# Abundance and spatial variability of invasive fishes related to environmental factors in a eutrophic Yunnan Plateau lake, Lake Dianchi, southwestern China

**Article** *in* Environmental Biology of Fishes · January 2015

DOI: 10.1007/s10641-014-0252-9



**6 authors**, including:

Shaowen Ye
Institute of Hydrobiology - Chinese Academy of Sciences


Mingli Lin
Institute of Deep-sea Science and Engineering, Chinese Academy of Science


Lin Li
Chinese Academy of Sciences

Environ Biol Fish
DOI 10.1007/s10641-014-0252-9

# Abundance and spatial variability of invasive fishes related to environmental factors in a eutrophic Yunnan Plateau lake, Lake Dianchi, southwestern China

**Shaowen Ye · Mingli Lin · Lin Li · Jiashou Liu · Lirong Song · Zhongjie Li**

Received: 24 July 2013 / Accepted: 9 March 2014


**Abstract** Lake Dianchi is the largest freshwater lake on the Yunnan Plateau and the sixth largest one in China. In recent decades, a number of non-native fish species have been introduced into the lake intentionally or accidentally while human-accelerated eutrophication has been occurring. In this study, we provided a whole-lake assessment of species composition and abundance of the accidentally-introduced fishes, and described the spatial variability of invasive small fish community in relation to eight physicochemical environmental factors. Fish were sampled quantitatively at 30 sites throughout the lake with multiple mesh-sized gillnets in the autumn of 2008. A total of 2,050 individuals from seven non-native small fish species were captured. Thin sharpbelly *Toxabramis swinhonis* and piper halfbeak *Hyporhamphus intermedius* were recognized as dominant species, followed by barcheek goby *Rhinogobius giurinus*, topmouth gudgeon *Pseudorasbora parva* and redfin culter *Culterichthys erythropterus*, according to their abundance and occurrence. Principal component analysis (PCA) suggested that the fish community structure in the northern part was distinct from those in the middle and southern parts of the lake, corresponding to the increase of lake eutrophic level from south to north. Redundancy analysis (RDA) showed that redfin culter, piper halfbeak and thin sharpbelly were positively related to nutrient variables (total phosphorus, total nitrogen), while topmouth gudgeon and barcheek goby were associated with relatively higher secchi depth and lower nutrition level. Water depth seemed to have moderately negative influence on spatial distribution of all the fish species. Regression tree analysis was applied to visualize decision rules for the prediction of fish abundances (CPUE, ind/fishing pass/h) from key environment variables, and explained 51.5–69.0 % of the total variance of response values. The details of these findings are beneficial to understanding the establishment of invasive fish in degraded environment, and to developing suitable conservation strategies for the restoration and management of fish resources in Lake Dianchi as well as the other lakes of Yunnan Plateau.

**Keywords** Accidentally-introduced fishes · Invasive fishes · Fish community structure · Environmental variables · Multivariate statistics · Plateau lake

S. Ye · M. Lin · L. Li · J. Liu (✉) · L. Song · Z. Li
State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology,
Chinese Academy of Sciences,
Wuhan 430072, China
e-mail: jsliu@ihb.ac.cn

M. Lin
Sanya Institute of Deep-sea Science and Engineering,
Chinese Academy of Sciences,
Sanya 572000, China

## Introduction

Invasive species are increasingly recognized as one of the main threats to biodiversity and one of the main drivers of global change (García-Berthou 2007). There is an impressive record of inland fish invasions that were caused by intentional or accident introduction and have

Published online: 20 March 2014

contributed to the loss of native species throughout the world (Kolar and Lodge 2002; Balirwa et al. 2003). Successful invasion by introduced organisms is widely regarded as being more likely in human-disturbed environments (Case 1996; Moyle and Light 1996; Lozon and MacIsaac 1997). Introduced freshwater fishes, in particular, have commonly been documented to thrive in degraded aquatic environments in many areas of the world (e.g. Leidy and Fiedler 1985; Gehrke et al. 1995; Brown 2000; Meador et al. 2003). Generally, key attributes of invasive fish successfully thriving in degraded environments include broad physiological tolerances, generalist resource requirements, and a variety of life history traits enabling them to persist where many native species could not (Kolar and Lodge 2002; García-Berthou 2007; Gozlan et al. 2010).

As a global environmental problem, human-accelerated eutrophication is characterized by high nitrogen and phosphorus contents and low transparency in water bodies. Water quality in many lakes worldwide has degraded considerably in recent decades due to increasing eutrophication by point- and nonpoint-source pollution in their watersheds (Søndergaard et al. 2007). The eutrophication of lakes induces changes in abiotic and biotic environmental factors, which are reflected in the structure of fish community. As an example, in temperate lakes of Europe, the characteristic shift of fish communities along a trophic gradient is from the dominance of salmoniformes in oligotrophic environments to the dominance of percids in moderately productive environments, and to the dominance of cyprinids in highly productive environments (Persson et al. 1991; Olin et al. 2002). The success of invasive cyprinids in eutrophic environments is determined by their omnivorous diets and ability to adapt to turbid waters (Persson et al. 1991). Moreover, the eutrophication process is responsible for marked changes in plankton and zoobenthic resources, on which fish communities depend (Olin et al. 2002). Examining how eutrophic environment influences fish abundance and/or distribution patterns and identifying relevant environmental thresholds can therefore be beneficial to understanding the establishment of invasive fish under degraded conditions.

The Yunnan Plateau, located in southwestern China and with about 30 natural lakes, ranges from the highest elevation of 6,740 masl in the northwest to the lowest of 76 masl in the southeast, and its average elevation is about 2,000 m above sea level. It has a distinctive monsoon climate with an annual mean temperature of about 15 °C and an annual mean precipitation of about 1,000 mm (Wang and Dou 1998). This unique combination of topographic complexity and favorable moisture conditions in the region supports an enormous richness of biological diversity and high degree of endemism (Zhang 1999). The Yunnan Plateau lakes are a Global 200 Priority Ecoregion of the Palearctic Lake Ecosystems (Olson and Dinerstein 1998). Ninety-four native fish species have been recorded in the lakes, most of which are endemic species with narrow geographic distribution (Yang 1996). Unfortunately, about two thirds of these species have been identified in critically endangered or extinct status due to overfishing, invasion of non-native fish species, and water pollution in recent decades (Yang 1996; Chen et al. 1998).

Lake Dianchi, with an altitude of 1,886 masl, is the largest lake in the Yunnan Plateau. Since the early 1960s, Chinese family carps (i.e. silver carp *Hypophthalmictuthys molitrix*, bighead carp *Aristichthys mobilis*, grass carp *Ctenopharyngodon idellus*, and black carp *Mylopharyngodon piceus*), Taihu icefish *Salangichthys tangkahkeii* and other non-native commercial fishes have been introduced from the Yangtze River Basin into the lake and other Yunnan Plateau lakes to enhance fishery production (Yang 1996; Xie and Chen 2001). In addition to these intentionally stocked fishes, several non-native small fish species (e.g. topmouth gudgeon *Pseudorasbora parva* and barcheek goby *Rhinogobius giurinus*) were introduced accidentally and have established reproductive populations in the lakes (Yang 1996). Meanwhile, with rapid increase in local population and massive untreated municipal and industrial sewage flows into Lake Dianchi, water pollution is accelerating and eutrophication level has increased considerably in the lake over the past decades (Fang et al. 2004; Gao et al. 2005); and now it is deemed to be hyper-eutrophic in some local areas. Theoretically, this rapid and substantial anthropogenic disturbance may create a mismatch between traits of native fishes and the current environment in the lake, while favor some of the introduced fishes originating from the Yangtze River Basin that usually adapt better to eutrophic environments (Ye 2007; Cheng et al. 2010).

To our knowledge, the existing studies concerning native and introduced fishes in Lake Dianchi and the other lakes of Yunnan Plateau are centered mainly on taxonomy, fauna, reproduction, feeding habit, toxicology, age and growth (e.g. Cheng 1958; Chu and Chen

1989; Liu and Zhu 1994; Li 2006; Wu et al. 2010; Yuan et al. 2010; Fei and Shao 2012; Guo et al. 2013). Few studies have been focused on the community level. In particular, little quantitative information is available on the distribution of invasive fishes in the lakes (Guo et al. 2012; Tang et al. 2013), so their relationships with environmental factors are poorly known. Thus, detailed examinations on species composition, abundance and distribution of fish community in the lakes, especially quantitative thresholds for species abundance and habitat use, are needed to assess such fish-environment relationships, which have the potential to inform ecological prediction for invasive fishes in the human-disturbed lake environments.

Here we use field sampling data and literature data sources to assess the current status, spatial variability and history of changes in the introduced fishes in Lake Dianchi. Specific objectives are to: (1) provide a whole-lake estimate for species composition, abundance, and occurrence of accidentally-introduced fishes, which are of low or no commercial values and receive little rigorous scientific examination in the previous studies, (2) describe spatial variations of invasive small fish community throughout the lake and assess the relative importance of physicochemical environmental factors in influencing their distribution, and (3) identify quantitative environmental thresholds for differentiating fish abundance and distribution patterns. Our observations are expected to inform recommendations for the restoration and management of fish resources in Lake Dianchi as well as the other lakes of Yunnan Plateau.

