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Ecosystem structure and functioning of Lake Taihu (China) and the impacts of fishing

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ABSTRACT

Lake Taihu is the third largest freshwater lake in China and has provided local communities with valuable fisheries for centuries. However, we have only a limited knowledge of its ecosystem. In this study, a trophic model was constructed for the Lake Taihu ecosystem. This model was used to evaluate and analyze the food web structure and other properties of this ecosystem using data covering the period from 1991 to 1995. Using the model, we evaluated the impacts on local fisheries of various management scenarios comprising two basic management regimes: (1) setting fishing mortality for the top predator (large culters, *Erythroculter mongolicus* and *Erythroculter ilishaeformis*) to 0, 0.3, 0.6, 0.9 and 1.2, and (2) adjusting overall fishing effort to 0.25, 0.5, 0.75 and 1.25 times the current level. For both scenarios, fishery profit and cost were evaluated to provide an understanding of how components of the ecosystem interact. We identified possible causes of fishery overexploitation in the lake ecosystem and described the necessity of developing ecosystem-based management. The results showed that Lake Taihu had six theoretical trophic levels (TLs), with the trophic flows primarily occurring through the first five TLs. System properties such as transfer efficiency, Finn's index, Finn's mean length, connectance index, system omnivory index, primary production/respiration ratio, and net primary production all indicated that Lake Taihu was an immature, fairly simple ecosystem in which a relatively low fraction of total primary production was utilized. At the same time, the ecosystem was also experiencing high fishing pressure. Yet despite this, the low ascendency index (25.9%) and high system overhead ratio (74.1%) indicated that the system was highly developed and relatively stable, a condition that might result from the high degree of recycling in the system. Among the harvesting strategies considered, a strategy of either decreasing the fishing mortality of the top predator (large culters) to 0.3 or, alternatively, reducing the overall effort on the system by a factor of 0.75 appeared to be most effective at increasing the efficiency of the fisheries.

1. Introduction

The overexploitation of aquatic living resources is common in today's fisheries worldwide. Both the inland and marine ecosystems are heavily influenced by intense fishing activities (Mchich et al., 2006). In view of these facts, it is widely recognized that an ecosystem-based approach to fisheries management is important for maintaining sustainable fisheries and healthy ecosystems (FAO, 1995; NRC, 1999). Although the objectives of ecosystem-based management are difficult to define, a general awareness exists that quantitative modeling is an important tool for exploring the ecological consequences of fishing and improving our understanding of how ecosystems function (Cury and Chirstensen, 2005). Ecosystem models are complimentary to single-species fisheries models in that they are potentially able to predict the otherwise unforeseen effects of trophic interactions; however, their high degree of complexity and large input data requirements have kept them from becoming a commonly used tool in stock assessment and fisheries management (Christensen et al., 2004; Cury and Shannon, 2004; Fletcher et al., 2005; Coll et al., 2006).

Lake Taihu, located in the southern Jiangsu province and northern Zhejiang province, is the third largest freshwater lake in China with an area of 2338 km^2 (Fig. 1). The lake plays an important role in flood control, water supply, fishery, shipping, tourism and culture. There are 38 cities and 34.2 million people living around the lake. Gross Domestic Production (GDP) in the lake drainage area is about one-seventh of the total GDP of China (Sun and Huang, 1993; Hu et al., 2006).

Wild fisheries in Lake Taihu began nearly 10,000 years ago, and were both productive and valuable (Chen, 1989; Sun and Huang,

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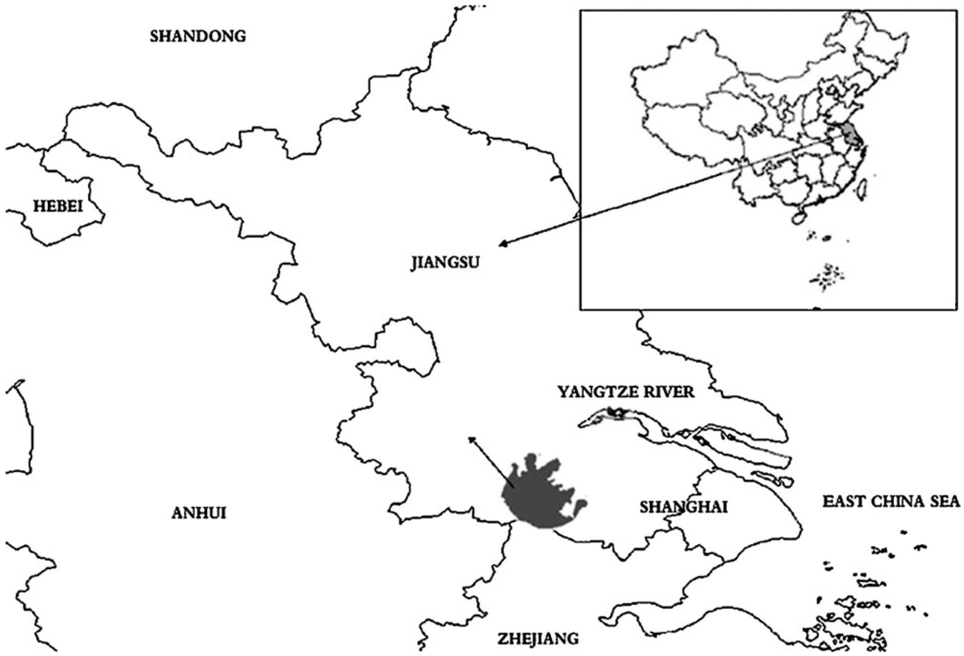

Fig. 1. The geographic location of Lake Taihu in Jiangsu Province and Zhejiang Province, China.

1993). Over the last few decades, Lake Taihu has sustained high stress from fisheries and pollution. The total catch (Fig. 2) and total fishing effort for commercial species has increased significantly. The top predators in Lake Taihu, such as the large culters (*Erythroculter mongolicus* and *Erythroculter ilishaeformi*), were subject to high fishing mortality (Xu, 1984). Because of prolonged intensive fishing pressure, we observed signs of "fishing down the food web" (Pauly et al., 1998) in Lake Taihu—in which the biodiversity declined significantly and the composition of landings was increasingly dominated by relatively small and less valuable species with high turnover rates from lower trophic levels, which also could be explained by the trend of catch started from 1994 (Fig. 2) (Sun and Huang, 1993; Yang, 1998; Yang et al., 2004; Zhu, 1999).

The Chinese government tried to solve the problems of eutrophication and resource degradation in Lake Taihu with an investment of 20.43 billion Yuan over the period from 1997 to 2010. At the same time, 4.1–9.24 million larval fishes were released into Lake Taihu every year in attempt to maintain fisheries resources (State Environmental Protection Administration of China, 2000). Although the pollution sources have been largely controlled, the attempted restoration of the aquatic ecosystem was not successful. Meanwhile, excessive aquaculture activity and the stocking programs continue altering the structure of the Taihu ecosystem. Furthermore, fishing intensity may still be too high. To better understand these issues, studies were undertaken concerning the

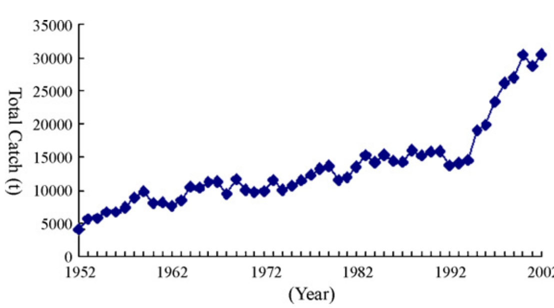

Fig. 2. Temporal trends in the total catch of Lake Taihu.

environment and the biology of fish species. To support these studies, large quantity of data were collected on fisheries statistics, population parameters, diet compositions, and physical and chemical variables (East China Normal University, 1959; Geography Department of Chinese Academy of Science, 1965; Chen et al., 1997; Cai, 1998; State Environmental Protection Administration of China, 2000; Taihu Environment Protection Administration, 2000; Wu, 2001). However, limited efforts were put into the development of an ecosystem-based fisheries resource management strategy.

