Aquatic Invasions (2021) Volume 16, Issue 2: 329–348

Research Article

Potential impact of population increases of non-native tilapia on fish catch and plankton structure: a case study of Tangxi Reservoir in southern China

Liang Peng[1,2], Xianguang Xue[1], Jian Liao[1], Jian Zhao[3], Quehui Tang[1], Qiuqi Lin[1], Qun Zhang[1] and Bo-Ping Han[1,2,*]

[1]*Department of Ecology, Jinan University, Guangzhou 510632, China*

[2]*Engineering Research Center of Tropical and Subtropical Aquatic Ecological Engineering, Ministry of Education, Guangzhou 510632, China*

[3]*Guangdong Hydrology Bureau Shantou Hydrology Sub-bureau, Shantou 515041, China*

**Corresponding author*

E-mails: *tbphan@jnu.edu.cn*, *tbphan@126.com*

Citation: Peng L, Xue X, Liao J, Zhao J, Tang Q, Lin Q, Zhang Q, Han B-P (2021) Potential impact of population increases of non-native tilapia on fish catch and plankton structure: a case study of Tangxi Reservoir in southern China. *Aquatic Invasions* 16(2): 329–348, https://doi.org/10.3391/ai.2021.16.2.08

Received: 18 October 2019

Accepted: 21 December 2020

Published: 18 February 2021

Thematic editor: Ian Duggan

Abstract

Several non-native tilapia species, including *Oreochromis mossambicus* (Peters, 1852), *O. niloticus* (Linnaeus, 1757) and their hybrids or strains, were introduced into China as major cultured species during the 1950s to 1980s. These are now among the dominant fish species in many tropical and some subtropical reservoirs. Eutrophication is assumed to accelerate their population growth. In the present study, we reported a sharp decline in the catch of stocked bighead carp (*Hypophthalmichthys nobilis* (Richardson, 1845)) with an extreme increase of tilapia catch in a large reservoir in southern China. In 2006, the catch of tilapia was 150 tons, which exceeded the catch of stocked bighead carp, and reached 500 tons in 2015. Long-term meteorological data over the past two decades did not show any significant change, especially in minimum air and water temperatures, which can be factors limiting tilapia growth. In contrast, water quality conditions, including total nitrogen, total phosphorus (TP), chlorophyll *a*, chemical oxygen demand, and trophic status, have significantly increased in the reservoir. The phytoplankton community has been mainly composed of small and filamentous species, while the total zooplankton biomass has decreased, with the community now mainly comprised of small rotifers and copepod species. The high ratio of chlorophyll *a*:TP indicates a weakening top-down effect of zooplankton on phytoplankton. The annual tilapia catch was significantly associated with trophic status of the reservoir, but not with meteorological and hydrological factors. We propose an ecological mechanism for increased population densities of the non-native tilapia under eutrophication, in which an increase in tilapia population size has been accompanied by a reduction in their body size, producing a stronger negative impact on zooplankton and water quality, which contributes to the turnover between bighead carp and tilapia catch. The proposed mechanism provides a useful framework for understanding the process and management of tilapia populations in tropical reservoirs.

Key words: phosphorus, chlorophyll *a*, eutrophication, bighead carp, phytoplankton, zooplankton

Introduction

Increases in population sizes of non-native fish largely depends on food composition, habitat, trophic status of the invaded waters, the biological characteristics of the introduced fish, and the scope of human activities

(Leprieur et al. 2008; Zengeya et al. 2013; Ovenden et al. 2015). Tilapia are members of the cichlid family of tropical omnivorous fish that were introduced into China from Africa, Vietnam, Thailand, and Philippines (De Silva et al. 2004). They have since become the major aquaculture species in tropical China and have invaded a variety of natural waters. *Oreochromis niloticus* (Linnaeus, 1757), *O. mossambicus* (Peters, 1852), *Sarotherodon galilaeus*, *Tilapia zillii*, *O. aureus* (Gu et al. 2016) and their hybrids are the most common non-native tilapia species in many parts of the world (Canonico et al. 2005; Casal 2006; Deines et al. 2016; Gu et al. 2018). These farmed species usually have a high individual growth rate (Grammer et al. 2012). Like other tilapia, they have a high intrinsic rate of population growth and a wide niche with a feeding habit covering a wide range of food (Peterson et al. 2006; Russell et al. 2012; Vicente and Fonseca-Alves 2013). They have formed feral populations in many natural waters of southern China and are presently distributed extensively in lakes, reservoirs, rivers and ponds (Chen and Ye 1994; Gu et al. 2015; Tan et al. 2012). Tilapia favor middle and lower layers of mainly shallow waters, such as the littoral zone (McDonald et al. 2007), and feed on plankton, benthic organisms and organic debris (Bruton and Boltt 1975; Peterson et al. 2006). Fishery production of tilapia is therefore mainly determined by the source and composition of foods in shallow littoral zones (Bruton and Boltt 1975). Eutrophication of tropical waters can enhance tilapia invasion and population expansion (Fernando 1991) as it provides more resources for tilapia (Bíró 1997). In reservoirs, the most common nutrients are nitrogen and phosphorus, derived mainly from high concentrations in upstream rivers, which result in eutrophication (Yang et al. 2010; Liu et al. 2012). Additionally, cyanobacterial blooms in reservoirs generally occur in littoral and riverine zones as a result of wind-induced accumulation, which in turn increases the amount of organic matter in sediments to provide a source of food for tilapia (Song et al. 2010).

Although early reviews on the impact of tilapis in Asia showed limited environmental impact (De Silva et al. 2004), a large tilapia population is capable of reducing the amount and quality of food and habitat for native fishes, leading to reductions in species richness and degradation in water quality (Canonico et al. 2005). For example, the invasion of spotted tilapia (*Tilapia mariae*) in Florida (USA) has restricted the spawning area of *Lepomis* sunfishes and reduced their growth (Brooks and Jordan 2009). Tilapia can also indirectly increase the biomass of small phytoplankton species by feeding on large and medium-sized zooplankton, such as large cladocerans (Okun et al. 2008; Fetahi et al. 2014). Further, tilapia forage the sediment for detrital matter (Balirwa 1992; Peterson et al. 2006), and can reduce zooplankton diapausing egg banks (Maia-Barbosa et al. 2003). In addition, the fish promote the recycling of nutrients such as nitrogen and phosphorus by suspending the sediments that favor phytoplankton growth and accelerate eutrophication (Starling et al. 2002; Figueredo and Giani 2005; da Silva et al. 2014). Change in plankton community structure with increasing eutrophication can further affect the ichthyofauna structure that feed on plankton (Ke et al. 2007; Jayasinghe et al. 2014).

Since the 1960s, the Chinese government has encouraged large-scale culture of four major Chinese carp species in freshwater lakes and reservoirs (Tang 1970; Liang et al. 1981). Among them silver carp (*Hypophthalmichthys molitrix* (Valenciennes, 1844)) and bighead carp (*H. nobilis* (Richardson, 1845)) have become the main aquaculture species in reservoirs as they could be fed on natural prey, i.e. phytoplankton and zooplankton (Liang et al. 1981; Miura 1990; Gu et al. 1996). Bighead carp differs from tilapia in habitat preference and feeding behavior; it is planktivorous and filter feeding, and prefers the pelagic zone. In contrast, tilapia are omnivorous fish (Bwanika et al. 2004; Peterson et al. 2006; Nagayi-Yawe et al. 2006) and prefer shallow water such as the littoral zone (McDonald et al. 2007; Vanessa and Éder 2012). Niche separation prevents their direct competition and so it is assumed that tilapia have little direct impact on bighead carp catch.

Tangxi Reservoir is a large reservoir located on the Tropic of Cancer in southern China. Bighead carp (*H. nobilis*) has been the most important stocked species in the reservoir since the 1970s. About 1.8×10^7 individuals of bighead carp fry (9–12 cm) and 2×10^5 individuals of silver carp fry (6–8 cm) were released per year into the reservoir since 1990. Starting from the mid-1990s, however, eutrophication has become a prominent problem in the reservoir, and two tilapia species, *O. mossambicus* and *Sarotherodon galilaeus* have expanded their population size and became the mainly harvested species. Each year all fish have been captured by multiple mesh-sized gill nets. Usually weights greater than 1.5 kg for silver and bighead carp and 0.2 kg of tilapia are collected, while smaller sized fish are immediately returned to the reservoir. In the late 1990s, the reservoir became an important source of drinking water for the local region and the government strengthened water quality management. Nevertheless, eutrophication of the Tangxi Reservoir has increased over the past two decades. Examining the yearly fish catch data, we found that the annual tilapia catch has increased sharply since 1999, and exceeded the annual bighead carp catch in 2006. In this study, we analyzed the changes in plankton and fish community structure under eutrophication in Tangxi Reservoir. The objective of our study was to understand the reasons for the tilapia population expansion and its impacts on water quality and bighead carp catch.

