Steady State Models

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O U T L I N E

4.1 STEADY STATE MODEL: ECOPATH AS AN EXAMPLE

4.1.1 Steady State Model

Steady state ecological models are established to describe conditions in which the modeled components (mass or energy) are stable, i.e., do not change over time (Jørgensen and Fath, 2011). Therefore, outputs from this model type represent the equilibrium of the ecosystems, which would be validated by average values of field observations over a period. In fact, under most conditions, the steady state is essentially dynamic equilibrium, in which the inflow and outflow of the ecosystems are balanced. A classic example of steady state model is to describe ecosystem with alternative stable states, such as the phytoplankton-dominant and vegetation-dominant states in shallow lake ecosystems (Scheffer et al., 1993, 2001). Steady state models were extensively applied in investigating this theory, which provided a deeper insight in understanding the mechanisms of hysteresis shown in many ecosystems. Importantly, the outcomes from steady state models might have critical implications for management.

4.1.2 Ecopath Model

Ecopath model is a well-established modeling tool with a user-friendly interface and a standard modeling procedure to document and analyze food web structure and ecosystem functioning at the steady state (Christensen et al., 2005), particularly focusing on trophic mass–balance analysis (Christensen and Walters, 2004). A typical Ecopath model is composed of multiple groups of state variables, which are usually termed as "functional groups". Each functional group corresponds to one linear equation, all of which could be solved simultaneously under steady state assumption. Ecopath model was firstly developed to evaluate the functioning of marine ecosystem (Polovina, 1984). The model was further modified by the ecological thermodynamic theory and gradually emerged into a powerful tool for analysis of energy flow (Christensen et al., 2005). By importing information for the functional groups such as biomass, production/consumption rate, and diet composition, the model would be able to provide important ecological properties including trophic levels, mass and energy flows, and ecosystem maturity and stability. The model is feasible to be applied for ecosystems with sufficient data. For a detailed review on the methods and capacity of Ecopath model, see Christensen and Walters (2004).

To date, the steady state Ecopath model was used abundantly in aquatic ecosystem including marine and freshwater ecosystems, particularly for gulfs and lakes, considering the fact that these two ecosystems are relatively stable than the others such as rivers and streams. These applications might be simply categorized into the following three groups: Ecopath model for one system at one specific period, for one system at multiple periods, and for multiple systems at one specific period. Different groups of researches were designed with distinct objectives, which would be briefly reviewed as follows.

For the first group, it has been conducted for multiple aquatic ecosystems around the globe (Fetahi and Mengistou, 2007; Fetahi et al., 2011; Hossain et al., 2010, 2012; Jia et al., 2012; Li et al., 2009; Liu et al., 2007b; Pedersen et al., 2008; Shan et al., 2014; Villanueva et al., 2006b, 2008). Outputs from Ecopath model for the studied system at one specific period provide a comprehensive understanding on the basic features of the ecosystems in terms of

food web structure, trophic interaction, energy flow, and ecosystem status such as stability and maturity. Moreover, one of the major objectives of Ecopath model approach is to evaluate the impact of fishery on the aquatic ecosystems and to provide suggestions for fishery strategy in a more sustainable way (Coll et al., 2006; Thapanand et al., 2007). For example, it was argued that an ecosystem-level perspective was urgent for fishery management in a fishery-intensive lake, illustrated by an Ecopath approach (Guo et al., 2013). For some other systems, Ecopath model was used to identify important functional groups or key species, such as autotrophs for an estuary (Pavés and González, 2008) and aquaculture fish for a marine ecosystem (López et al., 2008). In addition, the roles of exotic species in one specific ecosystem could be unraveled by Ecopath model (Kao et al., 2014). The introduced exotic fish, in general, exert a negative impact on the target system (Downing et al., 2012), but there are also occasions with positive consequences (Villanueva et al., 2008), where Ecopath played as the essential modeling tool. Overall, in most cases, the results from Ecopath model were considered as the scientific basis for ecological management.

For the second group, this type of research generally aims at investigating the changes in food web structure and ecosystem functioning during a relatively long-term temporary scale. By establishing Ecopath models during different periods, one would be able to compare the outcomes from the model and clearly observed the most significant changes in the properties of ecosystem, thereby obtaining a quantitative understanding of the ecosystem dynamics. For example, two Ecopath steady state models were built for a wetland in China before and after the flow regulation, and the model showed that this activity hampered the natural succession and increased the vulnerability of the wetland ecosystem (Yang and Chen, 2013). In addition, Ecopath models were used to investigate the consequences of the invasive species introduction. For example, Nile perch was introduced to Lake Victoria in East Africa about 30 years ago. Ecopath model showed that both changes in Nile perch's and detritivores' trophic levels were critical in driving the dynamics of the system, and the lake was unlikely to recover even though the main trophic levels would have been restored (Downing et al., 2012). Similar study was also conducted for other lakes to better understand the impact of invasive species at the ecosystem level (Stewart and Sprules, 2011). For lake ecosystems under complex disturbances, Ecopath models were also developed for several distinct periods to reach a quantitative evaluation of changes in ecosystem properties and a deduction of major driving factors (Kong et al., 2016; Li et al., 2010). Overall, to fulfill the research in this group, sufficient data from different periods with equal quality are required, which are, however, difficult to obtain for most of the ecosystems.

For the third group, this type of research is relatively scarce in comparison to the first two groups (Janjua et al., 2014; Mavuti et al., 1996). These studies focused on two or more similar and adjacent ecosystems (usually located in one region) with significant different features such as external conditions. Ecopath model outputs for each ecosystem were comparable, the differences of which would be directly linked to the difference in these features, thereby reaching a better understanding on the causality between driving factors and ecosystem properties. For example, it was revealed by Ecopath that the difference in ecosystem production in two adjacent lakes was attributed to the differences in principle source and pathway of energy flows, i.e., detritus-driven and algae-driven pathways (Villanueva et al., 2006a), which were suggested to play a significant role in determining the ecosystem stability (Moore et al., 2004).

4.1.3 Future Perspectives

Over the two decades of development and application, several hundreds of models based on Ecopath have been documented in literature (Jørgensen and Fath, 2011). As a steady state model, Ecopath has the advantages including (1) the capacity to characterize the food web structure and ecosystem functioning; (2) the small requirements of model input information; and (3) a user-friendly interface to facilitate model development, parameterization, and application. However, there are also disadvantages in Ecopath model, which have been systematically reviewed by Christensen and Walters (2004). Here, we point out that Ecopath is essentially a simplified food web model, in which many processes in nature, such as biogeochemical processes, are not fully considered in the model. This would lead to the deviation of model outputs from observations. Therefore, the model was designed to illustrate the ecosystem on a macroscale, instead of predicting the absolute values of specific ecosystem components. An interesting study attempted to couple a eutrophication model with an Ecopath model, which combined the advantages of both model types to obtain a comprehensive picture of ecosystem behavior in terms of both abiotic and biotic aspects (Cerco et al., 2010). As can be imagined, integration of Ecopath with other process-based ecological models will be a promising but challenging task, which is important for further researches. In addition, Ecopath model might also play a role in comparative limnology studies. As the model can provide multiple indicators representing ecological status for the modeled lake ecosystem, and more importantly, these information were usually provided in relevant literature, it is possible to use these results from steady state Ecopath model for lake classification using cluster analysis. This would be an interesting approach for a synthesis research for Ecopath model and for a promotion of the limnologic studies to categorize different lake types at the ecosystem-level in the future.

4.2 ECOPATH MODEL FOR A LARGE CHINESE LAKE: A CASE STUDY

In the following section, we illustrate a case of Ecopath model as a steady state model study. We managed to establish Ecopath mass–balance models for Lake Chaohu in China during the 1950s, 1980s, and 2000s. Our analysis with Ecopath provides a comprehensive and quantitative evaluation of the changes in the food web structure and ecosystem functioning during these three distinctly different periods. We further analyze the potential driving factors and underlying mechanisms. To our knowledge, this is the first analysis of this type for Lake Chaohu. We expect that the results will provide deeper insight into the changes that occurred in this lake and give essential input for sustainable management strategies by bridging the environmental and ecological perspectives.