The objectives of this study are to (1) understand how components of the Taihu ecosystem interact; (2) evaluate the impact of the fishing activity on the entire ecosystem, and (3) characterize the need for developing an ecosystem-based management strategy for Lake Taihu. Using Ecopath with Ecosim we constructed a mass-balanced food web model focusing on biomass flows among functional groups and species of ecological and commercial interests (Walters et al., 1997; Christensen et al., 2004). The model was used for evaluating the impacts of different fishing strategies on the ecosystem.

2. Methods and materials

2.1. Study area

Lake Taihu is located from 119°53′45″ to 120°36′15″E and 22°00′ to 27°10′N (Fig. 1). At its northern tip is Lake Wulihu, a lagoon with an area of approximately 10 km^2. Several tributaries connect the two lakes with other bodies of water such as the Yangtze River (Zou et al., 1996). The average depth of Taihu is 1.89 m and the maximum is 2.6 m. The annual precipitation in the area is 1100–1400 mm, and the mean temperature is approximately 16 °C. The frost-free period is over 230 days (Sun and Huang, 1993; Cai, 1998; Hu et al., 2006).

2.2. Mass-balanced modeling approach

A mass-balanced trophic model was constructed for Lake Taihu using Ecopath with Ecosim, version 5.0 (Walters et al., 1997; Christensen and Walters, 2004; Christensen et al., 2004). The basic equation for Ecopath is:

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot \mathrm{EE}_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot \mathrm{DC}_{ji} - \mathrm{EX}_i = 0 \qquad (1)$$

where B_i is the biomass of group i; P_i/B_i is the production/biomass ratio of group i; EE_i is the ecotrophic efficiency of group i; B_j is the biomass of predator j; Q_j/B_j: consumption/biomass ratio of predator j; DC_{ji} is fraction of prey i in the diet of predator j; EX_i is export of group i (Christensen et al., 2004).

The Ecopath model allows rapid construction and verification of a mass-balance model on an ecosystem and also identifies the biomass required for the assessment of marine carrying capacity (Tong et al., 2000; Christensen et al., 2004).

2.3. Parameterization

The model represents an annual average situation of the Lake Taihu ecosystem between the years 1991 and 1995. Biomass value were obtained from the lake survey and information available in the literature Production/biomass ratios (P/B), consumption/biomass ratios (Q/B), production/consumption ratios (P/Q), and unassimilated/consumption ratios (U/Q) were taken from the literature or obtained from the application of empirical equations using length and weight data (Pauly, 1980; Palomares and Pauly, 1998; Christensen et al., 2004). Diet compositions were compiled from published information. Official landings statistics covering the relevant time period acquired for the trawl fishery, the mollusc fishery and the macrophyte harvester fishery. These were mainly obtained from local landing statistics and stock assessment reports (Zhu, 1985; Zhu, 1999; Zhu, 2003).

The model compartments consist of 22 functional groups. Each group was represented using an Ecopath equation, as described above, so as to give a set of simultaneous linear equations – one for each species or group – that quantify trophic flows (Christensen and Pauly, 1992). Organisms were assigned to compartments based on their ecological function (mainly diet), their abundance, and also based on information availability (Christensen et al., 2004). The main commercial species were grouped separately because of their importance to fisheries and owing to the greater availability of information on these species. Species comprising the various functional groups are listed in Table A1. Model input data are compiled in Table A2, along with the main data sources and estimation methods used. The original diet composition data used to construct the initial, unbalanced model is given in Table A3.

2.4. Analysis and uncertainty

2.4.1. Uncertainty and sensitivity analysis

Data for this model was assigned a pedigree index of PI = 0.614. This index is understood as a coded statement categorizing the origin of a given input and specifying the likely uncertainty associated with it (Christensen et al., 2004). Based on this input data, annual mean values were estimated for the four basic parameters characterizing each group in the model: biomass, P/B ratio, Q/B ratio, and ecotrophic efficiency. These preliminary data and their resultant parameters were then subjected to the "Ecoranger" routine of Ecopath, from which a range (i.e. the coefficient of variation from pedigree analysis) was obtained. Random input variables were drawn from normal distributions for each basic parameter. This process was repeated in order to generate a theoretical frequency distribution for each basic parameter using Monte Carlo simulations. We ran 10,000 Lake Taihu models, of which 200 passed the selection criteria. The best fitting model (the one with the smallest residual) was chosen for further analysis. To compare the distributions of the initial parameter estimates against the theoretical frequency distributions, we carried out a chi-square test for goodness-of-fit. The distributions of the estimated basic parameters fitted well with the distributions of the initial estimates: biomass ($0.95 < P < 0.99$, $x^2 = 2.35$), P/B ($0.95 < P < 0.99$, $x^2 = 0.25$), Q/B ($0.95 < P < 0.99$, $x^2 = 2.31$), ecotrophic efficiencies ($0.95 < P < 0.99$, $x^2 = 0.1$). The sensitivity analysis showed that, by altering the input parameters of a functional group, the largest impacts were seen on the output parameters of that same group. Final input parameters, including those calculated by the model (in bold) are given in Table 1. Relying on these input parameters, the trophic level of each group was then determined, along with other important ecosystem statistics such as niche overlaps, mixed trophic impacts, and trophic transfer efficiencies by trophic levels (Christensen and Pauly, 1993). System summary statistics and network flow indices based on theoretical concepts of Odum (1969) and Ulanowicz (1986) were also obtained (Christensen, 1995).

Table 1
Basic inputs and estimated parameters (in bold) for the Taihu ecosystem model.

Group	Code	TL	Catch (t km^{-2})	Biomass (t km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
Large culters	LarC	**3.81**	0.212	0.275	0.974	3.200	**0.869**
Other piscivorous	OthP	**3.71**	0.040	0.130	1.665	6.100	**0.535**
Large icefish	LarI	**3.87**	0.066	0.110	1.862	16.650	**0.710**
Tapertail anchovy	TapA	**2.98**	2.925	4.343	1.283	11.350	**0.768**
Black carp	BlaC	**3.02**	0.043	0.055	0.912	11.544	**0.857**
Common carp	ComC	**2.92**	0.182	0.233	0.960	10.693	**0.840**
Goldfish	GolF	**2.26**	0.214	0.275	1.130	12.300	**0.821**
Bighead carp	BigC	**2.81**	0.470	0.610	0.990	6.900	**0.797**
Icefish	IceF	**3.02**	0.478	0.793	2.373	27.200	**0.568**
Other fishes	OthF	**2.79**	1.158	3.125	2.155	11.000	**0.302**
Silver carp	SilC	**2.20**	0.028	0.080	1.100	8.000	**0.589**
Herbivorous fishes	HerF	**2.00**	0.240	0.305	0.987	7.100	**0.797**
Macrocrustacean	MacC	**2.99**	0.466	1.575	**3.092**	**41.223**	0.850
Molluscs	Moll	**2.00**	31.22	35.965	1.326	**10.605**	**0.742**
Other benthos	OthB	**2.00**	0	1.16	4.130	**201.500**	**0.933**
Microzooplankton	Micz	**2.00**	0	1.304	**49.301**	**597.934**	0.950
Cladocera	Clad	**2.02**	0	3.506	**22.863**	**457.252**	0.900
Copepoda	Cope	**2.02**	0	4.243	**18.903**	**378.053**	0.900
Submerged macrophyte	SubM	**1.00**	242.912	150.292	2.253	–	0.73
Other macrophyte	OthM	**1.00**	13.416	146.36	1.000	–	**0.092**
Phytoplankton	Phyt	**1.00**	0	20.893	185.000	–	**0.413**
Detritus	Detr	**1.00**	0	311.62	–	–	**0.362**

TL: trophic level; P/B: production/biomass; Q/B: consumption/biomass; EE: ecotrophic efficiency.