Materials and methods

Study site

Tangxi Reservoir (N23°55′; E116°51′) is located in the middle reaches of Huanggang River in the northern part of Raoping County in Guangdong

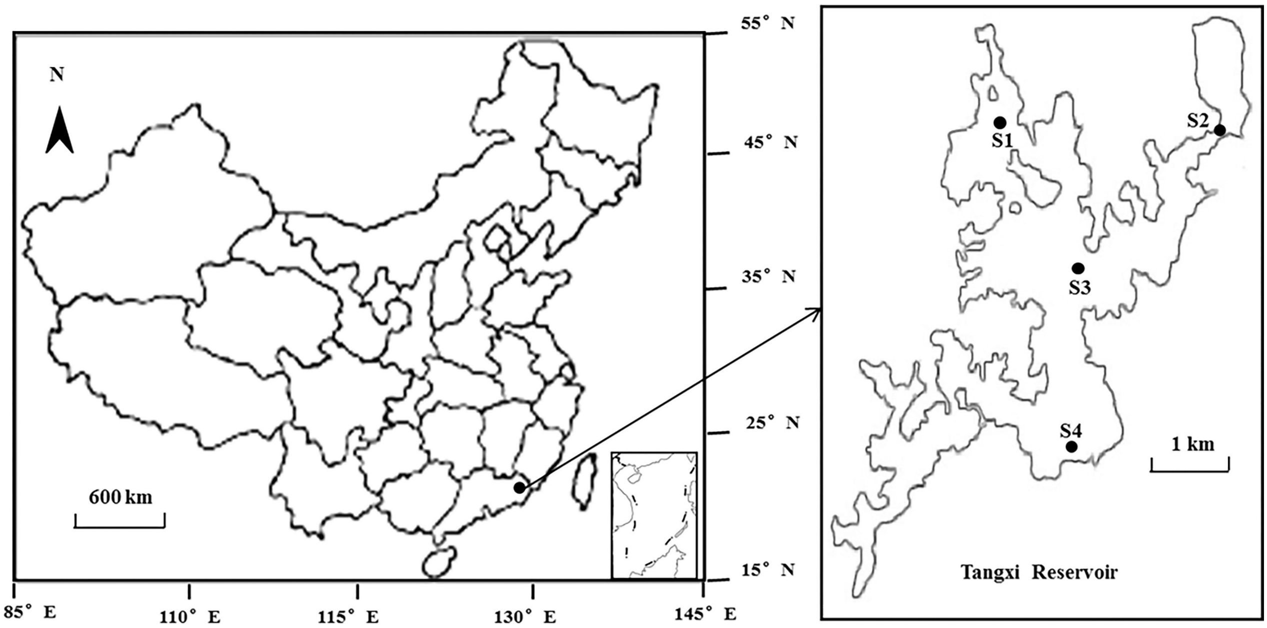

Figure 1. Map showing four sampling sites in Tangxi Reservoir: S1 and S2 at the riverine, S3 at the center, and S4 near the dam.

Province, southern China (Figure 1). The reservoir, constructed in 1960, is large and canyon-shaped with a catchment area of about 667 km^2. The total storage capacity is 381 million m^3 and the maximum water depth is 37 m. It has been used primarily for irrigation and flood control, but also for power generation, fish culture, and tourism. Currently it supplies drinking water for more than 1 million people in Raoping County and surrounding areas. The wet season lasts from April to September, and the mean annual precipitation is 1560 mm. The main inflow rivers are Jiucun River, Shifan River, and Jianrao River, with a drainage area of 118.9, 116.3 and 99.6 km^2, respectively. In the past three decades, the water quality of the reservoir has decreased as considerable domestic and livestock wastewater without effective treatment have been discharged into the reservoir through its tributaries. This is a result of population growth and industrial and agricultural development (Liu 2017) as well as increased fertilizer applied to *Eucalyptus* planted in entire watershed.

Data sources

Hydrological and meteorological data such as precipitation (mm), total outflow (m^3), minimum air and water temperature (°C), and annual mean water level (m), were collected from the Shantou Branch of Guangdong Province Hydrographic Bureau. Fish catch (t) data, mainly including tilapia and two stocked carp species, were obtained from the Management Office for Tangxi Reservoir. Two sampling sites, Xitou Inlet (S1) and Xinqiao Inlet (S2), were located in two main inflow rivers (Huanggang River and Jianhuan River) at the upper reaches of the reservoir that included riverine zones. The two other sampling sites were located in the reservoir transition zone (S3) and the lacustrine zone near the dam (S4). We collected data on plankton species and biomass (mg L^{-1}) from our own surveys at S4 (Figure 1). Sampling and monitoring were conducted in January, March, May, July, September, and November from 2000 to 2015. We measured water quality at S1, S2, and S3. Water quality data for site S4 were supplied by the Shantou Branch of the Guangdong Provincial Hydrographic Bureau.

Collection and identification of plankton

Phytoplankton were collected from samples of 1 L of water obtained at 0.5 m depth and immediately fixed with 5% formalin and 15 mL of Lugol's solution. Each water sample was precipitated in a sedimentation glass and phytoplankton were counted by the Utermöhl's technique using an inverted microscope (Lund et al. 1958; Edler and Elbrächter 2010). More than 400 phytoplankton individuals were counted per sample. Phytoplankton species were identified according to Hu and Wei (2006) in combination with descriptions and illustrations from relevant publications in the literature. Phytoplankton biovolume was estimated following Hillebrand et al. (1999) and biomass was estimated with an algal cell density of 1 g mL^{-1}.

For zooplankton, water samples were collected at intervals of 1-m depth using a 5-L water sampler. A total of 50 L of water was filtered through a 38-µm plankton net. Samples were fixed in 4% formalin, then allowed to stand for 48 hours and concentrated to a definite volume. After shaking, a 10 mL sub-sample was taken for species identification and counting under a microscope. More than 400 zooplankton individuals were counted per sample. Crustacean samples were identified by dissection under a dissecting microscope. Rotifer species were identified according to Koste (1978). Individual body size of zooplankton was estimated from body length (µm) and width (µm) measurements according to the appropriate formulae. Individual weight was calculated assuming a density of 1 g/m^3. Biomass of zooplankton was calculated according to Dumont et al. (1975) and Huang et al. (1984).

Tilapia species identification

In order to clarify tilapia species identification and potential hybridization, we collected tilapia using multiple mesh-sized gill nets in May and June 2020 at the three shallow water locations where the tilapia are commonly caught, and then picked out 36 tilapia individuals covering all possible species. These were identified based on their morphology as: *Sarotherodon galilaeus*, *Tilapia zillii* and *Oreochromis mossambicus*. We used the mitochondrial marker (COI) and two nuclear markers (PTR and SH3PX3) to sequence the 36 individuals. Tilapia muscle tissue was cut to extract genomic DNA. We used the COI amplification primers PTR (Liao et al. 2016) and SH3PX3 (Zheng et al. 2019). Sequences alignment was performed using MEGA version 7.0. COI sequences were imported into the Barcode of Life Data System (BOLD, http://www.boldsystems.org/index.php) for molecular barcode classification. Nuclear PTR and SH3PX3 gene sequences were imported into the National Center for Biotechnology Information (NCBI) Basic Local Alignment Search Tool (BLAST; https://blast.ncbi.nlm.nih.gov/Blast.cgi), and two phylogenetic trees were constructed for hybrid analysis. The mitochondrial COI gene was used to determine the maternal tilapia, and nuclear genes PTR or SH3PX3 contained both genetic information of maternal or paternal tilapia; hybrids can be recognized by comparing the two phylogenetic trees.

Measurement of water quality

Water quality variables included total nitrogen (TN, μg L^{-1}), total phosphorus (TP, μg L^{-1}) and chemical oxygen demand (COD_{Mn}, μg L^{-1}), which were measured following the standard national methods (Chinese EPA http://kjs.mee.gov.cn/hjbhbz/bzwb/shjbh/). Water transparency was measured using Secchi depth (SD, m). Chlorophyll *a* (Chl*a*, μg L^{-1}) concentrations were determined by ultraviolet spectrophotometry (Lorenzen 1967; Lin et al. 2005).

Data analysis

Trophic state index (TSI) was estimated using the weighted TSI method based on Chl *a* (Lin et al. 2003). We performed ANOVA to compare the difference of annual average TN, TP and Chl *a* concentration at sites S1, S2 and S3 between 2015 and 2000 (or 2003). Using ANOVA, we also compared interannual differences in water quality variables at sampling site S4 from 2000 to 2015. We used regression analysis to check the long-term trends of hydrological and meteorological variables over the past two decades. In addition, we used a variance partitioning technique to assess the relative contribution of environmental variables to variation in bighead carp and tilapia catch (Grömping 2007). Total variance of bighead carp catch was decomposed into the proportion explained (R^2) by the tilapia catch, TSI, water level and water temperature. A permutation test was conducted to test the significance explained by each independent variable (Borcard et al. 2018). The variance of tilapia catch was decomposed into TSI, water level and water temperature. All statistical analyses were performed using package "Vegan" in the R platform. We conducted variance partitioning using "varpart" function (https://www.r-project.org).

Results

Tilapia species identification

The 36 COI sequences were matched to three species of tilapia with both 100% similarity in BOLD database, indicating that there were three maternal parents: *Sarotherodon galilaeus* (17 individuals), *Tilapia zillii* (18 individuals) and *Oreochromis mossambicus* (1 individual). PTR and SH3PX3 were matched to *Orechromis nilotcus* (100% or 99.71%), *Orechromis aureus* (98.78%) and *Sarotherodon galilaeus* (99.56%), except for a few SH3PX3 sequences were not matched. Combined analysis of mitochondrial marker and nuclear markers indicated that all the 36 tilapia were heterozygous individuals, and were the hybrids of: (i) *Sarothrodon galilaeus*♀ × *Orechromis nilotcus*♂ (17), (ii) *Orechromis mossambicus*♀ × *Orechromis nilotcus*♂ (1), and (iii) *Tilapia zillii*♀ × *Orechromis aureus*♂ (18) (see Supplementary material Figure S1 in detail). As each hybrid group had a nearly identical sequence, it is unlikely that the hybrids were from natural hybridization but rather from the nearby fish farms.

Long-term change of hydrological and meteorological variables

Hydrobiological and meteorological variables have cycled widely over the last few decades. Between 1990 and 2015, annual precipitation over Tangxi Reservoir ranged from 796.7 to 2564.5 mm. The lowest precipitation occurred in 2011 and the highest in 2006 (Figure 2a). Total outflow ranged from 3.13 to 12.14 billion m^3 (Figure 2b). Minimum water temperature ranged from 11.5 to 13.0 °C. Annual mean water level changed little from 43.1 to 54.3 m (Figure 2c, d), and the lowest level (43.1 m) was observed in 2009. Minimum air temperature ranged from 1.3 to 5.8 °C (Figure 2e), and the lowest air temperature was observed in 2010. Regression analysis showed that the hydrological and meteorological variables did not significantly change over the past two decades (Table 1, $P > 0.05$).

