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The food web structure and ecosystem properties of a filter-feeding carps dominated deep reservoir ecosystem

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ABSTRACT

An Ecopath model was constructed to describe the ecosystem of Lake Qiandaohu, a stock-enhanced large deep Chinese reservoir with silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) dominated in its pelagic community. The food web structure and ecosystem property of the reservoir were analyzed and evaluated. The results showed that there were seven trophic levels (TLs) in the system, with the trophic flows primarily occurring through the first four TLs. The food web structure of this ecosystem was characterized with a bulged intermediate trophic level, which was contrary to the wasp-waist food web structure occurred in most natural aquatic ecosystems. The corresponding trophic flow pattern showing by transfer efficiencies (TEs) between TLs indicated that the trophic flows primarily went through from TL I to II with a high TE (of over 50%) and through a flow loop or short cut between detritus and TL II but greatly reduced from TL II to III with a lowest TE of 2.5% due to the bulged biomass at TL II. The trophic flow loop greatly increased the throughput recycled, which, together with high connectance index (CI), system omnivory index (SOI), Finn's cycled index (FCI) and Finn's mean path length (FML), might be beneficial to the maintaining of ecosystem stability. Finally, ecosystem property indices showed that this reservoir had a high value of P_p/R and P_p/B, indicating this ecosystem of short history was immature, but highly productive. This silver carp and bighead carp dominated deep reservoir ecosystem had both the characteristics of high productivity of an immature ecosystem and the feature of high stability of a mature ecosystem.

1. Introduction

Food web structure and interactions have a decisive role in determining the dynamics of an ecosystem, and are of interests of many ecological studies (e.g., Halfon et al., 1996; Elser et al., 1998; Kitchell et al., 2000; Aoki and Mizushima, 2001; Angelini and Agostinho, 2005; Gamito and Erzini, 2005). Lakes and reservoirs in China are particularly in need of the study of the food webs for the following two reasons: (1) the food webs of these ecosystems are usually characterized with the dominance of the two artificially stocked filter-feeding planktivorous Chinese carps, silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*), and their ecological effects on aquatic ecosystems have been controversial and contradictive (e.g., Januszko, 1974; Kajak et al., 1975; Opuszynski, 1979; Smith, 1985, 1989; Spataru and Gophen,

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1985; Shi et al., 1989; Starling and Rocha, 1990; Li et al., 1993; Opuszynski and Shireman, 1995; Domaizon and Devaux, 1999; Xie and Liu, 2001; Lu et al., 2002; Radke and Kahl, 2002; Liu et al., 2004); (2) the studies so far of the impacts of the two carps on the aquatic ecosystems are usually limited to top-down effects (i.e., the direct effects of the two carps on the plankton communities and water quality), while the indirect effects of the two carps on other planktivores and/or fish at higher trophic levels and on the stability and development of ecosystems are often not evaluated.

Silver carps mainly filter-feed on phytoplankton (and some small zooplankton such as rotifers, protozoan and nauplii) with the particle sizes between 8 and 100 μm while bighead carps primarily on zooplankton (especially copepods and cladocera) and large size phytoplankton with particle sizes of 17–3000 μm (Cremer and Smitherman, 1980; Xie, 1999, 2001). The two Chinese carps used to only naturally occur in lakes with connections to large rivers such as the Yangtze River and Pearl River, where they become sexually mature and reproduce naturally. However, the presence of the two carps in lakes or reservoirs now can only be through artificial stocking because their migrating passages are blocked by various hydraulic constructions. It almost becomes a routine practice of lake fisheries management to massively stock the two carps in lakes and reservoirs in China. The two fish often account for over 40% of the total fish biomass and almost 70% of the pelagic fish biomass in the lakes and reservoirs. This dominance imposes great influences on the biomass and structure of planktonic community, which, in turn, can trigger further trophic cascading effects on other planktivorous fish species and top predators. Thus the ecosystem dynamics are greatly affected by stocking of the two filter-feeding carps, and it is necessary to evaluate the role the two carps play in lake/reservoir food webs.

Various ecological models have been developed for evaluating the food web interactions, analyzing ecosystem structure and functioning, or addressing ecological dynamics ranging from the conventional Lotka-Volterra predator–prey model to more recent ecosystem-based or multispecies fisheries models (see reviews by Robinson and Frid, 2003; Babcock et al., 2005). These models differ in their complexity, input data requirement and outputs. The mass-balanced Ecopath with Ecosim (EwE) model is among the most updated and widely used ecosystem models and is considered as one of the effective and straightforward methods for quantifying the food web interactions and fisheries ecosystem dynamics. First built for estimating biomass and food consumption of the elements of an aquatic ecosystem, EwE was combined subsequently with various approaches from theoretical ecology, proposed by Odum (1969) and Ulanowicz (1986), for the analysis of energy flows between the elements of ecosystems and to reveal the maturity and stability of ecosystems. Later, the system has been further optimized for direct use in fisheries assessment, as well as for addressing environmental questions with the integration of the temporal dynamic model, Ecosim, in 1995, and the spatial dynamic model, Ecospace, in 1998 (Christensen et al., 2000). Since its initiation by Polovina (1984) in the early 1980s, the mass-balance based software EwE has been developed for about 20 years, and has been widely used for constructing food web models of marine and other ecosystems, serving parameterized systems, and predicting the changes in biomasses and trophic interactions in time and space in different environments. The information derived is useful in multispecies management decision (Vasconcellos et al., 1997; Christensen and Pauly, 1998; Wolff et al., 2000; Bundy and Pauly, 2001; Moreau et al., 2001), in analyses of effects of the trophic cascade (Polis et al., 2000; Ortiz and Wolff, 2002; Schmitz et al., 2004), in verifying the relationship between stability and diversity (Hastings, 1988; Naeem and Li, 1997; Tilman, 1999). Because the required input data are moderate, EwE is an ideal approach to quantifying the ecosystem dynamics of lakes and reservoirs in China.