2.4.2. Niche overlap analysis

To determine to what extent any two groups consumed the same prey, the prey overlap was considered using the Pianka index (1974) (which is symmetrical and has values between 0 and 1), as shown in Table 2. A value of 0 suggests that the two species do not compete for the same prey, whereas a value of one indicates complete overlap. Intermediate values show partial overlaps in resource utilization (Christensen et al., 2004).

2.4.3. Mixed trophic impacts analysis

Ulanowicz and Puccia (1990) developed a method to assess the direct and indirect interactions in a food web, which has been implemented in the Ecopath model (Christensen et al., 2004). The mixed trophic impact routine can also be regarded as a form of 'ordinary' sensitivity analysis (Majkowski, 1982). It is regarded as a tool for indicating the possible impact of direct and indirect interactions (including competition) in a steady-state system, not as an instrument for making long-term predictions because the changes in abundance may lead to changes in diet composition (Christensen et al., 2004).

2.4.4. Summary statistics and network flow indices

After balancing the model, ecological analysis integrated in EwE was used to examine a number of indictors describing trophic flows. These were variously derived from thermodynamic concepts, information theory, and network analysis (Christensen et al., 2004). Some of these results were related to ecosystem development theory, sensu Odum (Odum, 1969, 1971; Lindeman, 1942; Odum and Heald, 1975; Finn, 1976, 1980; Ulanowicz, 1986, 1995; Christensen and Pauly, 1993; Christensen, 1995).

2.5. Simulation of the impacts of fishing

The balanced model was used to initialize an Ecosim model, which in turn was used to explore the effects of different levels of fishing mortality rates applied to the top predators. This model was also employed to investigate the response of ecosystem structure and fishery profits to the use of total fishing effort as the forcing function in the system. Eq. (2) represents the basic Ecosim equation. Both current fishing mortality and total fishing effort could be determined by the balanced Ecopath model

$$\frac{dB_i}{d_t} = g\sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \tag{2}$$

where dB_i/dt represents the growth rate of group i during the time interval dt, expressed in terms of the change in its biomass, B_i. The term g_i refers to the net growth efficiency (production/consumption ratio), M_i to the rate of other natural mortality, F_i to the fishing mortality rate, e_i to the emigration rate, and I_i to the immigration rate. The consumption rate, Q_i, borne by group i is calculated based on the 'foraging arena' concept, whereby B_i is divided into vulnerable and invulnerable components (Christensen et al., 2004).

2.5.1. The cost calculation

Ecopath with Ecosim can be used for policy exploration regarding ecosystem-based fisheries management. To facilitate this, the routines have been designed to include various biological and economic information, giving the system the allure of a simple bio-economic model. This model is based on the following equations (Christensen et al., 2004):

$$\text{Profit} = \text{Total value} - \text{Cost} \tag{3}$$

Table 2
Estimates of prey overlap between trophic groups in Lake Taihu.

Group name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
LarC	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
OthP	0.543	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
LarI	0.082	0.032	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TapA	0.501	0.205	0.768	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BlaC	0.973	0.376	0.084	0.480	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ComC	0.329	0.962	0.013	0.079	0.155	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
GolF	0.196	0.901	0.002	0.010	0.021	0.984	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BigC	0.973	0.376	0.084	0.480	1.000	0.155	0.021	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–
IceF	0.101	0.041	0.736	0.849	0.097	0.016	0.002	0.097	1.000	–	–	–	–	–	–	–	–	–	–	–	–
OthF	0.500	0.527	0.760	0.879	0.416	0.428	0.356	0.416	0.658	1.000	–	–	–	–	–	–	–	–	–	–	–
SilC	0.973	0.376	0.084	0.480	1.000	0.155	0.021	1.000	0.097	0.416	1.000	–	–	–	–	–	–	–	–	–	–
HerF	0.973	0.376	0.084	0.480	1.000	0.155	0.021	1.000	0.097	0.416	1.000	1.000	–	–	–	–	–	–	–	–	–
MacC	0.162	0.750	0.289	0.263	0.023	0.766	0.737	0.023	0.245	0.584	0.023	0.023	1.000	–	–	–	–	–	–	–	–
Moll	0.005	0.026	–	0.229	–	0.027	0.026	–	0.485	0.011	–	–	0.304	1.000	–	–	–	–	–	–	–
OthB	0.003	0.017	–	–	–	0.018	0.018	–	–	0.007	–	–	0.071	0.078	1.000	–	–	–	–	–	–
MicZ	–	–	0.001	0.001	–	–	–	–	0.002	0.001	–	–	0.000	0.002	0.001	1.000	–	–	–	–	–
Clad	–	–	0.003	0.263	–	–	–	–	0.554	0.002	–	–	0.001	0.686	0.192	0.032	1.000	–	–	–	–
Cope	–	–	0.004	0.234	–	–	–	–	0.487	0.003	–	–	0.001	0.606	0.158	0.043	0.977	1.000	–	–	–
SubM	0.020	0.008	0.002	0.011	0.019	0.003	0.000	0.019	0.002	0.010	0.019	0.019	0.004	0.005	0.120	0.001	0.005	0.006	1.000	–	–
OthM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.000	–	–	0.712	1.000	–
phyt	0.000	0.000	–	0.001	–	0.000	0.000	–	0.002	0.000	–	–	0.000	0.002	0.004	0.841	0.003	0.003	0.002	–	1.000

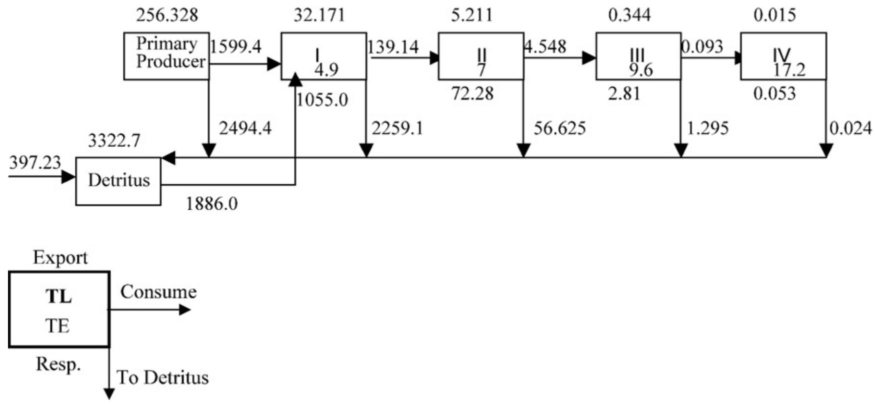

Fig. 3. The aggregation of the flows (t km^{-2} per year) into a concatenated chain of transfers through seven trophic levels (after Ulanowicz, 1995). The flows out of the top of the compartment represent exports and the flows out to the bottom represent respiration. Recycling of non-living materials is through compartment detritus. The percentages in the boxes represent the annual trophic efficiencies.

$$\text{Total value} = \sum_{i=1}^{n} C_i \cdot P_i \quad (4)$$

$$\text{Cost}_i = \frac{\text{Cost}_1 \cdot \text{FE}_i}{\text{FE}_1} \quad (5)$$

where C_i refers to the landings of group i and P_i to the market price of group i (China fishery website, 2004). Cost_1 is the initial cost value that Ecopath used, accounting for 32.8% of total value (Zhu, 1999). FE_i/FE_1 is the ratio between the simulated fishing effort that would occur under a particular policy and the current fishing effort. The market prices of the economic groups were obtained from the local fish market and the China Fishery Information website (http://www.china-fisheries.org/price/).

2.5.2. Scenarios

The following two scenarios were considered in the evaluation of impacts of different fisheries management strategies:

Scenario 1: Changing large culters mortality. In this set of runs the fishing mortality of large culters was set to be 0, 0.3, 0.6, 0.9 and 1.2. We assumed that the total fishing effort was not affected by the fishing mortality of large culters for the fishing efforts still stayed high. Thus, the cost of fishing did not change.