Water quality variables

Concentrations of TN, TP and Chl*a* at sites S1, S2 and S3 were higher in 2015 than in 2000 and 2003 (Figure 3). Concentrations of TN, TP, Chl*a*, and COD_{Mn} at site S4 (i.e., lacustrine zone near the dam) changed from 15.5 to 46.7 μg L^{-1}, 841.7 to 1555.0 μg L^{-1}, 2.38 to 20.5 μg L^{-1}, and 1550 to 2550 μg L^{-1}, respectively, all showing a general increasing trend at the S4 sampling site (Table 1, $P < 0.05$, Figure 4a–d). Secchi depth varied from 0.9 to 1.7 m, generally showing a decreasing trend at site S4 (Table 1, $P < 0.05$, Figure 4e). The trophic state index increased from 39 in 2000 to 53 in 2015 at S4 (Table 1, $P < 0.05$, Figure 4f). Ratios of Chl*a*:TN and Chl*a*:TP increased from 0.003 and 0.124 in 2000 to 0.012 and 0.392 in 2015, respectively at S4 (Table 1, $P < 0.05$, Figure 4g, h). Steep increases in the two ratios were observed between 2009 and 2012 (Table 1, $P < 0.05$).

Annual catch of tilapia and bighead carp

From 1991 to 2005, bighead carp dominated the fish catch, with an annual catch of more than 150 tons. The catch of silver carp was around six tons each year. The annual catch of tilapia was relatively low over the 15 years,

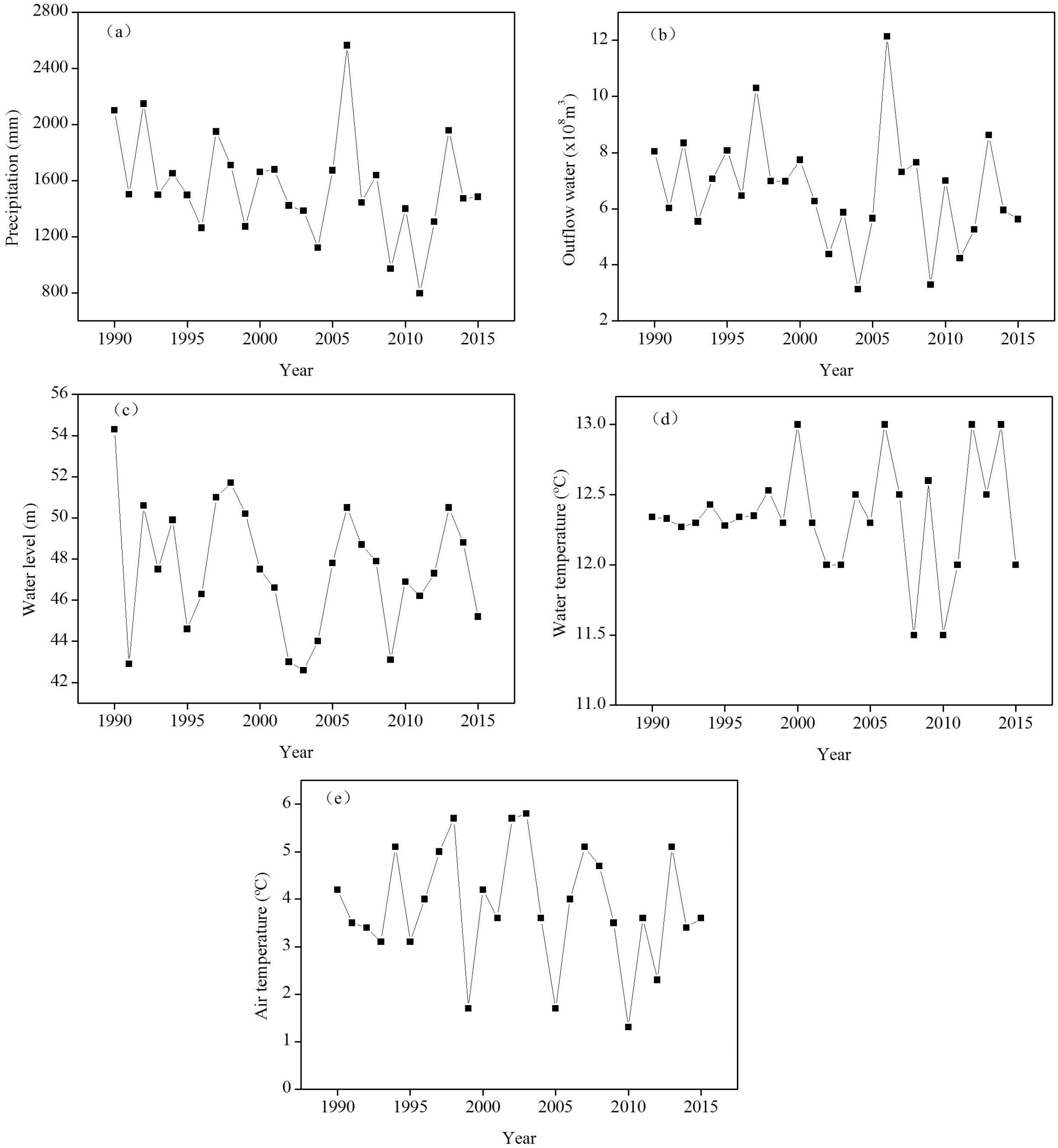

Figure 2. Precipitation (a), total outflow (b), water level (c), minimum water temperature (d), and minimum air temperature (e) of Tangxi Reservoir from 1990 to 2015.

ranging from 5 and 50 tons. The annual bighead carp catch declined sharply between 1991 and 1999, and then decreased at a slower rate since 1999, and became lower than that of tilapia from 2006. In contrast, the annual tilapia catch has increased throughout the study period, particularly after 2004, and reached 500 tons in 2015 (Figure 5). The maximum body weight of tilapia was 0.4 kg in 1995, 0.35 kg in 2005, and 0.3 kg in 2015.

Composition and change of phytoplankton and zooplankton

The total biomass of phytoplankton in July 2000 was 3.25 mg L^{-1}, comprised mainly of Cyanophyta, Chlorophyta and Bacillariophyta (Figure 6a).

Table 1. *F* test statistics for the regression relationships between water quality variables, hydrological variables and year.

Regression relationships	*F*	N	*P*
Air temperature (AT)~year	0.408	26	0.529
Water temperature (WT)~year	0.003	26	0.954
Water level (WL)~year	0.989	26	0.330
Precipitation ~year	2.259	26	0.146
Total outflow (TO)~year	1.348	26	0.257
Total nitrogen (TN)~year	77.87	16	< 0.01
Total phosphorus (TP)~year	60.99	16	< 0.01
chemical oxygen demand (COD)~year	33.45	16	< 0.01
Chlorophyll *a* (Chl*a*)~year	49.95	16	< 0.01
Secchi depth (SD)~year	14.18	16	< 0.01
Trophic state index (TSI)~year	99.2	16	< 0.01
Chl*a*:TN~year	36.16	16	< 0.01
Chl*a*:TP~year	25.32	16	< 0.01

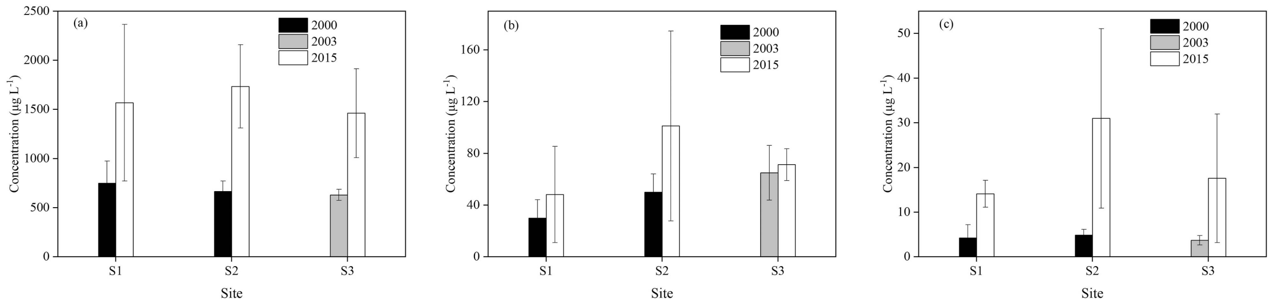

Figure 3. Concentrations of total nitrogen (TN) (a), total phosphorus (TP) (b), and chlorophyll a (Chl*a*) (c) at sampling sites S1, S2, and S3 in 2000, 2003, and 2015. Error bar indicates standard deviation (SD).

Cosmarium connatum and *Melosira* sp. were the dominant taxa. The total phytoplankton biomass in December 2000 was 0.87 mg L^{-1} and was dominated by *Eudorina elegans* and *Aulacoseira granulata*. In December 2014, the total phytoplankton biomass was 3.82 mg L^{-1}, with *Chroococcus* sp. and *Limnothrix redekei* the dominant species. The total phytplankton biomass in July 2015 was much higher with 12.42 mg L^{-1}, and dominated by *Limnothrix redekei* (Table 2).

The total biomass of zooplankton was 4.43 and 0.98 mg L^{-1} in July and December 2000, respectively (Figure 6b), and *Mesocyclops thermocyclopoides* was the dominant species. In December 2014, the biomass of zooplankton had decreased to 0.23 mg L^{-1}, with *Phyllodiaptomus tunguidus* and *Bosmina fatalis* the dominant species. In July 2015, the total biomass of zooplankton was 0.28 mg L^{-1}, dominated by *Phyllodiaptomus tunguidus* and *Moina micrura* (Table 2). There was a significant increase of phytoplankton biomass both in dry and wet seasons ($P < 0.05$), while for the zooplankton there was a significant decrease ($P < 0.05$).

