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Changes in the trophic interactions and the community structure of Lake Taihu (China) ecosystem from the 1960s to 1990s

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Abstract As the third largest freshwater lake in China, Lake Taihu has suffered from overfishing, eutrophication, and physical disturbance over the last several decades. Evaluating and quantifying changes in the ecosystem can help us better understand and develop hypotheses to explain the dynamics of the ecosystem. In this study, trophic interactions and community structure of commercial fisheries species of Lake Taihu ecosystem were analyzed and compared for three time periods (1961–1965, 1981–1987, and 1991–1995) using the Ecopath with Ecosim model with the aim of evaluating the changes in the population dynamics and ecosystem development mechanism spanning the period from the 1960s to 1990s. The results show that the biomass of large predators decreased over the three decades, while the biomass of small species increased. Increases in the P/B ratios and fishing mortality levels observed for species groups reveal rapidly intensifying fishery stress over the three decades. The fisheries operated at the highest trophic level during the 1980s, and there are some indications of "fishing down the food web" in this ecosystem between the 1980s and the 1990s. Drawing upon Odum's theory of ecosystem maturity, the structured, web-like ecosystem of the 1960s developed into a highly mature system during the 1980s; yet, in the 1990s, this structure became less complex and the system's maturity fell to its lowest observed level. During this period, the successional development of the system occurred in reverse.

Keywords Lake Taihu · Ecopath, Ecosystem impacts of fishing · Ecosystem modeling · Ecosystem development

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Introduction

Over the past few decades, an increasing number of terms and concepts have been proposed for the holistic management of aquatic natural resources

(Fletcher 2006). Ecosystem models are recognized as an invaluable tool in the assessment and management of aquatic living resources. Dynamics of species abundance and composition within an ecosystem can be quantified using an ecosystem model. Both the direct and indirect interspecies interactions can be explored, and the overall functioning of different ecosystems can be compared (Mercer 1982; Sherman and Alexander 1986).

One of the commonly used ecosystem models are mass-balanced models (Pauly et al. 1998; Heymans et al. 2004), which describe energy or biomass flows between species and ecological functional groups and can be used to facilitate the assessment of ecosystem-level properties. Mass-balanced models, following the theories of Odum (1969), Finn (1976), and Ulanowicz (1986), such as Ecopath with Ecosim, enable comparisons between different ecosystems with respect to ecological indices, food webs, trophic flows, and nutrient cycling regimes, as well as ecosystem properties such as maturity and habitat development. They also allow for comparisons of the same ecosystem in different time periods (Christensen and Pauly 1993; Christensen 1995; Moreau et al. 2001; Heymans et al. 2004; Brando et al. 2004; Neria et al. 2004).

Lake Taihu, China's third largest freshwater lake, lies in a densely populated and economically crucial areas. Although it accounts for only 0.4% of the total area of China and 2.9% of the nation's population, the Lake Taihu region provides more than 14% of China's GDP (Shen et al. 2000). Multiple uses tie Lake Taihu to the rapid economic growth of the past three decades. It provides the region's water supply, assists in flood control and waste disposal, and supports industries including shipping, commercial fishing, and tourism. It therefore plays an extremely important role in both economic and social development (Li et al. 2009). Historically, the Lake Taihu system has been very important as a valuable fishing ground (Hu et al. 2006), but it has also changed dramatically over the past few decades (1961–1995). In some instances, these changes reflected natural variability, but fishing practices in the Lake Taihu ecosystem have also changed with fishing management policy and economical development in the country.

Over the last few decades, Lake Taihu has sustained high stress from fishing and pollution. The total catch and total fishing effort for commercial species have increased significantly (Fishery Administration Department of Taihu). Because of prolonged and intense fishing pressure, we observed signs of "fishing down the food web" (Pauly et al. 1998) in Lake Taihu. Biodiversity has declined significantly; in addition, most large traditional food fish have been depleted, and catches are now dominated by small species with high turnover rates (Yang 1998). Moreover, algal blooms were observed more frequently, and the duration of blooming also became longer. Eutrophication has already seriously affected industrial and agricultural development and has threatened drinking water security in the Taihu basin (Zhang et al. 2008).

To properly manage the fisheries resources of Lake Taihu and address fishery depletion, it is particularly urgent to evaluate and quantify the changes in the ecosystem over the past few decades. Doing so can help diagnose problems with the past and current management (Pitcher 2004). The Lake Taihu ecosystem has been relatively well studied during this period, and a large quantity of data has been collected on fisheries statistics, fish population parameters, diet compositions, and physical and chemical variables (Wu et al. 1962; Chen et al. 1997; Li et al. 2009). Consequently, the objective of this paper is to investigate changes in the trophic interactions and the community structure of Lake Taihu ecosystem spanning the period from the 1960s to 1990s. To accomplish this objective, we constructed three mass-balanced ecotrophic models summarizing biomass, catches, and production of the main trophic groups, with an emphasis on fishery resources in the Lake Taihu ecosystem in the 1960s, 1980s, and 1990s.