Lake Qiandaohu, renamed from the reservoir of Xin'anjiang, was chosen for this study because it is a typical silver carp and bighead carp dominated deep reservoir ecosystem in China. Both silver carp and bighead carp have been stocked in the reservoir since its foundation in 1959. In this deep reservoir ecosystem, littoral zone is limited. This, together with the frequent seasonal and inter-annual fluctuation of water level, results in almost no vascular plants in the reservoir. Thus phytoplankton becomes almost the unique primary producer, resulting in a dominant food chain from phytoplankton to planktivores and to piscivores.

The reservoir had been renowned for its limpidity of water and water quality had been maintained at the Chinese national surface water Class I before the large-scale cyanobacterial bloom occurred in 1998 and 1999. The low population levels of the two Chinese carps in 1998 and 1999 (Fig. 1) were hypothesized to be responsible for the algal bloom (Liu et al., 2004). In order to prevent the recurrence of algal bloom and to improve water quality, silver carp and bighead carp have been stocked massively and maintained at a high biomass level since 2000 to restore or re-establish the two carp populations, which now account for about 80% of the pelagic fish production and thus play a crucial role in the ecosystem. The cyanobacterial bloom has not recurred since and the water quality has been greatly improved since the stocking of the two Chinese carps with no measures of nutrient control (Liu et al., 2004; Liu, 2005).

The objectives of this study are: (1) to document and quantify the trophic web structure of Lake Qiandaohu; (2) to evaluate the role that the silver carp and bighead carp play in the Lake Qiandaohu ecosystem; (3) to gain insight into the properties and development status of the ecosystem (maturity and resilience).

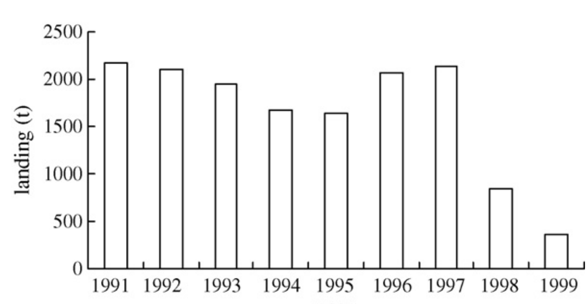

Fig. 1 – Historical landings of silver carp and bighead carp in Lake Qiandaohu.

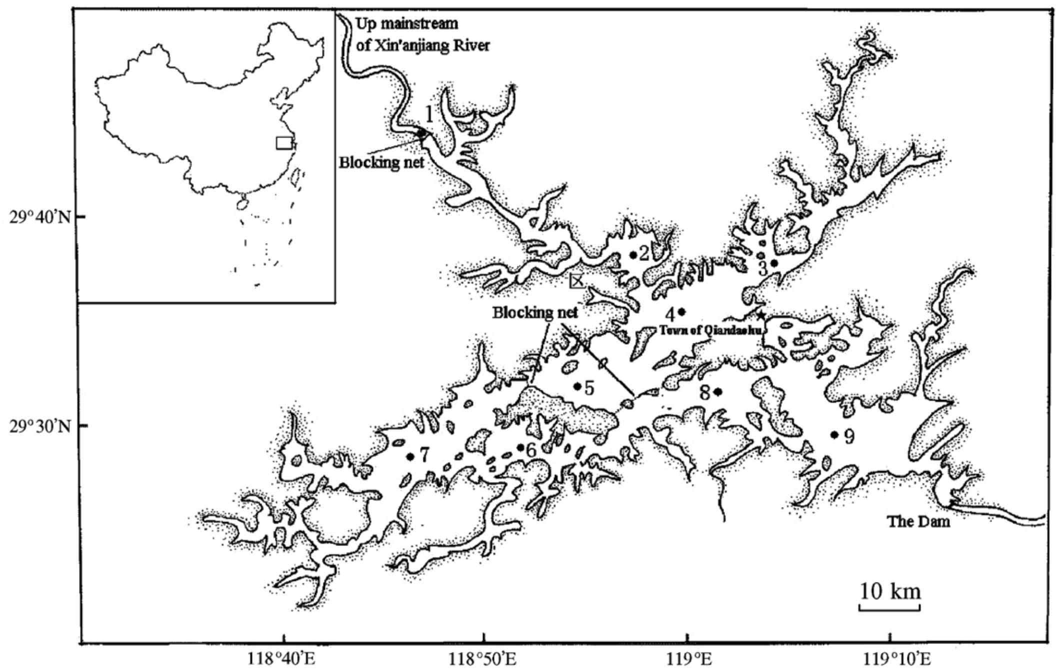

Fig. 2 – Map of Lake Qiandaohu.

2. Materials and methods

2.1. Study area

Lake Qiandaohu, located at Chun'an County, Zhejiang Province, PR China (29°22′–29°50′N, 118°34′–119°15′E) (Fig. 2), is one of the largest reservoirs in China, with a water surface area of 583 km^2 and an estimated volume of 178.4×10^8 m^3 when the water level is at 108 m above the sea level (the designed elevation with the corresponding average water depth of 30.44 m). The actual volume and water surface area vary with the change of water level (Table 1). The regression equations of surface water area (A) and average water depth (D) with the actual water level (L) can be described as: $A = 0.0484L^2 + 1.4127L - 132.76$ ($R^2 = 0.9997$) and $D = 0.0005L^2 + 0.302L - 7.6535$ ($R^2 = 0.9954$), respectively. The water surface area and water depth used in the construction of the Ecopath model in this study were 452.7 km^2 and 26 m, respectively, deduced from the actual average water level (96.35 m) in 2004. There are about 30 tributaries, of which, Xin'anjiang River is the largest and accounts for about 60% of the total inflows and thus water quality in this river has a great influence on water quality of Lake Qiandaohu.