Factors affecting bighead carp and tilapia catch

The variance of bighead carp catch was decomposed into those explained by tilapia + environmental variables (TSI + water level (WL) + water temperature (WT)) (Figure 7a). Much of the variance, 73.71%, was explained by tilapia

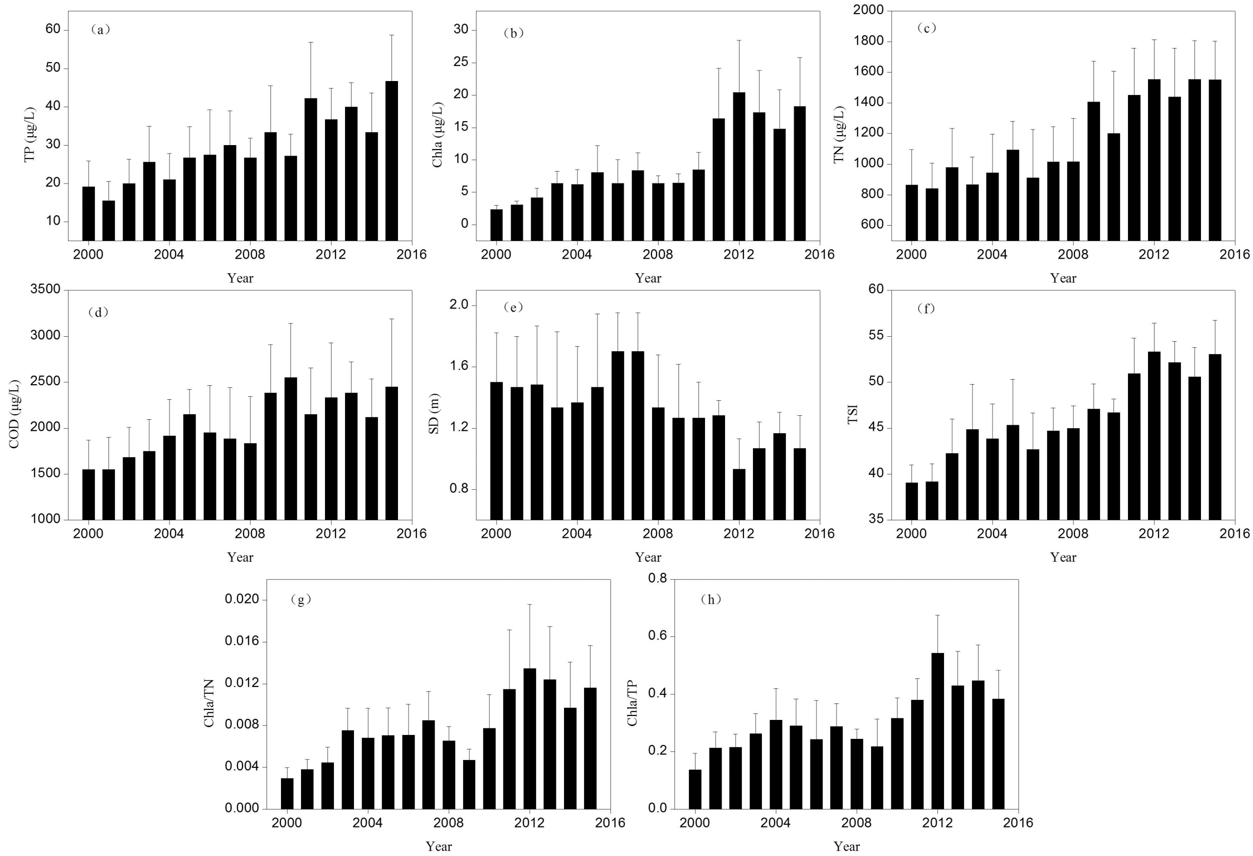

Figure 4. Annual variations in water quality variables at sampling site S4 from 2000 to 2015. TP: Total phosphorus, Chl*a*: Chlorophyll *a*, TN: Total nitrogen, COD: Chemical oxygen demand, SD: Secchi depth, TSI: Trophic state index. Error bar indicates standard deviation (SD).

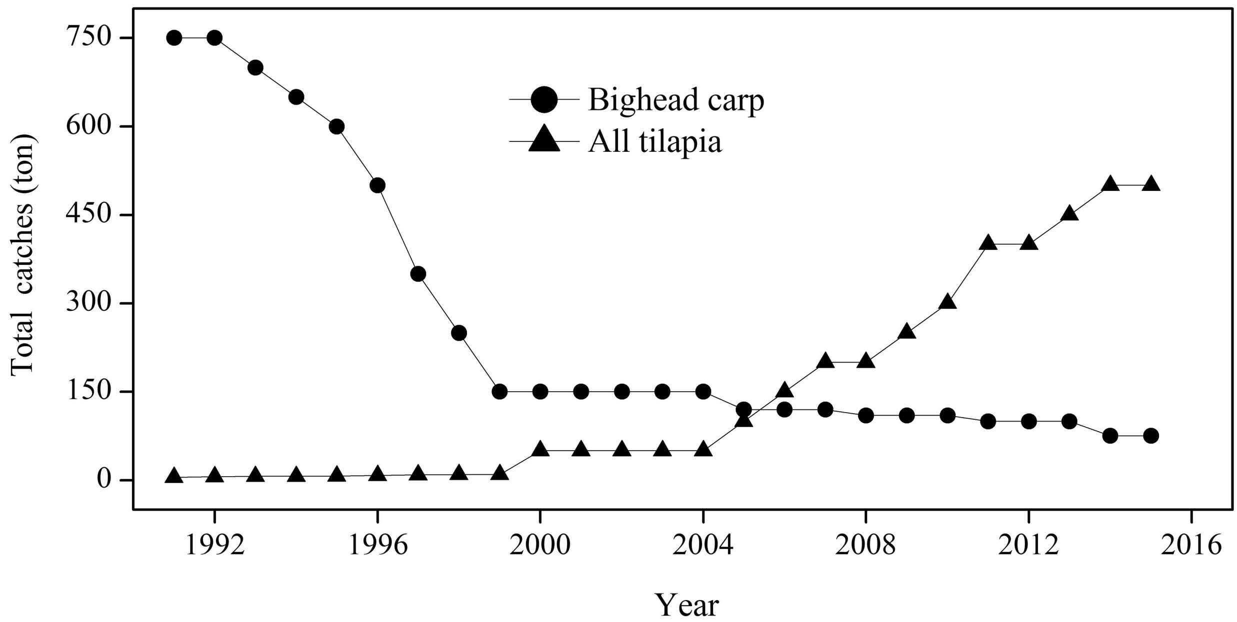

Figure 5. Long-term change in annual catch of all tilapia species and bighead carp from 1991 to 2015.

and TSI ($P < 0.05$), and 10.91% was explained by tilapia alone ($P < 0.05$). The variance of annual tilapia catch was decomposed into TSI + WT + WL (Figure 7b). The TSI explained 86.87% of the variance and WL 3.74% ($P <$ 0.05). Water temperature explained < 1% total variance of tilapia yield.

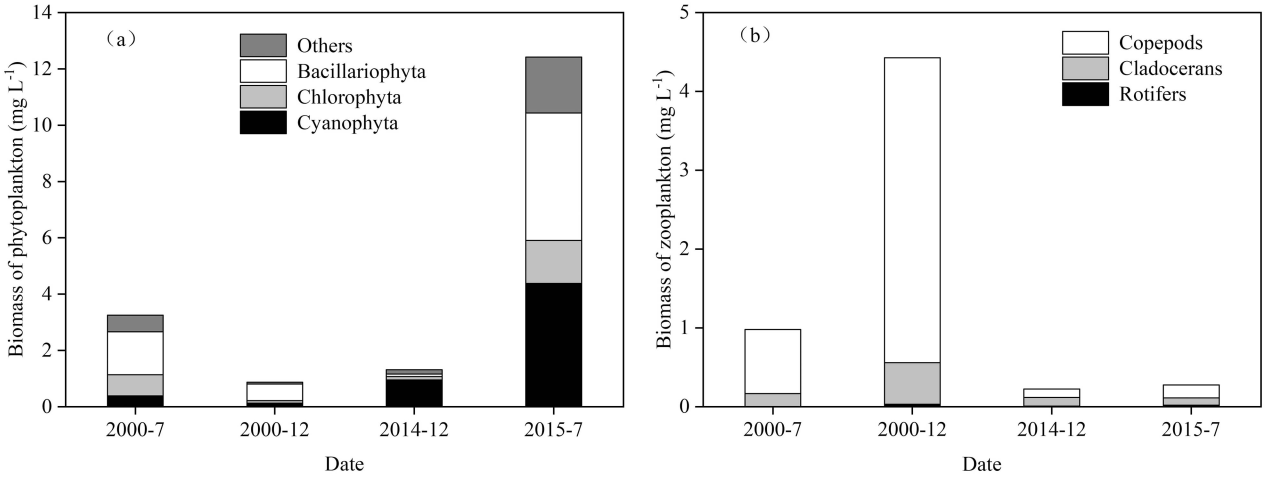

Figure 6. Phytoplankton biomass (a) and zooplankton biomass (b) in the pelagic zone near the dam (sampling site S4) in 2000, 2014 and 2015.

Table 2. Dominant species of phytoplankton and zooplankton in Tangxi Reservoir in 2000, 2014 and 2015.