Methods and data

Study site

Lake Taihu (31°30′N, 120°30′E) sits in the south portion of the Yangtze River delta (Fig. 1). It covers a water surface area of 2,428 km^2 with a mean depth of 1.9 m. The Lake Taihu Plain is dominated by monsoon climate, with annual mean air temperatures varying from 14.9 to 16.2°C. Precipitation averages between 1,000 and 1,400 mm annually, while evaporation

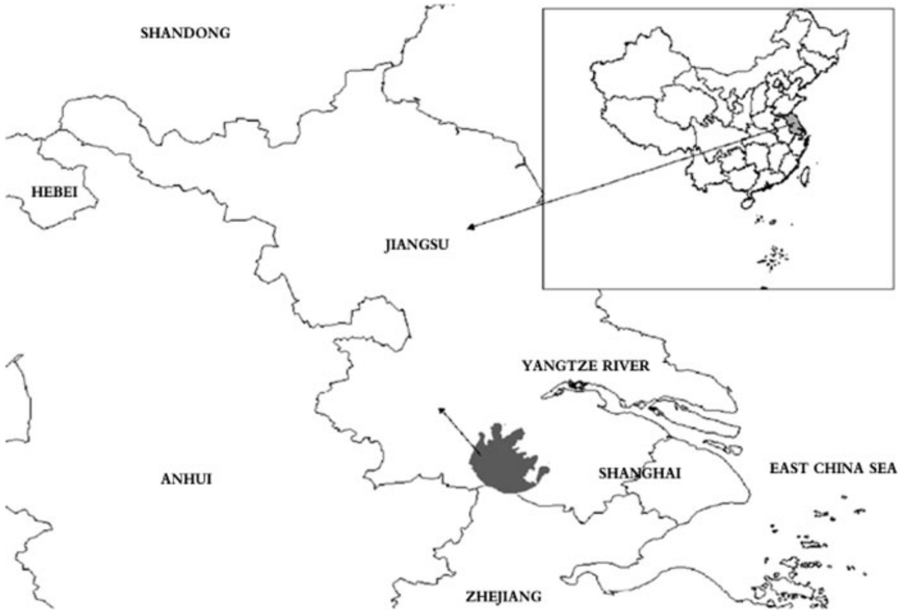

Fig. 1 The geographic location of Lake Taihu in Jiangsu and Zhejiang provinces, China

averages around 941 mm annually. Water temperature in the lake ranges from 0 to 38°C, with the lowest temperature occurring in January and the highest in August (Li et al. 2009).

Mass balance modeling approach

Trophic flow models of the Lake Taihu ecosystem were constructed and analyzed using Ecopath with Ecosim (Christensen et al. 2004). Ecopath is a static and mass-balanced ecosystem model that is used to analyze the structure of ecosystems and evaluate the impacts of trophic interactions among organisms at a given time (Christensen et al. 2004). The Ecopath model splits the production of each group (i) in a system into the following components:

$$P_i = Y_i + B_i \cdot M_{2i} + E_i + BA_i + P_i \cdot (1 - EE) \quad (1)$$

where i is a model component or group, P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), M_{2i} is the total predation rate for group (i), B_i is the biomass of the group, E_i is the net migration rate (emigration-immigration), BA_i is the biomass accumulation rate for (i), and $M_{0i} = P_i\,(1 - EE_i)$ is the other mortality rate on (i). EE_i is the ecotrophic efficiency of (i) and represents the total fraction of production that is either consumed by predators or exported from the system.

These components lead to the following linear equation:

$$Bi \cdot \left(\frac{P_i}{B_i}\right) \cdot EEi - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} - EX_i = 0 \quad (2)$$

where Q_i is the prey consumption of predator group j, DC_{ji} is the fraction that prey group i contributes to the overall stomach contents of predator group j, and EX_i is the export of group i from the system. In this study, EX_i consisted of fisheries catches (Christensen et al. 2004).

The mass balance of each component of the system is given by:

$$\text{Consumption } (Q_i) = \text{production } (P_i) + \text{respiration } (R_i) + \text{unassimilated food } (U_i) \quad (3)$$

This equation implicitly assumes that the energy inputs and outputs of all living groups must be balanced in an ecosystem (Christensen et al. 2004).

Model structure and parameterization

Using Ecopath, three models were constructed of Lake Taihu to represent its status during the early 1960s, 1980s, and early 1990s, respectively (hereafter termed the 1960s, 1980s, and 1990s models). To investigate fishing impacts on Lake Taihu and the resulting changes over these three decades, the ecosystem was structured into 22 compartments. These included 3 primary producers, 3 zooplankton groups, 3 groups of benthos, and 12 groups of fishes. Finally, detritus comprised of the only nonliving group in the model, being produced by the living groups. Organisms were classified into groups based on ecological function (mainly feeding), abundance, and information availability (Christensen et al. 2004). The main commercial species were grouped separately because of their importance to fisheries and the existence of sufficient information about them (Chen 1997; see Table A1).

