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Status and historical changes in the fish community in Erhai Lake*

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Abstract Erhai Lake is the second largest freshwater lake on the Yunnan Plateau, Southwest China. In recent decades, a number of exotic fish species have been introduced into the lake and the fish community has changed considerably. We evaluated the status of the fish community based on surveys with multi-mesh gillnet, trap net, and benthic fyke-net between May 2009 and April 2012. In addition, we evaluated the change in the community using historical data (1952–2010) describing the fish community and fishery harvest. The current fish community is dominated by small-sized fishes, including *Pseudorasbora parva*, *Rhinogobius giurinus*, *Micropercops swinhonis*, *Hemiculter leucisculus*, and *Rhinogobius cliffordpopei*. These accounted for 87.7% of the 22 546 total specimens collected. Omnivorous and carnivorous species dominated the community. A canonical correspondence analysis (CCA) plot revealed that the distribution of fishes in the lake is influenced by aquatic plants, water temperature, pH, and season. The abundance of indigenous species has declined sharply, and a majority of endemic species have been extirpated from the lake (a decrease from seven to two species). In contrast, the number of exotic species has increased since the 1960s to a total of 22 at present. The fishery harvest decreased initially following the 1960s, but has since increased due to the introduction of non-native fish and stocking of native fish. The fishery harvest was significantly correlated with total nitrogen, not total phosphorus, during the past 20 years. Based on our results, we discuss recommendations for the restoration and conservation of the fish resources in Erhai Lake.

Keyword: Erhai Lake; fish community; small fishes; indigenous fish species; exotic fish species

1 INTRODUCTION

Yunnan Plateau is located in southwestern China. The northern part of the plateau connects with western Sichuan and eastern Tibet. The average elevation of the plateau is ~2 000 m (Li et al., 1963), and the region has a distinctive subtropical monsoon climate with an annual mean temperature of 15°C and precipitation of 1 000 mm (Nanjing Institute of Geography and Limnology, 1989). Yunnan Plateau has about 30 lakes, of which Erhai Lake is the second largest (Chu and Chen, 1990). Because of the topographic complexity and favorable weather conditions, this region supports a high degree of endemic species and biological diversity (Zhang, 1999). For example, the lakes in the region support 94 native fish species, most of which are rare and unique, however, about two thirds of these species are critically endangered or extinct due to overfishing, invasion of exotic fish species, and water pollution from 1970s to 1990s (Yang, 1996; Chen et al., 1998;

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Zhou and Huang, 2005). Given these recent trends, the fish communities of the plateau lakes have changed significantly in recent decades.

Erhai Lake contains 17 native fish species, seven of which are endemic, including big-eye carp (*Cyprinus megalophthalmus*), long-pectoral carp (*Cyprinus longipectoralis*), Erhai carp (*Cyprinus barbatus*), Dali carp (*Cyprinus daliensis*), Dali schizothorax (*Schizothorax taliensis*), Dali barb (*Barbodes daliensis*), and oil barb (*Barbodes exigua*) (Chu and Chen, 1990; Xie and Chen, 1999). These endemic fish species are highly valued, both for conservation purposes and for research into speciation and ichthyofauna evolution (Li, 1982). Unfortunately, because of the increased disturbance associated with anthropogenic activities and environmental degradation, all the endemic species are classified as endangered, and some species have already become extinct (Du and Li, 2001).

The fish community of Erhai Lake was first described in the 1900s (e.g., Regan, 1907; Chaudhuri, 1911). Zhang (1945) was the first Chinese researcher to describe the fish community of Erhai Lake, in which he noted the presence of 10 fish species (Chu and Zhou, 1989). After 1949, more systematic research efforts have focused on the lake's fish assemblages (Cheng, 1958; Li et al., 1963; Wu et al., 1964, 1977; Li, 1982; Chu and Zhou, 1989; Du and Li, 2001; Fei et al., 2011). Despite the attentions, few studies have focused on the community level and historical variation, particularly the relationships between the fish community and the environment.

Our specific objectives were to (1) investigate the status of the fish community in Erhai Lake (2009 to 2012) and (2) analyze the changes (1952 to 2012) in the fish community of the lake by reviewing historical data. Our observations are expected to inform recommendations for the restoration and conservation of fishes in Erhai Lake as well as the other lakes in Yunnan Plateau.

2 MATERIAL AND METHOD

2.1 Study area

Erhai Lake (25°36′–25°58′N; 100°06′–100°18′E), a tectonic rift lake with a surface area of 249.0 km^2 and a volume of 25.31×10^8 m^3, is located in Dali City of Yunnan Province. The lake belongs to the climate zone under subtropical plateau monsoon, has a warm climate with an annual average air temperature of 15°C (minimum: 8.5°C, maximum: 20.1°C, in January and July, respectively). The lake is at an altitude of 1 973.66 m, and the maximum and average water depths are 20.7 and 10.17 m, respectively (Wang and Dou, 1998).