Date	Phytoplankton	Zooplankton
7/2000	*Cosmarium connatum* *Aulacoseira* sp.	*Mesocyclops thermocyclopoides*
12/2000	*Eudorina elegans* *Aulacoseira granulate*	*Mesocyclops thermocyclopoides*
12/2014	*Limnothrix redekei* *Chroococcus* sp.	*Phyllodiaptomus tunguidus* *Bosmina fatalis*
7/2015	*Limnothrix redekei*	*Phyllodiaptomus tunguidus* *Moina micrura*

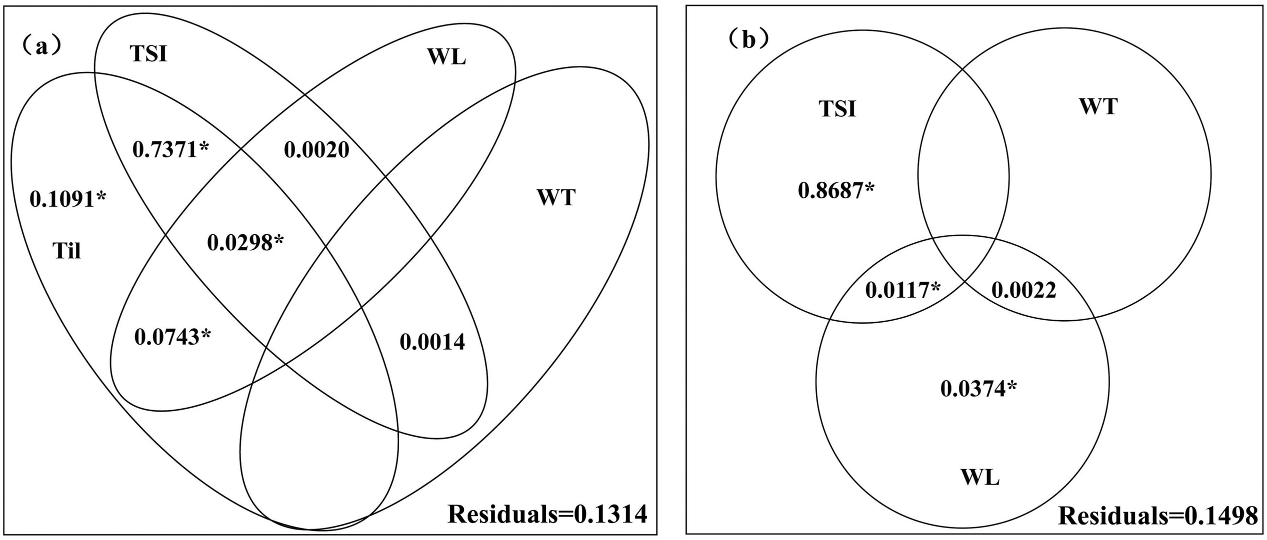

Figure 7. Decomposition of the bighead carp catch variance into tilapia catch and environmental variables (a) and of the tilapia catch variance into environmental variables (b). Til: Tilapia, TSI: Trophic state index, WL: Water level, WT: Water temperature. * indicates $P < 0.05$.

Discussion

Eutrophication and tilapia catch

Eutrophication of Tangxi Reservoir has increased over the past two decades. During that period, the annual tilapia catch increased and the catch of bighead carp has decreased. The tilapia catch has exceeded that of bighead carp since 2006. No pure tilapia species were detected, with all tilapia individuals in our study reservoir being hybrids; each hybrid had extreme low genetic diversity, indicating non-natural hybridization, but that this has occurred in culture.

Climate change (i.e., warming) and eutrophication are generally considered to be major contributors to tilapia establishment and subsequent population expansion (Fernando 1991; Jun et al. 2012; Lowe et al. 2012). Tilapia are distributed mainly in tropical and some subtropical regions (Canonico et al. 2005; Daga et al. 2016; Deines et al. 2016), and low temperature presents a physiologically limiting factor affecting their distributional range (Li et al. 2002; Schofield et al. 2011). The survival temperature for *O. niloticus* was reported to be about 10.6 °C (Atwood et al. 2003). In the past 26 years, the minimum water temperature in our reservoir was always above 11.5 °C. Therefore, tilapia can maintain their populations over winter. Variance decomposition of the annual catch further indicates that change in water temperature did not explain significant variation in tilapia catch.

Eutrophication invariably changes the structure of phytoplankton communities in aquatic ecosystems, and this change could further affect zooplankton and fish community structure through bottom-up effects (Bíró 1997; Smith and Schindler 2009). Phytoplankton and detritus are the main dietary items for some species of tilapia, such as *Oreochromis niloticus* and *Orechromis aureus*, which are efficient consumers of cyanobacteria (Semyalo et al. 2011; Moriarty and Moriarty 1973). Tilapia could assimilate up to 70–80% of ingested carbon from *Microcystis* spp. (Moriarty and Moriarty 1973). High nutrient loading from the input rivers would not only favor the biomass and proportion of cyanobacteria, but could also increase levels of organic matter in reservoirs (Wang and Wang 2009; O'Neil et al. 2012). This implies that eutrophication would enhance the growth and reproduction of tilapia (Fernando 1991). As an omnivorous fish (Gu et al. 1997; Peterson et al. 2006; Tesfahun and Temesgen 2018), tilapia not only feed on nanoplankton and suspended particulate matter (Northcott and Beveridge 1988; Sanderson et al. 1996), but also feed on benthic animals and plants, and on debris at the water bottom using its upper and lower pharyngeal and maxillary teeth (Bruton and Boltt 1975; Moor et al. 1986), thereby exhibiting a strong feeding flexibility.

Tangxi Reservoir was oligotrophic and mesotrophic prior to 2004. During this period, Bacillariophyta and Chlorophyta (e.g., *Melosira*, *Cyclotella* and *Arthrodesmus*) dominated the phytoplankton community, which had low abundance and biomass. Zooplankton had a high total biomass, particularly the cladoceran species *Bosminopsis deitersi* and *Bosmina longirostris* (Lin 1987; Zhao et al. 2002). Zooplankton provided about 150 tons of food for bighead carp, which supported a high catch of the stocked species, whereas tilapia catch was lower than 10 tons due to a lack of food resources. The reservoir became eutrophic after 2005. In 2012, Cyanophyta and Bacillariophyta (e.g., *Jaaginema angustissimum, M. flos-aquae*, and *Synedra acus*) dominated the phytoplankton community. Cyanophyta were observed to be dominant in 2015 (over 90% of total abundance), accounting for over 35% of total biomass; meanwhile, the composition of zooplankton shifted to small species such as rotifers and small cladocerans (e.g., *Keratella tecta* and *Bosmina* spp.). Jones et al. (2011) found that the Chla:TP ratio in a Missouri reservoir increased with increasing trophic state when the nutrient concentration was < 125 μg TP L^{-1}. The Chla:TP ratio was significantly reduced in the presence of large and medium-sized filter-feeding zooplankton (*Daphnia*) (Sarnelle 1992; Mazumder 1994a, b, c). Change in plankton community structure can alter fish community structure, and thus affect non-native fish species (Bíró 1997). The Chla:TP ratio in Tangxi Reservoir increased from 0.12 in 2000 to 0.39 in 2015, indicating that the distribution of nitrogen and phosphorus between phytoplankton and zooplankton has changed significantly through the reduced top-down effects of zooplankton. The zooplankton grazing effect on phytoplankton has been observed to decrease with increased fish biomass resulting from stocking of bighead carp in eutrophic reservoirs (Lin et al. 2020). Furthermore, the altered plankton community structure reduced the food quality for fish and consequently the energy conversion efficiency from plankton to fish. Inflow rivers provide a main input of nitrogen and phosphorus for reservoirs that result in high COD in the riverine zone. The COD in the Tangxi reservoir's littoral zone increased from 2 mg L^{-1} in 2000 to 3.5 mg L^{-1} in 2012 (Zhao et al. 2002). However, blooming cyanobacteria usually aggregate in the littoral zone driven by the wind. Debris is accumulated after cyanobacterial cell death and is then deposited as organic matter (Simon et al. 2002; Tang et al. 2010). Sediment in the littoral zone is easily re-suspended by wind and currents, thus providing a food source for tilapia.

In China, most lakes and reservoirs have been stocked with four major Chinese carp species since the 1970s, in particular with silver and bighead carp (Jia et al. 2013). Usually, the stocking rate of the two species ranges from 1 to 10 g m^{-3} and is dependent on plankton resources (Chen and He 2014). For algal control, the stocking rate would be up to 50 g m^{-3} (Xie and Liu 2001), of which silver carp account for major component as these filter and digest phytoplankton more efficiently (Li et al. 2013). The two species could not reproduce in most reservoirs as they are blocked form large rivers. In contrast to silver and bighead carp, tilapia can naturally reproduce in subtropical and tropical reservoirs (Costa-Pierce 2003; McDonald et al. 2007; Ovenden et al. 2015; Bradbeer et al. 2019), including the eutrophic Tangxi Reservoir. These factors have promoted a continuously increasing tilapia catch (Figure 8). After exceeding the bighead carp catch with 150 tons in 2006, tilapia reached a high annual catch of 500 tons in 2015 and took over the absolute dominance in the large reservoir.

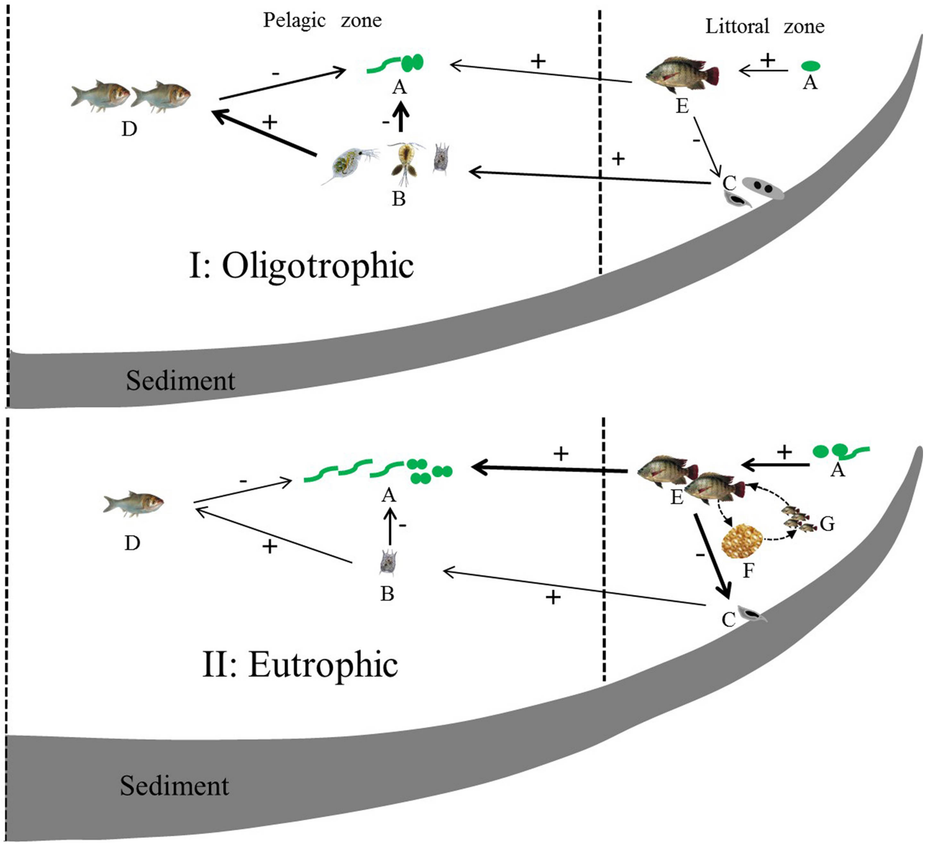

Figure 8. Conceptual model of the shift in ecological structure and processes with tilapia invasion and water quality change from oligotrophic (a) to eutrophic (b). A: phytoplankton; B: zooplankton; C: dormant egg; D: bighead carp; E: tilapia adult; F: tilapia egg; G: tilapia larvae.