## Materials and methods

### Study area

Lake Dianchi (24º40′–25º02′ N, 102º36′–102º47′ E, Fig. 1) is a tectonic lake located in the central part of the Yunnan Plateau. The lake, with a water surface of 306 km$^2$, mean depth of 4.4 m, watershed of 2,920 km$^2$, surface length (N–S) of 41.2 km, and width (W–E) of 7.2 km on average, is the sixth largest freshwater lake in China (Wang and Dou 1998). Kunming City, the capital of Yunnan Province, is located at its northern end and is upstream within its catchment region. Around the lake are mainly mountains, terraces and dammed river valleys, and the climate is of subtropical, humid, monsoon type. The annual precipitation varies from 795 to 1,010 mm, and the water temperature ranges from 9.8 to 24.5 °C with an annual average of about 16.0 °C.

The fish community of Lake Dianchi is characterized by the decline of high-degree endemics and increases in the invasion by introduced fishes in recent decades. A total of 26 native and 11 endemic fish species were recorded from the lake in the 1950s and 1960s (Appendix 1), and the endemic fishes accounted for 50–70 % of the fishery catches (Yang 1996). However, after the 1970s, with increasing fishing efforts, accelerating eutrophication process, disappearing macrophyte covers and diminishing spawning habitats, the number of native fish species deceased continuously and the majority (45.5–72.7 %) of the endemic species have not been found in the lake in recent years (Appendix 1). At present, apart from crucian carp *Carassius auratus auratus* that occurred frequently in fishermen's catches but contributed to less than 5 % of the total harvest, the other five remaining native species can only been seen occasionally (Appendix 1). On the other hand, a total of 21 non-native fish species have been recorded in Lake Dianchi since the 1960s, among which 11 were introduced intentionally for fisheries purpose and 10 accidentally through aquaculture activities (Appendix 2). More than half of these fishes were considered to be successful in invading the lake, either by continuous stocking or establishing naturalized and reproductive populations (see Appendix 2 and Discussion).

### Fish sampling and environmental measurement

According to the previous studies conducted on spatial patterns of water pollution in Lake Dianchi, the lake can be roughly divided into three main parts (northern, middle, and southern) at a large spatial scale (Fang et al. 2004; Gao et al. 2005). Sampling sites for this study were therefore established in the three lake parts to represent the main body of the lake and to identify fish spatial distributions in the whole lake. A total of 30 sites were oriented by GPS navigation in the lake, i.e. S1–10 in the northern part, S11–20 in the middle part, and S21–30 in the southern part (Fig. 1).

Fish were sampled at the 30 sites in the autumn of 2008, during the short legal fishing season from the middle of August to the end of September, with multiple mesh–sized gillnets (19.5, 6.25, 10, 35, 8, 12.5, 24, 15.5, 5, and 30 mm knot to knot); the length and depth of each section were 3 m and 2 m, respectively. Two types of

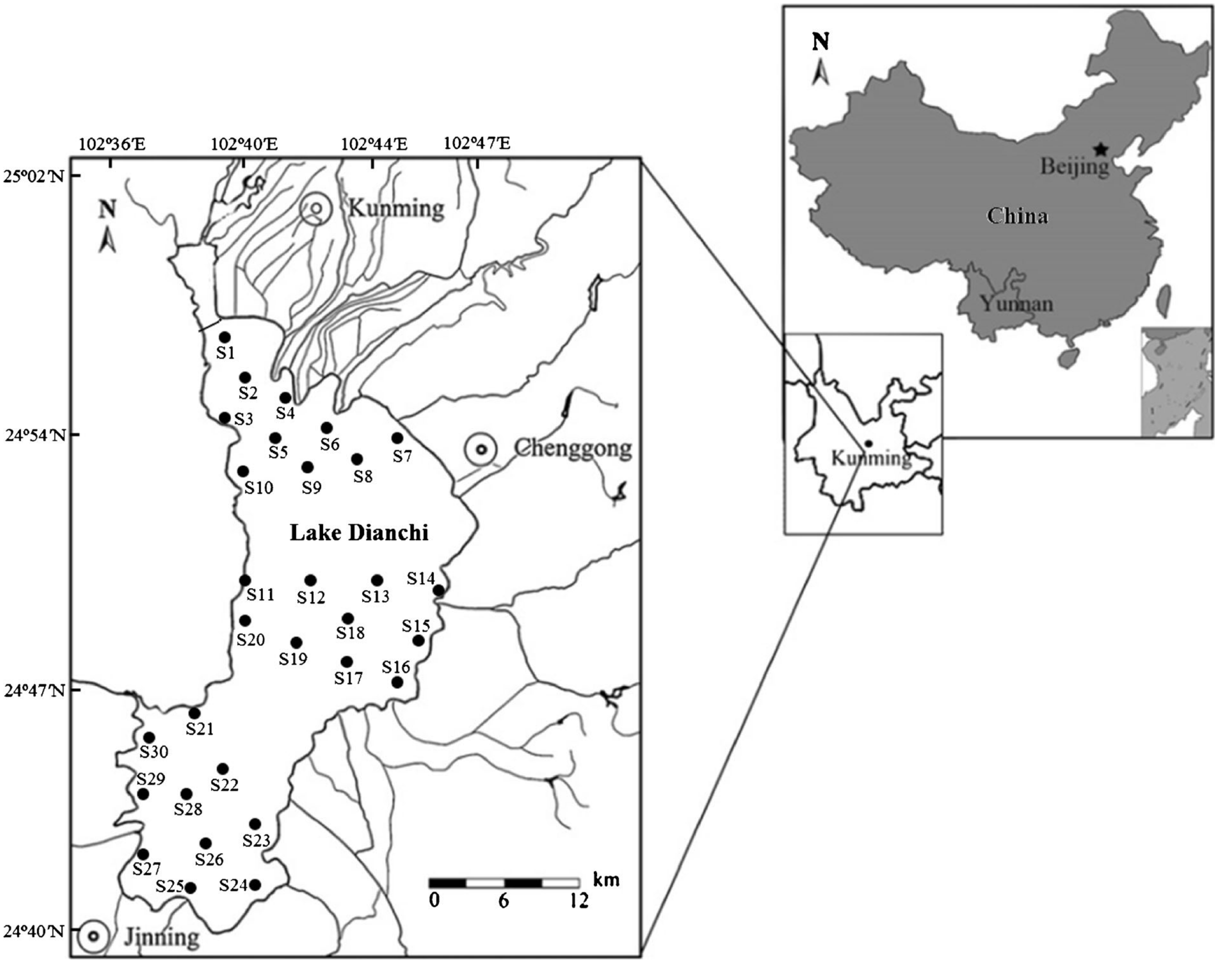


**Fig. 1** Geographic location and map of Lake Dianchi, showing the distribution of 30 fish sampling sites (S1~30) in the lake

multiple mesh–sized gillnets were used together at each sampling site: one benthic net was set close to the lake bottom and one floating net near the lake surface. The nets were set before dusk and retrieved after dawn in the following day with fishing hours being recorded. Fish captured were identified to species level, counted, individually weighed to the nearest 0.1 g and measured (total length, TL) to the nearest mm. The abundance of each species at each sampling site was expressed in terms of catch per unit effort (CPUE; number of fish per fishing pass per hour, unit: ind/fishing pass/h).

A measure of the relative importance of species i in the gillnet catches was calculated using the index of relative importance (Ye 2007): $IRI_i=(\%N_i+\%W_i)\times\%F_i$, where $\%N_i$ and $\%W_i$ are percentage number and percentage weight of species i in the total catches respectively, and $\%F_i$ is occurrence frequency of species i among the 30 sampling sites.

Environmental characteristics were determined along with fish sampling at each site. Physical environmental factors including: water depth (WD), secchi depth (SD) and pH were measured in situ. The average water temperature during the study was 22.1 °C. Water samples from slightly below the surface were collected and transported within 24 h to the laboratory for the measurement of chemical parameters. Total phosphorus (TP), total nitrogen (TN), ammonia nitrogen ($NH_4$-N), and chemical oxygen demand (COD) were analyzed with the national standard methods (China EPA 2004). Chlorophyll a (Chla) was extracted with 90 % acetone and then measured spectrophotometrically (China EPA 2004).

## Data analysis

The differences of the environmental factors between the three parts of the lake were examined by Kruskal-

Wallis and multiple comparison tests. The Kruskal-Wallis test is a nonparametric (distribution free) test used to compare three or more groups of sample data, and the following multiple comparison tests are pairwise comparison with a Mann–Whitney test with Bonferroni correction (Legendre and Legendre 2012).

Spatial variations of fish composition were analyzed and visualized using principal component analysis (PCA) on the fish abundance data across the 30 sampling sites. Geometrically, PCA is a rigid rotation of the original data matrix, and can be defined as a projection of samples onto a new set of axes. The maximum variance is projected or "extracted" along the first axis, the maximum variation uncorrelated with the first axis is projected on the second axis, the maximum variation uncorrelated with the first and second axis is projected on the third axis, and so on (Legendre and Legendre 2012).

The relationships between fish species and the measured environmental factors were analyzed by redundancy analysis (RDA). RDA is a constrained linear ordination technique that simultaneously relates two multivariate data sets and is commonly used to quantify the relationship between species and environmental factors (Legendre and Legendre 2012). The values of fish abundance and environmental factors at each sampling site were log $(x+1)$ transformed to stabilize variances. A Monte Carlo permutation test (999 permutations) was performed to test the significance of the relationships between environmental factors and species composition among the sampling sites (i.e. the significance of the sum of all eigenvalues).