4.2.1 Introduction

It is commonly accepted that natural and human systems are strongly coupled and that human activities have currently reached a level that may damage the natural system beyond its adaptive capacity (Liu et al., 2007a; Rockström et al., 2009). Many subsystems on the planet, such as aquatic ecosystems, will exhibit nonlinear behavior as certain thresholds

are crossed (Casini et al., 2009; Scheffer et al., 2001). For lake ecosystems, multiple anthropogenic stressors may have synergetic effects that lead to drastic ecological degradation (Yang and Lu, 2014). In addition to fertilization-induced nutrient enrichment and hydrological regulation, fishery in lakes provides important ecological services to local communities, but it is rarely sustainable around the globe (Pauly et al., 2002). Intensive fishery leads to biodiversity loss and simultaneous erosion of the structure and processes that confer stability in the food web (de Ruiter et al., 1995; Rooney et al., 2006), resulting in disastrous consequences, such as "fishing down the food web" (Pauly et al., 1998), food web collapses (Downing et al., 2012), and ultimately catastrophic regime shifts (Casini et al., 2009; Folke et al., 2004).

Over the last several decades, lakes along the Yangtze River floodplain in China have witnessed a strong ecological degradation (Dearing et al., 2012). Lake Chaohu, the fifth-largest freshwater shallow lake in China, is one of the three lakes in China (along with Lake Taihu and Lake Dianchi) that have attracted public concern regarding harmful cyanobacterial blooms (Shan et al., 2014). This lake has suffered from gradual nutrient enrichment from the 1950s onward (Kong et al., 2015), hydrological regulation, which disconnected the lake from the Yangtze River since 1963 (Xu et al., 1999b; Zhang et al., 2014) and intensive fishery since the 1980s (Zhang et al., 2012). Consequently, drastic changes have occurred in Lake Chaohu's ecosystem, resulting in significant changes in the food web structure, a decreasing biodiversity and catastrophic regime shifts toward an unfavorable turbid state dominated by phytoplankton and small-sized planktivorous fish (Liu et al., 2012; Zhang et al., 2015). A significant fourfold to fivefold increase in total biomass was observed, with an increasing dominance of the lower trophic levels (TLs) throughout these years. These changes in the food web structure may strongly influence the functioning of the ecosystem. To date, however, the quantitative changes in ecosystem functioning have not been documented for Lake Chaohu.

The availability of relevant data from the 1950s, 1980s, and 2000s make the present study feasible. Several studies have already used Ecopath for lakes in the Yangtze River floodplain (Guo et al., 2013; Jia et al., 2012; Li et al., 2010) and even a preliminary Ecopath model for Lake Chaohu (Liu et al., 2014), but studies that investigate the changes in the food web structure and ecosystem functioning over a long time span are scarce. The drastic changes in the Lake Chaohu ecosystem, however, urgently call for a quantitative analysis of food web dynamics and ecosystem functioning comparable with studies conducted in, e.g., Lake Taihu (Hu et al., 2011; Li et al., 2010), Lake Chozas (Marchi et al., 2011, 2012), and the Baltic Sea (Casini et al., 2009), to provide deeper insights into the effect of multiple anthropogenic stressors. Furthermore, the development of an integrated modeling tool is becoming imperative to support a sound policy for lake management with both environmental and ecological perspectives (Jørgensen and Nielsen, 2012).

Ecopath requires data of which it is difficult to obtain good empirical estimates (e.g., diet composition). Thus, a validation of the Ecopath model is strongly recommended. We provide a reliable method to validate the diet composition of the Ecopath model for Lake Chaohu using laboratory- and literature-based estimations of TLs from stable isotopes' determination for each functional group in the food web.

Overall, the goals of this study are as follows: (1) to establish three validated Ecopath mass—balance models for Lake Chaohu corresponding to the 1950s, 1980s, and 2000s, (2) to quantify the changes in food web structure in Lake Chaohu during different periods,

(3) to evaluate the changes in the ecosystem functioning of Lake Chaohu during the 1950s, 1980s, and 2000s, (4) to discuss the potential key factors driving the changes in the food web structure and ecosystem functioning, and (5) to provide a sound modeling basis for an integrated management tool with an illustrative example in Lake Chaohu.

4.2.2 Study Site

Lake Chaohu (31°33′59″N, 117°26′40″E) is the fifth-largest shallow lake in China. It covers an area of 760 km^2 and has a depth of 3 m on average (Fig. 4.1). Before the 1950s, the lake was famous for its beautiful scenery with a high water quality, a large amount of vegetation (30% of the surface area), and a high level of biodiversity (Kong et al., 2013; Xu et al., 1999a; Zhang et al., 2012; Zhang et al., 2014). However, in 1963, the connection of the lake with Yangtze River was blocked by the "Chaohu Sluice" on the Yuxi River, and as a result, the water level fluctuation in the lake was largely reduced. Since 1980, the rapid socioeconomic development in the drainage area of the lake led to a gradual elevation in nutrient loading and a deterioration of the water quality (Kong et al., 2015). Intensive fishery from the 1980s onward exacerbated the effect of eutrophication and water level control, resulting in rapid loss of ecological services. Natural riparian areas were reduced to less than 1% of the total area (Ren and Chen, 2011). The west part of the lake could no longer provide drinking water for the city of Hefei, primarily due to frequent cyanobacterial blooms. As the total fishery yield increased rapidly over the past decades (Fig. 4.2A, $p < 0.01$, approximately 2000 t from the 1950s to the 1970s and nearly 20,000 t in 2009), the total number of species in the fish community decreased from 84 (1963) to 62 (1973) to 78 (1981) to 54 (2002), indicating a considerable loss of biodiversity (Lv et al., 2011).
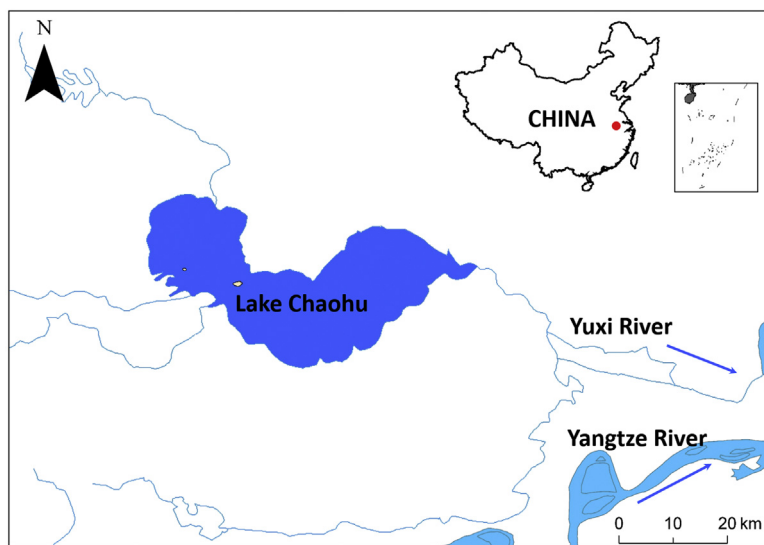
FIGURE 4.1   Location of the Lake Chaohu catchment in China. The blue arrows indicate the direction of water flows in the Yangtze River and in the river that connects Lake Chaohu and the Yangtze River (Yuxi River).
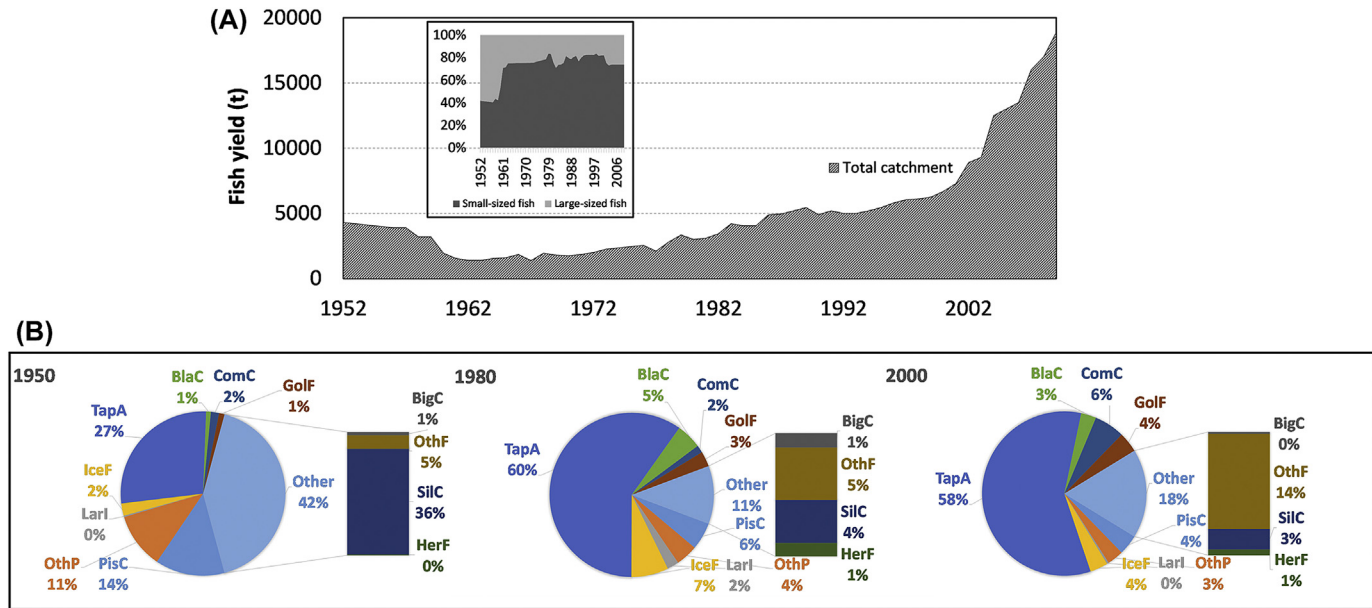
FIGURE 4.2 (A) Total fishery yield (t) from 1952 to 2009 and the fraction of small-sized and large sized fish in the yield. Small-sized fish include, e.g., *Coilia ectenes* and *Neosalanx taihuensis*, whereas large-sized fish include, e.g., *Culter*, silver carps, bighead carps, and common carps. Data collected from Guo (2005), Zhang et al. (2012), and Liu et al. (2014). (B) Composition of fishery yield in the 1950s, 1980s, and 2000s (Details of the abbreviations can be found in Table 4.1).