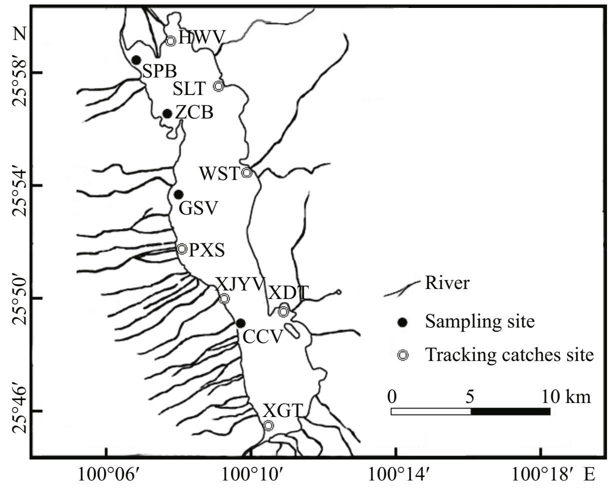

Fig.1 Map of Erhai Lake showing the sampling sites

SPB: Shaping Bay; ZCB: Zhoucheng Bay; GSV: Gusheng Village; PXS: Panxi Shipside; XJYV: Xiajiyi Village; CCV: Caicun Village; XGT: Xiaguan Town; HDT: Haidong Town; WST: Wase Town; SLT: Shuanglang Town; HWV: Hewei Village

2.2 Fish sampling and data collection

We surveyed the fish assemblage in the lake between May 2009 and April 2012. From May 2009 to July 2010, we used trap-nets, benthic fyke-nets and gillnets to collect monthly samples of fish in the area between Shaping Bay to Zhoucheng Bay. Between December 2010 to April 2012, we used multi-mesh gillnets to sample fishes seasonally. In addition, we monitored the local harvest in Shaping Bay, Zhoucheng Bay, Gusheng Village, Panxi Shipside, Xiajiyi Village, Caicun Village, Xiaguan Town, Haidong Town, Wase Town, Shuanglang Town, and Hewei Village (Fig.1).

The mesh size (knot to knot), length, and height of the trap-net was 5 mm, 70 m, and 2 m, respectively. The trap-net was used monthly to capture fish in Shaping Bay. We also used gillnets (L×H: 100×2 m) of four mesh sizes: 7.5, 20, 60, and 100 mm. The benthic fyke-net resembled a cuboid box and was used to catch benthic fish species. The mesh size, length, width, and height of benthic fyke-net were 5 mm, 15 m, 0.62 m and 0.35 m, respectively. The multi-mesh gillnets were made according to the European standard EN 14757 (CEN, 2005), with 12 mesh sizes (range: 5–55 mm), each mesh panel was 2.5 m long and 1.5 m high.

At each location where we set nets, we used portable instruments (YSI-550A and YSI-pH10, Ohio, USA) to measure water temperature, dissolved oxygen, and water pH. We use a modified iron clamp (stretch area: 0.3 m×0.5 m) to catch aquatic plants 4–6 times randomly within each sampling site, the average wet weight of each time is the biomass of macrophytes.

All fishes were identified to species, total length (TL) was measured to the nearest 1 mm. Body weight was measured with 0.01 g and 0.1 g accuracy for small and large fish, respectively. The data describing fishery yield (1952–2010) and water nutrients (mean total nitrogen (TN) and total phosphorus (TP): 1992–2010) were obtained from the Administration of Erhai Lake. The data describing fishery yield included three indices: total fish yield, large and medium-sized commercial fish yield, and ice-fish yield. Records of ice-fish yield began in 1991. The data describing the fish community between 1950s and 1990s were collected from published sources (Chu and Zhou, 1989; Chu and Chen, 1990; Du and Li, 2001).

2.3 Data analysis

Following the descriptions of Anonymous (1976) and Ye et al. (2006), we defined small fish as those that first mature at <2 years and have a maximum size (TL) of <240 mm. All the fishes in Erhai Lake were divided into five trophic guilds: omnivore, carnivore, planktivore, herbivore, and detritivore, based on the primary diet sources (Chu and Zhou, 1989; Chu and Chen, 1990; Zhang, 2005; Ye et al., 2006; our unpublished data) (Table 1). We then calculated the proportion of each trophic guild contributed to the total number of species during different periods (Ye et al., 2006).

We used a rank-abundance plot to evaluate fish abundance in Erhai Lake (Magurran, 2004). All species were ranked based on their abundance (percentage of total catch) and occurrence frequency (percentage of total sampling).

We used a canonical correspondence analysis (CCA) (ter Braak, 1986) to test the relationships between fish abundance (captured using the multi-mesh gillnet) and environmental variables, including macrophyte biomass (Macrophyte), water temperature (*T*), pH, dissolved oxygen concentration (DO), and season. Rare fish species were excluded if it had no effect on the analysis. The statistical significance of the CCA was tested by Monte Carlo tests (999 unrestricted permutations) (ter Braak and Šmilauer, 1998). CCA is a direct gradient analysis technique that can directly relate the pattern of community variation to the pattern of environmental variation, and has good performance in situations where species have nonlinear and unimodal relationships to environmental factors (ter Braak and Prentice, 1988). The environmental and biological data (fish abundance) were $\log_{10}(x+1)$ transformed to reduce the variance prior to analysis (James and McCulloch, 1990).

Linear regressions between nutrients (TN and TP) and biological data (algae biomass and fishery yield) were $\log_{10}$ transformed to improve linearity, and all regressions were judged to be statistically significant at the level of $P=0.05$ (Yurk and Ney, 1989). All statistical analysis were carried out in R (R Development Core Team, 2012; Version 2.14.2).

3 RESULT

3.1 Status of fish community

We collected a total of 31 species belonging to 11 families and 26 genera. Cyprinidae was the dominant family, and was represented by 14 genera and 18 species constituting 58.1% of the total fish assemblage. These were followed by Cobitidae with three species (9.7%) and Gobiieae with two species (6.4%). The remaining families, including Synbranchidae, Eleotridae, Salangidae, Channidae, Poeciliidae, Osmeridae, Belontiidae, and Bagridae comprised 25.8% of the total assemblage (Table 1). Seventeen species were classified as small fish, and accounted for >50% of the total species.

Based on the relative abundance and occurrence frequency of all fish species (Table 2), we constructed a diagram of the rank of fish abundance and occurrence (Fig.2). The 31 species were classified into three groups, i.e., dominant species, frequent species, and rare species.

