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Modeling trophic structure and energy flows in a shallow lake, Yangtze River Basin, China: a case analysis for culture-based fishery practices

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ABSTRACT: Culture-based fisheries (CBFs) in China are well developed in most lakes; however, an ecological approach is required to assess and improve them. This study aimed to describe the characteristics of the aquatic ecosystem of Lake Shangshe (Yangtze River Basin, China) and propose suggestions to improve CBF practices using an Ecopath with Ecosim model. Based on the direction of water flow and different product supply services, different practices were implemented in the 3 sub-lakes of Lake Shangshe (upper lake area, ULA; middle lake area, MLA; lower lake area, LLA) between 2014 and 2015. Asian carp (*Hypophthalmichthys molitrix*, *H. nobilis*, *Ctenopharyngodon idella*, *Cyprinus carpio*) and bream (*Megalobrama amblycephala*, *Parabramis pekinensis*) were stocked at 30.0 and 50.0 t km^{-2} in the ULA and MLA, respectively. In the LLA, the same fish species were stocked at 50.0 t km^{-2} and millet grass *Echinochloa* sp. was planted. Water quality, including physicochemical parameters, was monitored in the 3 sub-lakes. Total phosphorus and chemical oxygen demand were significantly lower in the ULA than in the MLA and LLA. Ecotrophic efficiency values were noticeably high for most of the functional groups, except small pelagic fishes and cyanobacteria. Mixed trophic impact analyses demonstrated high fishing pressure on piscivorous fishes. The total mean transfer efficiency (TE) was 14.4 %. The ratios of total primary production to total respiration, total primary production to total biomass, and total biomass to total throughput were 1.847, 46.131, and 0.008, respectively. In conclusion, the TE and ecosystem maturity of the aquatic ecosystem of Lake Shangshe were higher than those of other lakes in China, with the trialed CBF practices having a positive effect on both factors.

KEY WORDS: Culture-based fisheries · Trophic structure · Transfer efficiency · Ecopath with Ecosim · Lake Shangshe · Yangtze River Basin

INTRODUCTION

Aquaculture is a millennia-old tradition that is thought to have originated in China over 2500 yr ago, contributing to the success in global food security and the social economy (Wu et al. 1992). China is the largest inland fishery producer in the world, with a total production of 32.98 Mt in 2015, corresponding to 54.7 % of global inland fishery production (60.32 Mt), including capture and aquaculture production (FAO 2017). Culture-based fisheries (CBFs) are a mode of fisheries enhancement that is practiced in most lakes and reservoirs in China and recognized as a significant contributor to inland fish production (Li & Xu 1995, De Silva 2003, Wang et al. 2015). CBF practices exhibit broad diversity with respect to the type of water bodies utilized, species stocked, harvesting techniques, and management strategies (De Silva 2003). Various CBF practices are implemented in China, including those involving the modification of water bodies to stock silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*, the trans-

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plantation of macrophytes to culture grass carp *Ctenopharyngodon idella* and Chinese mitten crab *Eriocheir sinensis*, and the elimination of fish species with low economic value (Li & Xu 1995, De Silva 2003, Wang et al. 2015).

Modification of water bodies, cutting off small and controllable water areas from the main body by embankments, weirs, or nets to serve for extensive and intensive fishery practices, is widely implemented for stock enhancement in CBFs. These improvisations in a water body result in minimal loss of stocked seed, facilitate complete harvesting, and incur low cost in small water bodies (Li & Xu 1995, Welcomme & Bartley 1998, Ingram & De Silva 2015). During the 1980s and 1990s, semi-intensive and intensive aquaculture methods, including the use of pen and purse net cultures, were applied to lake fisheries in China. These practices substantially increased fishery production and incomes of fishers (Zeng 1995, Lian et al. 2016). However, these CBF practices in lakes have also generated a range of environmental problems, such as habitat fragmentation (Yang et al. 2010), deterioration of water quality, and eutrophication (Zhang & Mei 1996, Wang et al. 2009, Rico et al. 2012). Conflict between developing CBFs and protecting the environment has drawn the attention of stakeholders. Currently, the management strategies of lake fisheries in China are being gradually diverted from seeking high production exclusively to including water quality protection.

Macrophytes play a prominent role in primary production, water quality improvement (Jeppesen et al. 1998, Dhote & Dixit 2009), nutrient cycling (Carpenter et al. 1998), and phytoplankton biomass reduction (Søndergaard & Moss 1998). To reconcile fish production with environmental protection, it is necessary to transplant and/or recover macrophytes in lakes. Macrophytes have a high capacity for absorbing and storing nutrients from water and sediment (Boyd 1970, Dhote & Dixit 2009), resulting in their having substantial nutrient status (Mandal et al. 2010). Thus, the direct use of macrophytes as food or their indirect use when blended with feedstuffs as feed for herbivorous fishes could replace costly commercial feeds (Mandal et al. 2010), in parallel to extracting nitrogen and phosphorus from water, which will contribute towards environmental integrity (Barko & James 1998). Millet grass *Echinochloa* sp. was imported to China from Australia in 1983 and is an emergent macrophyte that can be transplanted to feed herbivorous and filter-feeding fishes (Gong et al. 1992, Li & Xu 1995). Previous studies have demonstrated that the transplantation of millet grass to cultivate grass carp *C. idella*, silver carp *H. molitrix*, and bighead carp *H. nobilis* reduces feed and manure costs, increases the flesh quality of fishes, and decreases production costs (Li & Xu 1995, Cheng et al. 2015, 2016).

Undoubtedly, CBF in China has contributed significantly towards increasing fish production, and emphasis is now being laid on enhancing environmental and ecological factors in these practices. A holistic ecological understanding is fundamental for optimizing the management of natural resources and maintaining the health of ecosystems (Chea et al. 2016). Trophic structure and interactions play a decisive role in determining the dynamics of an ecosystem and are of interest in many studies aimed at improving fisheries management (Kitchell et al. 2000, Guo et al. 2013, Zhou et al. 2015). In this regard, an ecological approach to assess and improve CBF practices in lakes is urgently required.

The Ecopath with Ecosim (EwE) model has a standard modeling procedure and a user-friendly interface and has thus become a commonly used software package for documenting and analyzing trophic structure and energy flows (Christensen et al. 2005). This model is based on the theories of Odum (1969), Finn (1976), and Ulanowicz (1986), facilitating comparisons among different ecosystems with respect to trophic structure, energy flows, and ecosystem properties. The EwE model was introduced to China by Tong (1999) and has since been used on many aquatic ecosystems, especially ocean systems (Tong et al. 2000, Chen et al. 2006). Today, the EwE model has been applied for many lakes in China, including Lakes Qiandao (Liu et al. 2007, 2010), Taihu (Li et al. 2009, 2010, 2014), Bao'an (Guo et al. 2013), Chaohu (Liu et al. 2014, Kong et al. 2016), and Dianchi (Shan et al. 2014).