Input data were collected from published stock assessment reports, peer-reviewed journal publications, and government reports. Some parameters were estimated from empirical modeling (see Table A2). Biomasses of most functional groups in the 1990s model were estimated directly based on data from the trawl survey conducted by the Lake Taihu Fishery Research Center (Li et al. 2009). The catch per unit of effort (CPUE) is often assumed to be proportional to the actual stock size (Hilborn and Walters 1992). Based on the detailed catch and effort statistics in Lake Taihu, in the 1960s and 1980s models, biomasses of many functional groups were back-calculated using the following equations from observed changes in CPUE between the 1960s and the 1990s,

$$B_{1960s} = \frac{CPUE_{1960s}}{q_{1960s}} \tag{4}$$

$$B_{1980s} = \frac{CPUE_{1980s}}{q_{1980s}} \tag{5}$$

$$B_{1990} = \frac{CPUE_{1990s}}{q_{1990s}} \tag{6}$$

$$B_{1960s} : B_{1980s} : B_{1990s} = \frac{CPUE_{1960s}}{q_{1960s}} : \frac{CPUE_{1980s}}{q_{1980s}} : \frac{CPUE_{1990}}{q_{1990}} \tag{7}$$

where q is the average catchability coefficient and B is the stock biomass. As reported in published literature and government reports (See Song 2004 for details), q for 1960s and 1980s was assumed to be 0.5–0.6 and 0.7–0.8 when the one of the 1990s was set to be 1, respectively (Taihu Fishery Research Center, personal communication). We used the mean of q in 1960s and 1980s to estimate the Biomasses. P/B ratios were estimated based on mortality estimates from length-based studies and empirical equations (Pauly 1980). Q/B ratios were estimated from empirical equations (Palomares and Pauly 1998). Diet compositions were derived from the published literature and the information available from FishBase (Froese and Pauly 2004; see Table A3). However, as diet composition was more uncertain than the other input parameters, the original data were modified in the course of balancing the model. This was done by adjusting the diets of individual groups and rerunning the parameterization procedure until ecotrophic efficiency values for all the functional groups were less than 1. Lastly, catches in the three models were based on the landings statistics reported by the Taihu Lake Fishery Research Center (Li et al. 2009).

Uncertainties and sensitivity analysis

Uncertainties of the input parameters were specified in “pedigree” index in Ecopath (Christensen et al. 2004). This index was a coded statement categorizing the origin of a given input and specifying the likely uncertainty associated with the input parameters (Christensen et al. 2004). Such a statement was given to each of the parameters by the pedigree routine. Inputs were rated according to how they had been derived from local data, other locations, “best guesses,” empirical relationships, other Ecopath models, or estimates of the current model. Associated with each of these categories was an index of quality that ranged from 0 to 1, with 0 denoting the lowest quality and 1 the highest quality.

Mean values of basic parameters (biomasses, P/B ratios, Q/B ratios, and ecotrophic efficiencies) were estimated for each time period of model based on input data. This preliminary data were introduced into the “Ecoranger” routine of Ecopath, and the coefficient of variation from the pedigree analysis was used to obtain a range for each parameter. Parameter values were repeatedly drawn from normal distributions defined in the pedigree analysis to generate frequency distribution for each basic parameter using Monte Carlo simulations. We ran 10,000 runs for estimating confidence limits for all input and output parameters of the three time periods of models. The sensitivity analysis was performed by systematically increasing and reducing the input parameters of each functional group by 50%.

Results

Biomass changes

Tables A4, A5, and A6 summarize the basic parameters and the results of the balanced ecotrophic model for the Lake Taihu ecosystem in the 1960s, 1980s, and 1990s. The models reveal a large change in ecosystem structure. The biomass of phytoplankton changed significantly over time, increasing from 6.636 t km^{-2} $year^{-1}$ in the 1960s to 8.959 t km^{-2} $year^{-1}$ in the 1980s, and finally to 20.893 t km^{-2} $year^{-1}$ in the 1990s. Notably, the biomass of phytoplankton increased by 133% from the 1980s to the 1990s, growing much faster than the biomass of zooplankton (Fig. 2). The biomass of major fish groups was lower in the 1990s than in either the 1960s or the 1980s. However, there was a steady increase in the biomasses of tapertail anchovy, other fishes, and macrocrustaceans over the three decades. Moreover, both groups of icefish were more abundant in the 1980s than in either the 1960s or the 1990s (Fig. 3).

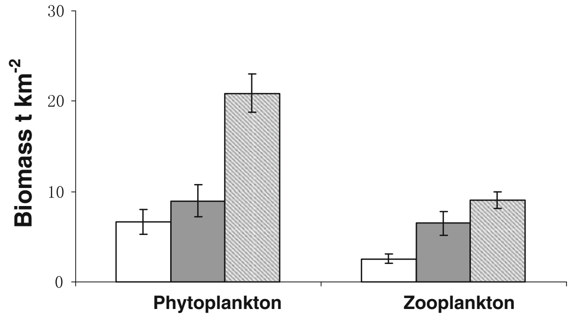

Fig. 2 Comparisons of phytoplankton and zooplankton biomasses in the 1960s (*open bars*), 1980s (*gray bars*), and 1990s (*shadow bars*) models. *Error bars* represent standard errors estimated from the pedigree analysis

The proportion of small fish species from low trophic levels seen in the total landings of Lake Taihu increased substantially from the 1960s to the 1990s. The percentage of tapertail anchovy and other fishes in these landings was seen an especially remarkable increase, rising from 9.99% in the 1960s to 30.65% in the 1980s, and eventually reaching 34.28% in the 1990s (Fig. 4).