The dominant species group included topmouth gudgeon (*Pseudorasbora parva*), barcheek goby (*Rhinogobius giurinus*), swinhon's sleeper (*Micropercops swinhonis*), sharpbelly (*Hemiculter leucisculus*), and *Rhinogobius cliffordpopei*. These five species exhibited high relative abundance (all>10%) and accounted for 87.70% of the 22 546 total specimens. The range of occurrence frequency was between 45.50%–87.50% for the 88 catch efforts.

The frequent species group consisted of rosy bitterling (*Rhodeus ocellatus*), crucian carp (*Carassius auratus*), mosquitofish (*Gambusia affinis*), icefish

Table 1 Changes in the fish community in Erhai Lake between the 1950s and 2012

Family	Species	Main food item	Trophic guild	Years					
				1950s	1960s	1970s	1980s	1990s	2012
Cyprinidae	1 *Schizothorax taliensis*‡ †	Zooplankton	Planktivore	+++	++	+	+	-	+
	2 *Schizothorax yunnanensis*‡	Aquatic plants	Herbivore	++	+	-	-	-	+
	3 *Schizothorax lissolabiatus*‡	Periphyton, algae	Detritivore	+	+	-	-	-	-
	4 *Schizothorax griseus*‡	Zoobenthos	Carnivore	+	+	-	-	-	-
	5 *Cyprinus barbatus*‡ †	Zooplankton	Planktivore	+	+	-	-	-	-
	6 *Cyprinus daliensis*‡ †	Fishes, shrimps	Carnivore	++	+	-	-	-	-
	7 *Cyprinus megalophthalmus*‡ †	Zooplankton	Planktivore	++	++	+	+	-	-
	8 *Cyprinus chilia*‡	Zoobenthos, insect larvae, aquatic plants, shrimps	Omnivore	+++	++	+	+	-	+
	9 *Cyprinus longipectoralis*‡ †	Zoobenthos, insect larvae	Carnivore	+	+	+	+	-	+
	10 *Barbodes daliensis*‡ †	Aquatic plants	Herbivore	+++	++	+	+	-	-
	11 *Barbodes exigua*‡ †	Aquatic plants	Herbivore	+	+	-	-	-	-
	12 *Cyprinus carpio*	Zoobenthos, plant detritus, insects	Omnivore	-	+	+	+	+	++
	13 *Carassius auratus*‡	Plant detritus, zooplankton	Omnivore	++	++	++	+++	+	++
	14 *Mylopharyngodon piceus*	Snail, mussel, shrimps	Carnivore	-	+	++	+	+	+
	15 *Ctenopharyngodon idellus*	Aquatic plants	Herbivore	-	++	++	++	+	+
	16 *Hypophthalmichthys molitrix*	Algae, zooplankton	Planktivore	-	++	++	+	+	++
	17 *Aristichthys nobilis*	Algae, zooplankton	Planktivore	-	++	++	+	+	+
	18 *Megalobrama amblycephala*	Aquatic plants	Herbivore	-	-	+	++	+	+
	19 *Pseudorasbora parva*	Zooplankton, insect larvae, algae	Omnivore	-	-	++	+++	+++	+++
	20 *Rhodeus ocellatus*	Plant detritus, algae	Detritivore	-	+	++	+++	+++	++
	21 *Acanthorhodeus chankaensis*	Plant detritus, algae	Detritivore	-	+	++	+++	++	++
	22 *Abbottina rivularis*	Zoobenthos, zooplankton, plant detritus	Omnivore	-	+	+	++	+	+
	23 *Cyprinus carpio haematopterus*	Zoobenthos, aquatic plants	Omnivore	-	-	-	-	-	+
	24 *Hemiculter leucisculus*	Zooplankton, algae	Planktivore	-	-	-	-	-	+++
	25 *Parabramis pekinensis*	Aquatic plants	Herbivore	-	-	-	-	-	+
Cobitidae	26 *Misgurnus anguillicaudatus*‡	Insect larvae, plant detritus, aquatic plants, algae	Omnivore	++	++	++	+	+	+
	27 *Yunnanilus pleurotaenia*‡	Insect larvae, plant detritus, algae	Omnivore	+	+	+	+	+	+
	28 *Homatula anguillioides*‡	Insect larvae, plant detritus, algae	Omnivore	+	+	+	+	+	+
Oryziidae	29 *Ortzias latipes sinensis*‡	Zooplankton, algae	Planktivore	+	+	+	+	+	-
Synbranchidae	30 *Monopterus albus*‡	Insect larvae, small fishes	Carnivore	++	++	+	+	+	+
Eleotridae	31 *Micropercops swinhonis*	Insect larvae, zooplankton, plant detritus	Omnivore	-	+	+	+	+	+++
Gobiieae	32 *Rhinogobius cliffordpopei*	Insect larvae, small shrimps, small fishes	Carnivore	-	+	+++	++	+++	+++
	33 *Rhinogobius giurinus*	Insect larvae, small shrimps, small fishes	Carnivore	-	+	+	+	++	+++
Salangidae	34 *Neosalanx taihuensis*	Zooplankton	Planktivore	-	-	-	++	+++	++
Channidae	35 *Channa argus*	Fishes, shrimps	Carnivore	-	-	-	-	-	+
Poeciliidae	36 *Gambusia affinis*	Mosquito larvae, zooplankton	Carnivore	-	-	-	-	-	++
Osmeridae	37 *Hypomesus olidus*	Zooplankton	Planktivore	-	-	-	-	-	+
Belontiidae	38 *Macropodus chinensis*	Insect larvae, zooplankton	Carnivore	-	-	-	-	-	+
Bagridae	39 *Pelteobagrus fulvidraco*	Small fishes, zoobenthos, shrimps	Carnivore	-	-	-	-	-	+

Note: fish data from 1950s–1990s cited by Chu and Zhou (1989), Chu and Chen (1990), and Du and Li (2001); the classification of trophic guilds were referred to Chu and Zhou (1989), Chu and Chen (1990), Zhang (2005), Ye et al. (2006), and our researches (unpublished data); ‡: Native species; †: Endemic species; +++: dominant species; ++: frequent species: +: rare species; -: none.