2.2. Modelling approach

The Ecopath model was used to create a static mass-balance model of the filter-feeding Chinese carps dominated Lake Qiandaohu. Details of the Ecopath model are given in Christensen et al. (2000). The balanced state was assumed to be reached when realistic estimates of the unknown parameters were obtained and there was a consistent view of the energy flow between the different compartments in the model (Gamito and Erzini, 2005). The balanced model was then used to analyze the trophic structure and ecosystem properties of Lake Qiandaohu ecosystem.

2.3. Choice of food web compartments

Table 2 shows a list of all compartments we selected to represent the food web structure in Lake Qiandaohu. The selection of compartments was based on the organisms' ecological

Table 1 – Variation of water areas, volume and mean water depths against water level of Lake Qiandaohu

	Water level (m)					
	58	68	78	88	98	108
Area (km^2)	112.0	186.7	274.7	361.3	474.7	583.3
Volume ($\times 10^8$ m^3)	13.0	28.0	50.0	85.0	128.0	178.4
Average depth (m)	11.6	14.97	18.18	23.42	26.19	30.44

Cited from Ma (1982).

Table 2 – Food web compartments in Lake Qiandaohu in 2004 included in the Ecopath model

Compartment name	Including organisms with their scientific names
Elopichthys	*Elopichthys bambusa*
Erythroculter	*Erythroculter ilishaeformis*, *E. mongolicus*, *E. dabryi*
Pseudolaubuca	*Pseudolaubuca sinensis*
Bighead carp	*Aristichthys nobilis*
Silver carp	*Hypophthalmichthys molitrix*
Common carp	*Cyprinus carpio*
Xenocypris	*Xenocypris davidi*, *X. argentea*, *Plagiognathops microleps*, *Distoechodon tumirostris*, etc.
Sinibrama	*Sinibrama macrops*
Other fish	*Ctenopharyngodon edellus*, *Megalobrama amblycephala*, *Parabramis pekinensis*, *Carassius auratus*, *Spinibarbus hollandi*, *Mylopharyngodon piceus*, etc.
Shrimp	*Macrobrachium* sp.
Mollusk	Freshwater snails, freshwater mussels and *Corbicula fleminea*
Macrobenthos	Oligochaetes and chironomids
Zooplankton	
Phytoplankton	
Benthic producer	Epiphyte, vascular plants
Detritus	

function (mainly feeding), abundance and information availability (Christensen et al., 2000). A group may be a single species (it is the case for most of the fish species in our system), taxonomically related species such as the group of Erythroculter in our system, which consisted of three related species under the genus of Erythroculter and shared a similar feeding composition, or ecologically related species such as the group of Xenocypris, which consisted of fish from different genus under the Xenocyprininae, but all were benthic fish and shared similar diet compositions. We also put grass carp (*Ctenopharyngodon edellus*), *Megalobrama amblycephala*, *Parabramis pekinensis*, crucial carp (*Carassius auratus*), *Spinibarbus hollandi* and black carp (*Mylopharyngodon piceus*) into one group (i.e., other fish group) because they were not abundant and were usually recorded as a group in fisheries statistics.

2.4. Field sampling and estimation of input parameters

Nine sampling stations were set up (Fig. 2) to monitor phytoplankton (monthly), zooplankton (monthly) and zoobenthos (quarterly) in 2004. The water temperature, dissolved oxygen, TN, TP, SD and chlorophyll *a* at each station were also determined monthly (Liu, 2005). Methods used for the ecological monitoring follow those routinely used in hydrobiological sampling (Zhang and He, 1991; Zhang and Huang, 1991).

2.4.1. Phytoplankton and zooplankton

Chlorophyll *a* concentrations of the nine sampling stations were determined monthly by spectrophotometry (Lorenzen, 1967; Wang and Wang, 1984; Zhang and He, 1991). The lowest chlorophyll *a* concentration observed was 0.22 mg m^{-3} while the highest 4.37 mg m^{-3} in 2004, with an average value of 2.36 mg m^{-3}. Phytoplankton biomass was estimated to be 0.786 g m^{-3} using the conversion factor of 0.3 mg chlorophyll *a* per 100 mg phytoplankton (Zhang and He, 1991). Using a mean depth of 26 m, we estimated the phytoplankton biomass of 20.44 g m^{-2}.

Biomass of zooplankton was determined directly from samples collected with modified opening–closing bongo nets (with a diameter of 37 cm and a mesh size of 0.03 mm) through the water column. The total biomass of zooplankton varied between 16.2 and 989.1 mg m^{-3} in 2004, with an average value of 396.2 mg m^{-3}. For a mean depth of 26 m, the corresponding value was estimated as 10.301 g m^{-2}.

Production/biomass (P/B) ratio was estimated to be 200.75 for phytoplankton, and 15.81 for zooplankton (He, 2000; Song, 2004). A production/consumption (P/Q) ratio of 0.05 was adopted for zooplankton (Park et al., 1974; Scavia et al., 1974; Song, 2004), which could then be converted into consumption/biomass ratio (Q/B) using $Q/B = (P/B)/(P/Q)$ (Christensen et al., 2000).