Regression tree analysis with binary recursive partitioning (Breiman et al. 1984) was used to visualize decision rules for predicting fish abundances (CPUE, ind/fishing pass/h) from the continuous environmental factors and identifying quantitative thresholds. During tree building, the initial node on a tree is called the root. From the root, data are broken into left and right branches with the splitting rules defined by the predictor variable values. Splitting continues down to the terminal nodes where response values are all the same within a node or data are too sparse for additional splitting. At the terminal node (leaf), the predicted response is given that is the average of the response values with the number of observations in that node.

All the statistical analyses were done under the version 2.13.1 of R (R Development Core Team 2011) using the "pgirmess" package (Giraudoux 2010) for the Kruskal-Wallis test, the "ade4" package (Dray et al. 2007) for the PCA and RA, and the "rpart" package (Therneau et al. 2010) for the regression tree models.

## Results

A total of 2,050 fish individuals from seven species and five families were caught by the gillnets throughout the lake (Table 1). All the species are non-native with two species introduced intentionally and five accidentally (Table 1). They are classified as small-sized fishes because of short life spans (less than 2 or 3 years) and low values of maximum, median and mean total lengths (Table 1, Fig. 2). With regard to trophic guild, redfin culter *Culterichthys erythropterus* and barcheek goby *R. giurinus* belong to small carnivores that prey mainly on shrimps and zoobenthos, and the other five species are omnivores consuming zooplankton, phytoplankton, detritus, and so on.

As shown in Table 1, thin sharpbelly *Toxabramis swinhonis* and piper halfbeak *Hyporhamphus intermedius* were identified as the most dominant fish species, according to their high relative abundances (>25 % of the total individuals) and high occurrence frequencies (≥90 % of the 30 sampling sites). Barcheek goby, topmouth gudgeon and redfin culter were also abundant species, displaying moderate relative abundances (6.8–13.9 %) and occurrence frequencies (60–76.7 %). Pond smelt *Hypomesus olidus* and Taihu icefish *S. tangkahkeii* were less important in the catches due to their low abundances and occurrences. The same order of fish dominance was obtained from the indexes of relative importance (IRI=0.7–65.4 %, Table 1), which include weight information for each species.

Spatial variations of the eight environmental factors during this study were presented in Table 2. The depth of the 30 sampling sites ranged between 2.0 m and 7.5 m, with the deepest site occurring in the southern lake. The northern sites on average were shallower than those in the other two parts of the lake. The secchi depth varied greatly from 19 cm to 125 cm, and the water appeared to be clearer in the southern part of the lake. In contrast, the pH varied with a range of 7.76–8.83, displaying similar alkalinity throughout the lake. In accordance with the secchi depth variation, the chlorophyll a concentration (9.6–183.9 μg/l) and chemical oxygen demand (4.80–19.01 mg/l) was also lower in the southern lake part than in the other two parts. For the

**Table 1** List of the seven non-native fish species caught from the 30 sampling sites in Lake Dianchi, with their common name, abundance, occurrence, index of relative importance (IRI), total length (TL) range, trophic guild, and species code used in the analyses

| Family | Species | Common name | Code | Abundance | Relative abundance (%) | Occurrence | Occurrence frequency (%) | IRI (%) | TL range (mm) | Trophic guild |
|---|---|---|---|---|---|---|---|---|---|---|
| Cyprinidae | [a]*Culterichthys erythropterus* | Redfin culter | CER | 139 | 6.8 | 23 | 76.7 | 12.7 | 41–154 | Carnivorous |
| | [a]*Pseudorasbora parva* | Topmouth gudgeon | PPA | 278 | 13.6 | 18 | 60.0 | 13.6 | 19–96 | Omnivorous |
| | [a]*Toxabramis swinhonis* | Thin sharpbelly | TSW | 765 | 37.3 | 28 | 93.3 | 65.4 | 43–125 | Omnivorous |
| Gobiidae | [a]*Rhinogobius giurinus* | Barcheek goby | RGI | 285 | 13.9 | 22 | 73.3 | 15.9 | 23–65 | Carnivorous |
| Hemiramphidae | [a]*Hyporhamphus intermedius* | Piper halfbeak | HIN | 515 | 25.1 | 27 | 90.0 | 55.0 | 86–173 | Omnivorous |
| Osmeridae | [b]*Hypomesus olidus* | Pond smelt | HOL | 33 | 1.6 | 13 | 43.3 | 2.6 | 87–112 | Omnivorous |
| Salangidae | [b]*Salangichthys tangkahkeii* | Taihu icefish | STA | 35 | 1.7 | 11 | 36.7 | 0.7 | 43–68 | Omnivorous |

[a] species introduced accidentally

[b] species introduced intentionally for fishery purpose

nutrient measurements, total phosphorus (0.05–0.89 mg/l), total nitrogen (1.25–7.13 mg/l) and ammonia nitrogen (0.06–2.72 mg/l) were all significantly higher in the northern lake, indicating highly eutrophic there.

The PCA on the abundances of the seven invasive fish species across the 30 sites (10 sites in each lake part) visualized spatial characteristics of the fish community. The first two principal components accounted for 42.3 % and 18.2 % of the total fish variation respectively (Fig. 3a). Distribution of the sampling sites regarding the three parts of the lake on the F1×F2 plane (Fig. 3b) indicated that fish community structure in the northern lake (with the highest eutrophication level) was different

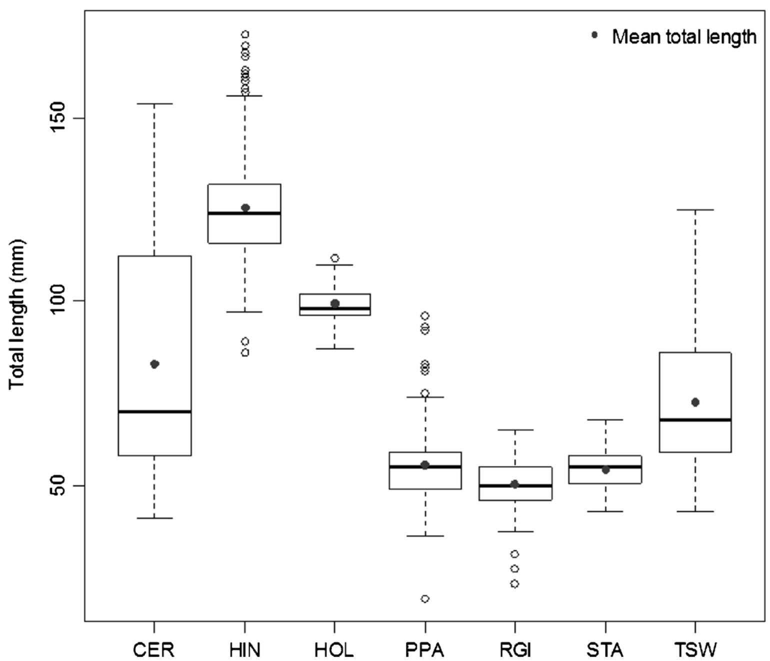


**Fig. 2** Box-Whiskers plots of total length for the seven fish species caught in Lake Dianchi. The central box covers 50 % of data values and the horizontal line in the box indicates the median. CER: redfin culter *C. erythropterus*, HIN: piper halfbeak *H. intermedius*, HOL: pond smelt *H. olidus*, PPA: topmouth gudgeon *P. parva*, RGI: barcheek goby *R. giurinus*, STA: Taihu icefish *S. tangkahkeii*, TSW: thin sharpbelly *T. swinhonis*

**Table 2** Spatial variations of the eight environmental characteristics of Lake Dianchi during the autumn of 2008. The environmental parameters are the mean values computed from 10 site measurements in each of the three parts (northern, middle, and southern parts) of the lake. *P* values for the Kruskal-Wallis tests were also given. Means with different letters are significantly different from each other at the 0.05 level

| Environmental factor | Abbr. | Northern (*n*=10) | | Middle (*n*=10) | | Southern (*n*=10) | | *P* |
|---|---|---|---|---|---|---|---|---|
| | | Range | Mean ± SD | Range | Mean ± SD | Range | Mean ± SD | |
| Water depth (m) | WD | 2.2–5.6 | [a]3.7±1.6 | 2.0–6.3 | [b]5.2±1.6 | 2.0–7.5 | [b]4.8±1.7 | 0.041 |
| Secchi depth (cm) | SD | 19–45 | [a]35±7 | 35–45 | [a]39±3 | 43–125 | [b]59±25 | <0.001 |
| pH | pH | 7.76–8.87 | [a]8.37±0.39 | 8.35–8.74 | [a]8.57±0.15 | 8.35–8.93 | [a]8.60±0.20 | 0.430 |
| Chlorophyll a (μg/l) | Chla | 38.4–183.9 | [a]86.8±4 2.6 | 70.8–124.4 | [a]90.3±16.5 | 9.6–77.5 | [b]47.7±21.6 | 0.002 |
| Chemical oxygen demand (mg/l) | COD | 6.55–19.01 | [a]12.88±4.32 | 4.80–16.80 | [a]13.52±3.34 | 5.33–13.67 | [b]8.67±2.55 | 0.013 |
| Total phosphorus (mg/l) | TP | 0.30–0.89 | [a]0.55±0.21 | 0.12–0.16 | [b]0.14±0.01 | 0.05–0.14 | [b]0.09±0.03 | <0.001 |
| Total nitrogen (mg/l) | TN | 2.79–7.13 | [a]4.78±1.57 | 1.55–1.92 | [b]1.71±0.13 | 1.25–2.26 | [b]1.75±0.32 | <0.001 |
| Ammonia nitrogen (mg/l) | $NH_4$-N | 0.14–2.72 | [a]0.63±0.91 | 0.09–0.57 | [b]0.19±0.16 | 0.06–0.45 | [b]0.20±0.12 | 0.077 |

from those in the other two lake parts. It can be inferred from the associations between species and sampling sites (Fig. 3b, c) that barcheek goby and topmouth gudgeon were abundant in the southern and middle parts of the lake, while the remaining five species (piper halfbeak, thin sharpbelly, pond smelt, redfin culter and