The biomass of trophic level I decreased from the 1960s to the 1980s, but increased significantly during the 1990s (Fig. 5). By way of comparison, biomass in the higher trophic levels, IV and V, decreased steadily over the three decades. The structure of the

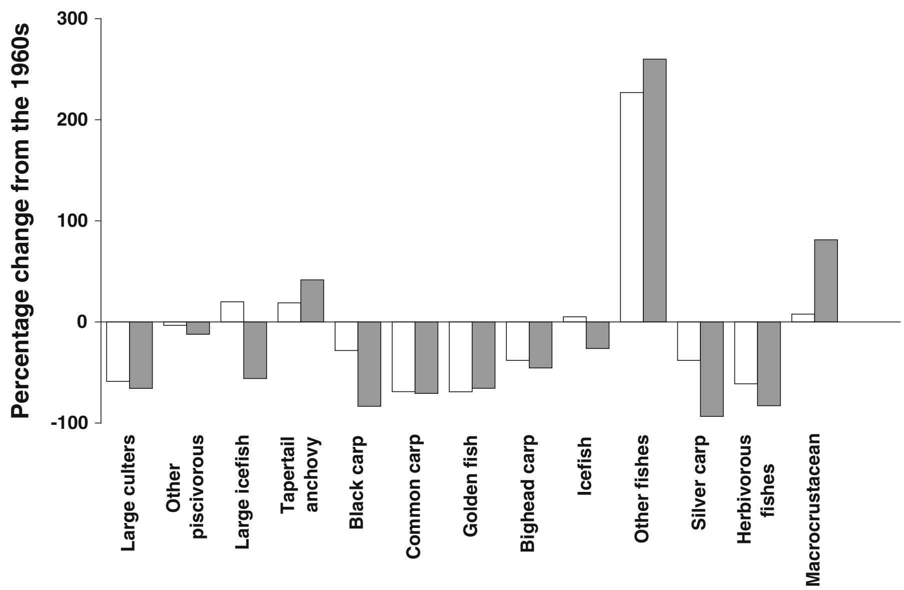

Fig. 3 Percentage changes in biomass from the 1960s to the 1980s (*open bars*) and 1990s (*gray bars*)

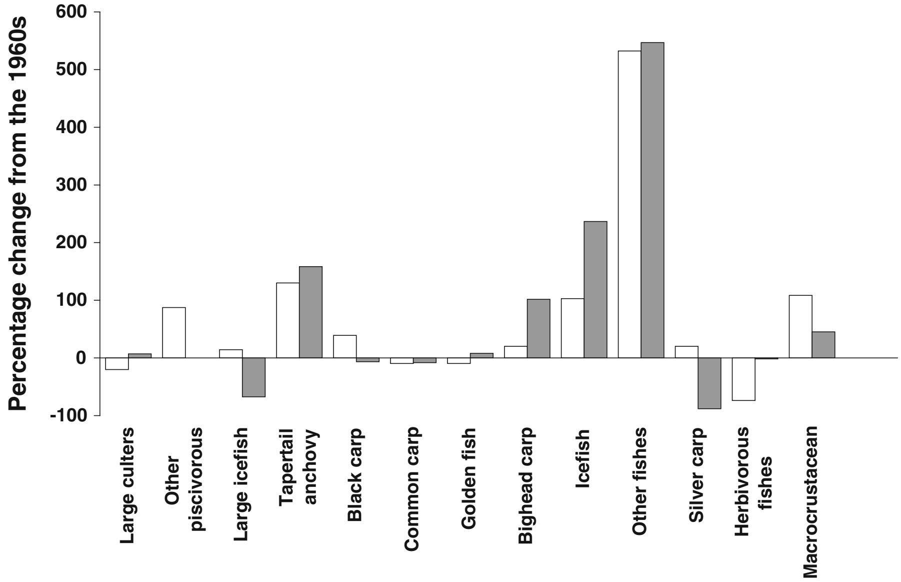

Fig. 4 Percentage changes in landings from the 1960s to the 1980s (*open bars*) and 1990s (*gray bars*)

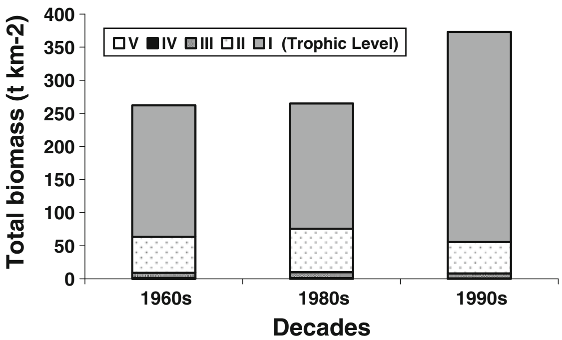

Fig. 5 Summary of total biomass per trophic level as an absolute value for the 1960s, 1980s, and 1990s

system, understood as the proportional contribution of each trophic level to total biomass, remained almost constant from the 1960s to the 1980s, but changed greatly in the 1990s. During this decade, about 99.85% of total biomass became concentrated in trophic levels I-III.