2.4.2. Benthic producer and detritus

The group of benthic producer includes various benthic algae (epiphytes) and a few vascular plants in the littoral zone of the reservoir, and all together they cover approximately 20% of the reservoir area. The biomass of benthic producer was one of a few parameters estimated in the Ecopath model. A P/B ratio of 80 was adopted for the group of benthic producer (Wang and Liang, 1995; He, 2000). The detritus group was defined to include DOC, POC and bacteria according to Heymans et al. (2004) who estimated the biomass of bacteria as 17.5% of that of the phytoplankton. The biomass of DOC and POC was estimated by the Ecoempire built-in in the EwE model (Christensen et al., 2000).

2.4.3. Macrobenthos and mollusks

We used macrobenthos as the group name to include both oligochaetes and chironomids. Since in the profoundal zone of this deep-water reservoir, which takes up over 80% of the reservoir bottom area, the benthic fauna only consisted of oligochaetes and some chironomids species. However, in the limited littoral zone of this reservoir, there did exist some gastropods and bivalve species, though the biomass of them was very limited. Thus we put the gastropods and bivalves into the group of mollusks.

Samples of macrobenthos were collected quarterly (i.e., in March, June, September and December of 2004, respectively) and at the nine sampling stations (Fig. 2) using a modified Peterson's grab sampler with an area of 0.0625 m^2 and sieved through a 450-μ mesh net (Zhang and He, 1991). The depths of the sampling stations varied among different sites and as a result of fluctuation of water level with a minimum depth of 24.0 m and a maximum depth of 50.0 m. Although water was stratified from May to November, the temperature was relatively stable (ranging from around 10 °C in winter to 15 °C in summer) and oxygen was abundant (no less than 4 g m^{-3} all year round in most of the sampling sites and no less than 2 g m^{-3} in all stations all year round) in the profoundal zone (see detailed information in Liu, 2005). The macrobenthos was only collected at the profoundal zone of the reservoir because this reservoir has a very steep and hard slope, on which no silts or soils could be accumulated. Thus neither the oligochaetes nor chironomids could grow there. This was also demonstrated by trial sampling using the grab sampler. The macrobenthos were picked alive manually in the laboratory. They were preserved with 75% ethanol for further identification and counting after the total biomass was weighed and recorded. The identification and counting of macrobenthos were performed under magnification (6.4–200×). Biomass of macrobenthos varied between 0.972 and 43.456 $g\,m^{-2}$, with an average value of 11.876 $g\,m^{-2}$.

Mollusks (gastropods and bivalves) were only found to be present on the limited littoral zone, which covers about 20% of the reservoir area. Samples of mollusks were collected quarterly by using a triangle haul-net with a 30 cm edge and hauling a 10 m distance in each sampling sites. The formation of this sampling net is similar to commercial haul nets used to catch freshwater snails in lakes in China. We chose this sampling method, not the commonly used grab sampler method, because it was demonstrated that the sampling efficiency and catchability was poor by the grab sampler in this oligo-mesotrophic reservoir (the gauge of the grab sampler is only 0.0625 m^2 and could catch few gastropods). It was also hard to sample anything in this reservoir with steep slope and hard bottom inshore in which the density of mollusk was low. The littoral areas near the nine sampling stations were chosen as mollusk sampling sites. Mollusks were dominant by *Bellamya* sp. and biomasses of gastropods were also much larger than those of bivalves, which could represent the whole mollusk group. The average biomass of the mollusks was estimated at 14.937 $g\,m^{-2}$ within their habitats.

The P/B and P/Q ratios adopted in this model were 3.800 and 0.02 for macrobenthos, 0.5 and 0.125 for mollusks, all were derived from Yan and Liang (2003).

2.4.4. *Shrimps and fish*

The biomass of shrimps was estimated along with the mollusks by using the same samples. But habitat of shrimps was assumed to cover the whole reservoir area. The average biomass of shrimps was estimated at 0.867 $g\,m^{-2}$. The P/B ratio of shrimps was 1.83, calculated by the Ecoempire of the EwE model (Christensen et al., 2000). The P/Q ratio of shrimps was assumed to be 0.075 (Halfon et al., 1996).

Fish biomass was estimated according to $F = Y/B$ and $F = Z - M$, where F, M and Z represent fishing mortality, natural mortality and total mortality, respectively, and Y and B represent the landing and biomass of fish. Data of landing statistics of various economic fish were from the Agriculture Bureau of Chun'an County and Hangzhou Qiandaohu Development Co. Ltd., Zhejiang Province, PR China (unpublished data) and were given in Table 3. Samples were taken for measuring body weight and fork length (to the nearest half centimeter), and scales were taken for age determination. Z (=P/B) were estimated by the method of Beverton and Holt (1957) and calculated using the FiSAT II. The average maximum attainable length L_∞ and average maximum attainable weight W_∞ were either estimated with the data collected in this study using the von Bertalanffy growth function (VBGF) or obtained from previous studies in the same reservoir (Chen et al., 1990). They were then used for the estimation of Z.

Table 3 – Landings of the main fish groups in Lake Qiandaohu in 2004

Group name	Landing (tonnes km^{-2} $year^{-1}$)
Elopichthys	0.0221
Erythroculter	1.104
Pseudolaubuca	0.309
Bighead carp	3.309
Silver carp	1.184
Common carp	0.110
Xenocypris	1.325
Sinibrama	2.068
Other fish	0.274
Shrimp	0.243
Mollusk	0.239

The Q/B ratios of various fish species were estimated using the empirical formula (Palomares and Pauly, 1998):

$$\log(Q/B) = 7.964 - 0.204 \log W_\infty - 1.965T' + 0.083A + 0.532h + 0.398d \quad (1)$$

where W_∞ is the asymptotic weight (g) estimated from the VBGF, T' an expression for the mean annual temperature of the water body expressed using $T' = 1000\,K^{-1}$ ($K = {}^\circ C + 273.15$), A the aspect ratio, calculated using $A = h^2/s$, where h the height of caudal fin and s its surface area (Christensen et al., 2000), and h is the dummy variable expressing food type (1 for detritivores, and 0 for herbivores and carnivores). Diet compositions were either directly estimated in this study or derived from previous work (e.g., Chen et al., 1990), and summarized in Table 4. The original Ecopath model input parameters and some estimates (in bold) by the EwE model were summarized in Table 5.