In the present study, the EwE model was developed for a shallow lake (Lake Shangshe) managed under CBFs to describe the characteristics of trophic structure, energy flows, and ecosystem properties. This information was used to develop suggestions to improve CBF practices.

MATERIALS AND METHODS

Study site

Lake Shangshe (30° 07′–30° 09′ N, 114° 12′ –114° 18′ E; Fig. 1) is a shallow lake (total area: 8.55 km^2; average water depth: 2.10 m) located on the Yangtze River Basin within Hubei province, central China. This lake has been separated into 3 sub-lakes by nets (Fig. 1). The lake is dominated by a northern subtrop-

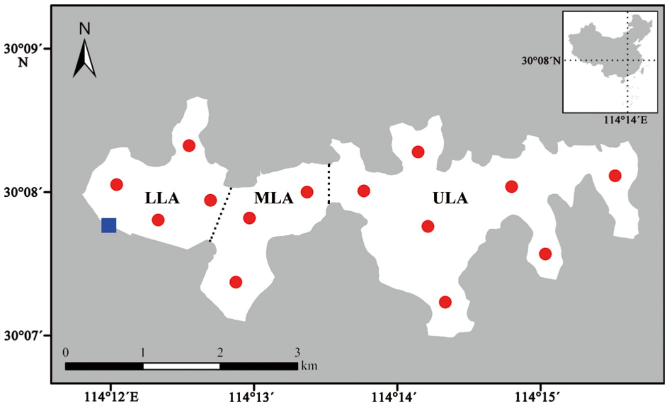


Fig. 1. Lake Shangshe, China. Red circles, blue square, and dotted lines represent sampling sites, sluice, and nets, respectively. LLA: lower lake area; MLA: middle lake area; ULA: upper lake area

ical monsoon climate. It has an annual mean air temperature of 16.20°C and an annual mean precipitation of 1250 mm (Wang & Dou 1998).

CBF practices and water quality assessment

Fish production and drinking water supply are the main ecosystem services of Lake Shangshe. Fish stocking and harvesting are done once a year within a narrow time span in winter. The culture-cycle is one year. To facilitate the harvesting of fish, the water level is regularly controlled by a sluice. From March to November, the sluice is shut and the water level rises following each rainfall event. In January, before the harvesting season, the sluice is opened and water flows from the upper lake area (ULA), through the middle lake area (MLA) to the lower lake area (LLA), and finally into the Yangtze River. CBF practices (Table 1) were implemented concurrently in the 3 sub-lakes of Lake Shangshe between 2014 and 2015, based on the direction of the water flow and different supply services. Drinking water supply is the principal ecosystem service in the ULA; thus, fish (including silver carp *Hypophthalmichthys molitrix*, bighead carp *H. nobilis*, grass carp *Ctenopharyngodon idella*, common carp *Cyprinus carpio* and bream ([*Megalobrama amblycephala*, *Parabramis pekinensis*]) were stocked at low density (30.0 t km^{-2}) in this lake area. Fish production is the main ecosystem service in the MLA and LLA. To make full use of nutrient flow from the ULA and to enhance fisheries yield, the above-mentioned fish species were stocked at high density (50.0 t km^{-2}) in the MLA. To utilize nutrients in the sediment and discharged effluent that flows from the ULA and MLA, the same species were stocked at high density (50.0 t km^{-2}) and millet grass *Echinochloa* sp. was planted in the LLA.

Water quality was monitored simultaneously at 14 sites during this study (Fig. 1). Water temperature, water depth, transparency, pH, conductivity, and dissolved oxygen were measured *in situ* using a YSI Professional Plus multimeter and Secchi disk. Water was sampled from 0.5 m below the water surface and 0.5 m above the sediment, with the samples being combined and collected for laboratory chemical analysis. Samples were kept at 4°C until analysis. Hydrochemical variables, including total nitrogen, total phosphorus, ammonium nitrogen, and chemical oxygen demand (permanganate index) (COD_{Mn}), were analyzed according to standard methods (APHA 1992, Huang 1999). Data were processed and statistically analyzed using SPSS (v. 22.0) and R (v. 3.3.3). Because the data sets were not independent and were abnormally distributed, the water quality of the 3 sub-lakes was analyzed using a non-parametric test (Kruskal-Wallis *H*-test). A non-parametric multiple comparison test was then performed using R when the results were significant. The significance of all statistical tests was set at α = 0.05.

Table 1. Fish stocking density and net yield in the 3 sub-lakes of Lake Shangshe. ULA: upper lake area; MLA: middle lake area; LLA: lower lake area

Fish species		Stocking density (t km^{-2})			Net yield (t km^{-2} yr^{-1})		
		ULA	MLA	LLA	ULA	MLA	LLA
Silver carp	*Hypophthalmichthys molitrix*	4.23	16.25	14.56	3.94	14.58	16.99
Bighead carp	*Hypophthalmichthys nobilis*	19.99	28.87	22.57	5.37	6.43	23.55
Grass carp	*Ctenopharyngodon idella*	3.98	4.06	5.34	−0.48	6.13	9.22
Common carp	*Cyprinus carpio*	1.32	0.63	4.85	1.68	6.60	14.56
Bream	*Megalobrama amblycephala*, *Parabramis pekinensis*	0.48	0.19	2.67	−0.18	3.25	4.61
Total		30.00	50.00	50.00	10.32	36.99	68.94

Modeling approach

A static mass-balance model for Lake Shangshe was constructed by using EwE (v. 6.2). To express mass balance, the model includes a set of linear equations. The basic mass-balance equation of EwE is formulated as follows:

$$B_i \times (P/B)_i \times \mathrm{EE}_i - \sum_{j=1}^{n} B_j \times (Q/B)_j \times \mathrm{DC}_{ji} - \mathrm{EX}_i = 0 \qquad (1)$$

where B_i, $(P/B)_i$, and EE_i represent the biomass, production/biomass ratio, and ecotrophic efficiency of group *i*, respectively; B_j and $(Q/B)_j$ are the biomass and the consumption/biomass ratio of predator *j*, respectively; DC_{ij} represents the contribution of prey *i* in the diet of predator *j*; and EX_i is the export of group *i* (Allen 1971, Christensen & Walters 2004, Christensen et al. 2005). To balance models, DC_{ij} and at least 3 of *B*, *P*/*B*, *Q*/*B*, and EE should be input. The rest of the unknown parameters can be calculated by Ecopath models.