Flow changes

By integrating the production of the fished species (groups 1 to 13), we found that total production increased markedly from 11.289 t km^{-2} year^{-1} in the 1960s to 16.521 t km^{-2} year^{-1} in the 1980s, but declined during the 1990s to 14.399 t km^{-2} year^{-1}. Production and throughput per trophic level were higher for almost all trophic levels during the 1980s than during either the 1960s or the 1990s. The only exception was for trophic level I. With respect to this trophic level, the 1990s values were the greatest, since this decade saw the largest amount of primary production. About 95.37% of total production and 79.23% of total throughput were concentrated in trophic level I during the 1990s. These values were much higher than those during either the 1960s or the 1980s.

Mortalities

The proportional contribution of fishing mortality to total mortality during each of the three decades increased from 30% in the 1960s to 37% in the 1980s and 46% in the 1990s. This increase came at the expense of predation mortality, which decreased proportionally from 51% in the 1960s to 48% in the 1980s and 26% in the 1990s (Fig. 6). This was a logical consequence of the dramatic increase in fishing effort over these decades.

Summary statistics

System indices obtained from the models suggest that the ecosystem changed considerably from the 1960s to the 1990s (Table 1). These system indices included

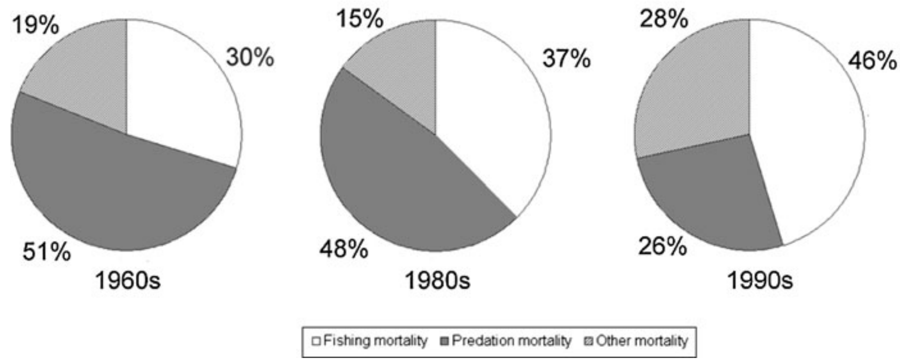

Fig. 6 Percentage of the production of fish and shrimps between fishery catch, consumption by predators, and other mortalities

Table 1 The overall system properties of the Lake Taihu ecosystem in the 1960s, 1980s and 1990s

Parameter (unit)	1960s	1980s	1990s
Sum of all consumption (t km^{-2} $year^{-1}$)	2,928.92	4,126.10	3,629.80
Sum of all exports (t km^{-2} $year^{-1}$)	578.10	738.89	3,616.77
Sum of all respiratory flows (t km^{-2} $year^{-1}$)	952.09	1,251.80	1,130.61
Sum of all flows into detritus (t km^{-2} $year^{-1}$)	2,092.83	2,970.08	5,208.73
Total system throughput (t km^{-2} $year^{-1}$)	6,552.00	9,087.00	13,586.00
Sum of all production (t km^{-2} $year^{-1}$)	1,613.00	2,089.00	4,561.00
Mean trophic level of the catch	1.44	1.62	1.15
Gross efficiency (catch/net p.p.)	0.0,688	0.0,374	0.068
Calculated total net primary production	1,430.19	1,845.32	4,350.15
Total primary production/total respiration	1.50	1.47	3.85
Net system production	478.11	593.52	3,219.54
Total primary production/total biomass	5.46	6.97	11.66
Total biomass/total throughput	0.04	0.03	0.03
Total biomass (excluding detritus) (t km^{-2} $year^{-1}$)	262.07	264.83	373.03
Total catches	78.80	109.44	294.07
Connectance Index	0.22	0.21	0.21
System Omnivory Index	0.05	0.04	0.04
Throughput cycled (excluding detritus) (t km^{-2} $year^{-1}$)	0.27	0.50	0.59
Throughput cycled (including detritus) (t km^{-2} $year^{-1}$)	1,585.48	2,413.74	1,572.83
Finn's cycling index (% of total throughput)	24.2	26.56	11.58
Finn's mean path length	4.28	4.57	2.87
Mean length of pathways of total cycles	5.17	4.69	4.56
Number of path ways of total cycles	632	383	335
Ascendancy	24.416	21.98	25.862
Overhead	75.584	78.02	74.138

summary statistics such as: the trophic level of the fishery; total biomass excluding detritus; total consumption, respiration, and production; total system throughput; and system connectance. Also obtained were the system's omnivory index, its ascendancy, and its overhead.