3. Results

Although most parameters were obtained or estimated from the direct observation and sampling, modification was necessary as for the diet composition of group 1 (Elopichthys) and group 2 (Erythroculter) in order to make the Ecopath model balance (see the modified diet matrix listed in Table 4).

The results of the aggregation of biomass and energy flows among trophic levels (TLs) showed the presence of seven trophic levels. The fractions of flows and biomass involved in the seven TLs for each trophic group are given in Table 6. Flows in TL I involved the groups of phytoplankton (the dominant producer), benthic producer and detritus. The TL II included zooplankton, macrobenthos, mollusk, shrimp, silver carp, Xenocypris and Sinibrama. All fish groups and shrimps were also partly involved in the flows at TL III. Flows at TL IV were dominated by the two top predators (Elopichthys and Erythroculter). Some other carnivorous or omnivorous fish groups (Pseudolaubuca and common carp), as well as the group of bighead carp, were partly involved at TL IV. Flows above TL IV were primarily involved by Elopichthys and Erythroculter. Although there were seven trophic levels, flows at TL VI and VII were so small (Fig. 3) and could be neglected. The trophic flows primarily occurred in the first four TLs and the food web structure in this reservoir ecosystem was characterized by the dominance of low trophic level organisms, with

Table 4 – Modified diet matrix of the Lake Qiandaohu ecosystem Ecopath model in 2004

Prey	Predator												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Elopichthys													
2. Erythroculter	0.370	0.082											
3. Pseudolaubuca	0.025	0.030											
4. Bighead carp	0.160	0.292	0.240										
5. Silver carp	0.130	0.114	0.100										
6. Common carp	0.012	0.012											
7. Xenocypris	0.075	0.078											
8. Sinibrama	0.220	0.235											
9. Other fish	0.008	0.007	0.040										
10. Shrimp		0.150	0.060			0.050							
11. Mollusk						0.200			0.300				
12. Meiobenthos						0.750	0.020	0.350	0.350	0.250			
13. Zooplankton			0.560	0.950	0.100								0.020
14. Phytoplankton				0.030	0.750						0.150		0.680
15. Benthic producer							0.680	0.500	0.350	0.550	0.450		
16. Detritus				0.020	0.150		0.300	0.150		0.200	0.400	1.000	0.300
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

the highest effective trophic level (ETL) of only 3.89 for the top predator, Elopichthys, and an ETL of 3.60 for another top predator, Erythroculter. The two top predators both primarily preyed on TL II and III (thus they themselves mainly became trophic III and IV; Table 6).

Primary production in the reservoir reached 4214.681 tonnes km^{-2} year^{-1}, accounting for 95.01% of the total system production (4437.0 tonnes km^{-2} year^{-1}; Table 7). Of the total primary production, 97.36% was contributed by phytoplankton (4103.33 tonnes km^{-2} year^{-1}), less than 3.0% by other primary producers. Thus food chains from phytoplankton, primarily through zooplankton or silver carp to higher TLs, should play a significant role in the dynamics of the reservoir ecosystem. This type of grazing food chains primarily included the one involved by algae, silver carp (bighead carp), (Pseudolaubuca), Erythroculter (Elopichthys) and Elopichthys, and the other by algae, zooplankton, bighead carp (Pseudolaubuca, silver carp), (Pseudolaubuca), Erythroculter (Elopichthys) and Elopichthys. In either case, silver carp and/or bighead carp were not only the main part of the catch, but also served as the intermediate link of the food chains, indicating the active role that the two carps played in the food web, with an EE of 0.981 for silver carp and 0.953 for bighead carp, respectively. The biomass and throughputs of the two carps were, however, much lower than those of the zooplankton.

The biomass of TL II was larger than that of TL I if the biomass of detritus was not taken into account (Table 7). This feature of food web structure was also consistent with the distinctive flow pattern and transfer efficiencies between TLs. Because of the large biomass of TL II, 50.98% of the trophic flows (i.e., 5202.688 tonnes km^{-2} year^{-1}) from TL I (of both

Table 5 – Input and estimated values (in bold) for the Lake Qiandaohu Ecopath model

Group	Habitat area (fraction)	Biomass in habitat (tonnes km^{-2})	Biomass (tonnes km^{-2})	*P/B* (tonnes year^{-1})	*Q/B* (tonnes year^{-1})	EE
1. Elopichthys	1	0.0385	0.0385	0.98	3.620	**0.585**
2. Erythroculter	1	1.958	1.958	1.054	3.830	**0.858**
3. Pseudolaubuca	1	0.466	0.466	1.170	3.970	**0.987**
4. Bighead carp	1	4.817	4.817	1.299	7.530	**0.953**
5. Silver carp	1	1.520	1.520	1.503	10.19	**0.981**
6. Common carp	1	0.210	0.210	1.035	3.550	**0.928**
7. Xenocypris	1	1.489	1.489	1.360	14.70	**0.948**
8. Sinibrama	1	2.922	2.922	1.360	14.70	**0.971**
9. Other fish	1	0.347	0.347	1.198	12.00	**0.965**
10. Shrimp	1	0.867	0.867	1.830	24.40	**0.956**
11. Mollusk	0.2	3.233	0.647	2.400	19.20	**0.948**
12. Meiobenthos	0.8	11.876	9.501	4.030	201.50	**0.595**
13. Zooplankton	1	10.301	10.301	15.810	316.20	**0.627**
14. Phytoplankton	1	20.440	20.440	200.75	–	**0.543**
15. Benthic producer	0.2	**7.170**	**1.434**	80.00	–	0.500
16. Detritus	1	6.677	6.677	–	–	**0.487**

Note: *P/B* stands for production/biomass ratio and *Q/B* is the consumption/biomass ration while EE represents the ecological efficiency.