Impact of tilapia on water quality and bighead carp catch

One direct impact of tilapia population expansion on ecosystems is the heavy nitrogen and phosphorus excretion, which promotes phytoplankton growth (Figueredo and Giani 2005; da Silva et al. 2014). Starling et al. (2002) reported that tilapia with individual wet weights ≥ 40 g excrete 1.12 μg TP g^{-1} wet weight h^{-1} and small tilapia (individual wet weight < 40 g) excrete 1.73 μg TP g^{-1}WW h^{-1}. Over the past two decades, the largest individual weights of tilapia in Tangxi Reservoir have decreased from 0.40 kg to 0.30 kg (data not shown). The higher metabolism of small-sized tilapia accelerates nutrient circulation. Moreover, tilapia are able to feed on large and medium-sized zooplankton (such as cladocerans), thereby weakening zooplankton's top-down control on small phytoplankton, and in so doing indirectly increases phytoplankton biomass (Okun et al. 2008; Fetahi et al. 2014; Wang et al. 2016). Zooplankton abundance in Tangxi Reservoir decreased substantially, which was related to grazing by tilapia, and the increased Chl*a*:TP ratio on average from 0.124 to 0.392. Furthermore, tilapia prefer the littoral zone (Bruton and Boltt 1975; McDonald et al. 2007) where the active zooplankton diapausing egg banks are primarily located, especially of cladocerans (Cáceres 1998). Fish feeding (Maia-Barbosa et al. 2003) and eutrophication (Brede et al. 2009; Bennion et al. 2015) impair egg banks and reduces seasonal recruitment of zooplankton. Xu et al. (2017) found that the zooplankton egg banks in shallow riverine zones in Liuxihe Reservoir, a mesotrophic water body also located on the Tropic of Cancer in China, contains more species and has an important role in zooplankton population dynamics. Eutrophication increases the anaerobic condition of sediments, which in turn may reduce hatching rates or even total hatchability of the diapausing eggs. In addition, tilapia is capable of inducing considerable disturbance and damage to the egg bank (Maia-Barbosa et al. 2003).

Bighead carp live in the pelagic zone and primarily filter-feed on zooplankton (Cremer and Smitherman 1980; Ke et al. 2007; Jayasinghe et al. 2014). Its catch is thus positively correlated with zooplankton biomass (Miura 1990). Bighead carp prefers to feed on large cladocerans in enclosure experiments (Cooke et al. 2009; Lin et al. 2013). In the 1980s and 1990s, the zooplankton biomass in Tangxi Reservoir was more than 3.0 mg L^{-1}, consisting mainly of *Keratella cochlearis*, *Bosmina longirostris*, and *Bosminopsis deitersi* (Lin 1987; Zhao et al. 2002). The bighead carp catch was more than 250 tons in that period. In 2000, however, the total zooplankton biomass in the reservoir decreased to 2.5 mg L^{-1}, and small rotifer species such as *Keratella cochlearis*, cladoceran *B. longirostris*, and copepod *Mesocyclops leuckarti* were also dominant (see Supplementary material Table S1 in detail). Meanwhile, the annual bighead carp catch declined to 150 tons. Yearly stocking of bighead carp inevitably results in high feeding pressure on zooplankton in the reservoir. On the other hand, eutrophication has impacted on the plankton community structure. In 2015, zooplankton in Tangxi Reservoir mainly comprised of *Keratella* and small cladocerans (e.g., *Bosmina* spp.), with a total biomass of 0.25 mg L^{-1}. Cladoceran biomass decreased from 0.35 mg L^{-1} in 2000 to just 0.10 mg L^{-1}, and the annual bighead carp catch decreased to 75 tons. A subsequent sharp decline in zooplankton biomass corresponded to an increase in eutrophication. This in turn led to a decline in bighead carp catch caused by food shortage and reduced food quality.

Variation partitioning analysis revealed that 74% of the bighead carp catch variation can be explained by TSI and tilapia catch. Therefore, the eutrophication of Tangxi Reservoir appears to have expanded food resources for tilapia. That is, the provision of more food, and the changes of plankton structure, would have been beneficial to the tilapia. The effect has been an accelerated growth of the tilapia population, and the resultant high population expansion in density and reduced body size has accelerated the nutrient cycling. This in turn has promoted phytoplankton growth in the pelagic water. Conversely, tilapia largely reduced the abundance of Cladocera in the water column and their diapausing egg hatching from the sediment, thereby indirectly affecting the phytoplankton community structure and bighead carp catch. We have summarized a mechanical framework for population expansion of tilapia and its ecological effects (Figure 8).

Conclusion

Long-term meteorological and hydrological data and water quality analysis showed that eutrophication promotes the Tangxi reservoir tilapia population. In our proposed conceptual model, increase in tilapia population size accelerates the nutrient cycle and reduces the seed bank and resting egg hatching of zooplankton, with a further impact on the phytoplankton community structure and bighead carp catch. This, in turn, leads to further degradation of the water quality.

Acknowledgements

We are grateful to two reviewers and the handing editor for their comments and suggestions which improved the manuscript. In particular, the suggestion to check hybridization pushed us to sequence for the species identification, which is valuable. We thank the Science and Technology Project of Guangdong Province (No. 2015B020235007) and the NSF of China (No. 31670460) to B.-P. Han. Dr. K. Chen, an ecologist from Australia, commented and revised the manuscript.

References

Atwood HL, Tomasso JR, Webb K, Gatlin DM (2003) Low-temperature tolerance of Nile tilapia, *Oreochromis niloticus*: Effects of environmental and dietary factors. *Aquaculture Research* 34: 241–251, https://doi.org/10.1046/j.1365-2109.2003.00811.x

Balirwa JS (1992) The evolution of the fishery of *Oreochromis niloticus* (Pisces, Cichlidae) in Lake Victoria. *Hydrobiologia* 232: 85–89, https://doi.org/10.1007/BF00014616

Bennion H, Davidson TA, Sayer CD, Simpson GL, Rose NL, Sadler JP (2015) Harnessing the potential of the multi-indicator palaeoecological approach: an assessment of the nature and causes of ecological change in a eutrophic shallow lake. *Freshwater Biology* 60: 1423–1442, https://doi.org/10.1111/fwb.12579

Bíró P (1997) Temporal variation in Lake Balaton and its fish populations. *Ecology of Freshwater Fish* 6: 196–216, https://doi.org/10.1111/j.1600-0633.1997.tb00163.x

Borcard D, Gillet F, Legendre P (2018) Numerical ecology with R. Springer, 450 pp, https://doi.org/10.1007/978-3-319-71404-2

Bradbeer SJ, Harrington J, Watson H, Warraich A, Shechonge A, Smith A, Tamatamah R, Ngatunga BP, Turner GF, Genner MJ (2019) Limited hybridization between introduced and critically Eedangered indigenous tilapia fishes in northern Tanzania. *Hydrobiologia* 832: 257–268, https://doi.org/10.1007/s10750-018-3572-5

Brede N, Sandrock C, Straile D, Spaak P, Jankowski T, Streit B, Schwenk K (2009) The impact of human-made ecological changes on the genetic architecture of *Daphnia* species. *Proceedings of The National Academy of Sciences* 106: 4758–4763, https://doi.org/10.1073/pnas.0807187106

Brooks WR, Jordan RC (2009) Enhanced interspecific territoriality and the invasion success of the spotted tilapia (*Tilapia mariae*) in South Florida. *Biological Invasions* 12: 865–874, https://doi.org/10.1007/s10530-009-9507-3

Bruton MN, Boltt RE (1975) Aspects of the biology of *Tilapia mossambica* Peters (Pisces: Cichlidae) in a natural freshwater lake (Lake Sibaya, South Africa). *Journal of Fish Biology* 7: 423–445, https://doi.org/10.1111/j.1095-8649.1975.tb04618.x

Bwanika GN, Makanga B, Kizito Y, Chapman LJ, Balirwa J (2004) Observations on the biology of Nile tilapia, *Oreochromis niloticus* L., in two Ugandan crater lakes. *African Journal of Ecology* 42: 93–101, https://doi.org/10.1111/j.1365-2028.2004.00468.x

Canonico GC, Arthington A, McCrary JK, Thieme ML (2005) The effects of introduced tilapias on native biodiversity. *Aquatic Conservation* 15: 463–483, https://doi.org/10.1002/aqc.699

Cáceres CE (1998) Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79: 1699–1710, https://doi.org/10.1890/0012-9658(1998)079[1699:IVITAP]2.0.CO;2

Casal CMV (2006) Global documentation of fish introductions: the growing crisis and recommendations for action. *Biological Invasions* 8: 3–11, https://doi.org/10.1007/s10530-005-0231-3

Chen DQ, He L (eds) (2014) Technical manual of fish breeding and releasing for four major Chinese carps. Science Press, Beijing, 152 pp [in Chinese]

Chen SZ, Ye W (1994) Study on introduced tilapia in China. *Chinese Journal of Zoology* 29: 18–23 [in Chinese]

Cooke SL, Hill WR, Meyer KP (2009) Feeding at different plankton densities alters invasive bighead carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition. *Hydrobiologia* 625: 185–193, https://doi.org/10.1007/s10750-009-9707-y

Costa-Pierce BA (2003) Rapid evolution of an established feral population (*Oreochromis* spp.): The need to incorporate invasion science into regulatory structures. *Biological Invasions* 5: 71–84, https://doi.org/10.1023/A:1024094606326

Cremer MC, Smitherman RO (1980) Food habits and growth of silver and bighead carp in cages and ponds. *Aquaculture* 20: 57–64, https://doi.org/10.1016/0044-8486(80)90061-7