Scenario 2: Changing effort. In this set of runs we considered the amount of fishing efforts to be 0.25, 0.5, 0.75 and 1.25 times current fishing efforts. The cost was assumed to be directly proportional to the fishing effort.

Vulnerability parameters, which are inputs governing bottom-up versus top-down control of the ecosystem, were difficult to estimate. Vulnerability factors in this study were calculated as nearly proportional to the trophic levels of the functional groups and also tuned by time-series simulation (Cheung et al., 2002; Song, 2004). All other settings in Ecosim assumed default values. The two scenario sets were examined over a simulation length of 35 years. At the end of each run, the Ecopath models representing the different scenarios were saved for comparison.

3. Results

3.1. Trophic structure and flows

A balanced model was successfully constructed for the Lake Taihu ecosystem. In general, primary production in the lake reached 4350.2 t km^{-2} year^{-1}. Of this production, the float grass industry and grazers at higher trophic levels consumed 256.2 t km^{-2} year^{-1} and 1599.4 t km^{-2} year^{-1}, accounting for 5.89% and 36.76% of total primary production, respectively. 5208.7 t of detritus were cycled through the system per square kilometer per year. Ecotrophic efficiencies in the system reflected these figures. EE values were generally high for fish groups, but low for macrophytes, phytoplankton, and detritus (Table 1). The low values for phytoplankton indicated that only a small proportion of total phytoplankton production was utilized, with the rest going toward detritus.

Ecopath calculated the fractional trophic level (TL) for each functional group by measuring the average trophic level at which the group received energy. Aggregating biomass and energy flows across trophic levels revealed the presence of six theoretical trophic levels, with the highest realized trophic level being 3.81. The trophic flows across the aggregated trophic levels in the Lake Taihu ecosystem are given in Fig. 3. Of the total detritus formed annually, 1886.032 t km^{-2} year^{-1} was consumed, while the remaining 3322.696 t km^{-2} year^{-1} was exported to the sediments. The trophic flow from TL I to TL II was 3485.421 t km^{-2} year^{-1}, although this only accounted for 35% of the biomass in TL I. The trophic flows across TLs II, III, IV, and V were, respectively, 3458.42 t km^{-2} year^{-1}, 139.14 t km^{-2} year^{-1}, 4.55 t km^{-2} year^{-1}, and 0.093 t km^{-2} year^{-1}. The transfer efficiencies associated with these flows were, respectively, 4.9%, 7%, 9.6% and 17.2%, with a mean transfer efficiency of 6.9% which was in the range of values reported in the published literature (Libralato et al., 2008).

3.2. Niche overlap analysis

High values of niche overlap appeared among fish from lower trophic levels, in some cases reaching one. In particular, it was high for many fish groups (tapertail anchovy, bighead fish, icefish, many of the carp groups and other fishes). It was also high between some of the fish and macrocrustaceans (see Table 2).

3.3. Mixed trophic impacts (MTI) analysis

Competiton interactions between functional groups of similar trophic levels were revealed by the analysis of the MTI. The results were shown in Fig. 4. Lower trophic levels and detritus had the most positive impacts on other groups in the system, providing an important food source for the other groups. While the groups had a smattering of negative and positive effects across the food web. Notably, tapertail anchovy and other fishes had some impacts that are greater on mid-trophic level groups. The trawl fishery fleets had strong negative impacts on almost all the groups. Similarly, the mollusks fishery also had some of the strongest negative impacts on the biomass of groups such as black carp, golden fish and mollusks.

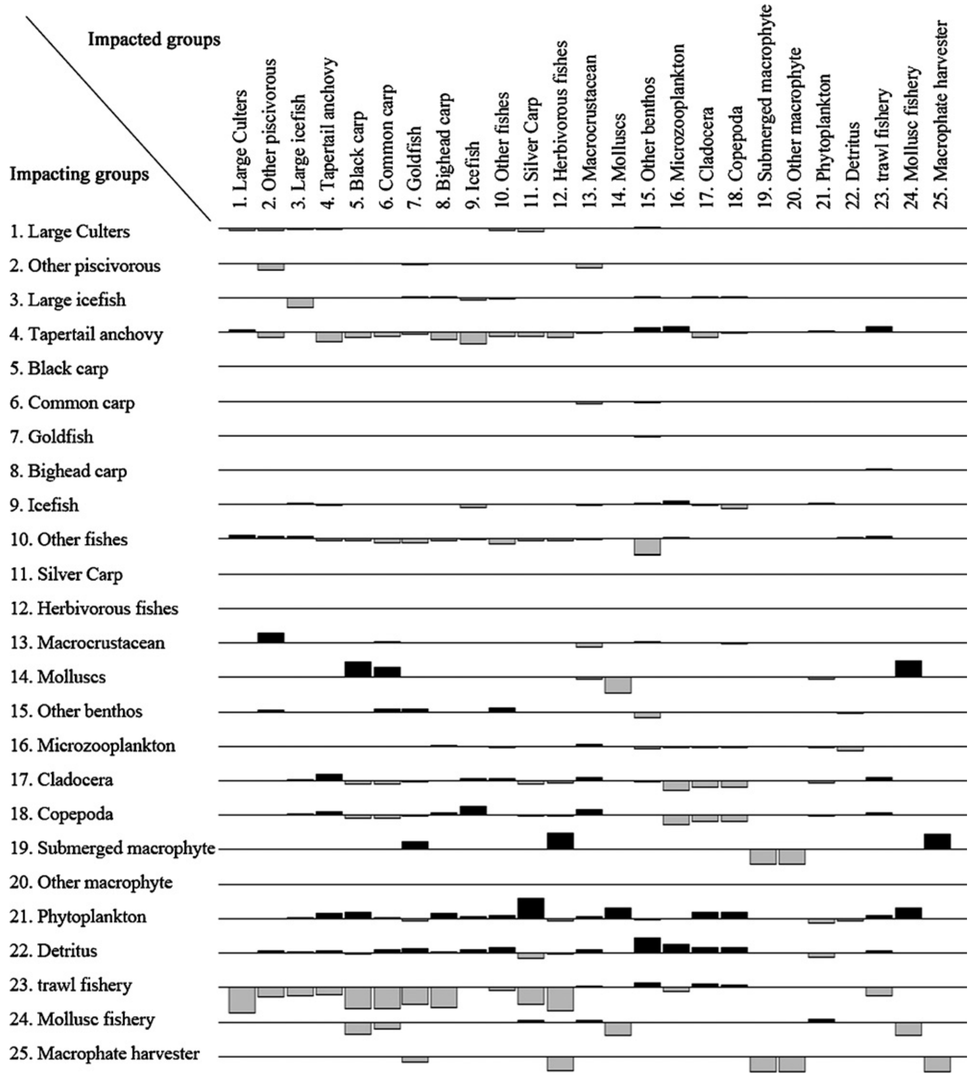

Fig. 4. Mixed trophic impacts in the Taihu ecosystem. Bars above the line represent a positive impact whereas bars underneath the line indicate a negative impact, and the height of the bars are proportionate to the degree of the impacts.

3.4. Summary statistics and network flow indices

For Lake Taihu, flows into detritus dominated the total system throughput (TST), accounting for 38.3% of overall ecosystem flow. These were followed by consumption flows (totaling 26.7%) and export flows (totaling 26.6%). The mean trophic level of fishery catch (TLc) was 2.92. Other important theoretical indices were also estimated from Ecopath. Many attributes related to the ecosystem's maturity were also obtained from the model, following the theories of Odum (1969) and Christensen (1995) regarding the developmental stages that ecosystems undergo. The ratio between total primary production (PP) and total respiration (R), considered to be another important descriptor of system maturity (Odum, 1971), was 3.848 for the lake, indicating that total primary production was approximately 285% greater than total respiration. The ratio of total primary production to total biomass, expected to be high in an immature ecosystem, was 11.66 t km^{-2} year^{-1}. The connectance index was estimated to be 0.206. The system omnivory index of the lake was 0.042, with a relatively low ascendency of 25.9%, and a high overhead of 74.1% (Christensen, 1995). All these system properties are listed in Table 3. The pair of the percentage of primary production required to sustain fisheries (%PPR) and the average tophic level of catch (TLc) of the system within the range of values of overfished

Table 3
The total system properties of Lake Taihu ecosystem.