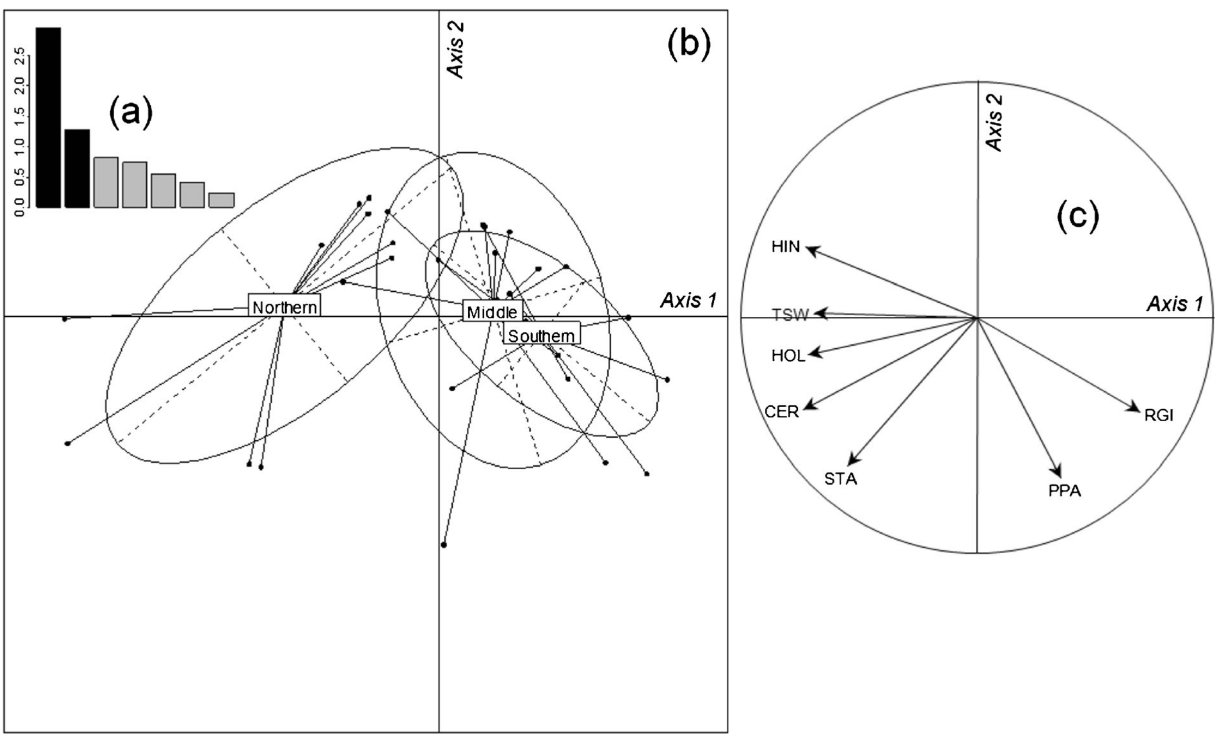


**Fig. 3** Results of principal component analysis (PCA) on the abundances of the seven fish species across the 30 sampling sites (represented as dots on the F1-F2 plane) in Lake Dianchi. **a** Axis 1 and Axis 2 described 42.3 % and 18.2 % of the total fish variation respectively. Each lake part is presented as an ellipsoid. **b** Histogram showing eigenvalues of the PCA. **c** Vector plot showing the contribution of different fish species to F1 and F2. CER: redfin culter *C. erythropterus*, HIN: piper halfbeak *H. intermedius*, HOL: pond smelt *H. olidus*, PPA: topmouth gudgeon *P. parva*, RGI: barcheek goby *R. giurinus*, STA: Taihu icefish *S. tangkahkeii*, TSW: thin sharpbelly *T. swinhonis*

Taihu icefish) were more common in the northern lake. Moreover, somewhat higher stability of the community was seen in the southern lake (smaller ellipsoid in Fig. 3b) than in the middle and northern lake.

The results of the RDA on the seven fish species to the environmental factors are shown in Fig. 4. According to the eigenvalue histogram (Fig. 4a), the first two axes accounted for 52.9 % and 18.9 % of the variability in the fish-environment relationship, respectively. The Monte Carlo randomization test indicated that: the most important factors describing species composition among the sampling sites were TP, TN and secchi depth for axis 1, and water depth and COD for axis 2 (Table 3, Fig. 4c). Based on the RDA results (Fig. 4b, c), redfin culter, piper halfbeak and thin sharpbelly were positively related to nutrient variables (TP and TN), topmouth gudgeon and barcheek goby were associated with relatively higher secchi depth and lower nutrition level, while pond smelt and Taihu icefish (near the center of Fig. 4b) were little influenced by the environmental factors. Overall, water depth and COD had negative impacts on all the fish species.

For thin sharpbelly, the regression tree explained 69.0 % of the total variance of abundance. Total phosphorus (TP) was the most important predictive variable and more fish (CPUE=3.879, 36.7 % of the 30 cases) was related to higher levels of eutrophication (TP> 0.155 mg/l) (Fig. 5a). Water depth and chemical oxygen demand (COD) were of secondary importance in the abundance prediction with the thresholds of 2.9 m and 14.63 mg/l respectively.

For piper halfbeak, the regression tree explained 64.4 % of the total variance of abundance. Total nitrogen (TN) and pH played first and second important roles in the prediction respectively (Fig. 5b). Under the condition of TN <2.89 mg/l, the lowest fish abundance (CPUE=0.496, 46.7 % cases) were predicted where pH was less than 8.68.

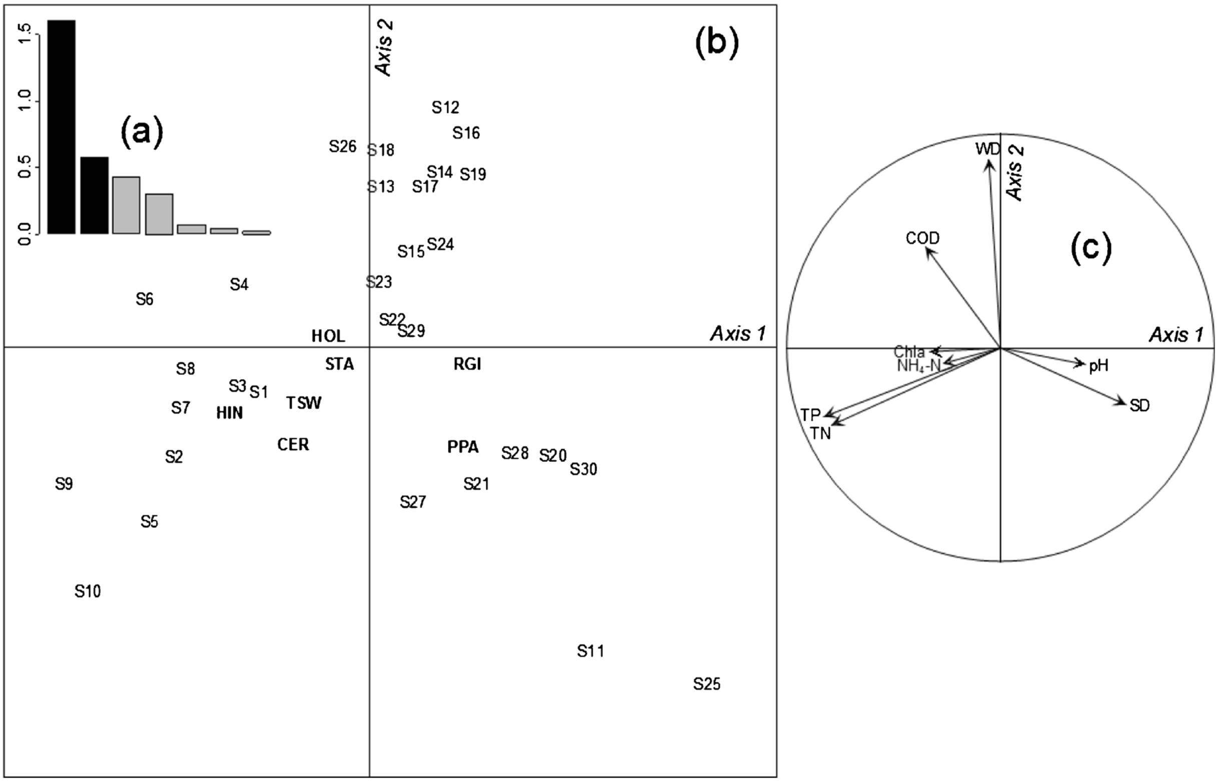


**Fig. 4** Results of redundancy analysis (RDA) on the relationships between the seven fish species and the eight environmental factors across the 30 sampling sites (represented as S1-30 on the F1-F2 plane) in Lake Dianchi. **a** Axis 1 and Axis 2 described 52.9 % and 18.9 % of the variability in the fish-environment relationship respectively. **b** Histogram showing eigenvalues of the PCA. (**c**) Vector plot showing the contribution of different environmental factors to F1 and F2. CER: redfin culter *C. erythropterus*, HIN: piper halfbeak *H. intermedius*, HOL: pond smelt *H. olidus*, PPA: topmouth gudgeon *P. parva*, RGI: barcheek goby *R. giurinus*, STA: Taihu icefish *S. tangkahkeii*, TSW: thin sharpbelly *T. swinhonis*. See Table 2 for environmental factor abbreviations