TABLE 4.1 Basic Input and Estimated Parameters (in Bold) for the Ecopath Models of Lake Chaohu in the 1950s, 1980s, and 2000s

Functional Group	Code	TL	Catchment (t/km²)			Biomass in Habitat Area (t/km²)			P/B			Q/B			Ecotrophic Efficiency			P/Q		
			1950s	1980s	2000s	1950s	1980s	2000s	1950s	1980s	2000s	1950s	1980s	2000s	1950s	1980s	2000s	1950s	1980s	2000s
Piscivorous	PisC	3.8	0.804	0.282	0.612	0.894	0.314	0.700	1.046	1.167	0.974	2.950	3.527	3.200	**0.930**	**0.846**	**0.983**	**0.355**	**0.331**	**0.304**
Other piscivorous	OthP	3.7	0.644	0.226	0.490	0.715	0.251	0.560	1.170	1.423	1.665	4.286	5.212	6.100	**0.871**	**0.734**	**0.621**	**0.273**	**0.273**	**0.273**
Large icefish	LarI	3.9	0.016	0.120	0.057	0.017	0.126	0.060	2.592	1.516	1.983	12.429	11.630	16.650	**0.986**	**0.974**	**0.947**	**0.209**	**0.130**	**0.119**
Other icefish	IceF	3.0	0.142	0.381	0.542	0.150	0.401	0.570	2.639	2.162	2.373	18.862	18.620	27.200	**0.944**	**0.999**	**0.994**	**0.140**	**0.116**	**0.087**
Tapertail anchovy	TapA	3.0	1.618	3.119	8.977	1.692	3.263	9.390	1.987	1.424	1.283	8.664	11.717	11.350	**0.925**	**0.948**	**0.914**	**0.229**	**0.122**	**0.113**
Black carp	BlaC	3.2	0.054	0.261	0.456	0.068	0.326	0.570	0.936	0.859	0.912	3.278	4.937	11.544	**0.896**	**0.935**	**0.882**	**0.286**	**0.174**	**0.079**
Common carp	ComC	2.8	0.095	0.077	0.919	0.123	0.100	1.190	1.069	0.906	0.960	4.767	10.067	10.693	**0.906**	**0.966**	**0.827**	**0.224**	**0.090**	**0.090**
Crucian carp	GolF	2.3	0.063	0.155	0.610	0.082	0.201	0.790	2.825	1.473	1.130	7.211	11.663	12.300	**0.974**	**0.757**	**0.885**	**0.392**	**0.126**	**0.092**
Bighead carp	BigC	2.8	0.068	0.069	0.041	0.076	0.077	0.046	1.436	1.123	1.690	4.693	4.357	6.900	**0.943**	**0.967**	**0.906**	**0.306**	**0.258**	**0.245**
Other fish	OthF	2.8	0.266	0.254	2.073	0.831	0.688	2.303	2.421	1.983	2.155	8.168	9.153	11.000	**0.987**	**0.971**	**0.799**	**0.296**	**0.217**	**0.196**
Silver carp	SilC	2.2	2.099	0.208	0.444	2.332	0.231	0.494	0.926	0.931	1.100	3.565	4.862	8.000	**0.978**	**0.992**	**0.839**	**0.260**	**0.191**	**0.138**
Herbivorous	HerF	2.0	0.014	0.065	0.126	0.025	0.112	0.140	0.697	0.639	0.987	2.424	2.108	7.100	**0.928**	**0.926**	**0.928**	**0.288**	**0.303**	**0.139**
Shrimp	MacS	2.9	0.658	1.118	2.904	0.823	1.398	3.630	4.500	4.500	4.500	21.324	24.400	24.400	**0.402**	**0.279**	**0.295**	**0.211**	**0.184**	**0.184**
Crab	MacC	3.0	0.329	0.559	0.019	0.346	0.588	1.500	2.823	2.120	2.120	8.480	8.480	8.480	**0.990**	**0.743**	**0.318**	**0.333**	**0.250**	**0.250**
Mollusks	Moll	2.1	6.750	11.006	1.010	13.500	22.012	2.020	1.326	1.326	1.326	10.605	10.605	10.000	**0.456**	**0.499**	**0.750**	**0.125**	**0.125**	**0.133**
Other benthos	OthB	2.0	–	–	–	0.775	2.000	0.910	4.030	4.030	4.130	201.500	201.500	50.000	**0.589**	**0.278**	**0.933**	**0.020**	**0.020**	**0.083**
Micro zooplankton	Micz	2.0	–	–	–	0.077	0.684	0.964	67.747	67.747	30.000	981.733	1354.950	600.000	**0.950**	**0.950**	**0.950**	**0.069**	**0.050**	**0.050**
Cladocera	Clad	2.0	–	–	–	0.344	0.379	7.910	21.093	21.093	15.300	826.440	421.858	457.000	**0.900**	**0.900**	**0.900**	**0.026**	**0.050**	**0.033**
Copepoda	Cope	2.0	–	–	–	0.344	0.641	1.820	15.973	15.973	12.165	780.473	319.469	378.000	**0.900**	**0.900**	**0.900**	**0.020**	**0.050**	**0.032**
Cyanobacteria	Cyan	1.0	–	–	–	1.540	16.751	27.386	150.000	150.000	150.000	–	–	–	**0.484**	**0.091**	**0.070**	–	–	–
Chlorophytes	Chlo	1.0	–	–	–	1.391	1.291	16.361	250.000	250.000	250.000	–	–	–	**0.512**	**0.890**	**0.287**	–	–	–
Bacillariophytes	Baci	1.0	–	–	–	1.172	1.956	12.418	200.000	200.000	200.000	–	–	–	**0.505**	**0.422**	**0.324**	–	–	–
Vegetation	SubM	1.0	–	–	–	75.000	5.146	4.457	1.250	1.250	2.253	–	–	–	**0.016**	**0.531**	**0.977**	–	–	–
Detritus	Detr	1.0	–	–	–	1.450	202.500	311.600	-	–	–	–	–	–	**0.980**	**0.471**	**0.312**	–	–	–

4.2.3 Model Development

4.2.3.1 Model Construction and Parameterization

We have built three static mass—balance models for Lake Chaohu, representative of the 1950s, 1980s, and 2000s, using Ecopath with Ecosim, version 6.4.3 (freely available at http://www.ecopath.org). The reasons we focus on these three different periods in the present study are that these three periods (1) represent three distinct stages in the development of the lake ecosystem and (2) correspond to the times when intensive investigations were conducted in Lake Chaohu, with abundant data available in the literature. The basic equation for this model is given in Eq. (4.1):

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot EE_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji} - EX_i = 0 \tag{4.1}$$

where B_i (t/km^2) and B_j (t/km^2) are the biomass of group i and j, respectively, P_i/B_i (per year) is the production/biomass ratio of group i, EE_i (−) is the ecotrophic efficiency of group i, Q_i/B_i (per year) is the consumption/biomass ratio of group j, n is the number of groups, DC_{ji} (−) is the contribution of prey i in the diet of predator j, and EX_i (t/km^2) is the export of group i.