Index	Value	Unit
Sum of all consumption	3629.80	t km^{-2} year^{-1}
Sum of all exports	3616.77	t km^{-2} year^{-1}
Sum of all respiratory flows	1130.61	t km^{-2} year^{-1}
Sum of all flows into detritus	5208.73	t km^{-2} year^{-1}
Total system throughput	13586.00	t km^{-2} year^{-1}
Sum of all production	4561.00	t km^{-2} year^{-1}
Primary production required/total primary production	22.08	%
Mean trophic level of the catch of fishes and shrimps	2.92	
Gross efficiency (catch/net primary production)	0.0087	
Net primary production	4350.15	t km^{-2} year^{-1}
Total primary production/total respiration	3.85	
Net system production	3219.54	t km^{-2} year^{-1}
Connectance index	0.206	
System omnivory index	0.042	
Throughput cycled (including detritus)	1572.84	t km^{-2} year^{-1}
Finn's cycling index	11.58	% of total throughput
Finn's mean path length	2.86	–
Ascendency	25.90%	
Overhead	74.10%	

Table 4
The effects of fishing mortality for large culters on the biomass of functional groups in the Taihu ecosystem model.

Fishing mortality	0	0.3	0.6	0.771	0.9	1.2
Group/biomass						
LarC	0.929	0.657	0.481	0.275	**0.072**	**0**
OthP	**0.120**	**0.123**	**0.128**	0.130	0.130	0.130
LarI	**0.058**	**0.069**	**0.089**	0.110	0.131	0.139
TapA	**0.834**	**1.628**	**3.148**	4.343	5.201	5.513
BlaC	0.056	0.056	**0.054**	0.055	0.059	0.063
ComC	0.382	0.337	0.273	0.232	**0.210**	**0.201**
GolF	0.360	0.332	0.296	0.275	**0.263**	**0.260**
BigC	**0.420**	**0.468**	**0.544**	0.610	0.661	0.668
IceF	2.077	1.767	1.209	0.793	**0.512**	**0.407**
OthF	**0.770**	**0.982**	**1.296**	1.525	1.699	1.755
SilC	**0.058**	**0.064**	**0.073**	0.080	0.085	0.087
HerF	**0.303**	**0.304**	**0.304**	0.305	0.306	0.306
MacC	0.827	0.765	0.658	0.575	**0.506**	**0.485**

Unit: t km^{-2} year^{-1}. The value in bold is lower than the control. Fishing mortality of 0.771 was set as the control value.

ecosystem status was identified by the framework developed by Tudela et al. (2005).

3.5. Simulated impacts of fishing

The current fishing mortality of large culters and the total fishing efforts were estimated to be 0.771 and 1307.42×10^4 horsepower day^{-1}, respectively. These values are extremely high compared to other inland fisheries in China.

3.5.1. Scenario 1

The biomass of large culters increased to 2.38 times its original level when fishing mortality for this species was reduced to 0. The biomasses of other piscivorous fish, bighead carp, silver carp, and grass carp all declined accordingly. The biomasses of tapertail anchovy and other fishes declined by 80.8% and 49.5%, respectively, while common carp, golden carp, icefish, and marcocrustaceans all saw biomass increases (Table 4).

For the scenarios involving different fishing mortalities upon large culters, the total catch increased significantly alongside fishing mortality up to the point at which the stock collapsed (F = 0.9). The catch of large culters decreased by 69% and disappeared from the landings altogether when fishing mortality reached 1.2 (Table 5). The profits from fishing reached their maximum of 32,559.81 Yuan km^{-2} year^{-1} when fishing mortality was set at 0.3.

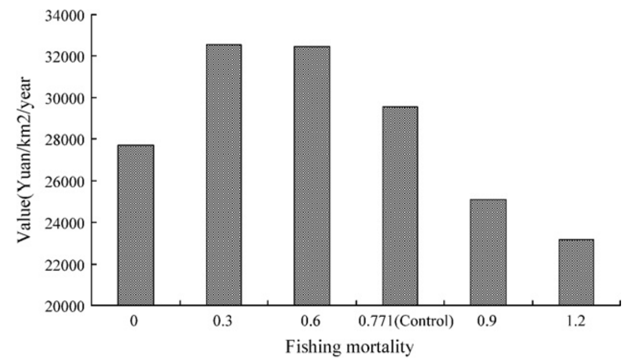

Fig. 5. The change of fishery profit with different scenarios of fishing mortality rates for large culters.

Their minimum of 23,164.92 Yuan km^{-2} year^{-1} occurred when fishing mortality was set to 1.2 (Fig. 5).

3.5.2. Scenario 2

When modeled fishing effort reached 1.25 times its current estimated level, a significant reduction in biomass occurred for most fish groups (with the exceptions of icefish and other fishes, whose biomasses increased). The biomasses of large culters, black carp, common carp, bighead carp, and golden carp decreased to 1.8%, 7.3%, 9.0%, 10.8%, and 52% of their original levels, respectively (Table 6). At the same time, total catch increased by only 3.0% as a consequence of reduced catches for these same five species. The catch of large culters increased to its maximum value of 0.544 t km^{-2} year^{-1} when relative fishing effort was reduced to 0.5 (Table 7). The highest fishery profit was obtained when fishing effort was reduced to 75% of its current level (Fig. 6). In this scenario, catch and cost declined by 17% and 25%, respectively, while value and profit increased by 8% and 24.5%, respectively.

4. Discussion

This contribution constituted the first attempt at modeling the food web of the inland lake in China and provided insights into the trophic structure and function of Lake Taihu and how they might be influenced by different fishing management strategies. The results provided guidance for future fisheries management in this lake and served as a strong platform for comparison with the case in marine systems.

Table 5
The effects of fishing mortality for large culters on the catch of functional groups in the Taihu ecosystem model.

Fishing mortality	0	0.3	0.6	0.771	0.9	1.2
Group/catch						
LarC	**0**	**0.197**	0.289	0.212	**0.065**	**0**
OthP	**0.037**	**0.038**	**0.039**	0.040	0.040	0.040
LarI	**0.035**	**0.041**	**0.053**	0.066	0.078	0.083
TapA	**0.562**	**1.097**	**2.121**	2.925	3.503	3.713
BlaC	0.044	0.043	**0.042**	0.043	0.046	0.049
ComC	0.299	0.264	0.214	0.182	**0.164**	**0.157**
GolF	0.280	0.259	0.231	0.214	**0.205**	**0.202**
BigC	**0.323**	**0.361**	**0.419**	0.470	0.510	0.530
IceF	1.253	1.066	0.729	0.478	**0.309**	**0.245**
OthF	**0.585**	**0.745**	**0.984**	1.158	1.290	1.333
SilC	**0.020**	**0.022**	**0.026**	0.028	0.030	0.031
HerF	**0.239**	**0.239**	**0.239**	0.240	0.241	0.241
MacC	0.670	0.620	0.534	0.466	**0.410**	**0.393**
Total catch	**4.347**	**4.992**	**5.920**	6.522	6.891	7.017

Unit: t km^{-2} year^{-1}. The value in bold is lower than the control. Fishing mortality of 0.771 was set as the control value.

Table 6
The effects of different fishing efforts on the biomass of functional groups in the Taihu ecosystem model.