**Table 3** Summary of the redundancy analysis on the environmental parameters measured for all the sites. Monte Carlo randomization test (999 permutations) run for the sum of all eigenvalues was significant when P<0.01. $r^2$: coefficient of determination. See Table 2 for environmental factor abbreviations

| | Axis 1 | Axis 2 | $r^2$ | *P* |
|---|---|---|---|---|
| WD | −0.037 | 0.999 | 0.776 | 0.001* |
| SD | 0.798 | −0.603 | 0.414 | 0.002** |
| pH | 0.949 | −0.315 | 0.165 | 0.088 |
| Chla | −0.995 | −0.095 | 0.109 | 0.225 |
| COD | −0.404 | 0.915 | 0.344 | 0.003** |
| TP | −0.835 | −0.551 | 0.784 | 0.001* |
| TN | −0.793 | −0.609 | 0.753 | 0.001* |
| $NH_4$-N | −0.831 | −0.556 | 0.084 | 0.282 |

Statistical significance: **P*<0.001, ***P*<0.01

For barcheek goby, the regression tree explained 55.3 % of the total variance of abundance. The first split at the root was based on total phosphorus (TP) and more fish (CPUE=2.976, 26.7 % cases) was related to lower TP (<0.12 mg/l) (Fig. 5c). The second important predictive determinants on the left and right branches were total phosphorus ($NH_4$-N) and total nitrogen (TN) respectively. The fish abundance was predicted lowest (CPUE=0.364, 56.7 % cases) where both TP and $NH_4$-N were high.

For topmouth gudgeon, the regression tree explained 51.5 % of the total variance. Water depth (WD) was the key determinant of abundance, and secchi depth (SD) played the second important role in the prediction (Fig. 5d). Low abundance (CPUE=0.240, 86.7 % cases) was related to deeper water (WD≥2.5 m), and the highest abundance were predicted in shallow water and relatively high transparence (SD>38 cm).

For redfin culter, the regression tree explained 68.4 % of the total variance. Total nitrogen (TN) played the most important role in the prediction and more fish (CPUE=1.548, 26.7 % cases) was predicted when TN>3.25 mg/l (Fig. 5e). Another determinant on the left branch was water depth (WD). The lowest abundance (CPUE=0.096, 46.7 % cases) was related to low TN and relatively deeper water (WD≥3.25).

## Discussion

We identified the seven non-native small-sized fishes caught in the present study as invasive species due to their wide distribution throughout the lake and established populations in the wild. The commercial species, Taihu icefish and pond smelt, were introduced intentionally into Lake Dianchi from the Yangtze River basin and northern China respectively in the 1980s, and the other five species of relatively low or no commercial values invaded the lake accidentally with the introduction of Chinese family carps from the Yangtze River basin since the 1960s. These species share a number of life history characteristics that may explain their successful invasion and high abundance in the lake. Specifically, they all are short-lived, but fecund for their size, less catchable than large-sized species, and have long reproductive seasons in lentic habitats (Chu and Chen 1989; Yang 1996; Gozlan et al. 2010; Guo et al. 2013); thus, it is unlikely that environmental disturbances would severely affect reproductive success of these species. Such disturbances can include fluctuations in water level, variations in water quality, increasing fishing efforts, and local, high concentrations of industrial effluents around the lake (Chen et al. 1998; Fang et al. 2004). The native species and other introduced species generally have more restricted spawning seasons and habitat requirements (Chu and Chen 1989; Yang 1996; Li 2006), making them more vulnerable to these disturbances or even unable to survive in the lake environments. For instance, some of the introduced species (listed in Appendix 2), such as breams (*Megalobrama amblycephala*, *Parabramis pekinensis*) and bitterlings (*Acheilognathus chankaensis*, *A. macropterus*, *Rhodeus ocellatus*), could not become naturalized in the wild due to unsuccessful reproduction and/or intolerance to water pollution, and they apparently vanished soon after their introduction (Yang 1996).

Our results revealed the high dominance of thin sharpbelly and piper halfbeak in Lake Dianchi, followed by barcheek goby and topmouth gudgeon, in terms of abundance and occurrence. It is surprising that the information of abundance status of these four invasive fishes in the lake were almost lacking in previous literatures [e.g. only listed as introduced fish species without any abundance description by Yang (1996)], and thus assessments of their ecological impacts on local fish community and ecosystem function are unavailable so far. This situation existed partly because these noncommercial species are not targeted by the artisan fisheries of Lake Dianchi and fishery-dependent sampling on the scale that is needed to truly understand fish distribution is costly and usually was given low priority

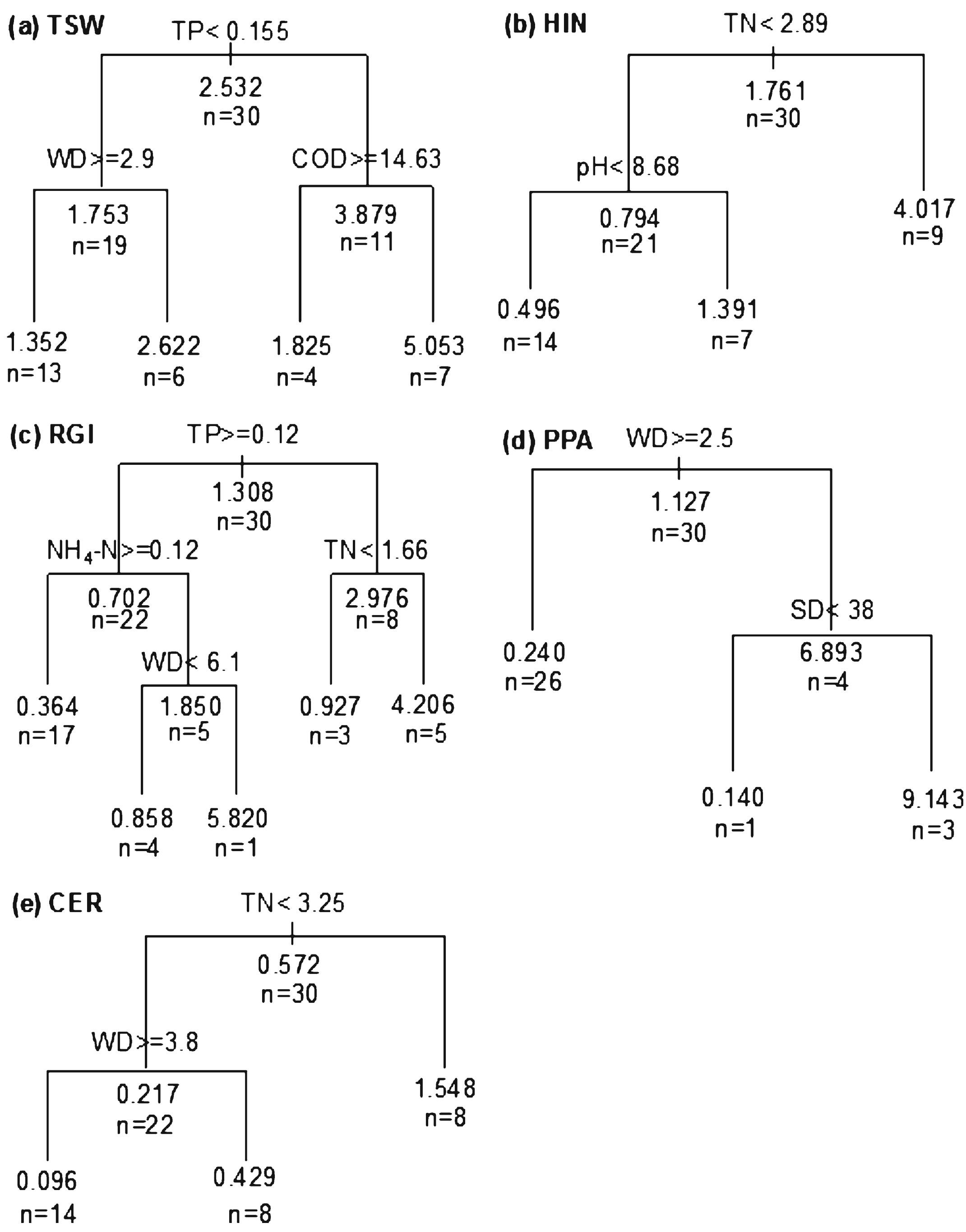


**Fig. 5** Regression tree models predicting fish abundance (CPUE, ind/fishing pass/h) of the five dominant species in Lake Dianchi. **a** TSW: thin sharpbelly *T. swinhonis*, **b** HIN: piper halfbeak *H. intermedius*, **c** RGI: barcheek goby *R. giurinus*, **d** PPA: topmouth gudgeon *P. parva*, and **e** CER: redfin culter *C. erythropterus*. The values at each node are the CPUE prediction for the node and the number of cases reaching the node. See Table 2 for environmental factor abbreviations and units

in lake management (Ye et al. 2006). In this light, our experimental sampling with the multiple mesh–sized gillnets can provide an alternative method to evaluate population status of these non-commercial small fish species as well as monitor their long-term dynamics. However, our passive gillnetting seemed to underestimate the abundance of Taihu icefish that is tiny and of low swimming activity. For this commercial species, fishery pelagic trawls in the lake are efficient in capturing and relative abundance derived from local fishery harvests could therefore be a better indicator of its population status (Liu and Zhu 1994).