Based on their feeding habits, fish can be categorized into several groups: planktivores, planktivores/benthivores, benthivores, benthivores/piscivores, piscivores, omnivores, detritivores, and herbivores. In Lake Chaohu, small-sized fish are dominated primarily by small pelagic and planktivorous fish, including *Coilia ectenes taihuensis* and *Neosalanx taihuensis*. Large-sized fish include piscivorous fish (e.g., *Erythroculter ilishaeformis*), planktivorous fish (e.g., *Aristichthys nobilis*), benthivorous fish (e.g., *Mylopharyngodon piceus*), herbivorous fish (e.g., *Ctenopharyngodon idella*), and omnivorous fish (e.g., *Hypophthalmichthys molitrix*, *Cyprinus carpio*, and *Carassius auratus*). We defined 24 functional groups in total for the Ecopath model in Lake Chaohu based on a previous study of the food web structure of Lake Chaohu (Zhang et al., 2012). All important biota components are covered by these 24 groups. We separated the phytoplankton group into three subgroups, i.e., Cyanobacteria (Cyan), Chlorophytes (Chlo), and Bacillariophytes (Baci), and added a new group accounting for macrocrustacean shrimp (MacS). For each model, the input data included biomass in certain period of time (*B*), the landings of fishery, diet composition, the parameter values for the production/biomass ratio (*P/B*), the consumption/biomass ratio (*Q/B*), and the ecotrophic efficiency (*EE*) for each functional group. The landing data were collected primarily from peer-reviewed publications, stock assessments, and government reports. Biomass was estimated based on the quote of landing data and estimated fishing mortality (Liu et al., 2014). *P/B* and *Q/B* ratios were primarily estimated according to length-based empirical relations (Palomares and Pauly, 1998; Pauly, 1980), and missing values were assigned based on similar approaches in the same area if data were not available. Most *EE* values were estimated by the model, with the exception of zooplankton. A complete list of data sources could be found in Kong et al. (2016). Diet composition was initially assigned according to the approaches conducted in Lake Taihu (Li et al., 2009), but we involved additional information from Lv et al. (2011) and Guo (2005). The proportion of the predation of different function groups in the three phytoplankton groups was estimated according to food web studies in lakes along the Yangtze River for fish (Guo, 2005), zoobenthos (Liu, 2006), and zooplankton

(Deng, 2004). All input values were adjusted during the model balancing. The values of diet composition were further calibrated based on the comparison between the model calculated and the measurement of TL for each group, and the diet composition with the best fit was applied. The determination of TL based on the nitrogen stable isotope analysis is demonstrated in Section 4.2.3.3.

4.2.3.2 Evaluation of Ecosystem Functioning

The Ecopath model software can calculate multiple indicators for the evaluation of ecosystem functioning (Christensen et al., 2005). The total system throughput (TST) is derived from the sum of all consumption (TC), exports (TEx), respiratory flows (TR), and flows into detritus (TD). It is suggested that TST is positively correlated with the turnover rate of the biomass in the ecosystem (Brando et al., 2004). Moreover, ecosystem maturity is a concept suggesting that ecosystems evolve in succession toward maturity (Odum, 1969). The total net primary production (TPP; $t/km^2/year$), net system production (NSP; $t/km^2/year$), the ratios of TPP with total respiration (TPP/TR), and the total biomass (TPP/TB) are important indicators of ecosystem maturity (Odum et al., 1971); e.g., TPP/TR equals 1 when the system becomes "mature." TPP/TB is positively correlated with a eutrophication state (Barausse et al., 2009). The system omnivory index (SOI) $= (\sum_{i=1}^{N}\sum_{j=1}^{N}(TL_j - (TL_i - 1))^2 \cdot DC_{ij})/N$, where N is the number of living groups, TL_i and TL_j are the trophic level of the predator i and the prey j, respectively, and DC_{ij} is the proportion of prey j that constitutes the diet of predator i. SOI is a weighted measure of food web connectance. Finn's cycling index (FCI) $=$ Tcy/TST, where Tcy is the throughput cycled (including detritus), and TST is the total system throughput. FCI represents the fraction of recycled throughput in the total system throughput (Finn, 1976). Finn's mean path length (FML) $=$ TST/(TEx $+$ TR), where TEx is the sum of all exports and TR is the sum of all respiratory flows. FML indicates the length of the food chain. The connectance index (CI) $= N/2(N - 1)$. CI measures the ratio of the observed links and the possible links in total (Gardner and Ashby, 1970).

Ascendancy $= \sum_{i=1}^{N}\sum_{j=1}^{N}T_{ij}\log\left(\frac{T_{ij}T_{..}}{T_{.j}T_{i.}}\right)$, where T_{ij} is the energy flow from j to i, and

$T_{j.} = \sum_{k=1}^{N}T_{jk}$, $T_{.i} = \sum_{k=1}^{N}T_{ki}$, and $T_{..} = \sum_{m=1}^{N}\sum_{k=1}^{N}T_{mk}$. Ascendency measures the average mutual information in a system, derived from information theory (Ulanowlcz and Norden, 1990). This indicator is negatively correlated with ecosystem maturity (Christensen, 1995) and positively reflects the gradient of eutrophication (Patrıcio et al., 2004). Overhead simply equals (1 − Ascendancy). The total transfer efficiencies (TE) is the average of transfer efficiencies between successive discrete TLs, calculated by the ratio between the sum of the exports from a given TL plus the flow that is transferred from one TL to the next and the throughput on the TL (Christensen et al., 2005). Transfer efficiencies from the primary producer (TE p.p.) and transfer efficiencies from detritus (TE det.) are thus the TE for the primary producer (macrophytes and phytoplankton) and detritus, respectively. In addition, mixed trophic impacts (MTI) analysis was utilized to determine trophic interactions, including both the predatory and competitive interactions of a certain functional group on the other groups in an ecosystem (Christensen and Walters, 2004). The element for the matrix, MTI_{ij}, equals $DC_{ij} - FC_{ij}$, where FC_{ij} is the proportion of the predation on j due to i as a predator (Shan et al., 2014). Simply put, FC_{ij} is the proportion of each element in Table 4.2 in the

TABLE 4.2 Diet Composition of the 24 Functional Groups in the Ecopath Model for Lake Chaohu (Details of the Abbreviations can be found in Table 4.1).

No.	Group	PisC	OthP	LarI	IceF	TapA	BlaC	ComC	GolF	BigC	OthF	SilC	HerF	MacS	MacC	Moll	OthB	Micz	Clad	Cope
1	PisC	0.02	0.004																	
2	OthP	0.008	0.021																	
3	LarI	0.007		0.04																
4	IceF	0.047		0.165		0.005														
5	TapA	0.51		0.36		0.005														
6	BlaC	0.001																		
7	ComC	0.001	0.007																	
8	GolF	0.001	0.052																	
9	BigC	0.013																		
10	OthF	0.306	0.281	0.248																
11	SilC	0.005																		
12	HerF	0.001																		
13	MacS	0.01	0.248	0.037				0.15		0.003										
14	MacC	0.003	0.2	0.037			0.025	0.008												
15	Moll		0.092			0.04	0.8	0.6			0.001									
16	OthB		0.076				0.025	0.157	0.156		0.186						0.001			
17	Micz			0.009	0.007	0.001		0.001	0.01	0.115	0.002	0.003	0.001	0.141	0.141	0.1	0.02		0.016	0.016
18	Clad			0.047	0.433	0.506			0.039	0.375	0.338	0.1		0.34	0.39					
19	Cope			0.057	0.56	0.4			0.05	0.31	0.253	0.097		0.449	0.449					
20	Cyan		0.001								0.01	0.6				0.5		0.1	0.05	0.05
21	Chlo		0.001			0.02		0.05	0.05	0.09	0.06	0.1				0.1	0.08	0.15	0.25	0.25
22	Baci		0.001			0.023		0.022	0.05	0.09	0.057	0.1				0.1		0.083	0.174	0.174
23	SubM	0.067						0.009	0.415		0.002		0.999	0.05			0.001			
24	Detr		0.016					0.153	0.227	0.02	0.091			0.02	0.02	0.2	0.898	0.667	0.51	0.51
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

sum of the corresponding row, whereas DC_{ij} is the proportion in the sum of the corresponding column. We obtained the MTI matrix from the Ecopath software and used R packages (corrplot and cairo) to present the results and obtain high-resolution graphs. More details for these indicators can be found in Christensen et al. (2005).