Fishing rate	0.25	0.50	0.75	1.00	1.25
Group/biomass					
LarC	2.155	1.411	0.816	0.275	**0.005**
OthP	0.164	0.178	0.149	0.130	**0.108**
LarI	0.129	**0.108**	**0.106**	0.110	**0.098**
TapA	**3.936**	**3.457**	**3.689**	4.343	**3.687**
BlaC	0.297	0.149	0.113	0.055	**0.004**
ComC	1.104	0.592	0.447	0.232	**0.021**
GolF	0.574	0.378	0.334	0.275	**0.143**
BigC	1.769	1.444	1.106	0.610	**0.066**
IceF	1.072	0.973	0.933	0.793	1.005
OthF	**2.442**	**2.598**	**2.836**	3.125	3.545
SilC	0.081	**0.079**	**0.079**	0.080	**0.075**
HerF	0.491	0.349	0.331	0.305	**0.248**
MacC	**1.499**	1.771	1.689	1.575	**1.529**

Unit: t km^{-2} year^{-1}. The value in bold is lower than the control. Fishing rate of 1.00 was set to be the control.

Table 7
The effects of different fishing efforts on the catch of functional groups in the Taihu ecosystem model.

Fishing rate	0.25	0.50	0.75	1.00	1.25
Group/catch					
LarC	0.415	0.544	0.472	0.212	**0.005**
OthP	**0.013**	**0.027**	**0.034**	0.040	0.041
LarI	**0.019**	**0.033**	**0.048**	0.066	0.074
TapA	**0.663**	**1.164**	**1.864**	2.925	3.104
BlaC	0.058	0.058	0.066	0.043	**0.004**
ComC	0.216	0.232	0.262	0.182	**0.021**
GolF	**0.112**	**0.144**	**0.195**	0.214	**0.139**
BigC	**0.341**	0.556	0.639	0.470	**0.064**
IceF	**0.162**	**0.294**	**0.422**	0.478	0.758
OthF	**0.226**	**0.481**	**0.788**	1.158	1.642
SilC	**0.007**	**0.014**	**0.021**	0.028	0.033
HerF	**0.097**	**0.137**	**0.195**	0.240	0.244
MacC	**0.111**	**0.262**	**0.375**	0.466	0.565
Total catch	**2.440**	**3.949**	**5.381**	6.522	6.694

Unit: $t\,km^{-2}\,year^{-1}$. The value in bold is lower than the control. Fishing rate of 1.00 was set to be the control.

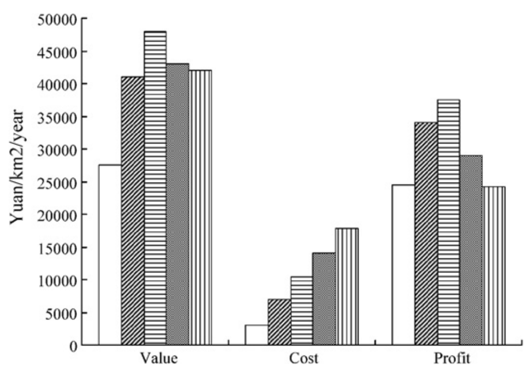

Fig. 6. The change of fishery values, costs and profits for different scenarios of fishing mortality rates.

As the energy sources of such ecosystems, both primary production pathways and detrital pathways are important in aquatic ecosystems, with each having significant impacts on the diets of groups at higher trophic levels (Pauly and Christensen, 1995). In Lake Taihu, EE values were high for most fish groups, indicating that the fish groups were highly constrained by combination of fishing and predation, but were low for phytoplankton and detritus. The low EE of phytoplankton indicated that only a small proportion of phytoplankton production was grazed in the water column, with the rest going toward detritus. Similarly, the low EE of detritus also indicated that a small fraction of detritus biomass was consumed, with the rest being buried in the sediment or being exported out of the system. As a consequence of this low ecotrophic efficiency, the accumulating detrital sediments continually released waste nutrients back into the system, resulting in its internal pollution (Yan and Shi, 1995; Chen et al., 1997; Zhu, 1999). The biomass, production and consumption of TL II indicated that zooplankton plays an important role in the food web, which was not only the direct consumer of primary production and detritus, but also the main food supply for TL III which was dominated by the relatively small zooplanktivores. It was well known that in natural lake ecosystems the biomass of phytoplanktivores was likely to be determined by both phytoplankton (bottom-up effect) and zooplanktivores (top-down controls; Liu et al., 2007). In this case, a low zooplanktivores biomass, as a result of high fishing pressure, might result in high biomass of primary production and low EE. This was considered as one of the main reasons for algal bloom that could last for nearly 6 months each year (Shapiro and Wright, 1984; Chen et al., 1997; Drenner and Hambright, 2002; Liu, 2005; Liu et al., 2007).

Numerous studies have suggested that biodiversity reduces variability in ecosystem productivity through compensatory effects (Naeem and Li, 1997; Lorenzen, 2000; Villanueva et al., 2006; Libralato et al., 2008), which means that one species increases in abundance in response to the reduction of another in a fluctuating environment. A high biodiversity enhances an ecosystem's reliability through an increase in the number of redundant species per functional group—where some groups occupying a given TL maintain ecosystem functioning by compensating for temporary loss of other groups in the same TL (Villanueva et al., 2006). In this case, mixed trophic impact analysis showed that fishing pressure had more impacts on most functional groups considered in this study compared with predation and competition (Christensen et al., 2004). Most of impacted fish groups were less negatively influenced by the top predators. Large culters consuming a large portion of tapertail anchovy had positive impacts on icefish and macrocrustacean which were strong competitors with other pelagic species.

Comparing this model with the model of Lake Superior, Canada (Table 8)—a lake much larger and deeper than Lake Taihu, we found that ratios of total system throughput and net primary production for Lake Taihu were, respectively, 3.83 and 2.74 times higher than for Lake Superior, respectively. This suggests that much higher energy is used in the Lake Taihu ecosystem. On the other hand, the export detritus was six times higher than Lake Superior's (Christensen, 1995; Kitchell et al., 2000). Similar results could also be found when compared the model with the model of Lake Kuvi expect for the mean trophic level of the catch, which in Lake Taihu was higher than that in Lake Kuvi (Villanueva et al., 2008). This could be explained as the fishery in Lake Taihu still mainly focused on the top predators on the higher trophic levels, although small species from lower trophic levels have increasingly comprised actual landings.

Pauly et al. (1998) explained that "fishing down the food web" was a symptom of ecosystem deterioration when fish species of high trophic levels were overexploited. The majority of landings in the Taihu fishery was fish species of lower trophic levels, suggesting that the top predators of the ecosystem were over exploited and the fishing intensity for the top predators was much higher than was the case in Lake Superior (Kitchell et al., 2000; Villanueva et al., 2006).

The low pair of TLc and %PPR and transfer efficiency (TE) parameters highlighted the overexploitation symptom of Lake Taihu (Tudela et al., 2005; Libralato et al., 2008). This result was in accordance with the previous studies carried out in the region (Zhu, 1999; Yang, 2003). The generally higher values observed for net primary production, net primary production/respiration, net system production, and catch, contrasted against the lower system omnivory index, the lower Finn's cycling index, and the shorter Finn's mean path length (Christensen et al., 2004) all indicated that Lake Taihu is an immature, unstable, and relatively less complex system. High fishing pressure and low utilization of primary production are key characteristics of Lake Taihu. The significant annual differences seen in the invertebrate biomasses and the

Table 8
The comparison of some system indices of different lakes.

	TST	SAE	NPP	NPP/R	NSP	SOI	TLc
Lake Taihu	13586.00	3616.77	4350.15	3.85	3219.54	0.04	2.92
Lake Superior	3549.10	602.16	1588.75	1.61	602.16	0.10	3.55
Lake Kuvi	6686	1499.85	2733.85	2.21	1499.85	0.148	2.90

TST: total system throughput; SAE: sum of all exports; NPP: net primary production; NPP/R: net primary production/respiration; NSP: net system production; SOI: system omnivory index; TLc: mean trophic level of the catch.

unpredictable, undulatory nature of most catches resulted from this unstable character of the system (Yan and Shi, 1995; Chen et al., 1997; Zhu, 1999). However, the high system overhead ratio (74.1%) would appear by itself to suggest that the system is highly developed and relatively stable (Christensen, 1995). This incongruously high overhead might have arisen as an artifact of the large recycling flow present in the system (Vasconcellos et al., 1997).