The mean trophic level of the fishery, calculated from the average trophic levels of the functional groups weighted by their total annual catches, increased from 1.44 in the 1960s to 1.62 in the 1980s, after which it decreased to 1.15 in the 1990s. At the same time, total catch from the Lake Taihu ecosystem increased from 78.8 to 294.07 t·km^{-2} during the period covered by the models. However, although total catch increased, lower trophic level groups contributed a higher fraction of the catch.

Statistics pertaining to production increased considerably over the modeled decades. Net primary production increased almost threefold from the 1960s to the 1990s, reflecting total net system production in the 1990s that was more than five times what was seen in the 1980s. The higher net primary production of the 1990s led to a similar rise in the formation of detritus and its conversion to sediment.

Ecopath yielded a number of statistics to assess the status of the ecosystem and to describe its maturity, stability, complexity, and scale (Christensen et al. 2004). The indices derived from Odum's attributes of ecosystem maturity (Odum 1969) indicate that maturity was highest in the 1980s and lowest in the 1990s. The ratio of total primary production to respiration decreased from 1.50 in the 1960s to 1.47 in the 1980s, after which it increased significantly in the 1990s to 3.85. Conversely, throughput cycled, Finn's cycling index, and Finn's mean path length were much higher during the 1980s than during either the 1960s or the 1990s. The overhead, an index that is positively related to a system's reserve strength, was highest in the 1980s model. Indices of the mean length and number of cyclic pathways were also estimated in order to analyze the structure and complexity of the system's food web (Christensen et al. 2004). These indices reveal that this complexity decreased over successive decades. Lastly, total consumption, total respiratory flow, and total throughput were all higher in the 1990s than in the 1960s, reflecting an increase in ecosystem scales.

Mixed trophic impacts

The mixed trophic impact routine of Ecopath (Ulanowitcz and Puccia 1990) was used to assess possible influences of increasing abundance of all groups by 10% to each considered group, which was regarded as a tool for indicating the possible impact of direct and indirect interactions in a steady-state system