4.2.3.3 Determination of Trophic Level

The established Ecopath models were validated by comparing calculated and measured TLs for most of the functional groups. Measured data were obtained from both field samples and the literature. For the field data, a total of six dominant fish species were sampled, identified, measured (length), and weighed in March, 2012, from a fishery catchment in Lake Chaohu, including *C. ectenes taihuensis*, *C. carpio*, *A. nobilis*, *Megalobrama amblycephala*, *Hemibarbus maculatus*, and *E. ilishaeformis*. Two benthic invertebrates (*Ballamya purificata* and *Palaemon modestus*) were also collected with a Peterson grab and subsequently kept alive for 24 h in the laboratory to allow for the evacuation of gut contents. Samples of primary producers for a stable isotope analysis were collected with a plankton net. The fish for gut-content analysis were preserved in formalin. Only the dorsal white muscle tissue samples from the adult fish were utilized for gut content analysis. All samples were dried to a constant weight at 60°C and crushed into a fine powder using a mortar and pestle. The TLs of certain functional groups in this study were determined based on nitrogen stable isotope analysis (δ^{15}N), following the method in Jepsen and Winemiller (1980). Nitrogen isotopes (δ^{15}N) were determined at the Institute of Geographic Sciences and Nature Resources Research, Chinese Academy of Sciences in Guangzhou, China, using a Flash EA CN elemental analyzer coupled with a Thermo Finnigan Delta Plus mass spectrometer. The formulation for the TL calculation is shown in Eq. (4.2):

$$TL = \left(\frac{\delta^{15}N_{Fish} - \delta^{15}N_{Reference}}{3.3} \right) + 1 \tag{4.2}$$

where $\delta^{15}N_{Reference}$ is the mean of phytoplankton δ^{15}N, and the denominator value (3.3) is an estimated mean enrichment (fractionation) of δ^{15}N between the fish and food sources (Pauly, 1980). In addition, more TL data for biota in Lake Chaohu were collected from the literature (Xu et al., 2005; Zhang et al., 2012).

4.2.4 Results and Discussion

4.2.4.1 Basic Model Performance

The basic input and the estimated parameters (in bold) for the Ecopath model of Lake Chaohu in the 1950s, 1980s, and 2000s are shown in Table 4.1. The diet composition is shown in Table 4.2. The model outputs of the food web structure and the trophic flows are illustrated in Fig. 4.3. Four TLs are identified by the model for Lake Chaohu's ecosystem, and the majority of the trophic flow occurred between these four TLs (Fig. 4.4). The performance of the Ecopath models was evaluated using the following criteria: calculated EE values for all the functional groups were less than 1, and most of the calculated P/Q ratios (simply the quotient of P/B and Q/B) were between 0.1 and 0.3, representing a mass−balance model (Christensen and Walters, 2004). EE values were generally higher for the fish groups and
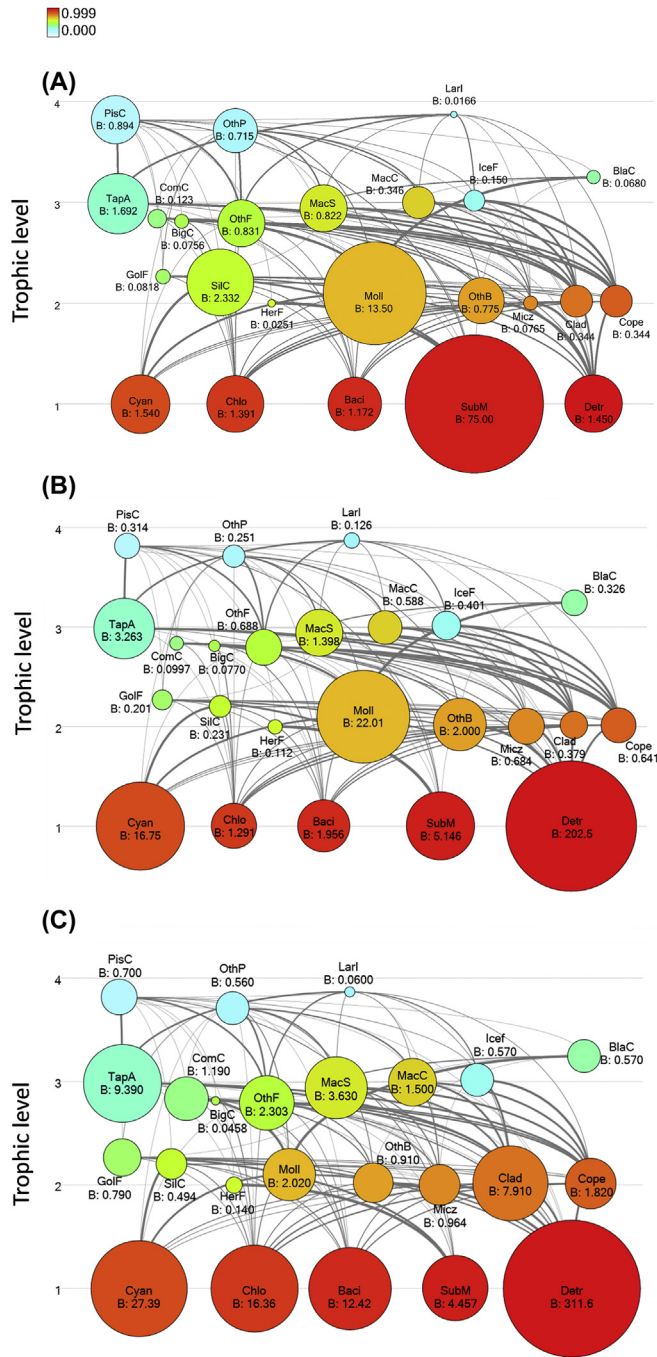
FIGURE 4.3 Food web structure and relative biomasses of Lake Chaohu, China, from the 1950s (A), 1980s (B), and 2000s (C) mass-balanced Ecopath models. The color bar in the left column represents the fraction of the biomass in the total biomass. (Details of the Abbreviations can be found in Table 4.1).
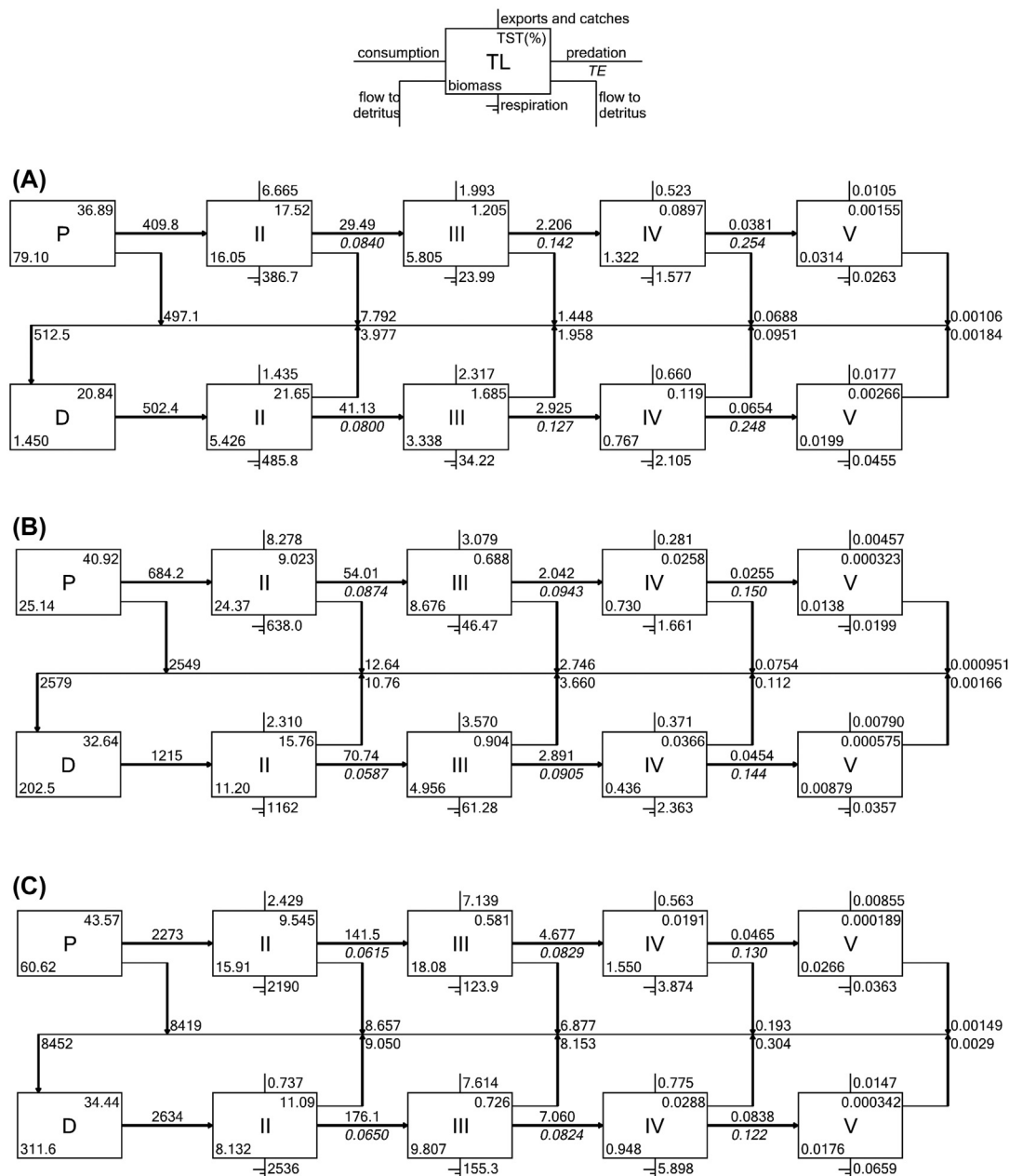
FIGURE 4.4   Lindeman spine representing the trophic flows of Lake Chaohu, China, from the 1950s (A), 1980s (B), and 2000s (C) mass-balanced Ecopath models. 'P' represents phytoplankton and 'D' represents detritus.