Data collection and parameter estimation

Based on the research objectives, availability of information, trophic habits, and abundance, 21 functional groups were defined to construct a mass-balance model for Lake Shangshe. Some commercial fish species were grouped separately due to their importance to fisheries yield and stocking. Overstocking of grass carp has resulted in the total elimination of submerged macrophytes in the 3 sub-lakes. Therefore, submerged macrophytes were not considered in the model. Table 2 shows a list of functional groups in the lake ecosystem.

The biomass of the fish group was estimated using the following 3 equations:

$$B = Y/F \qquad (2)$$

$$F = Z - M \qquad (3)$$

$$Z = P/B = K \times (L_\infty - \bar{L})/(\bar{L} - L') \qquad (4)$$

where B is the biomass (t km^{-2}), Y is the annual catch yield (t km^{-2} yr^{-1}), F is the fishing mortality (yr^{-1}), Z is the total mortality (yr^{-1}), and M is the natural mortality (yr^{-1}). K, L_∞, $\bar{L}$, and L' represent the growth rate of von Bertalanffy growth function, asymptotic length (cm), mean length (cm), and maximum length of fish (cm), respectively (Beverton & Holt 1957, Allen 1971). K, L_∞, $\bar{L}$, and L' were derived from a fish resource assessment and previously published studies. The fish resource assessment was performed with multi-mesh gillnets, with sampling every 3 mo to identify the composition of fish resources and determine the distribution of individual fish body length and weight. To calculate Z, the method of Beverton & Holt (1957) was used along with FiSAT software. Harvesting in Lake Shangshe was accomplished through a combination of unified fishing methods and fyke nets within a narrow time span in winter. The net yield (t km^{-2}), total fisheries yield (t km^{-2}), and composition (%) of the 3 sub-lakes and the whole lake between 2014 and 2015 were obtained from the Fisheries Management Department of Lake Shangshe and are shown in Table 1 and

Table 2. Functional groups and dominant species composition of Lake Shangshe in the model

No.	Functional group	Dominant species
1	Mandarin fish	*Siniperca chuatsi*, *S. knerii*
2	Snakehead fish	*Channa argus*
3	Topmouth culter	*Culter alburnus*
4	Other culters	*Culter dabryi*, *C. mongolicus*, *Cultrichthys erythropterus*
5	Common carp	*Cyprinus carpio*
6	Crucian carp	*Carassius auratus*
7	Small pelagic fishes	*Toxabramis swinhonis*, *Hemiculter leucisculus*, *H. bleekeri*
8	Small demersal fishes	*Pseudorasbora parva*, *Acheilognathus macropterus, Abbottina rivularis*
9	Silver carp	*Hypophthalmichthys molitrix*
10	Bighead carp	*H. nobilis*
11	Grass carp	*Ctenopharyngodon idella*
12	Bream	*Megalobrama amblycephala*, *Parabramis pekinensis*
13	Shrimp	*Macrobrachium nipponense*, *Procambarus clarkii*
14	Zoobenthos	*Propsilocerus akamusi*, *Limnodrilus hoffmeisteri*
15	Microzooplankton	*Keratella cochlearis*, *Trichocerca elongata*
16	Cladocera	*Diaphanosoma leuchtenbergianum*, *Bosmina longirostris*, *Moina micrura*
17	Copepoda	*Microcyclops varicans*, *Thermocyclops kawanurai*
18	Cyanobacteria	*Pseudanabaena* sp., *Microcystis* sp., *Merismopedia* sp., *Lyngbya* sp.
19	Other phytoplankton	*Synedra* sp., *Scenedesmus quadricauda*, *Cryptomonas rosa*, *Tetraedron minimum*
20	Millet grass	*Echinochloa* sp.
21	Detritus	Bioseston, abioseston, cereal

Fig. S1 in the Supplement at www.int-res.com/articles/suppl/q010p213_supp.pdf.

Natural mortality was estimated by Pauly's (1980) empirical equation:

$$\log M = -0.0066 - 0.279 \times \log L_\infty + 0.6543 \times \log K + 0.4634 \times \log T \quad (5)$$

where T is the mean annual water temperature (°C).

According to Palomares & Pauly (1998), Q/B of fish was calculated by the following empirical equation:

$$\log(Q/B) = 7.964 - 0.204 \times \log W_\infty - 1.965 \times T' + 0.083 \times A + 0.532 \times h + 0.398 \times d \quad (6)$$

where W_∞ is the asymptotic weight (g), T' is the mean temperature of the lake defined as $T' = 1000/(T + 273.15)$, A is the aspect ratio for a given fish, h is a dummy variable that expresses food type (0 for detritivores and carnivores, 1 for herbivores), and d is also a dummy variable expressing food type (0 for herbivores and carnivores, 1 for detritivores). The morphometric data and food type were derived from Zhang (2005). The biomass of shrimp was estimated from the field survey conducted by the Fisheries Management Department of Lake Shangshe. Because of the similarity in fisheries management practices and geographical conditions between Lake Shangshe and Lake Wuhu, the P/B and Q/B values of Lake Shangshe were defined as 2.50 and 12.50, respectively, derived from Lin (2012).

The zoobenthos community was composed of chironomids and oligochaetes. They were sampled every 3 mo between 2014 and 2015 for the 14 stations (Fig. 1) by using a Peterson's grab sampler (Huang 1999). Because of the similarity in the composition of dominant species and geographical conditions between Lake Shangshe and Lake Taihu, P/B and Q/B were considered as 15.00 and 300.00, respectively, derived from Li et al. (2014).

Three major functional groups of zooplankton were considered in this model, namely microzooplankton (protozoa, rotifers), Cladocera, and Copepoda. Zooplankton was sampled monthly between 2014 and 2015 at the 14 sampling stations (Fig. 1). After microscopic identification and counting, zooplankton biomass was estimated based on the length–weight relationship (Huang 1999). In general, for the 3 major functional groups of zooplankton, 0.05 was adopted for the production/consumption ratio (P/Q). For the EE values of microzooplankton, Cladocera, and Copepoda, 0.95, 0.90, and 0.90, respectively, were adopted (Park et al. 1974, Scavia et al. 1974).

The biomass of phytoplankton was measured/calculated between 2014 and 2015 each month at the 14 sampling stations (Fig. 1). Phytoplankton abundance was estimated by counting individuals, and their cell sizes were estimated to derive volumes by using a microscope. Biomass (wet weight) was calculated from abundance, cells, and wet weight density (1 g cm^{-3}). Gross primary production (GPP) was estimated using the vertically generalized production model (Zeng et al. 2011). Because of the similar geographical conditions and fishery practices between Lake Shangshe and Lake Chaohu, P/B of cyanobacteria was considered as 150.00, derived from Kong et al. (2016). The P/B ratio for other phytoplankton was calculated as 219.44.