Table 2 List of 31 fish species caught in Erhai Lake with common name, code, relative abundance, occurrence frequency, mean TL, and TL range

Family	Scientific name	Common name	Code	Relative abundance (%)	Occurrence frequency (%)	Mean TL±SE (mm)	TL range (mm)
Cyprinidae	*Schizothorax yunnanensis* ‡	Yunnan schizothorax	SYUN	0.009	2.27	286±39.5	246–325
	Schizothorax taliensis * ‡	Dali schizothorax	STA	0.018	2.27	106±9.0	97–115
	Cyprinus carpio	Common carp	CCA	0.727	7.95	164±8.9	60–300
	*Cyprinus longipectoralis**‡	Long-pectoral carp	CLO	0.040	2.27	88±5.1	67–118
	*Cyprinus chilia** ‡	Chilu carp	CCHI	0.191	2.27	91±3.0	58–168
	*Cyprinus carpio haematopterus**	Mirror carp	CHA	0.004	1.14	216	216
	Carassius auratus ‡	Crucian carp	CAU	2.475	45.45	76±2.1	28–217
	Hemiculter leucisculus	Sharpbelly	HLE	14.504	81.82	85±0.7	24–232
	Pseudorasbora parva	Topmouth gudgeon	PPA	25.432	87.50	54±0.4	17–119
	Hypophthalmichthys molitrix	Silver carp	HMO	0.701	14.77	306±6.0	120–498
	Aristichthys nobilis	Bighead carp	ANO	0.319	9.09	267±11.7	109–489
	Rhodeus ocellatus	Rosy bitterling	ROC	3.016	15.91	53±0.5	23–73
	Acanthorhodeus chankaensis	Khanka spiny bitterling	ACH	0.794	11.36	60±1.6	31–111
	*Mylopharyngodon piceus**	Black carp	MPI	0.009	1.14	154±9.9	147–161
	Ctenopharyngodon idellus	Grass carp	CID	0.071	3.41	276±30.4	84–784
	Megalobrama amblycephala	Bluntsnout bream	MAM	0.089	4.55	173±20.8	65–455
	Abbottina rivularis	Chinese false gudgeon	ARI	0.106	7.95	83±3.3	40–112
	*Parabramis pekinensis**	White bream	PPE	0.062	1.14	145±0.5	145–146
Cobitidae	*Misgurnus anguillicaudatus* ‡	Pond loach	MAN	0.412	13.64	68±5.2	26–133
	Yunnanilus pleurotaenia ‡		YPL	0.009	1.14	–	–
	Homatula anguillioides ‡		HAN	0.058	3.41	51±3.0	37–71
Synbranchidae	*Monopterus albus* ‡	Ricefield eel	MAL	0.013	1.14	–	–
Eleotridae	*Micropercops swinhonis*	Swinhon's sleeper	MSW	14.867	53.41	31±0.2	14–62
Gobiieae	*Rhinogobius giurinus*	Barcheek goby	RGI	19.338	50.00	32±0.3	16–65
	Rhinogobius cliffordpopei		RCL	13.559	45.45	32±0.2	21–50
Salangidae	*Neosalanx taihuensis*	Icefish	NTAI	0.847	11.36	61±2.5	46–98
Osmeridae	*Hypomesus olidus*	Pond smelt	HOL	0.031	4.55	89±13.4	50–140
Channidae	*Channa argus**	Snakeheaded fish	CAR	0.319	10.23	42±0.4	22–73
Poeciliidae	*Gambusia affinis*	Mosquitofish	GAF	1.889	26.14	24±0.2	15–40
Belontiidae	*Macropodus chinensis*	Roundtail paradise fish	MCH	0.084	3.41	54±2.7	41–86
Bagridae	*Pelteobagrus fulvidraco*	Yellow catfish	PFU	0.004	1.14	224	224

*: juveniles of large-bodied species; ‡: native species.

(*Neosalanx taihuensis*), Khanka spiny bitterling (*Acanthorhodeus chankaensis*), common carp (*Cyprinus carpio*), and silver carp (*Hypophthalmichthys molitrix*). These species were characterized by moderate relative abundance (0.70% to 3.02%, accounting for 10.45% of all specimens). The range of occurrence frequency varied from 7.95% to 45.45%.

The remaining 19 species were categorized as rare species, including pond loach (*Misgurnus anguillicaudatus*), snakeheaded fish (*Channa argus*), bighead carp (*Aristichthys nobilis*), and chilu carp (*Cyprinus chilia*) and so on. The relative abundance and occurrence frequency of these species was <0.450% and <14.00% respectively. The 19 species only accounted for 1.850% of all 22 546 specimens.