lower for zoobenthos and primary producers. In addition, the model-calculated TLs generally agree with the measured values for most functional groups (Fig. 4.5), indicating that the calibrated diet composition is in line with the real situations. For the Ecopath model, the TL for each functional group was largely determined by diet composition, which was, however, mostly arbitrarily assigned. This process has made the diet composition a subjective model input and a source of model uncertainty. An adjustment should be made for model inputs, particularly diet composition (Christensen and Walters, 2004). The calibration in the present study provides a solid basis for our analysis of the changes in the functioning of the ecosystem of Lake Chaohu. Thus, we suggest that the calibration process for diet composition by the comparison of calculated and measured TLs should be a standard procedure in analyses with the Ecopath model in the future.

4.2.4.2 Changes in Ecosystem Functioning

The calculated ecosystem properties of Lake Chaohu in the 1950s, 1980s, and 2000s are shown in Table 4.3. Multiple indicators show the changes in the ecosystem from different angles. TST (t/km^2/year) increased by one order of magnitude from the 1950s (2459.024) through the 1980s (7901.496) to the 2000s (24,541.850), indicating an increasing turnover rate of the biomass in the system related to cyanobacterial blooms (Shan et al., 2014). The profiles of TST were similar in the 1980s and 2000s. However, in the 1950s, the contribution of consumption and respiratory flows were much larger, but exports and flows into detritus were much lower. Similarly, the sum of all production (t/km^2/year) increased by one order of magnitude from the 1950s (960.843) through the 1980s (3351.219) to the 2000s (10,913.150), primarily due to nutrient enrichment from anthropogenic sources. The total catch (t/km^2/year) increased from 13,620 (1950s) to 17,900 (1980s) to 19,280 (2000s). The mean trophic level (MTL) of catch was similar in the 1950s (2.500) and 1980s (2.448) but slightly higher in the
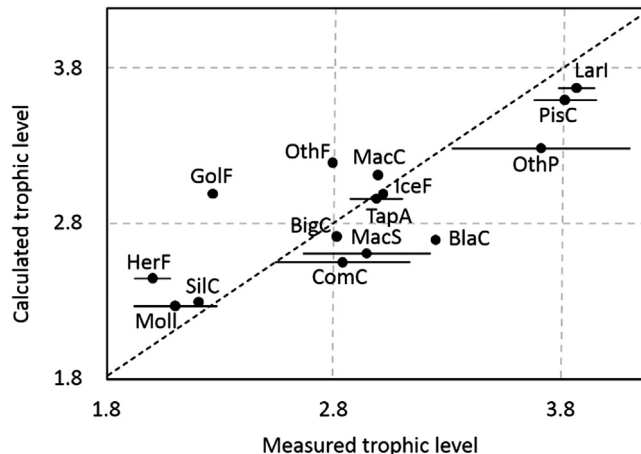

FIGURE 4.5 Comparison of measured and calculated TLs for different functional groups in Lake Chaohu, China. The measured values were based primarily on stable isotopes $\delta^{13}C$ and $\delta^{15}N$ from our laboratory measurement, also collected from Zhang et al. (2012) and Xu et al. (2005) (Details of the abbreviations can be found in Table 4.1.). The error bars represent one unit of standard deviation.

TABLE 4.3 Ecosystem Properties of Lake Chaohu in the 1950s (CH50′), 1980s (CH80′), and 2000s (CH00′) Based on Outputs From the Ecopath Model

Properties	Abbreviations	Units	CH50′	CH80′	CH00′
Sum of all consumption	TC	t/km^2/year	988.405	2029.502	5236.515
Sum of all exports	TEx	t/km^2/year	23.694	1381.892	5837.949
Sum of all respiratory flows	TR	t/km^2/year	934.462	1911.315	5015.073
Sum of all flows into detritus	TD	t/km^2/year	512.463	2578.786	8452.310
Total system throughput	TST	t/km^2/year	2459.024	7901.496	24,541.850
Sum of all production	TP	t/km^2/year	960.843	3351.219	10,913.150
Mean trophic level of the catch	MTL	—	2.500	2.448	2.912
Total catch	—	t/km^2/year	13.62	17.90	19.28
Gross efficiency	GE	—	0.015	0.006	0.002
Calculated total net primary production	TPP	t/km^2/year	906.900	3233.032	10,691.710
Total primary production/total respiration	TPP/TR	—	0.971	1.692	2.132
Net system production	NSP	t/km^2/year	27.562	1321.717	5676.638
Total primary production/total biomass	TPP/TB	—	8.864	54.858	111.154
Total biomass/total throughput	TB/TST	1/year	0.042	0.007	0.004
Total biomass (excluding detritus)	TB	t/km^2	102.316	58.935	96.188
System omnivory index	SOI	—	0.081	0.066	0.075
Throughput cycled (including detritus)	Tcy	t/km^2/year	836.068	1738.329	2208.767
Finn's cycling index	FCI	%	0.34	0.22	0.09
Finn's mean path length	FML	—	2.566	2.399	2.261
Connectance index	CI	—	0.238	0.238	0.238
Ascendancy	—	%	30.6	39.4	38.6
Overhead	—	%	69.4	60.6	61.4
Total transfer efficiencies	TE	%	14.0	9.8	8.7
Transfer efficiencies from primary producer	TE p.p.	%	14.5	10.7	8.7
Transfer efficiencies from detritus	TE det.	%	13.6	9.1	8.7

2000s (2.912). The gross efficiency ($-$) gradually decreased from 0.015 (1950s) to 0.006 (1980s) to 0.002 (2000s), suggesting the fraction of primary production that finally transferred into fishery products was decreasing during these years. From the 1950s to the 2000s, TPP, NSP, TPP/TR, and TPP/TB were rapidly increasing. The deviation of TPP/TR from 1 and the increasing TPP/TB in the 1980 and 2000s suggest that the ecosystem was approaching an immature and eutrophic state. SOI was highest in the 1950s (0.081) and lowest in the 1980s (0.066). This result demonstrates a general decrease in the complexity of the food web structure, indicating that the food web did not change from linear to web-like and that the system was not becoming more mature (Odum et al., 1971). Furthermore, the decreasing trend of FCI, FML, and ascendancy also demonstrated a decreasing maturity of system from the 1950s to the 2000s. Regarding to the TE, the geometric means for Lake Chaohu's ecosystem decreased from 14.0% (1950s) to 9.80% (1980s) to 8.70% (2000s), as did the TE p.p. and TE det (Table 4.3), lying in the acceptable range around a theoretical value of 10% (Lindeman, 1942). These results indicated that as the ecosystem of Lake Chaohu was adapting to the changing external conditions, the remaining ability of the system to utilize the available resources was reduced.