Detritus consists of soluble and particulate organic compounds, bacteria, and decaying matter. The total biomass of dissolved and particulate organic carbon was estimated using the empirical formula as follows (Heymans et al. 2004):

$$\log D = 0.954 \times \log \mathrm{PP} + 0.863 \times \log E - 2.41 \quad (7)$$

where D is the total biomass of dissolved and particulate organic carbon (g C m^{-2}), PP represents primary production (g C m^{-2} yr^{-1}), and E is the euphotic depth in meters (m). Bird & Kalff's (1984) formula was applied to calculate the bacterial biomass. This model considers the relationship between Chl$a$ and the abundance of bacteria as follows:

$$\log \mathrm{AODC} = 5.867 + 0.776 \times \log \mathrm{Chl}a \quad (8)$$

where AODC (acridine orange direct count) is the number of bacteria per millilitre (cells ml^{-1}) and Chl$a$ is the average concentration of chl a in lake water (µg l^{-1}). With the volume of bacteria estimated to be 0.5×10^{-3} ml (Cho & Azam 1990, Shan et al. 2014), the biomass of bacteria was calculated. Cereal, which is used to feed fishes, is a type of decaying organic matter; thus, it was considered as part of the detritus.

In this study, millet grass was planted in part of the LLA (17.3 % of the LLA, 0.36 km^2). Millet grass was considered as a second detritus group because it was not a living consumer group when it was flooded. Its biomass was estimated from the fishery sampling survey. The diet composition (consisting of fish, shrimp, zoobenthos, microzooplankton, Cladocera, and Copepoda) was synthesized from stomach content analysis and previous studies (Zhang 2005, Ye 2007, Lin 2012, Kong et al. 2016). The dietary composition of some groups was modified with slight adjustments to balance the model, if necessary (Table S2 in the Supplement).

Model balancing and uncertainty

By assigning the confidence intervals based on origins, the pedigree index was used to describe the quality of input data and evaluate the certainty of the model. Based on the individual pedigree index values, an overall pedigree index was estimated as follows:

$$P = \sum_{i=1}^{n} \sum_{j=1} l_{ij} / n \quad (9)$$

where l_{ij} is the pedigree index for group i and parameter j, and n is the total number of groups (Christensen & Walters 2004). In addition to the pedigree index, a measure of fit (t^*) was also used to scale the model uncertainty that described how well a given model is rooted in local data. The formula used was as follows:

$$t^* = P \times \sqrt{n-2} / \sqrt{1-P^2} \quad (10)$$

Ecosystem maturity

The ecosystem maturity of Lake Shangshe was quantitatively assessed by using the attributes given by the EwE model. Based on the ecosystem theories implemented by Odum (1969), Odum & Barrett (1971), and Ulanowicz (1986), a set of indicators was estimated to describe ecosystem properties using the model to assess the maturity and stability of the ecosystem, such as the ratios of total primary production to total respiration (TPP/TR), total primary production to total biomass (TPP/TB), and total biomass to total throughput (TB/TST) (Christensen et al. 2005).

RESULTS

Water quality

The water quality parameters of the 3 sub-lakes are listed in Table S1 in the Supplement. Conductivity, total phosphorus, and COD_{Mn} values were significantly lower in the ULA compared to the MLA and LLA ($p < 0.05$). Except for transparency, all parameters showed no significant differences between the MLA and LLA ($p > 0.05$).

Basic input and output variables

The basic input variables of the 3 sub-lakes and the whole of Lake Shangshe were calculated using Eqs. (1) to (8) and the values given in Table 3 & Table S3 in the Supplement. The pedigree index (0.488) fell in the upper range (0.164–0.675) in all 150 EwE models (Morissette et al. 2006), and the measure of fit was 2.304. This information supports that the input parameters of the models were based on reliable sources and that the model was robust with high confidence. A set of estimated parameters from the model is listed in Table 3. The EE values were estimated to be >0.5 for commercial fish groups such as silver carp (0.933), bighead carp (0.931), grass carp (0.718), common carp (0.823), and bream (0.735) in Lake Shangshe. However, the EE values of small

Table 3. Basic input (not bold) and estimated parameters (**bold**) in the model of Lake Shangshe. *P/B*: production/biomass ratio; *Q/B*: consumption/biomass ratio; EE: ecotrophic efficiency; *P/Q*: production/consumption ratio; –: no data