Table 6 – Trophic structure decomposition of the groups in Lake Qiandaohu ecosystem

Groups	Trophic levels							ETL	OI
	I	II	III	IV	V	VI	VII		
1. Elopichthys			0.344	0.446	0.188	0.020	0.002	3.89	0.395
2. Erythroculter			0.461	0.480	0.054	0.005		3.60	0.226
3. Pseudolaubuca			0.710	0.285	0.005			3.30	0.160
4. Bighead carp		0.050	0.931	0.019				2.97	0.049
5. Silver carp		0.900	0.098	0.002				2.10	0.094
6. Common carp			0.988	0.012				3.01	0.003
7. Xenocypris		0.980	0.020					2.02	0.020
8. Sinibrama		0.650	0.350					2.35	0.228
9. Other fish		0.350	0.650					2.65	0.228
10. Shrimp		0.750	0.250					2.25	0.188
11. Mollusk		1						2	0
12. Meiobenthos		1						2	0
13. Zooplankton		0.98	0.02					2.02	0.02
14. Phytoplankton	1							1	0
15. Benthic producer	1							1	0
16. Detritus	1							1	0.229

Note: ETL stands for effective trophic level while OI stands for omnivory index.

primary production and detritus) went to TL II. The transfer efficiency from TL I to TL II was thus high. However, the trophic flow from TL II to III was only 65.055 tonnes km^{-2} year^{-1}, with a low transfer efficiency (TE) of 2.5%, the lowest TE among TLs. The TEs for TL III and above were among 8.7–23.0 (see Fig. 3).

The trophic flow from TL II to detritus reached 3993.111 tonnes km^{-2} year^{-1}, this large flow, together with the large part from detritus to detritivores (2917.351 tonnes km^{-2} year^{-1}), indicated that there existed a short cut or a loop of trophic flows in this ecosystem. This might be of great advantage for the recirculation of nutrients. The trophic flow from detritus to TL II was larger than that from primary producers (Fig. 3), indicating that the detritus food chains played an even more important role than the grazing chains in this system.

The ecosystem properties were summarized at Table 7. According to Odum (1971), the ratio between primary production and total system respiration (P_P/R) would decline to 1.0 as an ecosystem develops toward “mature”. Biomass accumulated as the system develops, thus lead to a lower ratio between primary production and biomass (P_P/B). The P_P/R of this system was 3.725, much larger than 1.0 of mature systems. P_P/B is 73.956, also much larger than those for most mature systems such as 10.52 in the Ria Formosa in south Portugal (Gamito and Erzini, 2005), 3.7 of the Broa reservoir (Angelini and Petrere, 1996) and 0.239 of Caete Mangrove Estuary (Wolff et al., 2000) in Brazil, and even larger than the immature ecosystem, Lake Taihu (11.60), the third largest Chinese lake (Song, 2004). All these suggested that the Lake Qiandaohu ecosystem was still an immature ecosystem and in a developing stage.

The connectance index (CI) and system omnivory index (SOI) were also used as a parameter describing the ecosystem maturity and were expected to be higher in mature ecosystems (Odum, 1971). However, CI and SOI in this developing ecosystem were comparatively high (0.222 and 0.087, respectively). So were the other parameters such as throughput cycled (3748.28 tonnes km^{-2} year^{-1}), Fin’s cycling index (FCI, 24.12% total throughput) and Finn’s mean path length (FML, 3.688), which were close to a character of mature ecosystems but differed from usual immature ecosystems. The absolute system ascendancy was 16513.2 flowbits, which was 33.4% of the total capacity with an overhead of 66.6% (Table 8).

Table 7 – Distribution of throughput, biomass and catches through aggregated trophic levels in Lake Qiandaohu ecosystem

Trophic level	Throughput	Biomass	Production	Catch
VII	0.003	0.001	0.0009	0
VI	0.038	0.010	0.011	0.006
V	0.478	0.117	0.126	0.066
IV	6.180	1.189	1.353	0.693
III	128.155	7.786	12.971	5.031
II	5202.688	26.055	207.891	4.391
I	10204.980	21.832	4214.681	0
Sum	15542.520	56.990	4437.034	10.188

Note: biomass and production at TL I only included those of the producers, those of detritus were not included.