In addition, omnivorous species were the highest proportion in total species number and specimens

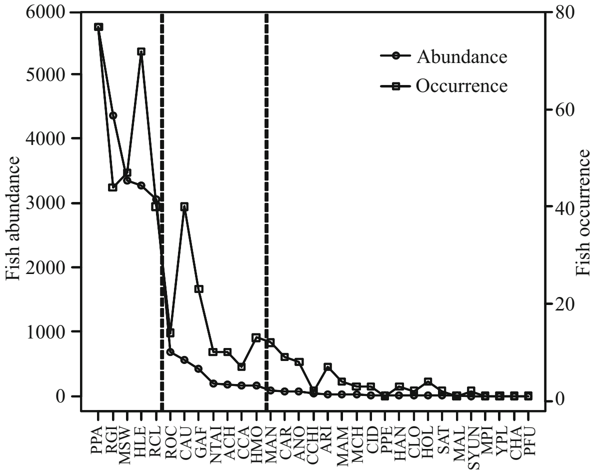

Fig.2 Rank-abundance and occurrence of the 31 fish species caught in Erhai Lake from 2009 to 2012, represented by fish code (see Table 2)

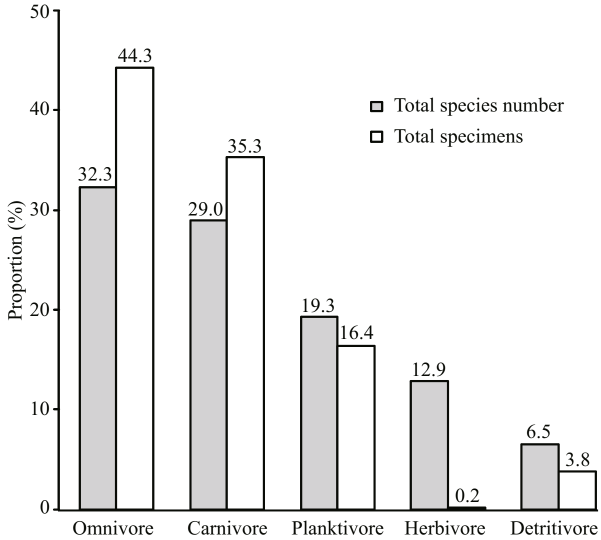

Fig.3 Proportions of the five trophic guilds relative to the total species number and the number of specimens captured in Erhai Lake from 2009 to 2012

number, i. e. 32.3% (10 species) and 44.3%, respectively; followed by the carnivorous species with 29.0% (nine species) and 35.3%. Planktivorous, herbivorous, and detritivorous guilds had 19.3% (six species), 12.9% (four species) and 6.5% (two species), respectively (Fig.3).

3.2 Relationships between current fish community and environmental variables

The CCA plot of the 13 species and four environmental variables (Macrophyte, *T*, pH, DO) was statistically significant (P=0.014) and the two axes accounted for 88.2% (57.7% and 30.5% respectively) of the variability (Fig.4). The primary outcomes were: (1) *A. nobilis*, *Ctenopharyngodon idellus*, *C. longipectoralis*, *C. auratus*, *C. carpio*, and *H. molitrix* preferred dense macrophyte habitat; (2) the distribution of *H. leucisculus*, *N. taihuensis*, *R. giurinus* and *R. ocellatus* was primarily influenced by *T* and pH; (3) The distribution of *P. parva* and *A. chankaensis* was not explained by the four variables.

The CCA of the seasonal distribution of the 13 fish species was also statistically significant (P=0.004) with the first two axes accounting for 80.5% and 13.7% of the variability in the fish-season relationships, respectively (Fig.5). The pattern of fish distribution differed between spring/summer (high water temperature), and autumn/winter (low water temperature). Furthermore, the majority of the 13 species were appeared in spring and summer, particularly the big cyprinid fishes, whereas there were fewer species appeared in autumn and winter. *P. parva* was the most common species throughout the whole year.

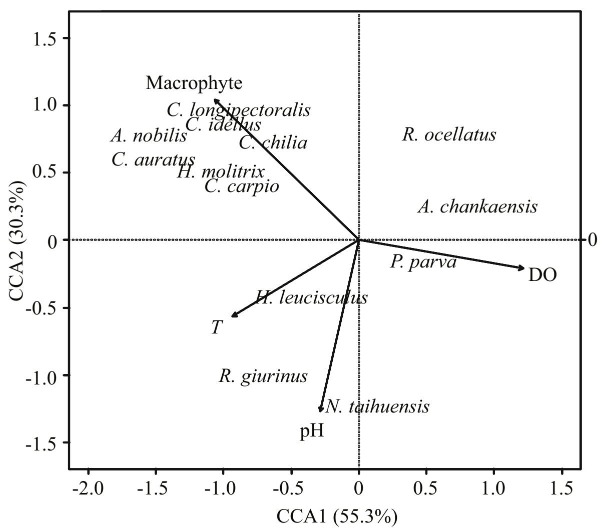

Fig.4 Canonical correspondence analysis (CCA) plot of the abundances of 13 fish species to water temperature (*T*), dissolved oxygen (DO), pH, and macrophytes in Erhai Lake from 2009 to 2012

3.3 Historical changes in fish assemblages and fishery yield

The number of native fish species has decreased since the 1960s, and only nine species remain in the lake at present. The number of endemic species has decreased from seven to two. In contrast, the number of exotic species has increased since the 1960s, to the current level of 22 species (Fig.6). The five trophic guilds have also changed over time. The numerical fluctuations in planktivorous, herbivorous, and

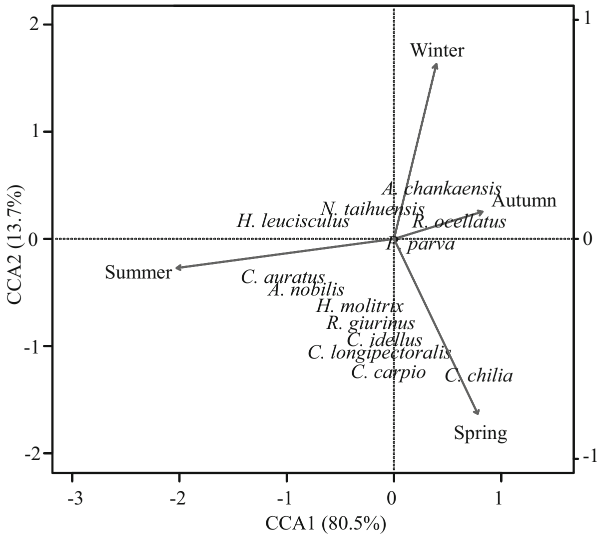

Fig.5 Canonical correspondence analysis (CCA) plot of the abundances of 13 fish species to the four seasons