Deines AM, Wittmann ME, Deines JM, Lodge DM (2016) Tradeoffs among ecosystem services associated with global *Tilapia* introductions. *Reviews in Fisheries Science & Aquaculture* 24: 178–191, https://doi.org/10.1080/23308249.2015.1115466

da Silva LHS, Arcifa MS, Salazar-Torres G, Huszar VLM (2014) *Tilapia rendalli* increases phytoplankton biomass of a shallow tropical lake. *Acta Limnologica Brasiliensia* 26: 429–441, https://doi.org/10.1590/S2179-975X2014000400010

Daga VS, Debona T, Abilhoa V, Gubiani ÉA, Vitule JRS (2016) Non-native fish invasions of a Neotropical ecoregion with high endemism: A review of the Iguaçu River. *Aquatic Invasions* 11: 209–223, https://doi.org/10.3391/ai.2016.11.2.10

De Silva SS, Subasinghe RP, Bartley DM, Lowther A (2004) Tilapias as alien aquatics in Asia and the Pacific: a review. FAO Fisheries Technical Paper. No. 453. FAO, Rome, pp 56–60

Dumont HJ, Van de Velde I, Dumont S (1975) The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75–97, https://doi.org/10.1007/BF00377592

Edler L, Elbrächter M (2010) The Utermöhl method for quantitative phytoplankton analysis. In: Karlson B, Cusack C, Bresnan (eds), Microscopic and Molecular Methods for Quantitative Phytoplankton Analysis. UNESCO, Paris, pp 13–20

Fernando CH (1991) Impacts of fish introductions in tropical Asia and America. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 24–32, https://doi.org/10.1139/f91-301

Fetahi T, Schagerl M, Mengistou S (2014) Key drivers for phytoplankton composition and biomass in an Ethiopian highland lake. *Limnologica* 46: 77–83, https://doi.org/10.1016/j.limno.2013.10.007

Figueredo CC, Giani A (2005) Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). *Freshwater Biology* 50: 1391–1403, https://doi.org/10.1111/j.1365-2427.2005.01407.x

Grammer GL, Slack WT, Peterson MS, Dugo MA (2012) Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) establishment in temperate Mississippi, USA: Multi-year survival confirmed by otolith ages. *Aquatic Invasions* 7: 367–376, https://doi.org/10.3391/ai.2012.7.3.008

Grömping U (2007) Estimators of relative importance in linear regression based on variance decomposition. *The American Statistician* 61: 139–147, https://doi.org/10.1198/000313007X188252

Gu B, Schell DM, Huang X, Yie Fei (1996) Stable isotope evidence for dietary overlap between two planktivorous fishes in aquaculture ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2814–2818, https://doi.org/10.1139/f96-242

Gu B, Schelske CL, Hoyer MV (1997) Intrapopulation feeding diversity in blue tilapia: Evidence from stable-isotope analyses. *Ecology* 78: 2263–2266, https://doi.org/10.1890/0012-9658(1997)078[2263:IFDIBT]2.0.CO;2

Gu DE, Ma GM, Zhu YJ, Luo D, Li YY, Wei H, Mu XD, Luo JR, Hu YC (2015) The impacts of invasive Nile tilapia (*Oreochromis niloticus*) on the fisheries in the main rivers of Guangdong Province, China. *Biochemical Systematics and Ecology* 59: 1–7, https://doi.org/10.1016/j.bse.2015.01.004

Gu DE, Mu XD, Xu M, Luo D, Wei H, Li YY, Zhu YJ, Luo JR, Hu YC (2016) Identification of wild tilapia species in the main rivers of south China using mitochondrial control region sequence andmorphology. *Biochemical Systematics and Ecology* 65: 100–107, https://doi.org/10.1016/j.bse.2016.02.007

Gu DE, Yu FD, Xu M Wei H, Mu XD, Luo D (2018) Temperature effects on the distribution of two invasive tilapia species (*Tilapia zillii* and *Oreochromis niloticus*) in the rivers of South China. *Journal of Freshwater Ecology* 33: 511–524, https://doi.org/10.1080/02705060.2018.1517698

Hillebrand H, Kirschtel D, Pollinger U, Pollinger U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35: 403–424, https://doi.org/10.1046/j.1529-8817.1999.3520403.x

Hu HJ, Wei YX (eds) (2006) The Freshwater Algae of China - Systematics, Taxonomy and Ecology. Science Press, Beijing, 1023 pp [in Chinese]

Huang XF, Chen XM, Wu ZT, Hu CY (1984) Study on the change in abundance and biomass of zooplankton in lake Donghu Wuhan. *Acta Hydybiology Sinica* 8: 345–358 [in Chinese]

Jayasinghe UAD, García-Berthou E, Li ZJ, Li W, Zhang TL (2014) Co-occurring bighead and silver carps show similar food preference but different isotopic niche overlap in different lakes. *Environmental Biology of Fishes* 98: 1185–1199, https://doi.org/10.1007/s10641-014-0351-7

Jia PQ, Zhang WB, Liu QG (2013) Lake fisheries in China: Challenges and opportunities. *Fisheries Research* 140: 66–72, https://doi.org/10.1016/j.fishres.2012.12.007

Jones JR, Obrecht DV, Thorpe AP (2011) Chlorophyll maxima and chlorophyll: Total phosphorus ratios in Missouri reservoirs. *Lake and Reservoir Management* 27: 321–328, https://doi.org/10.1080/07438141.2011.627625

Jun Q, Xu P, Wang HZ, Li RH, Wang H (2012) Combined effect of temperature, salinity and density on the growth and feed utilization of Nile tilapia juveniles (*Oreochromis niloticus*). *Aquaculture Research* 43: 1344–1356, https://doi.org/10.1111/j.1365-2109.2011.02938.x

Ke Z, Xie P, Guo L, Liu Y, Yang H (2007) In situ study on the control of toxic *Microcystis* blooms using phytoplanktivorous fish in the subtropical Lake Taihu of China: A large fish pen experiment. *Aquaculture* 265: 127–138, https://doi.org/10.1016/j.aquaculture.2007.01.049

Koste W (1978) Rotatoria. Die Rädertiere Mitteleuropas, 2 Vols. Gebrüder orntraeger, 1141 pp, 234 pl

Leprieur F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish invasions in the world's river systems: When natural processes are blurred by human activities. *PLoS biology* 6: 404–410, https://doi.org/10.1371/journal.pbio.0060028

Li S, Li C, Dey M, Gagalac F, Dunham R (2002) Cold tolerance of three strains of Nile tilapia, *Oreochromis niloticus*, in China. *Aquaculture* 213: 123–129, https://doi.org/10.1016/S0044-8486(02)00068-6

Li KY, Xu ZH, Liu ZW, Gu BH (2013) Stable isotope enrichment, dietary sources and trophic overlap between silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*). *Aquaculture* 402/403: 8–12, https://doi.org/10.1016/j.aquaculture.2013.03.020

Liang Y, Melack JM, Wang J (1981) Primary production and fish yields in Chinese ponds and lakes. *Transactions of the American Fisheries Society* 110: 346–350, https://doi.org/10.1577/1548-8659(1981)110<346:PPAFYI>2.0.CO;2

Liao J, Zhang S, Long S, Huang C, GuoY, Wang Z, Liu C (2016) Sequence variation and molecular phylogeny of mitochondrial COI gene segments from five species of gobiidae family. *Journal of Guangdong Ocean University* 36(1): 7–12

Lin YT (1987) Evaluation of fishery performance and improvement of fish productivity in reservoirs of Guangdong Province. *Reservoir Fisheries* 4: 29–34 [in Chinese]

Lin QQ, Hu R, Duan SS, Han BP (2003) Reservoir trophic states and the response of plankton in Guangdong Province. *Acta Ecologica Sinica* 23: 1101–1108, https://doi.org/10.3321/j.issn:1000-0933.2003.06.010 [in Chinese]

Lin QQ, Zhao PP, Wu QT, Wei ZH, Li HM, Han BP (2013) Predation pressure induced by seasonal fishing moratorium changes the dynamics of subtropical Cladocera populations. *Hydrobiologia* 710: 73–81, https://doi.org/10.1007/s10750-012-1260-4

Lin QQ, Chen QH, Peng, Xiao LJ, Lei LM, Jeppesen E (2020) Do bigheaded carp act as a phosphorus source for phytoplankton in (sub) tropical Chinese reservoirs? *Water Research* 180: 115841, https://doi.org/10.1016/j.watres.2020.115841

Lin SJ, He LJ, Huang PS, Han BP (2005) Comparison and improvement on the extraction method for chlorophyll *a* in phytoplankton. *Ecological Science* 24: 9–11, https://doi.org/10.1007/s10971-005-6694-y [in Chinese]

Liu ZW (2017) Present situation of water quality and pollution source analysis in Tangxi Reservoir. *Journal of Green Science and Technology* 14: 59–61, https://doi.org/10.16663/j.cnki.lskj.2017.14.024 [in Chinese]

Liu Y, Yang PJ, Sheng H, Guo HC, Zhou F, Xiang N, Wang CY, Yang YH, Yan XP, Chen X, Zhang S (2012) Watershed pollution prevention planning and eutrophication control strategy for Lake Dianchi. *Acta Scientiae Circumstantiae* 32: 1962–1972, https://doi.org/10.13671/j.hjkxxb.2012.08.024 [in Chinese]

Lowe MR, Wu W, Peterson MS, Brown-Peterson NJ, Slack WT, Schofield PJ (2012) Survival, growth and reproduction of non-native Nile tilapia II: Fundamental niche projections and invasion potential in the northern Gulf of Mexico. *PLoS ONE* 7: e41580, https://doi.org/10.1371/journal.pone.0041580

Lorenzen CJ (1967) Determination of chlorophyll and pheo-pigments: spectrophotometric equations. *Limnology and Oceanography* 12: 343–346, https://doi.org/10.4319/lo.1967.12.2.0343

Lund JWG, Kipling C, Cren EDL (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia* 11: 143–170, https://doi.org/10.1007/BF00007865