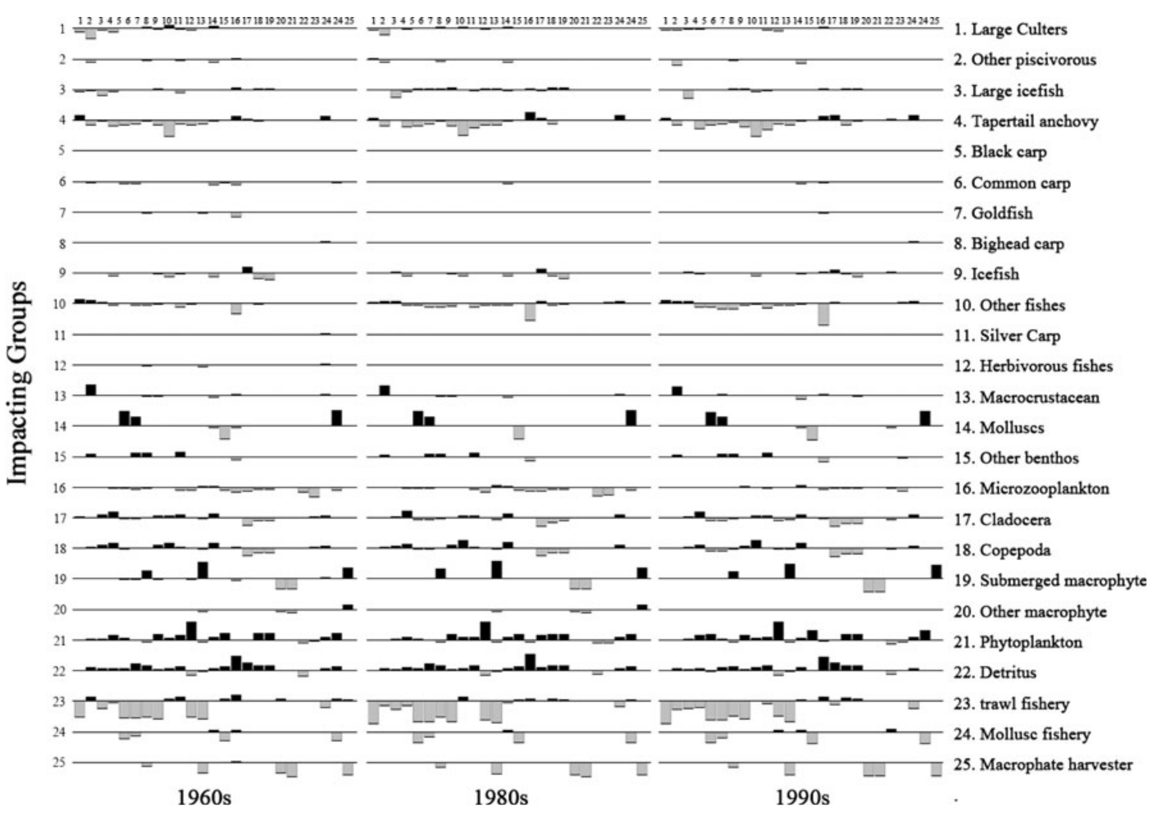

Fig. 7 The mixed trophic impact comparison over the decades

(Christensen et al. 2004). The result of Mixed trophic impact comparison is shown in Figure 7. As expected, most groups had a negative direct impact on their prey and a positive impact on their direct predators. Predators that had a negative impact on the system included large culters, other piscivorous, and large icefish. Numerous functional groups in the model were impacted by groups at the base of the food web such as detritus, phytoplankton, macrophytes, and zooplankton. This could be related to possible bottom-up predator–prey interactions occurring in the ecosystem (Hunter and Price 1992). Some groups such as black carp, common carp, golden carp, bighead carp, silver carp, and grass carp had little or no impact on other groups, either because these fish species had low biomass levels compared with the dominant groups in the ecosystem or because their diets consisted mostly of primary production, whose biomass accounted for a great percentage of the total biomass in the system. Finally, fishing activities had negative direct impacts on most commercial fish groups.

One of the most important differences among the three decades was the decrease in magnitude of the impacts (both positive and negative) of large culters, other piscivorous, and large icefish. This was due to the decrease in the biomasses of these groups from the 1960s to the 1990s. Groups whose biomasses increased from the 1960s to the 1990s, such as tapertail anchovy and other fishes, had an increased overall impact.

Uncertainty and sensitivity analysis

The input parameters for the 1960s model might be estimated less reliably than those for the 1980s and 1990s models. Based on the pedigree matrices assigned, estimation indices of uncertainty from 1960s, 1980s, and 1990s models were 0.431, 0.478, and 0.514, respectively. This trend indicates that parameter values of the 1990s model were based on more reliable data sources than were those of the other two models. The estimated parameters were sensitive to the input parameters within a functional group, whereas these outputs were generally robust to parameters from other functional groups. It was observed in all three models that when an input parameter for one group was changed by 50%, the output parameters of that group could vary by more than 80%. This was expected, as the input data for particular functional groups were tightly linked with each other. The 1960s model showed more sensitivity to input parameters, reflecting the larger uncertainties associated with its estimated parameters.

Discussion

This study showed that the Lake Taihu ecosystem underwent great change over the time period examined. Results showed that the biomass of most fish groups, especially top predators such as large culters and species at higher trophic levels, declined greatly over the decades in the face of steady increases in the total fishery catch. Notably, large icefish stocks became depleted following the 1980s, seeing a dramatic decrease in their biomass. However, the biomasses of tapertail anchovy, other fishes, and species from lower trophic levels all increased significantly over the decades. This increase was driven not only by the low P/B ratios and high turnover rates of these species, but also by the decline that occurred among their predators. Enhanced primary production also played a role, since herbivorous species made the greatest single contribution to the diets of all these groups.

Changes similar to these have been observed in many other exploited lake ecosystems and typically have two principal explanations: (1) technological improvements in fishing power that, together with greater fishing effort, increase the fishing mortality for large predators of high trophic levels; and (2) increased eutrophication that enhances primary productivity, to the benefit of herbivorous fishes at lower trophic levels (Song 2004; Cheung 2007).

Pauly et al. (1998) showed that in many aquatic ecosystems, there had been in recent decades an increase in the proportion of catches taken from lower trophic levels. Pauly termed this trend “fishing down the food web.” Fisheries were initially operated at the highest trophic levels during the 1980s. However, from the 1980s onward the fisheries became increasingly dependent on lower trophic levels. There are some indications that “fishing down the food web” occurred in the Lake Taihu ecosystem between the 1980s and the 1990s, the most prominent of these being the decrease seen in the mean trophic level of catch.

The results show that the P/B ratios of all groups increased over the decades. However, any absolute increases notwithstanding, relatively low P/B ratios have always been found among the small species with high turnover rates (Cai 1998). This previously documented pattern, in combination with many other results of the present study, reflects the depletion of large predatory and graduate replacement of the k-selected species by the r-selected species. Many fish species in Lake Taihu can today be considered as being highly overfished because of exceptionally higher annual fishing mortality, especially the 1990s. Fishing mortality in this decade was much higher than in the 1980s, while total production was much lower than that in the 1980s, a sign of fishery degeneration.

Fundamental features of population interactions, such as predation and competition have been elucidated by empirical and theoretical investigations of the dynamics between two species (Bondavalli and Ulanowicz 1999). Using the mixed trophic impact charts, we can assess the impacts of changes in the biomass of one group on the biomasses of the other groups in the system. This technique can be regarded as a tool for identifying and quantifying the direct and indirect interactions (including competition) that may be occurring within a steady-state system (Christensen et al. 2004). The results of mixed trophic impact analysis indicate that the impact of species occupying lower trophic levels, such as tapertail anchovy and other fishes, increased over time. This might have resulted from the increase in their biomass.