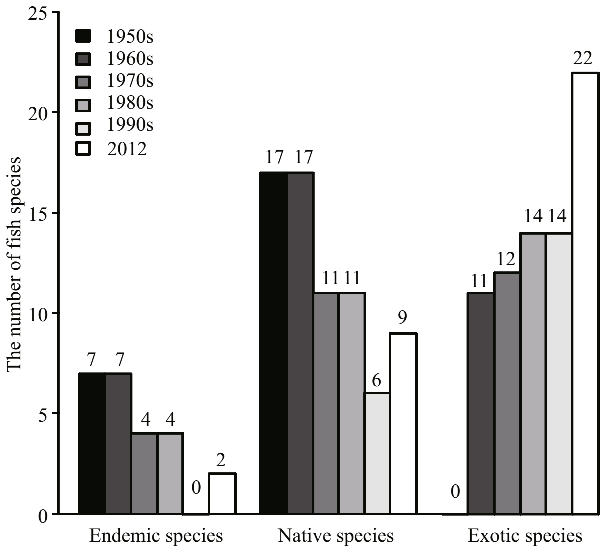

Fig.6 Changes in endemic, native and exotic fish species between the 1950s and 2012 in Erhai Lake

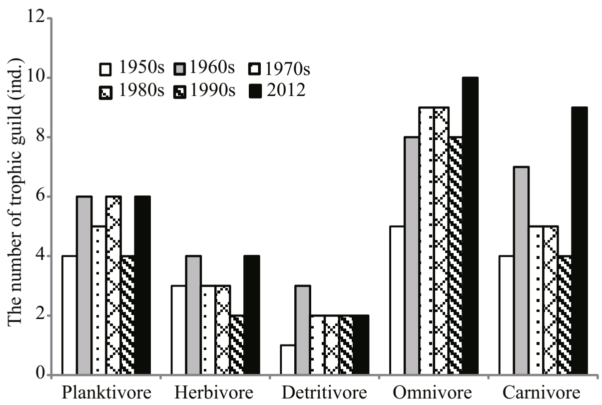

Fig.7 Changes in the abundance of fish in the five trophic guilds between the 1950s and 2012 in Erhai Lake

detritivorous species have been relatively small, however, the number of omnivorous and carnivorous species has doubled since the 1950s (Fig.7).

Prior to the 1960s, there were 17 indigenous fish species in Erhai Lake, of which the large and medium-sized indigenous species such as *S. taliensis*, *C. chilia*, *B. daliensis*, and *Schizothorax yunnanensis* dominated the harvest (Table 1).

Between the 1960s and 1970s, four Chinese carp species (*Mylopharyngodon piceus*, *C. idellus*, *H. molitrix*, *A. nobilis*), *C. carpio* and bluntsnout bream (*Megalobrama amblycephala*) were introduced into the lake (Chu and Zhou, 1989). Concurrently, a number of indigenous species such as *S. yunnanensis*, bare-lip schizothorax (*Schizothorax lissolabiatus*), and grey schizothorax (*Schizothorax griseus*) were extirpated from the lake by the 1970s. In addition, some emerging small fishes (*P. parva*, *R. ocellatus*, and *R. cliffordpopei*) began to boom during this time (Table 1). In general though, there was a downward trend in the annual harvest during this period (Fig.8).

In the 1980s, the number of indigenous fishes declined further. In stark contrast to indigenous species, the size of exotic fishes, particularly the small fishes, were increasing rapidly. Another exotic species, *N. taihuensis*, was also introduced to the lake in the mid-1980s and quickly became a dominant species by the 1990s. The numbers of indigenous species declined to their lowest level during the 1990s (Table 1).

In the 2000s, the large and medium-sized commercial fish yield was in a period of sustainable growth (Fig.8). However, the composition had shifted from indigenous species to exotic species (Table 1). Furthermore, an additional eight exotic fish species (*Cyprinus carpio haematopterus*, *H. leucisculus*, *Parabramis pekinensis*, *C. argus*, *G. affinis*, *Hypomesus olidus*, *Macropodus chinensis*, and *Pelteobagrus fulvidraco*) were first captured in the lake during this period (Table 1).

3.4 Relationship between fish yield and nutrients

Total fish yield and TN concentration increased concurrently in Erhai Lake after 1997 (Fig.9). Between 1999 and 2010, total fish biomass increased by 51% and the TN concentration increased by 70%. The linear regression of fish yield and nutrients in Erhai Lake between 1992 and 2010 revealed a significant correlation between fish yield and TN, except for commercial fish yield (Fig.10; Table 3). In contrast, there was no significant correlation between fish yield and TP concentration (Table 3).