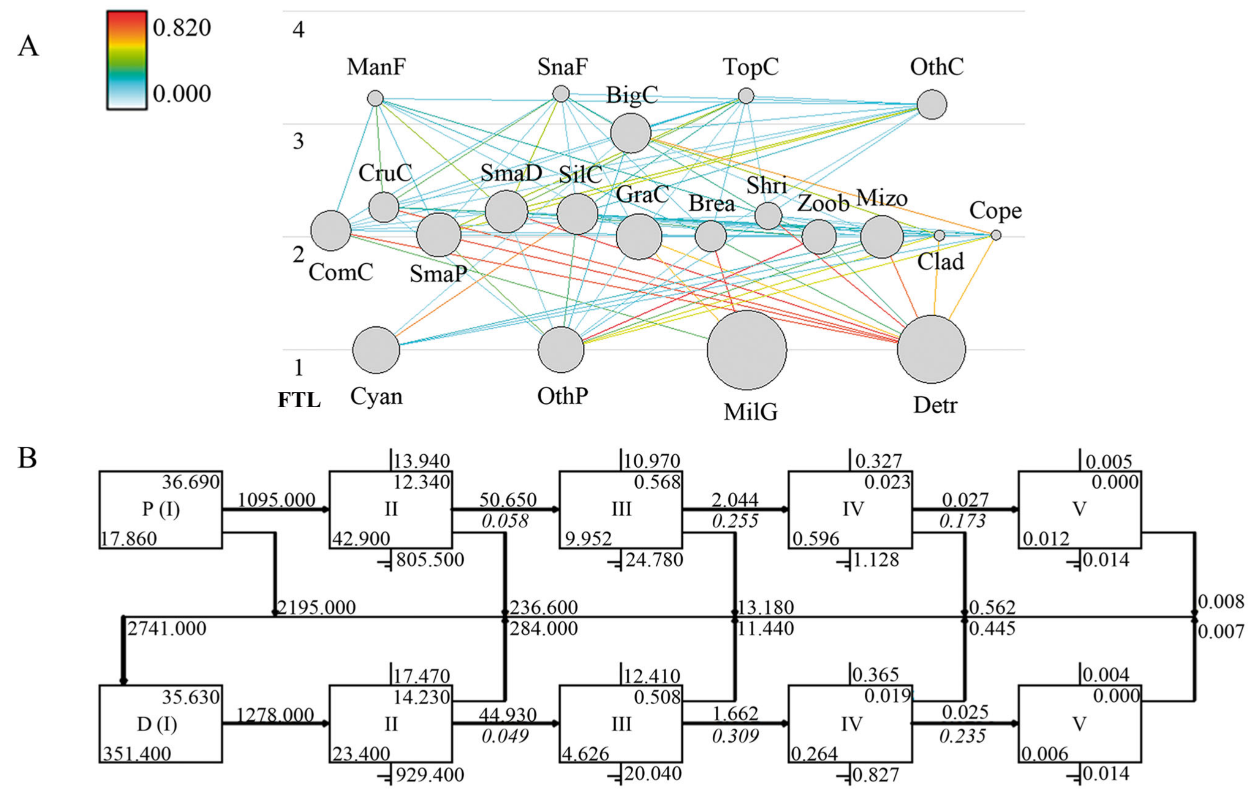
Functional group	Code	Fractional trophic level	Biomass (t km^{-2})	*P/B* (yr^{-1})	*Q/B* (yr^{-1})	EE	*P/Q*
Mandarin fish	ManF	**3.22**	0.30	1.04	3.27	**0.721**	**0.318**
Snakehead fish	SnaF	**3.27**	0.33	0.96	3.36	**0.496**	**0.285**
Topmouth culter	TopC	**3.25**	0.31	1.28	4.22	**0.756**	**0.303**
Other culters	OthC	**3.17**	1.58	1.25	6.94	**0.579**	**0.180**
Common carp	ComC	**2.06**	4.65	2.04	8.37	**0.823**	**0.244**
Crucian carp	CruC	**2.27**	1.72	2.57	15.92	**0.619**	**0.161**
Small pelagic fishes	SmaP	**2.02**	7.18	2.59	25.67	**0.266**	**0.101**
Small demersal fishes	SmaD	**2.22**	6.21	2.18	15.58	**0.408**	**0.140**
Silver carp	SilC	**2.20**	5.28	3.31	11.84	**0.933**	**0.279**
Bighead carp	BigC	**2.92**	4.95	4.56	7.65	**0.931**	**0.596**
Grass carp	GraC	**2.00**	8.84	1.09	13.60	**0.718**	**0.080**
Bream	Brea	**2.01**	1.88	1.66	21.78	**0.735**	**0.076**
Shrimp	Shri	**2.19**	1.22	2.50	12.50	**0.379**	**0.200**
Zoobenthos	Zoob	**2.00**	2.59	15.00	300.00	**0.625**	**0.050**
Microzooplankton	Mizo	**2.00**	6.15	**8.38**	**167.51**	0.950	0.050
Cladocera	Clad	**2.02**	0.14	**5.44**	**108.88**	0.900	0.050
Copepoda	Cope	**2.02**	0.13	**4.60**	**92.07**	0.900	0.050
Cyanobacteria	Cyan	**1.00**	9.06	150.00	–	**0.105**	–
Other phytoplankton	OthP	**1.00**	8.80	219.44	–	**0.494**	–
Millet grass	MilG	**1.00**	268.18	–	–	**0.544**	–
Detritus	Detr	**1.00**	83.22	–	–	**0.417**	–

pelagic fishes (0.266) and cyanobacteria (0.105) were noticeably lower than those of all other functional groups.

Trophic structure and energy flows

The fractional trophic levels (FTLs) of all of the 21 functional groups in Lake Shangshe ranged from 1.00 (cyanobacteria, other phytoplankton, millet grass, and detritus) to 3.27 (snakehead fish) (Table 3). A concise web-like representation was developed to show the FTLs of functional groups and energy flows in the lake food webs (Fig. 2A).

To describe the proportion of energy transferred from one trophic level to the next, all of the functional groups in the models were assigned to 1 of 5 aggregated trophic levels (ATLs, Fig. 2). Table 4 shows the ATL decomposition of the groups in the Lake Shangshe ecosystem. Flows at ATL I involved groups of cyanobacteria, other phytoplankton, millet grass, and detritus. ATL II included zooplankton, zoobenthos, shrimp, silver carp, small fishes, herbivorous fishes, and omnivorous fishes. ATL III contained mandarin fish, snakehead fish, topmouth culter, other culters, and bighead carp. Crucian carp, small demersal fishes, silver carp, and shrimp were also partly involved in the flows at ATL III. Flows at ATL IV and ATL V were dominated by predators (mandarin fish, snakehead fish, and topmouth culter). From the Lindeman spine of lakes, a detritus-based food chain and a grazing food chain were detected (Fig. 2B). For the grazing food chain of the Lake Shangshe ecosystem, the transfer efficiencies (TEs) from ATL II to ATL III, ATL III to ATL IV, ATL IV to ATL V were 5.8, 25.5, and 17.3 %, respectively, with a mean value of 13.7 %. For the detrital food chain, TEs were 4.9, 30.9, and 23.5 %, respectively, with a mean value of 15.2 %. The total mean TE of the Lake Shangshe ecosystem was 14.4 %.



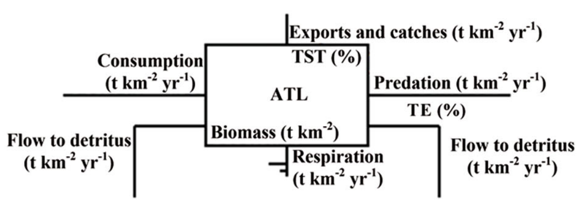


Fig. 2. (A) Food web structure and trophic flows and (B) Lindeman spine of the Lake Shangshe ecosystem. (A) The circles represent functional groups; circle sizes are proportional to biomass (t km^{-2}); lines reflect trophic flows; color key (dimensionless) represents the proportion that the prey contributed to a predator's diet; FTL: fractional trophic level; group abbreviations as in Table 3. (B) P: primary producers; D: detritus; I to V: aggregated trophic levels (ATLs); TE: transfer efficiency; TST: total system throughput; exports and catches: harvest of cultured fishes

Table 4. Aggregated trophic level decomposition of the functional groups in the Lake Shangshe ecosystem. –: no data