Along with various industrial and agricultural activities, overfishing is responsible for a wide variety of impacts on fish communities. These include the modification of population structures and the imposition of stress conditions that force ecosystems to adapt to their changing environments (Myers and Worm, 2003; Watson and Pauly, 2001; Pauly, 2003). Xu (1984) explained that overfishing of large culters, which are considered a main predator of less valuable fishes such as tapertail anchovy, might be one cause of the current problems facing the Taihu fishery and the environment of Lake Taihu. Our results support this hypothesis. When the fishing mortality upon large culters was increased in the first simulation scenario, the biomasses of common carp, golden carp, icefish, and macrocrustaceans all declined as the result of a trophic cascade mediated by an expansion among mesopredators. Yet at the same time, certain smaller, less valuable species consisting of tapertail anchovy and "other fishes" increased in abundance, owing to a reduction in the competitive pressures they faced as the biomasses of these other groups declined. These results indicate that recent increases in the abundances of tapertail anchovy and other fishes might have resulted from increased fishing effort on their predators.

The nature of the link between fishing effort on top predators and the abundance of small species is further clarified by the scenarios that reduced fishing mortality upon large culters. In these simulations, the biomasses of most fish groups declined because of the increase in the biomass of their predators (Chen et al., 1997; Song, 2004). This decrease among mesopredators could effectively control the biomass of small species by prompting an expansion of lower trophic levels and an increase in competition. Small, inferior competitors declined. As a result, the biomasses of tapertail anchovy and other fishes declined by 63.28% and 35.61%, respectively. Furthermore, Fig. 5 shows that decreasing the fishing mortality upon large culters might optimize the structure and profits of the fishery, allowing a greater number of valuable fish and fewer less valuable fish to be caught. The fishery could reach its maximum productivity (both in terms of biomass and profit) if the fishing mortality upon large culters were set at 0.3.

The mean trophic level of the species groups reported in the fisheries statistics of the Food and Agricultural Organization declined from 1950 to 1994 in the face of overcapitalization and excess fishing effort (Pauly et al., 1998). In light of this trend, we used our second set of scenarios to analyze how ecosystem structure and fishery profits changed with fishing effort in the Taihu ecosystem. When fishing effort increased, the biomasses of almost all groups declined significantly. This was especially true for species of economic importance. Although overall landings rose with increasing fishing effort, profitability declined because of high operating costs and the lower value of those species caught. Conversely, when we reduced fishing mortality to 75% of its current level, the biomasses of most groups recovered and fishery profits increased by 8%. Based on this evidence, we argue that a reduction in overall fishing effort may help resolve the problems currently facing the Taihu fishery and its supporting ecosystem.

The EwE model developed in this study provides an analytical approach for evaluating interactions of all components in a complex ecosystem. Deficiencies in available biological data have been identified. Further effort to better characterize key elements of the ecosystem, such as the aspect ratio of fishes and the biomass of detritus, could be an important step forward towards the improvement of the input data and the characterization of the ecosystem. Data are also scarce in estimating the cost of fishing. The incorporation of fishery economic study would also be appropriate to increase the quality of the model. Moreover, considerations of the discard and import portions in the model would also be an important step forward towards the improvement of the model. Thus, although the pedigree index of the model was high and the sensitivity analysis proved the robustness of the model, the continuous incorporation of new empirical data from the region into the model would improve the results. If these hurdles can be overcome, an ecosystem modeling approach could become a productive complement to other fisheries stock assessment approaches currently in use, hopefully leading to the development of ecosystem-based management for lake fisheries in China.

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Appendix A

See Tables A1–A3 .

Table A1
Species and descriptions by functional groups for the Lake Taihu model.

Functional groups	Species	Description
Large culters	*Erythroculter mongolicus*	67.5% of the total biomass of large culters
	Erythroculter ilishaeformis	32.5% of the total biomass of large culters
Other piscivorous	*Cultrichthys erythropterus*	
	Pelteobagrus fulvidraco	
	Channa argus	
	S. chuatsi and *S. kneri*	
	Odontobutis obscurus	
Large icefish	*Protosalanx chineniss*	Main economic fishery species in Lake Taihu
Tapertail anchovy	*Coilia ectenes taihuensis*	*Coilia ectenes taihuensis* has a wide distribution in Lake Taihu. It is the most productive species (Zhang, 2001; Yang, 2003) that accounts for nearly 46% of the total annual catch in the lake (Zhang and Zhu, 2004)
Black carp	*Mylopharyngodon piceus*	Traditional species in the Taihu fisheries
Common carp	*Cyprinus carpio*	
Goldfish	*Carassius auratus*	
Bighead carp	*Aristichthys nobilis*	
Silver carp	*Hypophthalmichthys molitrix*	
Iicefish	*Neosalanx taihuensis*	A total of 95% of the icefish biomass was from *Neosalanx taihuensis* that inhabits the whole lake. Other species in this group are *Neosalanx ologodontis* and *Reganisalanx branchyrostralis*
	Neosalanx ologodontis	
	Reganisalanx branchyrostralis	
Other fishes	*Toxabramis swinhonis*	Together these make up of 80% of the biomass of 'other fishes', according to the bottom trawl surveys (Deng et al., 1997)
	Hemirhamphus kurumeus	
	Xenocypris argentea	
	Ctenogobius giurinus	
	Macropodus chinensis	
	Oryzias latipes	
	Toxabramis swinhonis	
	Hemirhamphus kurumeus	
Herbivorous fishes	*Ctenopharyngodon idella*	
	Megalobrama amblycephala	
Macrocrustaceans	*Palaemon modestus*	
	Erocheir sinensis	
Mollusks	*Corbicula fluminea*	
Benthos	*Nephthy* sp.	
Microzooplankton	*Vorticella aequilata*	
	Polyathra trigla	
Cladocera	*Ceriodaphima cornuta*	
	Daphina longispina	
	Diaphanosoma sarsi	
Copepoda	*Sinocalanus dorrii*	
	Limnothora sinensis	
Macrophyte	*Potamogeton maackianus*, *Zizaniz latifolia* and *Nymphoides peltata*	
Phytoplankton	*Cyanophyta*, *Bacillariophyta*, *Cryptophyta*, *Chlorophyta*, *Pyrrophyta*, *Euglenophyta*, and *Chrysophyta*	In Lake Taihu, there exist about 228 species of phytoplankton. *Cyanophyta*, *Bacillariophyta*, *Cryptophyta*, *Chlorophyta*, *Pyrrophyta*, *Euglenophyta*, and *Chrysophyta* biomasses accounted for 42.75%, 18.78%, 18.08%, 11.09%, 8.59%, 0.4%, and 0.1% of total phytoplankton biomass, respectively (Sun, 1993)

Table A2
Input data and references by functional groups for the Lake Taihu model.