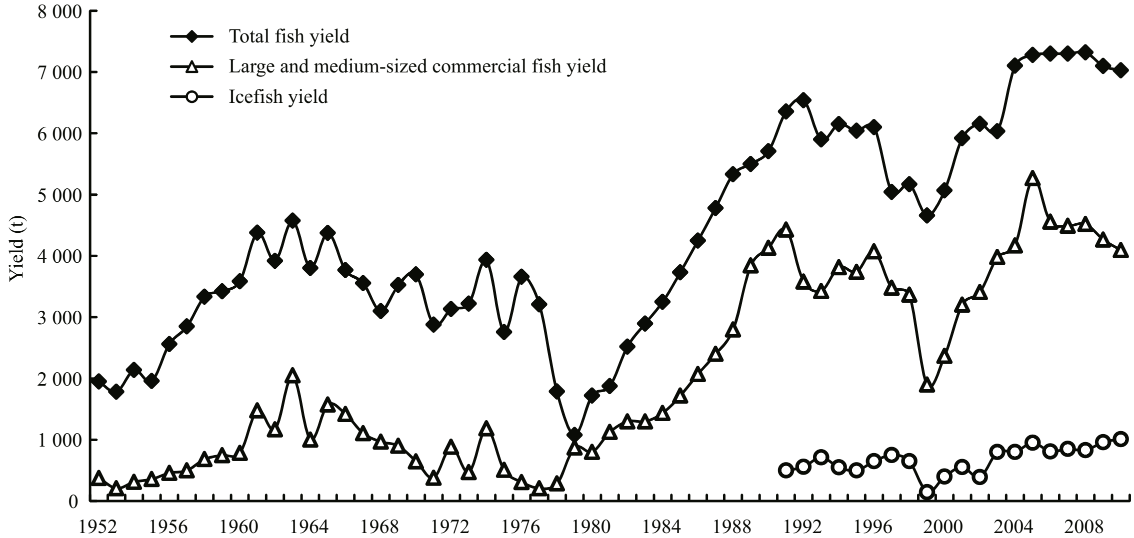

Fig.8 Annual changes in fish harvest (t) between 1952 and 2010 in Erhai Lake

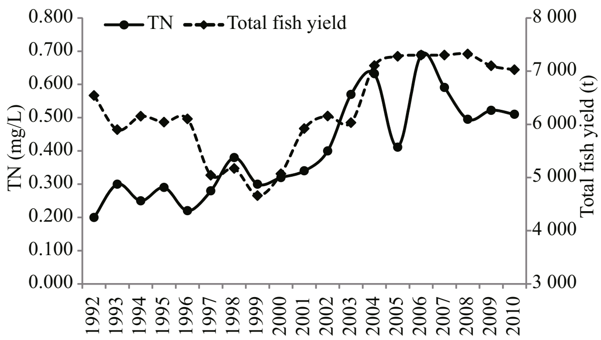

Fig.9 Dynamics of mean TN (total nitrogen concentration, mg/L) and total fish harvest (t) in Erhai Lake, 1992–2010

Table 3 Log_{10} linear regressions between nutrients and biological variables in Erhai Lake, 1992–2010

Nutrients	Category	R^2	P
TN	Total fish yield	0.314	0.01
	Commercial fish yield	0.196	0.06
	Icefish yield	0.218	0.04
TP	Total fish yield	0.004	0.79
	Commercial fish yield	0.002	0.84
	Icefish yield	0.011	0.67

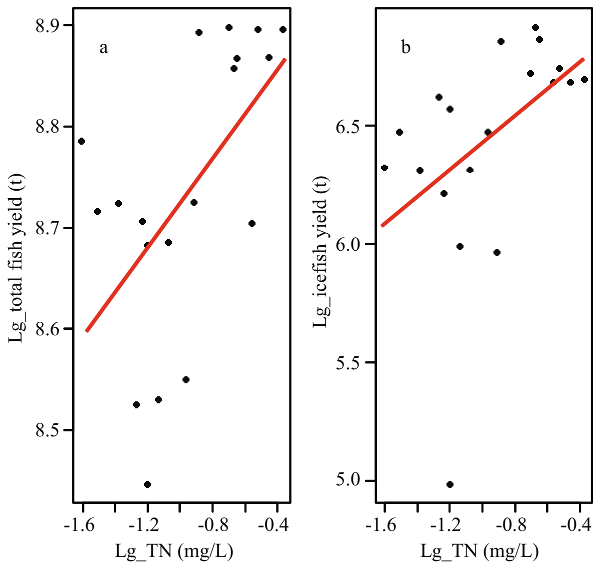

Fig.10 Log_{10} linear regression of fish yields (a. total fish yield; b. icefish yield) on total nitrogen concentration (TN) for Erhai Lake, 1992–2010

a. Log_{10} total fish yield=8.94+0.217×log_{10} TN, R^2=0.314; b: log_{10} icefish yield=6.99+0.568×log_{10}TN, R^2=0.218

4 DISCUSSION

Biological invasions are a global issue because of their effects on biodiversity and degradation or destruction of ecosystems (Vitousek et al., 1996; Sala et al., 2000). We noted the presence of 22 exotic fish species, accounting for 70% of the total number of species in Erhai Lake. Other Yunnan Plateau lakes such as Fuxian Lake, Dianchi Lake and Qilu Lake also contain exotic fish species that dominate the local fish communities (Xiong et al., 2006; Yuan et al., 2010).

4.1 Changes of fish community and fishery yield

The fish community of Erhai Lake currently includes 17 small fish species (54.8% of the total species), among which *P. parva* and *H. leucisculus* are well-known invasive species that exhibit a high degree of plasticity in life history traits and habitat utilization (Patimar, 2008; Gozlan et al., 2010). Sax

(2001) suggested that water bodies with high species richness were at lower risk of invasion than those with low species richness. Historically, Erhai Lake, had low richness (only 17 fish species) and a variety of empty ecological niches available for exotic fishes to colonize. In addition, the population dynamics of larger, native fish species in Erhai Lake have been heavily influenced by overfishing (Du and Li, 2001). Fishing pressure is known to have a significant effect on fish communities in a range of environments (Kangur et al., 2002; Tambets et al., 2003). For example, species that mature at an early age and have a short life span (i.e., small fishes) can better withstand heavy fishing pressure (Sarvala et al., 1999).