The results of the MTI analysis are presented in Fig. 4.6. Only a few differences were observed for the three periods. Piscivorous fish generally had negative effects on other fish groups and on phytoplankton, and they had positive effects on zoobenthos and zooplankton. However, this effect was weakened in the years approaching the 2000s. Planktivorous fish, particularly the tapertail anchovy (TapA), had negative effects on most fish groups and on zooplankton, whereas they positively affected phytoplankton. Most fish groups benefitted from phytoplankton. Fishing (Fleet1) was apparently negatively influencing most fish groups, particularly commercial stocks, such as piscivorous and silver carp. Simultaneously, this anthropogenic activity had a positive effect on phytoplankton, manifesting the intensive fishery in the lake may contribute to the recent blooming of phytoplankton.

4.2.4.3 Collapse in the Food Web: Differences in Structure

Our results clearly illustrate a collapse in the food web structure in Lake Chaohu during the 1950s, 1980s, and 2000s (Fig. 4.3). Here, we demonstrate the structural differences by clusters of functional groups, as follows.

The total fish biomass increased rapidly, but it is clear that the catch composition of the fishery showed an abrupt change in the beginning of 1960s after the onset of the sluice (Fig. 4.2). The dominant group of fish shifted from large-sized piscivorous fish (62.9% in 1952) to small-sized (80% after the 1980s) zooplanktivorous fish, such as pelagic *C. ectenes taihuensis* and *N. taihuensis*. The fraction of young large-sized fish in the fishery catchment was increasing—yet another sign of a growing trend toward small-sized fish in the lake.

Zooplankton and zoobenthos occupied the middle TLs in the lake ecosystem, thereby playing a vital role in the mass and energy cycling. The abundance of zooplankton, including cladocerans (Clad), copepods (Cope), and small-sized zooplankton (Micz) such as rotifers, increased from the 1950s to the 2000s, based on field data (Deng, 2004). The dominant species in the cladocerans changed from the large-sized *Daphnia pulex* and *Daphnia hyalina* to the small-sized *Bosmina coregoni*, whereas in copepods, *Sinocalanus dorii* and *Limnothona sinensis* became the dominant species. Zoobenthos fed primarily on microorganisms such as diatoms, protozoans, rotifers, and detritus and were eaten by carnivorous fish. The dominance of
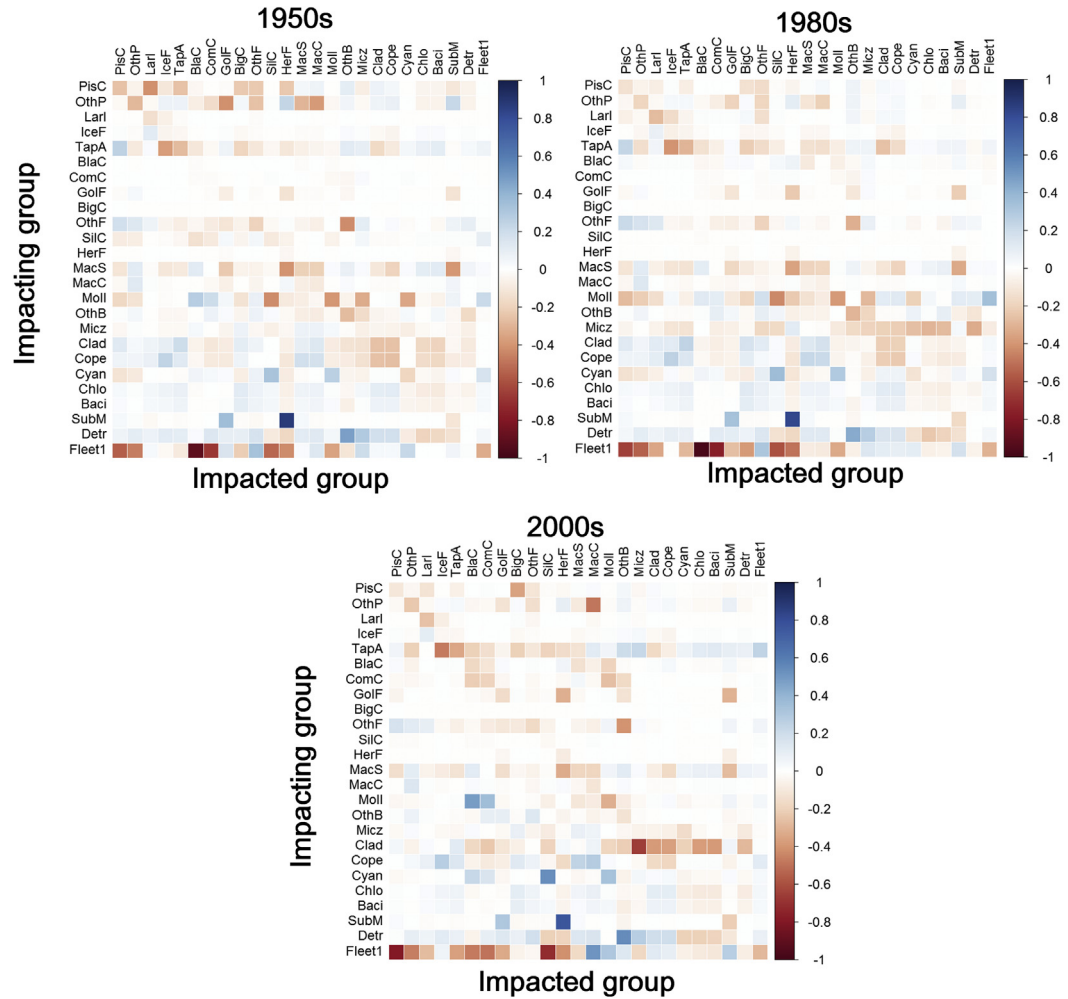
FIGURE 4.6 Mixed trophic impacts of Lake Chaohu's ecosystem in the 1950s, 1980s, and 2000s. Blue values represent a positive impact, whereas red values represent a negative impact, and the absolute values are proportionate to the degree of the impact.

Mollusca (Moll) in the 1960s (*Corbicula fluminea*, *Limnoperna lacustris*, and *Semisulcospira cancellata*) indicates the oligotrophic state of the lake at that time. Later, in the 1980s, the biomass of Moll had increased approximately sixfold (Cai et al., 2012; Hu and Yao, 1981). However, recent studies have shown that the composition of benthic assemblages was largely altered during the 2000s, shifting from a dominance of Moll to oligochaetes and chironomids (OthB; biomass was still primarily attributed to the Moll; Cai et al., 2012; Ning et al., 2012). In addition, the abundance of macrocrustacean shrimp (MacS) and crab (MacC) gradually increased throughout these years, whereas the dominant shrimp species transitioned from *Macrobrachium nipponensis* to a more sedentary *P. modestus* (Hu and Yao, 1981).

At the bottom of the food web, the primary producer shifted from macrophytes in the 1950s to phytoplankton in the 1980s and 2000s. Abundant submerged macrophytes were recorded before the flood in 1954, covering 25−30% of the lake area according to field observation (Xie, 2009; Zhang et al., 2014). The flood led to the degradation but not the extinction of the macrophytes, which recovered to 25% of coverage before 1960, according to field observation, primarily due to the surviving seed banks (Zhang et al., 2014). Thereafter, the macrophytes community gradually shifted toward floating and emergent plants (Xu et al., 1999a), and the observed coverage of macrophytes were as low as 2.54% and 1.54% in the 1980s and 2000s, respectively. Phytoplankton took over and accounted for more than 90% of the lake's primary productivity, with the dominant species of *Microcystis aeruginosa* and *Anabaena spirodies*. The total biomass of phytoplankton in the 2000s became even higher than that in the 1980s with increasing contributions from chlorophytes and bacillariophytes (Guo, 2005).

Overall, we observed a collapse of food web structures toward a simplified structure and decreasing biodiversity in Lake Chaohu's ecosystem. This observation is further supported by the generally decreasing SOI and FML calculated by model (Table 4.3), suggesting a shorter food chain length and a less complex structure. In addition, field data suggest that the MTL of Lake Chaohu declined steadily since 1970, indicating a decrease in the abundance of higher TL species (e.g., large piscivorous bottom fish) relative to lower TL ones (e.g., small pelagic fish; Zhang et al., 2012). This phenomenon, known as "fishing down the food web" (Pauly et al., 1998), has led to a loss of trophic interactions and lower structure complexity in the ecosystem of Lake Chaohu (Zhang et al., 2012). However, in the present study, the MTL of the catch was highest in the 2000s (Table 4.3), which was largely attributed to the relatively high TL of dominant stocks of the TapA (3.0). This value was in line with earlier measurements (2.9−4.1; Xu et al., 2005) and was kept constant due to a fixed diet composition in all three models here, but it could be dynamic in a long time scale. An overestimation of the TL in the 2000s and a bias in the fishery catch data may have led to this result. However, we argue that the TapA could be a special case that occupies high TL but has a specialized diet of zooplankton, thereby simplifying the food web structure and reducing biodiversity and trophic interactions.