Functional group	Original value	Reference	Observations
Submerged macrophyte			
Biomass	150.292 t km^{-2}	Bao (1991), Yang (1998)	
P/B	1.25 $year^{-1}$	Liu (1992)	
Catch	242.912 t km^{-2}	Yang (1998)	
Other macrophyte			
Biomass	146.36 t km^{-2}	Bao (1991), Yang (1998)	
P/B	1.00	Liu (1992)	
Catch	13.416 t km^{-2}	Yang (1998)	
Phytoplankton			
Biomass	20.893 t km^{-2}	Tang (1995)	
P/B	185 $year^{-1}$	Sun and Huang (1993)	
Detritus			
Biomass	311.62 t km^{-2}	State Environmental Protection Administration of China (2000)	Used conversion factor that estimated the biomass of bacteria as 17.5% of that for phytoplankton (Heymans et al., 2004). The biomass of DOC and POC was estimated by the Ecoempire in the EwE model (Christensen and Pauly, 1992, 1993; Christensen et al., 2004)
Zooplankton			
Microzooplankton			
Biomass	0.69 mg/L	Yan and Shi (1995)	Used conversion factor from dry weight to wet weight of 16.7% (Gong et al., 2001)
U/Q	0.65	Park et al. (1974)	
P/B	29.897 $year^{-1}$	Estimated by Ecopath	EE was assumed to be 0.95 (Christensen et al., 2004)
Q/B	597.934 $year^{-1}$		*P/Q* ratio of 0.05 was adopted for zooplankton (Park et al., 1974; Scavia et al., 1974; Yang, 2003), which could then be converted into consumption/biomass ratio (*Q/B*) using $Q/B = (P/B)/(P/Q)$
Cladocera			
Biomass	1.86 mg/L	Yan and Shi (1995)	Used conversion factor from dry weight to wet weight of 16.7% (Gong et al., 2001)
P/B	15.394 $year^{-1}$	Estimated by Ecopath	
Q/B	307.882 $year^{-1}$		*P/Q* ratio of 0.05 was adopted for zooplankton (Park et al., 1974; Scavia et al., 1974; Yang, 2003), which could then be converted into consumption/biomass ratio (*Q/B*) using $Q/B = (P/B)/(P/Q)$
Copepoda			
Biomass	2.25 mg/L	Yan and Shi (1995)	Used conversion factor from dry weight to wet weight of 16.7% (Gong et al., 2001)
P/B	12.165 $year^{-1}$	Estimated by Ecopath	
Q/B	234.3 $year^{-1}$		*P/Q* ratio of 0.05 was adopted for zooplankton (Park et al., 1974; Scavia et al., 1974; Yang, 2003), which could then be converted into consumption/biomass ratio (*Q/B*) using $Q/B = (P/B)/(P/Q)$
Trophic data		Liu (1999)	
Benthos			
Biomass	1.16 t km^{-2}		
P/B	4.03 $year^{-1}$	Empirical equation from Brey (1999)	Used conversion factor from dry weight to wet weight of 16.7% (Gong et al., 2001)
Q/B	201.5 $year^{-1}$	Estimated by Ecopath	*P/Q* ratio of 0.05 was adopted for benthos (Park et al., 1974; Scavia et al., 1974; Yang, 2003), which could then be converted into consumption/biomass ratio (*Q/B*) using $Q/B = (P/B)/(P/Q)$
U/N	0.94	Yan (2003)	
Trophic data		Liu (1999)	
Mollucs			
Biomass	35.965 t km^{-2}	Deng et al. (1997)	
P/B	1.326 $year^{-1}$	Yang (2003)	
Q/B	10.605 $year^{-1}$	Estimated by Ecopath	*P/Q* ratio of 0.05 was adopted for mollucs (Park et al., 1974; Scavia et al., 1974; Yang, 2003), which could then be converted into consumption/biomass ratio (*Q/B*) using $Q/B = (P/B)/(P/Q)$
U/N	0.4	Scavia et al. (1974)	
Catch	31.22 t km^{-2}	Zhu (1998)	
Trophic data		Liu (1999)	
Macrocrustacean			
Biomass	0.575 t km^{-2}	Zhu (2003)	
P/B	2.42 $year^{-1}$	Estimated by Ecopath	
Q/B	32.268 $year^{-1}$	Estimated by Ecopath	
U/Q	0.7	Halfon et al. (1996)	

Table A2 (*Continued*)

Functional group	Original value	Reference	Observations
Catch	0.466 t km^{-2}	Zhu (1998)	
Trophic data		Shi et al., 1995	
Herbivorous fishes			
Biomass	0.305 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	0.987 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	7.1 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*N*	0.41	Winberg (1956), Brett and Groves (1979)	
Catch	0.24 t km^{-2}	Zhu (1999)	
Trophic data		Liu (1992)	
Other fishes			
Biomass	1.525 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	2.155 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	11 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.2	Winberg (1956), Brett and Groves (1979)	
Catch	1.158 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Zhu (1999)	
Icefish			
Biomass	0.793 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	2.373 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	27.2 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.2	Winberg (1956), Brett and Groves (1979)	
Catch	0.793 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Bing (1995)	
Black carp			
Biomass	0.055 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	0.912 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/B	11.544 $year^{-1}$	*P*/*Q* was assumed to be 0.079	
U/*Q*	0.724	Winberg (1956), Brett and Groves (1979)	
Catch	0.043 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Liu (1992)	
Common carp			
Biomass	0.233 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	0.96 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	10.693 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.35	Winberg (1956), Brett and Groves (1979)	
Catch	0.182 t km^{-2}	Zhu (2003)	
Trophic data		Liu (1992)	
Goldfish			
Biomass	0.275 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	1.13 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	12.3 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.35	Winberg (1956), Brett and Groves (1979)	
Catch	0.214 t km^{-2}		

Table A2 (*Continued*)

Functional group	Original value	Reference	Observations
Trophic data		Liu (1992)	
Bighead carp			
Biomass	0.61 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	0.99 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	6.9 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.3	Winberg (1956), Brett and Groves (1979)	
Catch	0.47 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Liu (1992)	
Silver carp			
Biomass	0.035 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	1.1 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	8 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.41	Winberg (1956), Brett and Groves (1979)	
Catch	0.028 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Liu (1992)	
Tapertail anchovy			
Biomass	4.343 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	1.283 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	11.35 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.2	Winberg (1956), Brett and Groves (1979)	
Catch	2.92 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Tang (1995)	
Large Icefish			
Biomass	0.11 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	1.862 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	16.65 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.2	Winberg (1956), Brett and Groves (1979)	
Catch	0.066 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Zhu (1985)	
Other priscivorous			
Biomass	0.13 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu
P/*B*	1.665 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	6.1 $year^{-1}$	Empirical equation from Palomares and Pauly (1998)	
U/*Q*	0.2	Winberg (1956), Brett and Groves (1979)	
Catch	0.04 t km^{-2}	Zhu (1999), Zhu (2003)	
Trophic data		Tan (1997)	
Large culers			
Biomass	0.275 t km^{-2}	Zhu (2003)	Biomass estimated from the trawling surveys (1991–1998) in the Lake Taihu.
P/*B*	0.974 $year^{-1}$	$F = C/B$ and $Z = F + M = P/B$, M = empirical equation from Pauly (1980)	
Q/*B*	3.2 $year^{-1}$	Fishbase	
U/*Q*	0.2	Winberg (1956), Brett and Groves (1979)	
Catch	0.212 t km^{-2}	Zhu (2003)	
Trophic data		Xu (1984)	

Table A3
The input diet composition data in proportions for the Lake Taihu ecosystem.

Prey/predator		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	LarC	0.020	0.004																
2	OthP	0.008	0.021																
3	LarI	0.007		0.040															
4	TapA	0.510		0.360	0.005														
5	BlaC	0.001																	
6	ComC	0.001	0.007																
7	GolF	0.001	0.052																
8	BigC	0.013																	
9	Icef	0.047		0.165	0.005														
10	OthF	0.306	0.281	0.248															
11	SilC	0.005																	
12	HerF	0.001																	
13	MacC	0.013	0.448	0.074		0.025	0.080												
14	Moll		0.092		0.040	0.950	0.600				0.001								
15	OthB		0.076			0.025	0.157	0.159			0.186					0.001			
16	Micz			0.009	0.001		0.001	0.010	0.115	0.007	0.002	0.003	0.001	0.141				0.016	0.016
17	Clad			0.047	0.506			0.039	0.31	0.433	0.338	0.097		0.38					
18	Cope			0.057	0.400			0.050	0.375	0.560	0.253	0.100		0.459					
19	SubM	0.067					0.009	0.515			0.002		0.998			0.001			
20	OthM												0.001						
21	Phyt		0.004		0.043				0.18		0.129	0.800			0.800	0.100	0.333	0.474	0.474
22	Detr		0.016				0.153	0.227	0.02		0.091			0.02	0.200	0.898	0.667	0.510	0.51
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

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