Functional group	Aggregated trophic level				
	I	II	III	IV	V
Mandarin fish	–	–	0.786	0.204	0.010
Snakehead fish	–	–	0.742	0.248	0.011
Topmouth culter	–	–	0.765	0.224	0.011
Other culters	–	–	0.829	0.169	0.001
Common carp	–	0.945	0.051	0.004	–
Crucian carp	–	0.737	0.259	0.003	–
Small pelagic fishes	–	0.982	0.018	0.000	–
Small demersal fishes	–	0.777	0.222	0.001	–
Silver carp	–	0.800	0.197	0.003	–
Bighead carp	–	0.091	0.894	0.015	–
Grass carp	–	0.998	0.002	–	–
Bream	–	0.994	0.006	–	–
Shrimp	–	0.810	0.190	–	–
Zoobenthos	–	–1.000	–	–	–
Microzooplankton	–	–1.000	–	–	–
Cladocera	–	0.984	0.016	–	–
Copepoda	–	0.984	0.016	–	–
Cyanobacteria	1.000	–	–	–	–
Other phytoplankton	1.000	–	–	–	–
Millet grass	1.000	–	–	–	–
Detritus	1.000	–	–	–	–

Prey overlap indices and mixed trophic impacts

Table 5 shows the prey overlap indices between the functional groups of Lake Shangshe. The prey overlap indices between small pelagic fishes and stocked fishes (common carp, crucian carp, and grass carp) were 0.90, 0.93, and 0.66, respectively. The results of mixed trophic impacts (MTIs) exhibited both positive and negative effects on each other (Fig. 3). The main food sources (e.g. detritus and millet grass) had positive effects on other groups, especially common carp, crucian carp, grass carp, and bream. The other compartments showed direct predator−prey interactions, cascading effects, and competition. Filter-feeding fishes (e.g. silver carp and bighead carp) had negative effects on cyanobacteria, Cladocera, and Copepoda. Piscivorous fishes (such as mandarin fish, snakehead carp, topmouth culter, and other culters) had negative effects on forage fishes (e.g. small pelagic fishes and small demersal fishes). The fishery (fleet group) had relatively strong negative effects on all commercial fishes (such as piscivorous fishes, silver carp, bighead carp, and grass carp) but was beneficial for small pelagic fishes, small demersal fishes, shrimp, zooplankton, and cyanobacteria.

Ecosystem properties

The ecosystem properties of Lake Shangshe are listed in Table 6. The TPP/TR, TPP/TB, and TB/TST values were 1.847, 46.131, and 0.008, respectively.

DISCUSSION

Trophic structure and energy flows

In this study, a set of indicators was derived by the model to analyze the trophic structure and energy flows of Lake Shangshe, China. One of the most prominent features of the trophic structure was variation in the estimated EE values (Table 3). EE values are the fractions of production that are consumed by

Table 5. Predator overlap indices between functional groups in the Lake Shangshe ecosystem. –: no data

	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Mandarin fish	1.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	Snakehead fish	0.98	1.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	Topmouth culter	0.59	0.56	1.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	Other culters	0.61	0.60	0.95	1.00	–	–	–	–	–	–	–	–	–	–	–	–	–
5	Common carp	0.01	0.01	0.01	0.01	1.00	–	–	–	–	–	–	–	–	–	–	–	–
6	Crucian carp	–	–	–	–	0.92	1.00	–	–	–	–	–	–	–	–	–	–	–
7	Small pelagic fishes	–	–	–	–	0.90	0.93	1.00	–	–	–	–	–	–	–	–	–	–
8	Small demersal fishes	–	–	–	–	0.93	0.96	0.92	1.00	–	–	–	–	–	–	–	–	–
9	Silver carp	–	–	–	–	–	0.05	0.10	0.01	1.00	–	–	–	–	–	–	–	–
10	Bighead carp	–	–	–	–	–	0.23	0.06	0.03	0.25	1.00	–	–	–	–	–	–	–
11	Grass carp	–	–	–	–	0.88	0.68	0.66	0.68	–	–	1.00	–	–	–	–	–	–
12	Bream	–	–	–	–	0.55	0.26	0.26	0.26	–	–	0.87	1.00	–	–	–	–	–
13	Shrimp	–	–	–	–	0.94	0.96	0.94	1.00	0.02	0.02	0.68	0.26	1.00	–	–	–	–
14	Zoobenthos	–	–	–	–	0.20	0.23	0.52	0.22	0.29	0.12	0.15	0.07	0.27	1.00	–	–	–
15	Microzooplankton	–	–	–	–	0.89	0.91	0.99	0.91	0.23	0.04	0.66	0.25	0.93	0.51	1.00	–	–
16	Cladocera	–	–	–	–	0.72	0.75	0.92	0.74	0.27	0.08	0.54	0.21	0.78	0.77	0.93	1.00	–
17	Copepoda	–	–	–	–	0.72	0.75	0.92	0.74	0.27	0.08	0.54	0.21	0.78	0.77	0.93	1.00	1.00

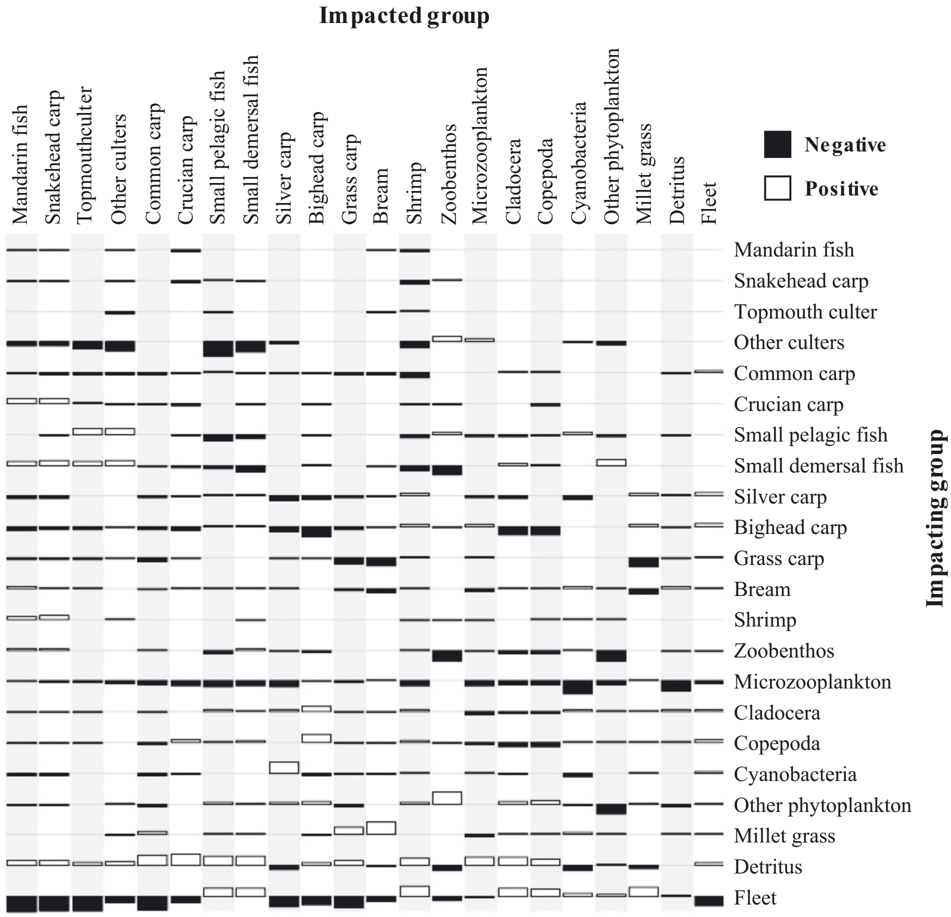


Fig. 3. Mixed trophic impacts of the Lake Shangshe ecosystem. The black bars pointing downwards show the negative impact on the functional groups, while the white bars pointing upwards indicate the positive impacts. The heights of the bars are proportionate to the degree of the impact, and values range from −1 to +1