Primary production, total biomass, and total throughput all increased over the three decades. This was especially true for the period from the 1980s to the 1990s, during which these three indices increased by 135.7%, 40.9%, and 49.5%, respectively. Such an expansion suggests that the ecosystem productivity grew progressively larger over the decades. Similarly, while detritus export out of the system rose by only 24% from the 1960s to the 1980s, it jumped 442% from the 1980s to the 1990s. Consequently, much more nutrient-rich sediment began to accumulate in the lake, a process that would be expected to exacerbate eutrophication and organic pollution in the Lake Taihu ecosystem.

Ecosystem maturity and stability declined remarkably, especially from the 1980s to the 1990s. During this period, ecological succession reversed itself, driven by the overfishing of large, long-lived species. Intense fishing effort, growing numbers of fishers, and the use of highly efficient, technologically sophisticated fishing gear all were to blame. By contrast, the ecosystem developed normally during the preceding period spanning the interval from the 1960s to the 1980s. According to Odum's attributes of ecosystem maturity (Odum 1969), the ratio between system primary production and respiration is considered an important parameter describing the maturity of an ecosystem (Odum, 1971). For a mature system, the ratio should approach 1; for a system in an early developmental stage, production is expected to exceed respiration, and the ratio is likely to be greater than 1. An ecosystem with a ratio less than 1 might be suffering from organic pollution (Christensen 1995; Christensen et al. 2004; Zhang and Chen 2007). The Pp/R ratios seen in ecosystem models of the three decades were 1.50 (1960s model), 1.47 (1980s model), and 3.84 (1990s model). The dramatic rise from the 1980s to the 1990s suggests that the ecosystem regressed to a much less mature and stable state. This conclusion is further backed by the equally dramatic change in net system production that took place between these two decades. Net system production (the difference between total primary production and total respiration) tends to be large in immature systems and close to zero in mature ones (Christensen et al. 2004). In Lake Taihu, net system production increased more than fivefold from the 1980s to the 1990s. Finally, the change in ecosystem overhead across the decades also supports the conclusion that the maturity of the Lake Taihu ecosystem decreased.

The dominance of high turnover species in Lake Taihu and the increased fishery dependence on lower trophic levels could increase the volatility of the ecosystem and its fisheries. It is known that population dynamics of small, fast-growing fishes with high fecundities are often strongly affected by the environment (Paul et al. 1998; Halpern et al. 2008) and are subject to large interannual variability (Spencer and Collie 1997). Moreover, as intensive fishing has removed a large proportion of the adult biomass, juveniles have come to dominate the population. Such truncation of the age structure of fish populations may further increase their variability (Cheung 2007). If catch levels respond sensitively to changes in stock size, the greater short-term variability of catches that would result from these ecological changes might cause considerable socioeconomic dislocation within fishing communities. A much healthier, pre-1990s state of Lake Taihu with abundant predatory species would be beneficial both ecologically and economically (Pitcher 2004). Ecological restoration would not only prevent depletion, extirpation, or even extinction of the species that have been heavily fished in Lake Taihu; but would also improve the maturity, stability, and resilience of the ecosystem, helping to dampen the effects of environmental change (Peterson et al. 1998; Hsieh et al. 2006). This is especially important, as eutrophication increase in inland lakes and global climate change may further increase the variability of the environment (Yang 1998; Cheung 2007). Economically, restoration could increase stock abundance and improve the profitability of fisheries. On the other hand, any restoration effort would likely require a reduction in fishing effort, meaning that the fishing community would have to face some short-term social and economic difficulties. Moreover, restoration and conservation-based management are sometimes costly to implement (Cheung 2007).

This study found that phytoplankton biomass had increased significantly during the study period, which was considered as an evidence of bottom-up control of the Lake Taihu food web dynamics. This conclusion was drawn from considering the quantitative changes. If we consider the qualitative changes in the plankton communities, the answer might not be so simple. The nutrient enrichment in Lake Taihu had induced structural shifts in the phytoplankton community with the most profound being the cyanobacteria dominance. Cyanobacteria are considered to have low food quality due to their morphological characteristics, toxin production, and low fatty acid content. Thus, they can impose limitations to the growth of herbivorous zooplankton. The faster growth of the phytoplankton relative to zooplankton biomass may be a testament to this hypothesis. However, the tapertail anchovy, herbivorous fishes, and other fishes in the ecosystem benefited from the increasing number of cyanobacteria that are one of their food sources, which supports bottom-up forcing of the Lake Taihu food web.

This study provides a summary of current knowledge of the dynamic of the biomass, consumption, production, food web, and trophic structure in an ecosystem exploited by the Taihu fishery over decades. The Ecopath model can be a valuable tool for understanding ecosystem functioning and for design of ecosystem-scale adaptive management experiments. Further effort to better characterize key elements of the ecosystem, such as the biomasses of fish groups and the detritus in the 1960s and 1980s, can be an important step forward toward the improvement of the input data and the characterization of the ecosystem. Data are also scarce in diet composition of the models in the 1960s and the 1980s. Moreover, considerations of the discard and import portions in the models would also be an important step forward toward the improvement of the model. Thus, although 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. In a future step, we would simulate the consequences of certain management measure based on these models using Ecosim and Ecospace module in order to improve input data and to reduce the uncertainty of the results.

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