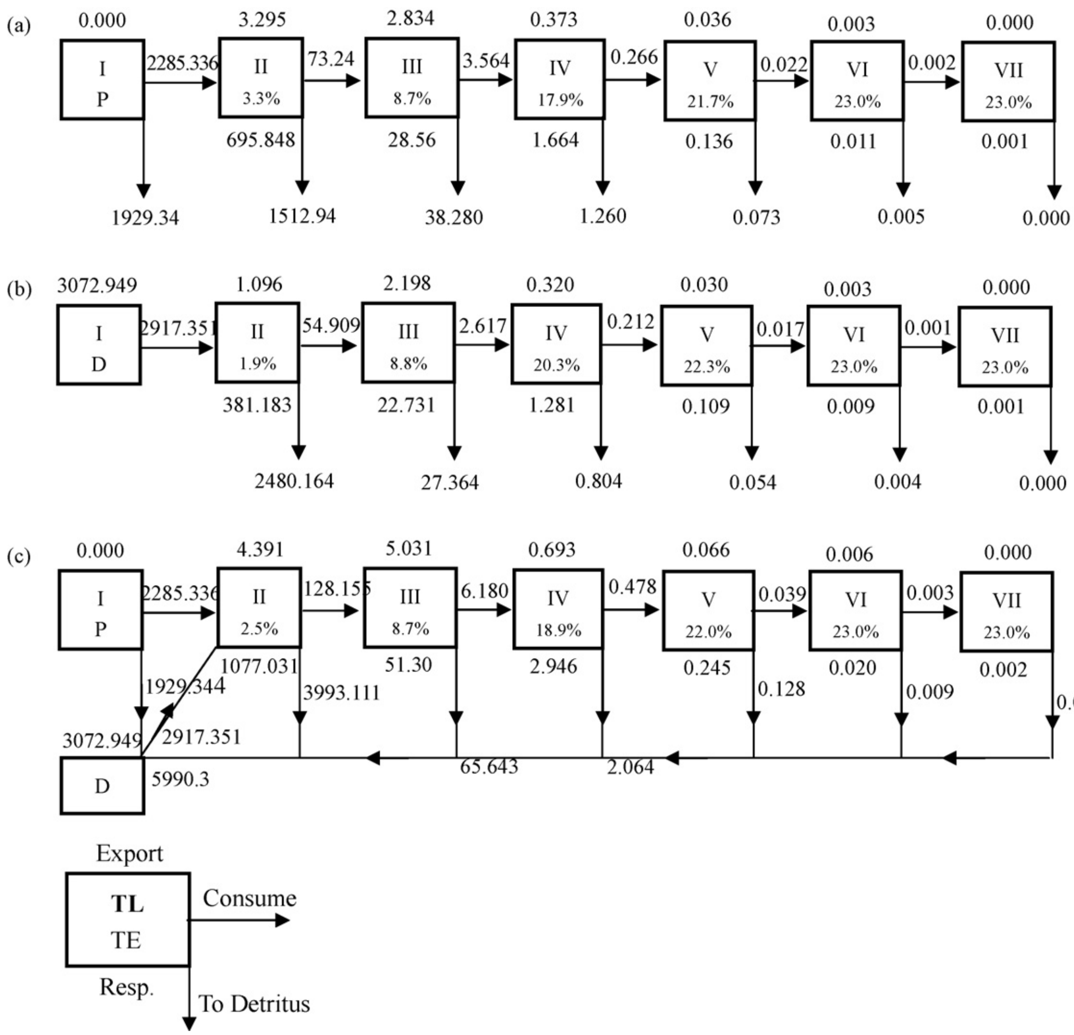

Fig. 3 – The aggregation of the flows (tonnes km^{-2} year^{-1}) into a concatenated chain of transfers through seven trophic levels (after Ulanowicz, 1995). (a) Trophic flows from producers; (b) trophic flows from detritus; (c) trophic flows combined. The flows out of the top of the compartment represent exports and the flows out to the bottom represent respiration. Recycling of non-living material is through compartment D (detritus). The percentages in the boxes represent the annual trophic efficiencies.

4. Discussion

One of the most prominent features of the food web in this reservoir is perhaps its bulging intermediate trophic levels. This is different from the so-called wasp-waist food web structure in many natural or nonstock-enhanced aquatic ecosystems, where the intermediate trophic levels (such as planktivores) were often occupied by a small plankton-feeding pelagic species (Rice, 1995; Bakun, 1996; Vasconcellos et al., 1997). This feature was likely to be associated with the stocking of the two filter-feeding carps, although the biomass of the two carps alone was not large enough to make the biomass at TL II surpass that of TL I. The stocking effectively brought down the biomass level of phytoplankton.

In a natural deep lake ecosystem, it is conceivable that biomass of phytoplanktivores (mainly zooplankton) are determined by both phytoplankton (bottom-up effect) and zooplanktivores (top-down controls). Thus the population of zooplankton is usually not large enough unless the zooplanktivores are effectively controlled or eliminated (the so-called biomanipulation; e.g., Shapiro and Wright, 1984; Drenner and Hambright, 2002) while the phytoplankton density is high. Even in this case, however, biomass of zooplankton should still be less than that of phytoplankton due to the limited ecological transferring efficiency.

In the case of artificial stocking of the two carps, however, the density or biomass of the two carps was not determined either by phytoplankton density (bottom-up forces) or the size of piscivorous fish population (top-down forces), but initially by the stocking density and survival rate of the two carps stocked and then by their growth rates. In Lake Qiandaohu, silver carp and bighead carp were maintained at a high level so that the ever-occurred algal bloom could be prevented. This strategic high biomass of the two carps did effectively decrease the biomass of phytoplankton (Liu et al., 2004; Liu,