Maia-Barbosa PM, Eskinazi-Sant'Anna EM, Valadares CF, Pessoa GCD (2003) The resting eggs of zooplankton from a tropical, eutrophic reservoir (Pampulha Reservoir, southeast Brazil). *Lakes & Reservoirs: Research and Management* 8: 269–275, https://doi.org/10.1111/j.1440-1770.2003.00229.x

Mazumder A (1994a) Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. *Ecology* 75: 1141–1149, https://doi.org/10.2307/1939437

Mazumder A (1994b) Phosphorus-chlorophyll Relationships under contrasting herbivory and thermal stratification: Predictions and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 390–400, https://doi.org/10.1139/f94-040

Mazumder A (1994c) Phosphorus-chlorophyll relationships under contrasting zooplankton community structure: potential mechanisms. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 401–407, https://doi.org/10.1139/f94-041

McDonald JL, Peterson MS, Slack WT (2007) Morphology, density, and spatial patterning of reproductive bowers in an established alien population of Nile tilapia, *Oreochromis niloticus* Linnaeus. *Journal of Freshwater Ecology* 22: 461–468, https://doi.org/10.1080/02705060.2007.9664176

Miura T (1990) The effects of planktivorous fishes on the plankton community in a eutrophic lake. *Hydrobiologia* 200/201: 567–579, https://doi.org/10.1007/BF02530374

Moor FCD, Wilkinson RC, Herbst HM (1986) Food and feeding habits of *Oreochromis mossambicus* (Peters) in hypertrophic Hartbeespoort Dam, South Africa. *African Zoology* 21: 170–176, https://doi.org/10.1080/02541858.1986.11447976

Moriarty DJW, Moriarty CM (1973) The assimilation of carbon from phytoplankton by two herbivourous fishes: *Tilapia nilotica* and *Haplochromis nigripinnis*. *Journal of Zoology* 171: 41–55

Nagayi-Yawe KJ, Ogutu-Ohwayo R, Kizito YS (2006) Population characteristics of *Oreochromis esculentus* in the Victoria and Kyoga lake basins. Implications for conservation and improvement of the stocks. *African Journal of Ecology* 44: 423–430, https://doi.org/10.1111/j.1365-2028.2006.00645.x

Northcott ME, Beveridge MCM (1988) The development and structure of pharyngeal apparatus associated with filter feeding in tilapias (*Oreochromis niloticus*). *Journal of Zoology* 215: 133–149, https://doi.org/10.1111/j.1469-7998.1988.tb04889.x

Okun N, Brasil J, Attayde JL, Costa IAS (2008) Omnivory does not prevent trophic cascades in pelagic food webs. *Freshwater Biology* 53: 129–138, https://doi.org/10.1111/j.1365-2427.2007.01872.x

O'Neil JM, Davis TW, Burford MA, Gobler CJ (2012) The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change. *Harmful Algae* 14: 313–334, https://doi.org/10.1016/j.hal.2011.10.027

Ovenden JR, Macbeth GM, Pope L, Thuesen P, Street R, Broderick D (2015) Translocation between freshwater catchments has facilitated the spread of tilapia in eastern Australia. *Biological Invasions* 17: 637–650, https://doi.org/10.1007/s10530-014-0754-6

Peterson MS, Slack WT, Waggy GL, Finley J, Woodley CW, Partyka ML (2006) Foraging in non-native environments: Comparison of Nile tilapia and three co-occurring native centrarchids in invaded coastal Mississippi watersheds. *Environmental Biology of Fishes* 76: 283–301, https://doi.org/10.1007/s10641-006-9033-4

Russell DJ, Thuesen PA, Thomson FE (2012) A review of the biology, ecology, distribution and control of Mozambique tilapia, *Oreochromis mossambicus* (Peters 1852) (Pisces: Cichlidae) with particular emphasis on invasive Australian populations. *Reviews in Fish Biology and Fisheries* 22: 533–554, https://doi.org/10.1007/s11160-011-9249-z

Sanderson S, Stebar M, Ackermann K, Jones SH, Batjakas IE, Kaufman L (1996) Mucus entrapment of particles by a suspension-feeding tilapia (Pisces: Cichlidae). *The Journal of Experimental Biology* 199: 1743–1756

Sarnelle O (1992) Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* 73: 551–560, https://doi.org/10.2307/1940761

Schofield PJ, Peterson MS, Lowe MR, Brown-Peterson NJ, Slack WT (2011) Survival, growth and reproduction of non-indigenous Nile tilapia, *Oreochromis niloticus* (Linnaeus 1758). I. Physiological capabilities in various temperatures and salinities. *Marine and Freshwater Research* 62: 439–449, https://doi.org/10.1071/MF10207

Semyalo R, Rohrlack T, Kayiira D, Kizito YS, Byarujali S, Nyakairu G, Larsson P (2011) On the diet of Nile tilapia in two eutrophic tropical lakes containing toxin producing cyanobacteria. *Limnologica* 41: 30–36, https://doi.org/10.1016/j.limno.2010.04.002

Simon M, Grossart HP, Schweitzer B, Ploug H (2002) Microbial ecology of organic aggregates in aquatic ecosystems. *Aquatic Microbial Ecology* 28: 175–211, https://doi.org/10.3354/ame028175

Smith VH, Schindler DW (2009) Eutrophication science: where do we go from here? *Trends in Ecology & Evolution* 24: 201–207, https://doi.org/10.1016/j.tree.2008.11.009

Song XL, Liu ZW, Yang GJ, Chen YW (2010) Effects of resuspension and eutrophication level on summer phytoplankton dynamics in two hypertrophic areas of Lake Taihu, China. *Aquatic Ecology* 44: 41–54, https://doi.org/10.1007/s10452-009-9258-3

Starling F, Lazzaro XC, Cavalcanti C, Moreira R (2002) Contribution of omnivorous tilapia to eutrophication of a shallow tropical reservoir: evidence from a fish kill. *Freshwater Biology* 47: 2443–2452, https://doi.org/10.1046/j.1365-2427.2002.01013.x

Tan XC, Li XH, Li YF, Li J (2012) Early development and spatial distribution of the Nile tilapia (*Oreochromis niloticus*) in the Pearl River. *Journal of Biosafety* 21: 295–299, https://doi.org/10.3969/j.issn.2095-1787.2012.04.011 [in Chinese]

Tang YA (1970) Evaluation of balance between fishes and available fish foods in multispecies fish culture ponds in Taiwan. *Transactions of the American Fisheries Society* 99: 708–718, https://doi.org/10.1577/1548-8659(1970)99<708:EOBBFA>2.0.CO;2

Tang XM, Gao GA, Chao JY, Wang XD, Zhu GW, Qin BQ (2010) Dynamics of organic-aggregate-associated bacterial communities and related environmental factors in Lake Taihu, a large eutrophic shallow lake in China. *Limnology and Oceanography* 55: 469–480, https://doi.org/10.4319/lo.2010.55.2.0469

Tesfahun A, Temesgen M (2018) Food and feeding habits of Nile tilapia *Oreochromis niloticus* (L.) in Ethiopian water bodies: A review. *International Journal of Fisheries and Aquatic Studies* 6: 43–47

Vanessa SD, Éder AG (2012) Variations in the endemic fish assemblage of a global freshwater ecoregion: Associations with introduced species in cascading reservoirs. *Acta Oecologica* 41: 95–105, https://doi.org/10.1016/j.actao.2012.04.005

Vicente IST, Fonseca-Alves CE (2013) Impact of introduced Nile tilapia (*Oreochromis niloticus*) on non-native aquatic ecosystems. *Pakistan Journal of Biological Sciences* 16: 121–126, https://doi.org/10.3923/pjbs.2013.121.126

Wang HJ, Wang HZ (2009) Mitigation of lake eutrophication: Loosen nitrogen control and focus on phosphorus abatement. *Progress in Natural Science* 19: 1445–1451, https://doi.org/10.1016/j.pnsc.2009.03.009

Wang Y, Gu X, Zeng Q, Mao Z, Wang W (2016) Contrasting response of a plankton community to two filter-feeding fish and their feces: An in-situ enclosure experiment. *Aquaculture* 465: 330–340, https://doi.org/10.1016/j.aquaculture.2016.08.014

Xie P, Liu JK (2001) Practical success of biomanipulation using filter-feeding fish to control cyanobacteria blooms: a synthesis of decades of research and application in a subtropical hypereutrophic lake. *The Scientific World Journal* 1: 337–356, https://doi.org/10.1100/tsw.2001.67

Xu L, Xu SL, Han XX, Li SJ, Dumont H, Han BP (2017) Spatial heterogeneity and long-term dynamics of Cladoceran ephippia in a monsoonal reservoir, driven by hydrology and eutrophication. *Journal of Paleolimnology* 58: 571–584, https://doi.org/10.1007/s10933-017-9993-8

Yang YG, He ZL, Lin Y, Stoffella PJ (2010) Phosphorus availability in sediments from a tidal river receiving runoff water from agricultural fields. *Agricultural Water Management* 97: 1722–1730, https://doi.org/10.1016/j.agwat.2010.06.003

Zengeya TA, Robertson MP, Booth AJ, Chimimba CT (2013) Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: concerns and implications for the conservation of indigenous congenerics. *Biological Invasions* 15: 1507–1521, https://doi.org/10.1007/s10530-012-0386-7

Zhao SY, Lin QQ, Hu R, Wang ZH, Han BP, Liu AJ (2002) Current eutrophication in Tangxi Reservoir of Guangdong Province. *Ecological Science* 21: 316–319, https://doi.org/10.1007/s11769-002-0041-9 [in Chinese]

Zheng X, Zhao L, Wu Z, Zhang J, Hunag L, Wang K, Zhang M (2019) Wild tilapia population and its hybridization in Youjiang River, Guangxi. *Journal of Southern Agriculture* 50(12): 2797–2805 [in Chinese]

Supplementary material

The following supplementary material is available for this article:

Figure S1. Maximum likelihood tree of 36 tilapia individuals with sequences based on mitochondrial maker (COI) and nuclear markers (PTR and SH3PX3).

Table S1. Species of phytoplankton and zooplankton at pelagic site (S4).

This material is available as part of online article from:
http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Peng_etal_SupplementaryTable.xlsx
http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Peng_etal_SupplementaryFigure.pdf