According to the measurements of water quality and fish composition on the whole lake scale, we found that the eutrophic level of Lake Dianchi increased from south to north and invasive fish community structure in the northern lake was distinct from those in the middle and southern parts of the lake, in accord with shifting environmental conditions. This spatial pattern of lake trophic status was consistent with the results reported by Fang et al. (2004) and Gao et al. 2005, who suggested that the hyper-eutrophication in the northern area was associated with more dense industrial estates, farmlands and human habitation surrounding the northeast lake-shore. On the other hand, the multivariate analyses (PCA, RDA and regression trees) indicated that thin sharpbelly, piper halfbeak and redfin culter were more common in the northern lake and positively correlated with total nitrogen and total phosphorus (TP). Based on our previous investigations in the lakes within the Yangtze River basin, these small-sized fish species are generally tolerant of environmental changes, presenting high growth rates in the presence of high level of plankton in eutrophic environments (Ye 2007). As these tolerant species have a great resistance to environmental stress, it is assumed that the increase of their population abundance could be used as an indicator to reflect degradation of environmental conditions (Karr 1981; Schleiger 2000; Kennard et al. 2005).

Studies on the relationships between fish and abiotic environmental factors are of particular importance to conservation ecology because of their value in quantifying the effects of habitat quality that control the size and dynamics of fish communities (Moyle and Light 1996; Lozon and MacIsaac 1997). Physical characteristics and water quality parameters can directly influence lake productivity and affect invertebrate prey resources and fish abundance. For example, increases in fish production have been reported to be associated with increases in phosphorus (Hanson and Leggett 1982; Downing and Plante 1993) and chlorophyll a concentrations (Jones and Hoyer 1982). Abundance of omnivorous fishes in particular may increase with lake eutrophication (Jeppesen et al. 2000; Egertson and Downing 2004). In Lake Dianchi, increasing total nitrogen and total phosphorus concentrations have caused significant changes in plankton and zoobenthic communities (Wang et al. 2007, 2008; Sun 2010), which might benefit some invasive fishes (e.g. thin sharpbelly and piper halfbeak) that have broader physiological tolerances to polluted conditions, generalist food habits and unrestricted spawning habitat requirements. Water depth (maximum measurement=7.5 m) seemed to have a moderately negative influence on the spatial distribution of the small invasive fishes in Lake Dianchi, perhaps due to relatively complex habitats and abundant prey close to the lake shoreline, and more active feeding in shallower areas during autumn.

The aquatic macrophytes of Lake Dianchi have declined dramatically in the past half century owing to anthropogenic alteration of the lake environment, e.g. increasing untreated municipal and industrial sewage flows into the lake, decreasing transparency (secchi depth), and construction of concrete breakwater (Yu et al. 2000). The coverage of macrophytes decreased from 88 % in 1961 to only 2 % of the lake area by 2010 (Lu et al. 2012). As a consequence, our study cannot provide direct evidence for the roles of macrophyte in structuring fish communities of Lake Dianchi. A lot of empirical studies undertaken in temperate and subtropical lakes have shown that macrophytes offer fish increased foraging opportunities, reduced predation risk, and suitable spawning sites (Dibble et al. 1996). Our previous studies in the shallows Yangtze lakes found that the spatial distributions of many fishes are positively associated with submerged macrophytes due to the benefits provided by macrophyte cover (Ye et al. 2006). Our research in Lake Erhai, the second largest lake in the Yunnan Plateau, also indicated that the majority of fish species in the lake preferred habitats with abundant macrophytes (Tang et al. 2013). Moreover, it is generally accepted that invasive fish have a higher degree of plasticity in life history traits and habitat utilization than native species (Kolar and Lodge 2002; García-Berthou 2007; Gozlan et al. 2010), enabling them more tolerant to rapid and substantial environmental changes. Thus, the disappearing macrophyte cover in Lake Dianchi may play an important role in the historical changes of the lake fish communities (Appendix 1 and 2), i.e. a considerable decline of endemic fishes and the shift of fish community from the dominance by native species to the dominance by invasive fishes.

The regression trees built for the abundances of the dominant invasive fishes in Lake Dianchi explained more than half (51.5–69.0 %) of the total variance of response values. More sharpbelly were found in shallow waters, with high total nitrogen and low chemical oxygen demand. High abundances of piper halfbeak were predicted in the enviroment of high total nitrogen and pH. Barcheek goby seemed to prefer low total phosphorus and ammonia nitrogen, but high total nitrogen and deep water. High numbers of topmouth gudgeon were asscociated with shallow and clean waters, while redfin culter with deep areas with high total nitrogen. All the predictive criterion and corresponding thresholds of the key environmental variables for spatial distribution of the invasive fishes could be helpful in evaluating and controlling fish habitat quality, which is an important issue in conservation ecology (Kolar and Lodge 2002; García-Berthou 2007).

On a larger spatial scale, some of the seven non-native small fish species were also recorded from the other Yunnan Plateau lakes, which vary in area, altitude and depth (Appendix 3). Three species invaded all the nine investigated lakes of different trophic status, but through different processes: Taihu icefish *S. tangkahkeii* has been widely introduced into the lakes since the 1980s to enhance local fishery, while barcheek goby *R. giurinus* and topmouth gudgeon *P. parva* entered the lakes accompanying the introduction of target fishery species (i.e. the Chinese family carps) (Yang 1996). The presence of piper halfbeak *H. intermedius* was reported in Lake Fuxian, Lake Xingyun and Lake Yangzong without abundance data. Pond smelt *H. olidus* and redfin culter *C. erythropterus* were also observed in Lake Erhai and Lake Fuxian respectively. However, no record of thin sharpbelly *T. swinhonis* is available in the plateau lakes except in Lake Dianchi. The reasons for spatial distribution patterns of non-native fish species among the lakes are likely because of geographic isolation, limnological characteristics, different levels of human disturbances, and various sampling methods (Chen et al. 1998). Further quantitative/semi-quantitative field investigations with comparable sampling procedures on fish communities of these plateau lakes are required to assess population status of invasive fishes and identify key environmental filters for their spatial diffusions on the Yunnan Plateau.

Fish introduction is important disturbance to aquatic ecosystems, especially to plateau lakes that are generally considered to be vulnerable ecosystems (Huber et al. 2005). Lake ecosystems in the Yunnan plateau are usually isolated and the food webs are relatively simple (Xie and Chen 2001). Ecological impacts of invasive fish on local fish community and ecosystem function are mainly focused on intentionally introduced species in these lakes. For instance, the disastrous impacts made by planktivorous bighead and silver carp have been striking in many of the lakes, where the continuous stocking of fingerlings has taken place on a wide scale since the late 1950s (Yang 1996; Xie and Chen 2001). Taihu icefish *S. tangkahkeii* was largely introduced into the Yunnan Plateau lakes since 1980s and became predominant after introduction in many lakes (Liu and Zhu 1994; Wang and Dou 1998). These invaders have suppressed and in some instances eliminated the native or endemic species (Wang and Dou 1998; Li 2006), by competing for plankton food with native fishes. However, there is much less knowledge on ecological impacts of the accidentally-introduced fishes that are presently uncontrolled because of non-target by fisheries and devoid of predatory fish species in the lakes. Thus, the possible impacts of the ignored small fish species on local fish communities urgently need to be assessed, especially in those lakes (e.g. Lake Dianchi) where the fishes have successfully established reproducing populations.

In general, the fish community of Lake Dianchi has changed significantly during the past half century. The abundance of native species has declined sharply, and a majority of endemic species have been extirpated from the lake. Of the non-native fish species that have been introduced, some of the accidentally introduced small fishes have become dominant. To suppress the invasive fish species and encourage restoration of the native fish community, managers should consider the following: (1) develop economically and/or ecologically effective controlling strategies, e.g. physical removals, chemical eradication or bio-manipulation of invasive small fishes by incorporating their spatial distribution characteristics and potential trophic interaction, (2) regulate loading nutrients, and restore submerged macrophytes in shallower areas with turbidity-tolerant species, (3) support stocking programs for the restoration of indigenous species and improve enforcement to avoid overfishing. 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 non-native fishes, trophic dynamics in the food web, fish biogeography distribution, and the effects of eutrophication on lake ecosystems.