Table 8 – Ecosystem properties of Lake Qiandaohu in 2004

Parameter	Value	Unit
Sum of all consumption	5337.542	tonnes km^{-2} year^{-1}
Sum of all exports	3083.137	tonnes km^{-2} year^{-1}
Sum of all respiratory flows	1131.544	tonnes km^{-2} year^{-1}
Sum of all flows into detritus	5990.300	tonnes km^{-2} year^{-1}
Total system throughput	15543.0	tonnes km^{-2} year^{-1}
Sum of all production	4436.000	tonnes km^{-2} year^{-1}
Mean trophic level of the catch	2.65	
Gross efficiency (catch/net primary production)	0.002417	
Net primary production	4214.681	tonnes km^{-2} year^{-1}
Total primary production/total respiration	3.725	
Net system production	3083.137	tonnes km^{-2} year^{-1}
Total primary production/total biomass	73.956	
Total biomass/total throughput	0.004	
Connectance index	0.222	
System omnivory index	0.087	
Throughput cycled (including detritus)	3748.28	tonnes km^{-2} year^{-1}
Finn's cycling index	24.12	% of total throughput
Finn's mean path length	3.688	
Ascendancy (flowbits)	16513.2	
Ascendancy (%)	33.4	
System overhead (flowbits)	32966.7	
System overhead (%)	66.6	

2005). In addition, in order to increase the survival rate of stocked silver and bighead carp fingerlings, piscivorous fish such as *Elopichthys bambusa* and *Erythroculter ilishaeformis* were also drastically eliminated in 1999 and 2000, which resulted in a low biomass of the two fish that might be responsible for the growing of other fish populations such as the detritivorous Xenocypris and Sinibrama (Liu, 2005). The naturally occurred zooplankton population supported by the phytoplankton, the addition of artificially stocked carp biomass, the decreased biomass of phytoplankton resulting from the grazing of the two carps and zooplankton, and the increased detritivorous fish populations which were also at TL II, might all be responsible for a comparatively higher biomass at TL II in this ecosystem.

The feature of food web structure in Lake Qiandaohu includes distinctive trophic flow pattern and the corresponding ecological transfer efficiencies between TLs. Due to the larger biomass at TL II, the transfer efficiency (TE) between TL I and II was high (50.98%), but the TE between II and III dropped to an extremely low level (only 2.5%), which was much lower than those of the many unstocked ecosystems such as 40.4% of L. Ontario (Halfon et al., 1996), 32.0% of the Barents Sea ecosystem (Blanchard et al., 2002) and 15.2% of the Orbetello Lagoon, Italy (Brando et al., 2004). In these natural ecosystems, TEs at TL II were all showing a higher value, if not the highest. The low value of TE at TL II in this system might result from the large exportation at TL II, which became the main part of the reservoir fishery, and the large proportion of flows to detritus and respiration (Fig. 3).

Another characteristic of the food web structure is probably the existence of a loop or short cut for trophic flow at TL II, which mainly resulted from abundant detritivores. The large trophic flow between phytoplankton and planktivores, together with this loop made it possible for the system to transfer both energy and materials (nutrients) efficiently at the low levels of food chains, which might be accountable for the improvement of water quality (clarity) since the stocking of the two carps. In 1998 and 1999, large algal blooms repeatedly occurred in the central and upstream zones of the reservoir. But since 2000 when large numbers of silver carp and bighead carp were stocked in the reservoir (no carps were allowed to capture in the first 3 years of stocking) with no measures of nutrient control, the water quality parameters (such as the TP, chlorophyll *a* and SD, etc.) were all showing improvement (Liu, 2005). In addition, it is worth noticing that Lake Qiandaohu is actually a water reservoir founded in 1959. The short history may be accountable for the developing or immature stage of the ecosystem.

This artificially stocked immature reservoir ecosystem also showed some characteristics of a mature ecosystem. In general, according to Odum (1969), in an immature ecosystem the food web structure is more linear with the grazing food chain being dominant. However, in Lake Qiandaohu trophic flows from the detritivorous food chains were even larger than those of the grazing food chains (Fig. 3). Besides, indices such as CI, SOI, FCI and FML all showed high connectances between the various food chains, a characteristic often seen in a mature ecosystem. With high food web connectance, the ecosystem seemed to be more stable: with the similar nutrient loading, algal bloom had not recurred, and water quality was better than it was in 1998 and 1999 and was restored to a state the ecosystem had before the algal bloom occurred.

This study suggests a shortcut in trophic transfers that would increase greatly the recycling of nutrients. A question that may arise is that if this is just an artifact of having a single detritus compartment. It has been shown that compacting detritus into a single compartment in aquatic systems has a major effect in some ecosystem indexes described in this study (Allesina et al., 2006). Most studies of Ecopath models do not include compartments such as sediment carbon, POC, DOC but rather a single compartment including them all. However, the results derived in this study are likely to be robust to a change in the network topology for the following reasons: (1) the main objective of our study is focusing on the effects of fish composition on the ecosystem property, especially the impacts of the dominance of the two filter-feeding Chinese carps. This study is designed for setting up the stage for our planned studies to examine the effects of the changes in the biomass of the two filter-feeding carps on the ecosystem structure and function. In this regard, we believe that the number of detritus compartments is unlikely to alter the analysis results. (2) This reservoir ecosystem is rich in many detritivorous fish species such as Xenocyprininae and *Sinibrama macrops*, along with the silver carp and bighead carp, which play an important role in the recycling of nutrients in this ecosystem. That is to say, various detritivorous fish species are abundant in this reservoir ecosystem and they do actually compose a recycling shortcut of nutrients.

We only considered the property of the Lake Qiandaohu ecosystem in a given time period, and did not quantify the dynamics of the ecosystem in this study. It would be interesting to simulate what would happen if these two carp species were stocked at much lower (or even at higher) density or even more interesting to run the model using data relative to the "algal bloom" years with low carp densities. This, however, needs to establish a dynamic ecosystem model using approaches such as Ecosim (Christensen et al., 2000), which is beyond the scope of this study, but will be the focus of our future research.

In summary, we found that this silver carp and bighead carp dominated deep-water reservoir ecosystem had high production, a feature of an immature ecosystem, and high stability, a characteristic of a mature ecosystem.

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