predators within the system or exported out of the system through fishing (Coll et al. 2009). The high EE values of fish groups showed that fishing activities and predation pressure negatively impacted the fishes. In the Lake Shangshe ecosystem, EE values were estimated to be >0.5 for the commercial fish groups (including silver carp, bighead carp, grass carp, common carp, mandarin fish, and topmouth culter). These results were consistent with the fisheries yield of Lake Shangshe between 2014 and 2015, which showed that commercial fishes were the main fishing targets, accounting for 93.7 % of the total fisheries yield (55.48 t km^{-2}, Fig. S1). Similar results were observed in other lakes and ponds where the EE values of stocked commercial fishes (such as silver carp, bighead carp, and grass carp) were higher than 0.9 (Liu et al. 2007, Zhou et al. 2015, Kong et al. 2016).

In comparison, the estimated EE values of small pelagic fishes and cyanobacteria were extremely low, indicating that these groups were not well utilized in the Lake Shangshe ecosystem. The prey overlap index was calculated to determine the consumed extent of 2 functional groups for the same

Table 6. Ecosystem properties of the Lake Shangshe ecosystem

Parameter	Lake Shangshe
Sum of all exports (t km^{-2} yr^{-1})	1703.039
Sum of all consumption (t km^{-2} yr^{-1})	2473.011
Sum of all respiratory flows (t km^{-2} yr^{-1})	1781.766
Sum of all flows into detritus (t km^{-2} yr^{-1})	3010.137
Sum of all production (t km^{-2} yr^{-1})	3486.715
Total system throughput (t km^{-2} yr^{-1})	8967.953
Total biomass (excluding detritus) (t km^{-2})	71.320
Total primary production/total respiration	1.847
Total primary production/total biomass	46.131
Total biomass/total throughput	0.008
Pedigree index	0.488
Measure of fit (t^*)	2.304

prey (Table S4 in the Supplement). This index is symmetrical, and its values ranged between 0 and 1. A value of 0 indicates that the 2 species do not compete for the same prey, whereas a value of 1 indicates complete overlap. Intermediate values indicate partial overlaps in resource utilization between the functional groups (Christensen & Walters 2004). The values of the predator overlap indices between small pelagic fishes and commercial fishes (common carp, crucian carp, and grass carp) were relatively higher (0.90, 0.93, and 0.66, respectively) (Table 5). Thus, competition for prey resources among these species will lead to less energy being transferred to fishery products. In addition to their competition for food with economically important fishes, small pelagic fishes are of low economic value, and some of them feed on the eggs and fry of other species (Li & Xu 1995). Therefore, stock enhancement of piscivorous fishes to eliminate these unwanted species is urgently needed. In addition to economic benefits, silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis* are also useful for controlling algal blooms, because of their abilities to ingest masses of phytoplankton directly and to adjust the water environment (Xie 2003, Guo et al. 2015). Artificial stock enhancement of silver carp and bighead carp to control cyanobacterial blooms has been tested and used successfully in many eutrophic lakes in China, such as Lake Donghu (Xie & Liu 2001) and Lake Qiandao (Liu et al. 2007). Various studies have demonstrated that the stocking density and ratio between silver carp and bighead carp can be used to control cyanobacteria levels (Xie & Liu 2001, Yi et al. 2016). Silver carp and bighead carp reared at 30 to 70 g m^{-3} provide the most effective way of preventing the rapid growth of algae, with a proportion of >2.33 silver carp being recommended for use (Zhang et al. 2008, Yi et al. 2016). In the present study, the density of silver carp and bighead carp was 4.87 g m^{-3} and the ratio was 1.07. These were lower than the recommended values. Therefore, to enhance the EE value of cyanobacteria and the TE in Lake Shangshe, the stocking strategies of silver carp and bighead carp need to be optimized.

The MTI routine, described by Ulanowicz & Puccia (1990), is used to determine the trophic interactions of one functional group with the other groups in an ecosystem (Christensen & Walters 2004, our Table S4). In the Lake Shangshe ecosystem, MTI analyses showed that fishing pressure was higher on top predators (i.e. mandarin fish, snakehead fish, and topmouth culter) than on other species and had positive impacts on small fish resources under the effects of fish selectivity and trophic cascades, which was consistent with fisheries yield composition (Fig. S1). The EE values combined with MTI analyses demonstrated that fishing pressure on piscivorous fishes was high. Furthermore, optimizing capture strategies is essential when stock enhancement is implemented.

TEs are the ratios between the sum of exports and flows predated on by the next level and the throughput on the trophic level (Table S4). ATL III included mandarin fish, snakehead fish, topmouth culter, other culters, and bighead carp (Table 4). Consistent with the high EE values for these species, the TE value increased significantly from ATL III to ATL IV. The EwE model has been established for numerous lakes to assess energy flows in aquatic ecosystems. Compared with other lakes in China, the total mean TE of the Lake Shangshe ecosystem was relatively higher, indicating that primary production was efficiently utilized; thus, more nutrients were transferred to fishery products (Table 7).

Assessment of ecosystem maturity

According to the ecosystem development described by Odum (1969) and Christensen (1995), energy that is fixed tends to be balanced by the energy cost of maintenance. Thus, TPP/TR is >1 in the immature ecosystem and will approach 1 when the ecosystem becomes mature. As long as TPP exceeds TR, biomass will accumulate in the system, which will lead to a decrease in TPP/TB (Odum 1969). Therefore, the TPP/TB ratio is lower in a mature system than in a developing system. According to Ulanowicz (1986), the TB/TST ratio is expected to increase as systems mature.