**Acknowledgments** We are grateful to Bangding Xiao, Neng Wang and Xinhai Tu of the Institute of Hydrobiology, Chinese Academy of Science, for their kind help during the laboratory analysis. Special thanks to Sovan Lek of Université de Toulouse for his help in data analysis. We appreciate the valuable comments of the three anonymous reviewers on an early version of this paper. This research was supported by the National Special Program of Water Environment (2013ZX07102-005), the National Natural Science Foundation of China (30900182) and the knowledge Innovation Program of the Chinese Academy of Sciences. This study was approved by animal ethic committee of Institute of Hydrobiology, Chinese Academy of Sciences, and was conducted according to "Instructive notions with respect to caring for laboratory animals" issued by the Ministry of Science and technology of the People's Republic of China.

## Appendixes

### Appendix 1

**Table 4** Historical changes of native and endemic fish species composition in Lake Dianchi during the recent decades

| Species | [a]1950s | [a]1960s | [a]1970s | [a]1980s | [a]1990s | [b]2007-2008 |
|---|---|---|---|---|---|---|
| *Acheilognathus elongates** | + | + | – | – | – | – |
| *Acrossocheilus yunnanensis* | + | + | + | + | + | – |
| *Anabarilius alburnops** | ++ | ++ | + | + | + | + |
| *Anabarilius polylepis** | ++ | ++ | – | – | – | – |
| *Carassius auratus auratus* | ++ | ++ | ++ | ++ | ++ | ++ |
| *Channa argus* | + | + | + | – | – | – |
| *Cyprinus carpio chilia* | + | + | – | – | – | – |
| *Cyprinus micristius** | + | + | – | – | – | – |
| *Discogobio yunnanensis* | + | + | + | + | + | – |
| *Liobagrus kingi** | + | + | – | – | – | – |
| *Liobagrus nigricauda* | + | + | – | – | – | – |
| *Misgurnus anguillicadatus* | ++ | ++ | ++ | + | + | + |
| *Monopterus albus* | ++ | ++ | + | + | + | + |
| *Oryzias latipes sinensis* | + | + | + | – | – | – |
| *Paracobitis variegatus* | + | + | – | – | – | – |
| *Pseudobagrus medianalis** | + | + | + | + | + | + |
| *Schizothorax grahami* | + | + | + | + | + | – |
| *Silurus mento** | + | + | + | + | – | – |
| *Sinocyclocheilus grahami** | ++ | + | + | + | + | + |
| *Sphaerophysa dianchiensis** | + | + | – | – | – | – |
| *Spinibarbus sinensis* | + | + | + | – | – | – |
| *Triplophysa grahami* | + | + | – | – | – | – |
| *Xenocypris yunnanensis** | ++ | ++ | + | + | – | – |
| *Yunnanilus discoloris** | + | + | + | + | + | – |
| *Yunnanilus nigromaculatus* | + | + | – | – | – | – |
| *Yunnanilus pleurotaenia* | + | + | + | + | + | – |
| Number of native species | 26 | 26 | 16 | 13 | 11 | 6 |
| Number of endemic species | 11 | 11 | 6 | 6 | 4 | 3 |

++: frequently seen species; +: infrequently seen species; −: not found. *: endemic species

[a] compiled from Cheng (1958); Li et al. (1963); Chu and Chen (1989); Yang (1996); Chen et al. (2001)

[b] from our surveys on fishery catches during that period

## Appendix 2

**Table 5** List of 21 introduced fish species in Lake Dianchi recorded since the 1960s, with the reasons for introduction and their relevant ecological characteristics compiled from Chu and Chen (1989) and Yang et al. (1996). The first four species are the Chinese family carps. The species in bold are small-sized invasive fishes caught in the present study

| Family | Species | Common name | Reasons for introduction | Abundance status and acclimatization | Body size | Commercial species or not | Spawning habitat | Sensitivity to pollution |
|---|---|---|---|---|---|---|---|---|
| Cyprinidae | *Hypophthalmictuthys molitrix* | Silver carp | Improve fisheries, control plankton | Abundant, dependent on stocking | Large | Yes | Lotic | Tolerant |
| | *Aristichthys mobilis* | Bighead carp | Improve fisheries, control plankton | Abundant, dependent on stocking | Large | Yes | Lotic | Tolerant |
| | *Ctenopharyngodon idellus* | Grass carp | Improve fisheries | Frequent, dependent on stocking | Large | Yes | Lotic | Tolerant |
| | *Mylopharyngodon piceus* | Black carp | Improve fisheries | Rare, dependent on stocking | Large | Yes | Lotic | Tolerant |
| | *Cyprinus carpio* | Common carp | Improve fisheries | Abundant, successful invasion | Large | Yes | Lentic | Tolerant |
| | *Megalobrama amblycephala* | Wuchang bream | Improve fisheries | Absent, not acclimatized | Large | Yes | Lentic | Intolerant |
| | *Parabramis pekinensis* | White Amur bream | Improve fisheries | Absent, not acclimatized | Large | Yes | Lentic | Intolerant |
| | *Cirrhinus molitorella* | Chinese mud carp | Improve fisheries | Absent, not acclimatized | Large | Yes | Lentic | Unknown |
| | *Culterichthys erythropterus* | Redfin culter | Accidentally | Abundant, successful invasion | Small | Yes | Lentic | Tolerant |
| | *Pseudorasbora parva* | Topmouth gudgeon | Accidentally | Abundant, successful invasion | Small | No | Lentic | Tolerant |
| | *Toxabramis swinhonis* | Thin sharpbelly | Accidentally | Abundant, successful invasion | Small | No | Lentic | Tolerant |
| | *Elopichthys bambusa* | Yellowcheek carp | Accidentally | Absent, not acclimatized | Large | Yes | Lotic | Unknown |
| | *Luciobrama macrocephalus* | Spiky-head carp | Accidentally | Absent, not acclimatized | Large | Yes | Lotic | Unknown |
| | *Acheilognathus chankaensis* | Xingkai bitterling | Accidentally | Absent, not acclimatized | Small | No | Lentic | Intolerant |
| | *Acheilognathus macropterus* | Largefin bitterling | Accidentally | Absent, not acclimatized | Small | No | Lentic | Intolerant |
| | *Rhodeus ocellatus* | Rosy bitterling | Accidentally | Absent, not acclimatized | Small | No | Lentic | Intolerant |
| Gobiidae | *Rhinogobius giurinus* | Barcheek goby | Accidentally | Abundant, successful invasion | Small | No | Lentic | Tolerant |
| Hemiramphidae | *Hyporhamphus intermedius* | Piper halfbeak | Accidentally | Abundant, successful invasion | Small | No | Lentic | Tolerant |
| Osmeridae | *Hypomesus olidus* | Pond smelt | Improve fisheries | Frequent, successful invasion | Small | Yes | Lentic | Tolerant |
| Salangidae | *Salangichthys tangkahkeii* | Taihu icefish | Improve fisheries | Abundant, successful invasion | Small | Yes | Lentic | Tolerant |
| Serranidae | *Siniperca chuatsi* | Chinese perch | Improve fisheries | Absent, not acclimatized | Large | Yes | Lentic | Intolerant |

## Appendix 3

**Table 6** Records of the presence of the seven non-native fish species from the nine lakes on the Yunnan Plateau. The information of lake area, altitude, maximum depth, and trophic status is adapted from Yu et al. (2010). The lakes are listed in the order of their areas. O: oligotrophic, M: mesotrophic, E: eutrophic lakes. 0: not recorded, 1: recorded. CER: redfin culter *C. erythropterus*, HIN: piper halfbeak *H. intermedius*, HOL: pond smelt *H. olidus*, PPA: topmouth gudgeon *P. parva*, RGI: barcheek goby *R. giurinus*, STA: Taihu icefish *S. tangkahkeii*, TSW: thin sharpbelly *T. swinhonis*

| Lake name | Area ($km^2$) | Altitude (m) | Max depth (m). | Trophic status | Non-native fish species | | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | CER | HIN | HOL | PPA | RGI | STA | TSW | |
| Lake Dianchi | 297.9 | 1886 | 7.5 | E | 1 | 1 | 1 | 1 | 1 | 1 | 1 | This study |
| Lake Erhai | 249 | 1974 | 20.7 | M | 0 | 0 | 1 | 1 | 1 | 1 | 0 | Tang et al. (2013), Fei et al. (2012) |
| Lake Fuxian | 211 | 1721 | 155 | O | 1 | 1 | 0 | 1 | 1 | 1 | 0 | Li (2006), Xiong et al. (2008) |
| Lake Chenghai | 77.2 | 1503 | 35.1 | M | 0 | 0 | 0 | 1 | 1 | 1 | 0 | Yuan et al. (2010) |
| Lake Lugu | 48.5 | 2691 | 93.5 | O | 0 | 0 | 0 | 1 | 1 | 1 | 0 | Kong et al. (2006) |
| Lake Qilu | 36.9 | 1797 | 6.8 | E | 0 | 0 | 0 | 1 | 1 | 1 | 0 | Li (2006); Yuan et al. (2010) |
| Lake Xingyun | 34.7 | 1722 | 11 | E | 0 | 1 | 0 | 1 | 1 | 1 | 0 | Li (2006); Yuan et al. (2010) |
| Lake Yangzong | 31.7 | 1771 | 30 | M | 0 | 1 | 0 | 1 | 1 | 1 | 0 | Li (2006); Yuan et al. (2010) |
| Lake Datun | 12.3 | 1286 | 5 | E | 0 | 0 | 0 | 1 | 1 | 1 | 0 | Yuan et al. (2010) |