Most of the fishes in Erhai Lake were omnivorous and carnivorous species. However, the current fish community lacked big carnivorous species. Indeed, the scale of the largest species (*C. argus*) was still too small to effectively control the small fishes. As a result, small and exotic fishes have become dominant (Fig.2). Interestingly, Winemiller (1990) and Starling et al. (2002) have suggested that fish communities are dominated by omnivorous species in warm climates, or by omnivorous planktivorous fishes in (sub-) tropical lakes owing to their plastic foraging ability at various trophic levels.

Those introduced species can alter the biodiversity of habitat by predation, competition, or changing the habitat structure (McDowall, 2006; Yonekura et al., 2007). As a result, a number of indigenous species, particularly highly endemic species, have become endangered or extinct (Harrison and Stiassny, 1999). Non-native fishes have been introduced into Erhai Lake since the 1960s with the intent of improving fishery production. Unfortunately, a number of species were also unintentionally introduced with the target species, including *P. parva*, *R. giurinus*, and *H. leucisculus*.

Both the endemic species *S. taliensis*, *C. barbatus*, and *C. megalophthalmus* and introduced species such as silver carp, bighead carp, sharpbelly, and icefish prey primarily on zooplankton such as cladocera and copepods (Chu and Chen, 1990; Zhang, 2005). As the abundance of the introduced species has increased it has likely led to increased competition (Liu et al., 2007). For example, the introduction of silver carp and bighead carp into Xingyun Lake (another lake on the Yunnan Plateau) resulted in a steep decline in the harvest of native species (*Cyprinus pellegrini*) between the 1950s and 1980s (Xie and Chen, 2001). Silver carp and bighead carp also caused a decline in the species richness of native filter-feeding species (*Polyodon spathula*) in the Mississippi River (Chick and Pegg, 2001). Moreover, topmouth gudgeon and gobies (*R. giurinus* and *R. cliffordpopei*) threaten indigenous fishes by competing for food and spawning ground and preying on eggs and larvae (Chu and Chen, 1990; Du and Li, 2001). These factors led to the decline or extinction of the indigenous species, and also significantly reduced the fishery yield in the 1960s through 1970s (Figs.6, 8). However, the increasing abundance of commercially stocked species, including four Chinese carps, bluntsnout bream, and common carp, since the 1980s, has resulted in increased fishery yield during the past 30 years (Fig.8).

4.2 The impacts of TN and TP on fishery yield changes

Phosphorus is thought to play a major role on influencing primary production (algae and macrophytes) and, as a result, fish communities (Yurk and Ney, 1989). Oglesby (1977) found that phytoplankton biomass explained 84% (R^2=0.84) of the variation in total fish yield among 46 lakes on four continents. Our research, however, suggested that TN is the primary factor limiting fish yields and primary production (algae biomass) in Erhai Lake (Table 3). It is possible that TP failed to explain variation in fish yield because it is not a limiting nutrient in Erhai Lake (Yurk and Ney, 1989). The commercial fish harvest consisted primarily of planktivores (silver carp and bighead carp) and omnivores (common carp and crucian carp). Hence, many factors may affect the yield, aside from TN and TP. These include, mean depth, lake surface area, aquatic plants, and error in estimation of fish catch (Egertson and Downing, 2004). Moreover, fishery management actions such as fish stocking may have buffered fish yields from the effects of changing TP concentrations (Carline et al., 1984). Although our regression analysis does not reveal whether the correlation is causative, our results do suggest that TN concentrations maybe a good predictor of fishery productivity in Erhai Lake (Yurk and Ney, 1989).

4.3 Spatial and seasonal variations of fish community

Aquatic plants have important effects on structuring fish communities. We noted that the majority of fish species in Erhai Lake preferred habitats with abundant vegetation (Fig.4). This is likely because aquatic plants provide increased foraging opportunities, reduce the predation risk and provide spawning sites (Persson and Eklőv, 1995; Xie et al., 2001; Ye et al., 2006). As an example, the cyprinid fishes (*C. carpio*, *C. chilia*, *C. longipectoralis*) in Erhai Lake lay viscous eggs that are attached to aquatic plants (Chu and Chen, 1990).

The distribution of the fish community varied among seasons. Most species were readily captured in the spring and summer, likely because of the timing of their reproductive cycle, seasonal activity, and availability of food resources as well as the occurrence of overwintering mortality (Yin, 1995; Guan et al., 2005; Zhang, 2005). *P. parva* exhibits highly plastic habitat preferences, and is highly tolerant of environmental changes (Zhang, 2005; Gozlan et al., 2010). Thus, *P. parva* is present year round in Erhai Lake.

4.4 Management implications

In general, the fish community of Erhai Lake has changed significantly during the past seven decades. The abundance of indigenous species has declined sharply, and a majority of endemic species have already been extirpated from the lake. Concurrently, an increasing number of exotic fish species have been introduced into Erhai Lake, of which, some of the small species have become dominant. Some of the native fish species such as *S. taliensis*, *C. chilia*, and *C. longipectoralis*, have begun to recover in recent years because of stocking programs. To encourage further restoration and conservation of the native fish community, managers should consider the followings: (1) habitat restoration, particularly in spawning grounds along the lakeshore and river estuary, areas that should also be closed to access; (2) control the scale of exotic fishes, and limit new foreign species from entering the Lake. For example, snakeheaded fish may could be used to control some of the small fish species such as sharpbelly and gobies; (3) regulate loading nutrients, limit nutrients within an appropriate concentration range that balances the needs for clean water and fisheries; (4) maintain the stocking programs for the restoration of indigenous species and improve enforcement to avoid overfishing, particularly in spring and summer. In addition, a more thorough understanding of the changes in fish community structure and latent cascading effects can only be gained by research on the life history alteration of exotic fishes, trophic dynamics in the food web, fish biogeography distribution, and the effects of warming climate on lacustrine ecosystems.

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