The EwE model has been constructed for many lakes to assess the maturity of aquatic ecosystems (Table 8). The TPP/TR ratio was 1.847 in the Lake Shangshe ecosystem. This ratio was lower than that of most lakes in China, including Lakes Qiandao (1999–2000, 2004), Taihu (1991–1995), Gehu (1986–1989), Chaohu (2007–2010, 2000s), Niushan (2002–2004), and Ehai (2009–2012). In addition, this ratio was higher than that obtained for lakes Taihu (1961–1965, 1981–1987), Wuli (2009), Bao'an (1992–1993), Dianchi (2009–2010), Chaohu (1950s, 1980s), and Wuhu (2006–2007, 2008–2011). The TPP/TB ratio of the Lake Shangshe ecosystem was 46.131; between the immature lake ecosystem (Lake Chaohu, 2007–2010) and the mature ecosystem (Lake Gehu, 1986–1989). The TB/TST ratio in this study was 0.008;

Table 7. Transfer efficiencies (from primary producers, from detritus, and total mean) of lake ecosystems in China. –: no data

Lake	Period	Primary producers (%)	Detritus (%)	Mean (%)	Source
Shangshe	2014–2015	13.7	15.2	14.4	Present study
Qiandao	2004	3.5	2.1	2.7	Liu et al. (2007)
Wuli	2009	4.8	4.1	5.7	Huang et al. (2012)
Gehu	1986–1989	–	–	12.35	Jia et al. (2012)
Bao'an	1992–1993	8.96	8.40	8.68	Guo et al. (2013)
Dianchi	2009–2010	5.1	4.9	4.9	Shan et al. (2014)
Chaohu	2007–2010	6.9	6.8	6.9	Liu et al. (2014)
Chaohu	1950s	14.5	13.6	14.0	Kong et al. (2016)
Chaohu	1980s	10.7	9.1	9.8	Kong et al. (2016)
Chaohu	2000s	8.7	8.7	8.7	Kong et al. (2016)
Niushan	2002–2004	–	–	13.5	Ye (2007)
Wuhu	2006–2007	–	–	10.0	Lin (2012)
Wuhu	2006–2007	–	–	12.1	Lin (2012)
Ehai	2009–2012	–	–	8.3	Tang (2013)

between the immature ecosystem (Lake Chaohu, 2007–2010; Lake Chaohu, 2000s) and the mature ecosystem (Lake Bao'an, 1992–1993; Lake Chaohu, 1950s). Thus, the Lake Shangshe ecosystem is a relatively mature ecosystem compared to other immature (Lake Qiandao, 2004; Lake Chaohu, 2007–2010, 2000s) and mature (Lake Wuli, 2009; Lake Bao'an, 1992–1993) ecosystems (Q. Liu et al. 2007, 2010, Ye 2007, Huang et al. 2012, Jia et al. 2012, Lin 2012, Guo et al. 2013, Tang 2013, E. Liu et al. 2014, Shan et al. 2014, Kong et al. 2016).

Table 8. Ecosystem properties of lake ecosystems in China. TPP: total primary production; TR: total respiration; TB: total biomass; TST: total throughput. –: no data

Lake	Period	TPP/TR	TPP/TB	TB/TST	Source
Shangshe	2014–2015	1.847	46.131	0.008	Present study
Qiandao	1999–2000	2.073	89.598	0.003	Liu et al. (2010)
Qiandao	2004	3.725	73.956	0.004	Liu et al. (2007)
Taihu	1961–1965	1.50	5.46	0.04	Li et al. (2010)
Taihu	1981–1987	1.47	6.97	0.03	Li et al. (2010)
Taihu	1991–1995	3.85	11.66	0.03	Li et al. (2010)
Wuli	2009	1.339	10.431	0.029	Huang et al. (2012)
Gehu	1986–1989	2.761	1.76	–	Jia et al. (2012)
Bao'an	1992–1993	1.640	6.993	0.049	Guo et al. (2013)
Dianchi	2009–2010	1.665	61.812	0.003	Shan et al. (2014)
Chaohu	2007–2010	13.53	137.92	0.003	Liu et al. (2014)
Chaohu	1950s	0.971	8.864	0.042	Kong et al. (2016)
Chaohu	1980s	1.629	54.858	0.007	Kong et al. (2016)
Chaohu	2000s	2.132	111.154	0.004	Kong et al. (2016)
Niushan	2002–2004	2.642	–	–	Ye (2007)
Wuhu	2006–2007	1.458	9.164	0.037	Lin (2012)
Wuhu	2008–20011	1.359	5.004	0.067	Lin (2012)
Ehai	2009–2012	9.952	5.178	0.056	Tang (2013)

Suggestions for improvements of CBF practice

It is widely accepted that an ecosystem-based approach to lake ecosystem fisheries management is relevant for sustainable fisheries and the maintenance of healthy ecosystems. Through analyses of trophic structure and energy flows in Lake Shangshe, ecosystem-oriented fisheries management strategies have emerged.

First, due to the low EE value of small pelagic fishes, stock enhancement of piscivorous fishes is urgently needed. The fish species that are selected for CBF should have fast growth and high economic value, feed on a wide range of food types, and have an easily available and reliable supply of fry. Moreover, such species should not harm other economically important fish species (Li & Xu 1995). Topmouth culter is an indigenous species that feeds on small fishes in the middle and upper layers of open waters (Li & Xu 1995, Zhang 2005), and it has almost no negative effects on stocked fishes according to the MTI results (Fig. 3). Therefore, stocking of topmouth culter in Lake Shangshe is recommended. CBF practices are dependent on regular stocking. Excess stocking results in decreased growth and/or increased mortality, leading to lower yields (De Silva 2003). Thus, it is important to estimate the carrying capacity by calculating the biomass and production of small fishes and their bioenergetics before stocking lakes with topmouth culter. The addition of seed stock to a water body with the view of enhancing fish production is only one facet of stock enhancement. Stock enhancement also includes other practices, such as the introduction of closed seasons, gear restrictions, establishment of conservation zones, and improvement and/or establishment of spawning grounds (De Silva et al. 2015). Our EE and MTI outputs demonstrate that greater effort should be placed on optimizing capture strategies that reduce pressure on piscivorous fishes in Lake Shangshe, especially for juvenile (young) stages. Because of the low EE value of cyanobacteria, stronger focus should be placed on how primary production is utilized to enhance the TE and water quality of the Lake Shangshe ecosystem. Consistent with the utilization of cyanobacteria, high stocking density and proportion of silver carp *H. molitrix* in Lake Shangshe appear to be favorable at present.

From the perspectives of the ecosystem model and water quality assessment, implementation of these CBF practices, considering ecosystem services and the direction of water flow, has a positive effect on the ecosystem health of Lake Shangshe. Our results are expected to contribute towards maintaining the sustainability of fisheries in our study lake while potentially serving as a reference for other lakes where the traditional stocking of Asian carp remains a popular practice.

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