## References


Balirwa JS, Chapman CA, Chapman LJ et al (2003) Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? Bioscience 53:703–716

Breiman L, Friedman JH, Olshen RA et al (1984) Classification and regression trees. Chapman and Hall, New York

Brown LR (2000) Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. Environ Biol Fish 57:251–269

Case TJ (1996) Global patterns in the establishment and distribution of exotic birds. Biol Conserv 78:69–96

Chen YR, Yang JX, Li ZY (1998) The diversity and present status of fishes in Yunnan Province. Chinese Biodivers 6:272–277, in Chinese with English abstract

Chen ZM, Yang JX, Su RF et al (2001) Present status of the indigenous fishes in Dianchi Lake, Yunnan. Biodivers Sci 9:407–413, in Chinese with English abstract

Cheng QT (1958) Fishes in Yunnan. Chinese J Zool 3:153–165 (in Chinese)

Cheng L, Lek S, Loot G et al (2010) Variations of fish composition and diversity related to environmental variables in shallow lakes in the Yangtze River basin. Aquat Living Resour 23:417–426

China EPA (Environmental Protection Agency) (2004) Analytical methods for the examination of water and wastewater, 4th edn. China Environmental Science Press, Beijing, in Chinese

Chu XL, Chen YR (1989) The fishes of Yunnan. Science Press, Beijing (in Chinese)

Dibble ED, Killgore KJ, Harrel SL (1996) Assessment of fish-plant interactions. Am Fish Soc Symp 16:357–372

Downing JA, Plante C (1993) Production of fish populations in lakes. Can J Fish Aquat Sci 50:110–120

Dray S, Dufour A-B et al (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20

Egertson CJ, Downing JA (2004) Relationship of fish catch and composition to water quality in a suite of agriculturally eutrophic lakes. Can J Fish Aquat Sci 61:1784–1796

Fang T, Ao HY, Liu JT et al (2004) The spatial patterns of water environmental status in Dianchi Lake. Acta Hydrobiologia Sinica 28:124–130, in Chinese with English abstract

Fei JH, Shao XY (2012) Studies on the growth characteristics and morphological differences of fish in plateau lakes. Oceanologia et Limnologia Sinica 43:789–796, in Chinese with English abstract

Gao L, Zhou JM, Yang H et al (2005) Phosphorus fractions in sediment profiles and their potential contributions to eutrophication in Dianchi Lake. Environ Geol 48:835–844

García-Berthou E (2007) The characteristics of invasive fishes: what has been learned so far? J Fish Biol 71:33–55

Gehrke PC, Brown P, Schiller CB et al (1995) River regulation and fish communities in the Murray-Darling river system, Australia. Regul River Res Manag 11:363–375

Giraudoux P (2010) Pgirmess: data analysis in ecology. R Packag Vers 1(4):5

Gozlan RE, Andreou D, Asaeda T et al (2010) Pan-continental invasion of Pseudorasbora parva: towards a better understanding of freshwater fish invasions. Fish Fish 11:315–340

Guo ZQ, Liu JS, Lek S (2012) Habitat segregation between two congeneric and introduced goby species. Fundam Appl Limnol 181:241–251

Guo ZQ, Cucherousset J, Lek S et al (2013) Comparative study of the reproductive biology of two congeneric and introduced goby species: implications for management strategies. Hydrobiologia 709:89–99

Hanson JM, Leggett WC (1982) Empirical prediction of fish biomass and yield. Can J Fish Aquat Sci 42:280–286

Huber UM, Bugmann HKM, Reasoner MA (2005) Global change and mountain regions: an overview of current knowledge. Springer, Dordrecht

Jeppesen E, Jensen JP, Sondergaard M et al (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshw Biol 45:201–218

Jones JR, Hoyer MV (1982) Sportfish harvest predicted by summer chlorophyll-a concentration in Midwestern lakes and reservoirs. Trans Am Fish Soc 111:176–179

Karr JR (1981) Assessment of biotic integrity using fish communities. Fisheries 6:21–27

Kennard MJ, Arthington AH, Pusey BJ, Harch BD (2005) Are alien fish a reliable indicator of river health? Freshw Biol 50:174–193

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–1236

Kong DP, Chen XY, Yang JX (2006) Fish fauna status in the Lugu Lake with preliminary analysis on cause and effect of human impacts. Zool Res 27:94–97

Legendre P, Legendre L (2012) Numerical ecology, 3rd edn. Elsevier, Amsterdam

Leidy RA, Fiedler PL (1985) Human disturbance and patterns of fish species diversity in the San Francisco Bay drainage, California. Biol Conserv 33:247–267

Li K (2006) Studies on biology and genetic diversity of two endemic fishes in lakes of Yunnan Plateau. PhD Dissertation. Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan (in Chinese with English abstract)

Li SH, Yu MJ, Li GZ et al (1963) Limnological survey of the lakes of Yunnan Plateau. Oceanologia et Limnologia Sinica 5:87–114 (in Chinese with English abstract)

Liu WZ, Zhu SQ (1994) Food and feeding behavior of ice-fish (Neosalanx taihuensis Chen) in Dianchi Lake. Acta Zool Sin 40:253–261 (in Chinese with English abstract)

Lozon JD, MacIsaac HJ (1997) Biological invasions: are they dependent on disturbance? Environ Rev 5:131–144

Lu J, Wang HB, Pan M et al (2012) Using sediment seed banks and historical vegetation change data to develop restoration criteria for a eutrophic lake in China. Ecol Eng 39:95–103

Meador MR, Brown LR, Short T (2003) Relations between introduced fish and environmental conditions at large geographic scales. Ecol Indic 3:81–92

Moyle PB, Light T (1996) Fish invasions in California: do abiotic factors determine success? Ecology 77:1666–1670

Olin M, Rask M, Ruuhljärvi J et al (2002) Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. J Fish Biol 60:593–612

Olson DM, Dinerstein E (1998) The Global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. Conserv Biol 12:502–515

Persson L, Diehl S, Johansson L et al (1991) Shifts in fish communities along the productivity gradient of temperate lakes-patterns and the importance of size-structured interactions. J Fish Biol 38:281–293

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Schleiger SL (2000) Use of an index of biotic integrity to detect effects of land uses on stream fish communities in West-Central Georgia. Trans Am Fish Soc 129:1118–1133

Søndergaard M, Jeppesen E, Lauridsen TL et al (2007) Lake restoration: successes, failures and long-term effects. J Appl Ecol 44:1095–1105

Sun CQ (2010) The study on the community structure and the variation of population quantity in Dianchi Lake. Master Dissertation. Yunnan University, Kunming (in Chinese with English abstract)

Tang JF, Ye SW, Li W (2013) Status and historical changes of fish community in Erhai Lake. Chinese J Oceanol Limnol (In press)

Therneau T, Atkinson B, Ripley B (2010) rpart: Recursive Partitioning. R Package Version 3.1-46

Wang SM, Dou HS (1998) Lakes in China. Science Press, Beijing (in Chinese)

Wang LZ, Liu YD, Chen L (2007) Benthic macroinvertebrate communities in Dianchi Lake and assessment of water quality. Acta Hydrobiologia Sinica 31:590–593 (in Chinese with English abstract)

Wang N, Song LR, Wang RN et al (2008) The spatio-temporal distribution of algal biomass in Dianchi Lake and its impact factors. Acta Hydrobiologica Sinica 32:184–188 (in Chinese with English abstract)

Wu XQ, Gong Y, Wang Z et al (2010) Residue levels and distribution features of microcystins in fish samples from Lake Dianchi. Acta Hydrobiologica Sinica 34:388–393 (in Chinese with English abstract)

Xie P, Chen Y (2001) Invasive carp in China's plateau lakes. Science 294:999–1000

Yang JX (1996) The exotic and native fishes in Yunnan: the study of impact ways and degrees and other related problems. In: Wang S, Xie BD, Xie Y (eds) Biodiversity conservation for China (Part II). China Environmental Science Press, Beijing, pp 129–138 (in Chinese)

Ye SW (2007) Studies on fish communities and trophic network model of shallow lakes along the middle reach of the Yangtze River. PhD Dissertation. Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan (in Chinese with English abstract)

Ye SW, Li ZK, Lek-Ang S et al (2006) Community structure of small fishes in a shallow macrophytic lake (Niushan Lake) along the middle reach of the Yangtze River, China. Aquat Living Resour 19:349–359

Yu GY, Liu YD, Qiu CQ et al (2000) Macrophyte succession in Dianchi Lake and relations with the environment. J Lake Sci 12:73–80 (in Chinese with English abstract)

Yu Y, Zhang M, Qian SQ et al (2010) Current status and development of water quality of lakes in Yunnan-Guizhou Plateau. J Lake Sci 22:820–828 (in Chinese with English abstract)

Yuan G, Ru HJ, Liu XQ (2010) Fish diversity and fishery resources in lakes of Yunnan Plateau during 2007–2008. J Lake Sci 22:837–841 (in Chinese with English abstract)

Zhang RZ (1999) Zoogeography of China. Science Press, Beijing (in Chinese)