4.2.4.4 Toward an Immature but Stable Ecosystem

The changes in the food web structure could be the major explanation for the changes in ecosystem functioning, which can be observed in multiple ecosystem property indicators from model outputs (Table 4.3). We have demonstrated that the ecosystem of Lake Chaohu was moving toward an immature state from the 1950s to the 2000s, according to changes in multiple related indicators (TPP/TR, SOI, FCI, FML, and ascendancy). Nonetheless, the stability of the system might have developed in another way such that immature ecosystems were thought to be more stable and vice versa (Pérez-España and Arreguín-Sánchez, 2001). In general, the stability of lake ecosystem decreases as the nutrient loading increases due to the loss of system resilience and maturity (Scheffer et al., 2001). A recent study showed, however, that after the catastrophic shift to the turbid ecosystem state in lakes, there will be a shift toward a higher stability (Kuiper et al., 2015). Because a catastrophic shift in Lake Chaohu was identified around 1980 (Liu et al., 2012), the stability of the ecosystem could have been lower in the 1980s than in the 1950s and 2000s. In addition, the stability of Lake Chaohu ecosystem could be interpreted from the proportion of detritus and primary producer energy

channels in the food web such that a stable ecosystem derived energy from both rather than a single pathway to enhance the plasticity and resilience (Fetahi et al., 2011; Moore et al., 2004). What we found was that energy flows were evenly distributed in the 1950s and 2000s, whereas the detritus pathway was more dominant in the 1980s in Lake Chaohu (Fig. 4.4). Additionally, detritus itself increases the stability and persistence of the food web by influencing the composition and dynamics (Moore et al., 2004). The biomass of detritus in the food web in Lake Chaohu kept increasing throughout time (Fig. 4.3), primarily due to increasing production and throughput in the system and decreasing gross efficiency (Table 4.3). Primary production was not utilized efficiently to transfer into fish production but flowed back into detritus through a potential shortcut (Shan et al., 2014). Overall, the ecosystem of Lake Chaohu may develop toward an immature but stable state. The discussion above may contribute to the debate on the relationships among the stability, maturity, and complexity of ecosystems. Further studies may be conducted using thermodynamic ecosystem-level indicators such as exergy and structural exergy (Marchi et al., 2012; Xu et al., 2001) for a more comprehensive evaluation of lake ecosystem status.

4.2.4.5 *Potential Driving Factors and Underlying Mechanisms*

Unfortunately, as we are using steady state Ecopath model that accounts for the food web components only, the potential external driving factors and underlying mechanisms of the changes in food web structure and ecosystem functioning cannot be directly identified in the present study. We speculated that anthropogenic stressors, including nutrient-loading discharge, intensified fishery, and hydrological regulation, were the major drivers that led to a switch from top-down to bottom-up control in the food web. The onset of the sluice in 1963 might have blocked the migratory route for juvenile large-sized fish, particularly migratory piscivorous, herbivorous, and omnivorous fish, thereby strongly suppressing the survival and growth of these fish in the lake and subsequently favoring the dominance of small-sized, sedentary stocks. The regulated higher water level in spring thereafter led to the abrupt degradation of macrophytes (Zhang et al., 2014), which used to provide refuge for both piscivorous/herbivorous fish and large-sized zooplankton (Carpenter et al., 2008; Schriver et al., 1995). Consequently, the top-down control and trophic cascading were destroyed, resulting in the limitation of piscivorous/herbivorous fish, the domination of zooplanktivorous fish and the enhanced suppression of large-sized zooplankton, all of which favored the dominance of phytoplankton as the primary producer. From the 1980s, the gradual intensification of fishery and eutrophication (Kong et al., 2015; Zhang et al., 2012) might have further overexploited predatory fish and triggered cyanobacterial blooms, which are inedible to zooplankton. All of these factors contributed to the strongly increased productivity and flux cycling in the low TLs of the ecosystem, which might give rise to the bottom-up control in the food web (Oksanen, 1988), stabilize the ecosystem in eutrophic state, enhance the resistance to restoration efforts, and hinder the recovery toward a prior state. As a result, anaerobic conditions caused by cyanobacterial blooms and organic matter accumulation in the benthic environment, along with the toxicity of microcystins produced by cyanobacteria, exerted high pressure on the species of low hypoxia-tolerant Mollusca, such as *C. fluminea*, and favored the dominance of high

hypoxia-tolerant oligochaetes and chironomids, thereby largely reducing the biodiversity of benthic communities (Cai et al., 2012; Lv et al., 2011).

Overall, Lake Chaohu might be affected by multiple driving factors, but it remains unclear which factors contribute to the dramatic changes; further evaluation is required. In the Baltic Sea ecosystem, the strong removal of piscivorous fish by fishery may lead to a collapse in the top predators, cascading effects down the food web, and a subsequent shift in ecosystem functioning (Casini et al., 2009). In addition, human-introduced invasive species may alter the food web structure, cause a loss of complexity and in turn trigger a critical transition in ecosystems such as Lake Chozas (Marchi et al., 2011, 2012). However, other than in the Baltic Sea and Lake Chozas, the collapse in the food web structure in Lake Chaohu might initially be triggered by the water level control due to the onset of the sluice. Thus, the major driving factors and the underlying mechanisms for the changes in food web structure and ecosystem function may be unique in each specific case, which requires careful evaluation.

4.2.4.6 Hints for Future Lake Fishery and Restoration

Fishery can be put on a path toward sustainability by limiting fishing effort (Pauly et al., 2002). In fact, there has been a fishery regulation in Lake Chaohu in recent years that releases pressure on economic stocks by prohibiting fishery from February to July. However, this strategy has not led to significant improvements in the lake's state. The alternative stable state theory suggests that the new state after the collapse of the food web may be stabilized by certain mechanisms, which results in difficulties of lake ecosystem restoration even under robust management. There could be a threshold in density of zooplanktivorous fish that separates the ecosystem into two alternative states with different structures and functioning (Casini et al., 2009). It is generally difficult to control small-sized planktivorous fish, but the large-sized fish are much easier to regulate. Thus, we propose that, first, we should evaluate the value of this planktivorous fish density threshold and that the increase in the abundance of large-sized fish should be large enough to keep planktivorous fish density under the threshold, thereby favoring the restoration of the food web. Second, nutrient loading should be controlled; two-thirds of the current loading needs to be cut down to restore the lake to a clear state (Kong et al., 2015). Third, a multiobjective water level control for the hydrological regulation in this lake is strongly suggested (Kong et al., 2013; Zhang et al., 2014). Overall, an integrated strategy incorporating all the strategies above will bring about direct or indirect positive effects on the food web and ecosystem functioning of this lake and together promote the lake toward a mature, stable, and healthy state in the future.

Furthermore, using Ecopath in the case of Lake Chaohu in the present study, we have shown it is possible to develop a new management tool for lakes that considers the changes in the food web and ecosystem functioning as a consequence of the increased anthropogenic effects on the ecosystem. As illustrated in Fig. 4.3 and Table 4.3, the model shows its ability to follow the food web collapse and evaluate the changes in the functioning of an ecosystem, which will undoubtedly bridge environmental and ecological management. In general, there is an increasingly urgent need for integrated ecological—environmental management in lakes (Jørgensen and Nielsen, 2012), where the Ecopath model may play a role.

4.3 CONCLUSIONS

The present study managed to establish Ecopath-based mass—balance models for the 1950s, 1980s, and 2000s to describe systematically the changes in the food web structure and ecosystem functioning in Lake Chaohu, China. We found significant changes in the food web structure throughout these periods and the degradation of the lake ecosystem, which was approaching an immature but stable state. Nutrient enrichment, intensive fishery, and hydrological regulation might be the key drivers of these changes in the food web structure and ecosystem functioning. The present study provided a first comprehensive and quantitative evaluation of the effect of multiple anthropogenic stressors on Lake Chaohu's ecosystem, and it provided hints toward the sustainable management of this important ecosystem. We deem that the Ecopath model can be considered a new management tool for lakes because it incorporates a food web perspective and bridges the strategy of environmental and ecological management, as shown in the concrete case of Lake Chaohu.

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