Tropical Ecology **57**(3): 567-581, 2016 ISSN 0564-3295

www.tropecol.com

Fish diversity and trophic interactions in Lake Sampaloc (Luzon Is., Philippines)

JONATHAN CARLO A. BRIONES[1,2*], REY DONNE S. PAPA[1,2,3*], GIL A. CAUYAN[1,3], NORMAN MENDOZA[1,4] & NOBORU OKUDA[5,6]

[1]The Graduate School, [2]Department of Biological Sciences and [3]Research Center for the Natural and Applied Sciences of the University of Santo Tomas, Manila, Philippines
[4]Philippine Nuclear Research Institute, Department of Science and Technology, Quezon City, Philippines
[5]Center for Ecological Research, Kyoto University, Japan
[6]Research Institute for Humanity and Nature, Kyoto, Japan

Abstract: In this paper, we aimed to contribute to the conservation research of a heavily impacted tropical lake ecosystem by characterizing its previously undescribed fish diversity and also elucidating the trophic structure of its fish community. Our study area is Lake Sampaloc, a small crater lake in the southern region of Luzon Island, Philippines. This lake has been heavily used for economic resource functions, such as aquaculture, for decades. Hindrances to the effective implementation of regulatory provisions have produced detrimental ecological effects on the lake, which has recently been declared as "Threatened Lake of the Year 2014". We employed several sporadic fish surveys during a span of two years (2012 to 2014) to identify fishes in the lake. We also used stable isotope analysis to elucidate the trophic level and production reliance of important aquatic consumers. We discovered that the lake fish populations are heavily reliant on periphyton production and are mostly composed of non-native and potentially established invasive fish species. In addition, trophic niche overlaps are observed among non-native fish and native species. For the past three decades, Lake Sampaloc has been classified as eutrophic with high phytoplankton standing biomass. A possible direction for lake rehabilitation research is to investigate ways to change the present turbid state into a clear water system that is predominantly composed of submerged native vegetation. Such a macrophyte-based environment may help sustain the development and recruitment of native juvenile fish and also provide a more diverse functional habitat for fish assemblages that have overlapping trophic niches.

Key words: Introduced fish, *Leiopotherapon plumbeus*, periphyton, small lakes, stable isotope analysis, trophic niche.

Handling Editor: Donna Marie Bilkovic

Introduction

Human society has always utilized inland water bodies for many necessary economic services, but in doing so, has overlooked its value as a supporting ecosystem. Freshwater ecosystems accumulate the detrimental impacts of human activities (Zalewski & Welcomme 2001) and are altered or degraded much faster than they are being restored (NRC 1992). While research on the

---

[*] *Corresponding Author*; e-mail: jonathancarlo@ymail.com
Postal Address: Room 308, Biology Laboratory, Thomas Aquinas Research Complex, University of Santo Tomas, Sampaloc, Manila 1015, Philippines

role of anthropogenic stressors has been focused mainly on its effects to the ecology of large lakes (Wetzel 2001), smaller lakes have received much less attention despite their rich biodiversity (Scheffer *et al.* 2006). In fact, lake size has little association with species richness across several taxonomic groups (Oertli *et al.* 2002; William *et al.* 2003) suggesting that small lakes, or even ponds, are equally important areas for conservation.

Lake Sampaloc is among many small lakes in the Philippines that have been tapped as an economic resource, most notably as a pioneer site for aquaculture in the 1970s (Santiago *et al.* 2001). By the late 1980s, however, floating cages for tilapia culture in the lake expanded from 0.06 to 0.33 km^2 of its total surface area, with at most 6,000 t of fish feeds used in the lake annually (Santiago & Arcilla 1993). The resulting increase in allochthonous organic matter caused the worst occurrences of mass fish kills in Lake Sampaloc in the early 1990s, resulting in revenue loss and the risk of lake faunal extinction. These events prompted the revision of aquaculture and integrated water resources management plans in the lake which resulted to the reduction of the allowable cage area to only 0.12 km^2 which is approximately 10 % of the lake surface area (Cariño 2003). These new provisions were geared towards lake rehabilitation and the protection of local stakeholders through responsible aquaculture practices. However, just recently, Global Nature Fund (GNF 2014) proclaimed Lake Sampaloc as the "Threatened Lake of the Year 2014". GNF cited the local government's difficulty in implementing the imposed regulations due to inadequacy of manpower and funding, and highlighted the continuing degradation of the Lake Sampaloc ecosystem. This issue has raised concerns regarding the current status and potential threats to Lake Sampaloc's biodiversity. However, to date, most of the published research done in the lake has been related only to aquaculture implications (Cariño 2003; Santiago 2001; Santiago & Arcilla 1993; Tan *et al.*1994) with only a handful of studies on the lake's actual biota (Quilang *et al.* 2007; Santos *et al.* 2010). As a result, there is a gap on what is currently known regarding the lake's biodiversity. An assessment of the present ecology and establishment of baseline information regarding the various biota of Lake Sampaloc is therefore needed.

Analyzing the trophic structure of Lake Sampaloc would be an ideal approach to understand its current state as an ecosystem. However, comprehensively detailing lake trophic dynamics will be a significant feat due to the lack of baseline data. This is compounded by the fact that trophic interactions in lake ecosystems are complex, with a need to characterize both benthic and pelagic pathways which undergo different processes but are equally important for understanding the whole-lake perspective (Carpenter & Kitchell 1993; Jeppensen *et al.* 1997; Vadeboncoeur *et al.* 2002). An alternative option to comprehensively detailing the trophic dynamics of all lake biota would be to study fish species diversity through field surveys and fish trophic dynamics using stable isotope analysis, since fish are understood to be integrators of benthic and pelagic food webs in lakes (Vander Zanden & Vadeboncoeur 2002). Fish species profiles and stable isotope analyses have been successfully used in tandem to determine the presence of anthropogenic activities in small freshwater ecosystems (Lake *et al.* 2001), provide evidence for the food web consequences of fish species invasions in lakes (Vander Zanden *et al.* 1999), predict the impact and occurrences of fish introductions in lakes (Vander Zanden *et al.* 2004), and provide historically relevant restoration targets for the lake-wide rehabilitation of native aquatic communities (Vander Zanden *et al.* 2003).

This paper intends to produce baseline information on the fish species profile of Lake Sampaloc and also describe the present trophic structure of the lake's threatened ecosystem in relation to its ecologically important fish species. We aim to contribute to the body of knowledge that is urgently required for the sustainable resource management of Lake Sampaloc, in light of recent calls for its conservation due to persistent habitat degradation.

Materials and methods

Study site

Lake Sampaloc (14.079° N 121.33° E) is the largest among the seven crater lakes of San Pablo City, Laguna, Philippines (Fig. 1). It is an inactive volcanic maar with a maximum width of 1.2 km, a surface area of 1.04 km^2, an average depth of 10 m in most areas, and a maximum depth of 27 m (LLDA 2005).

Fish sampling

We conducted rapid fish surveys in Lake Sampaloc from April to November 2012 (excluding

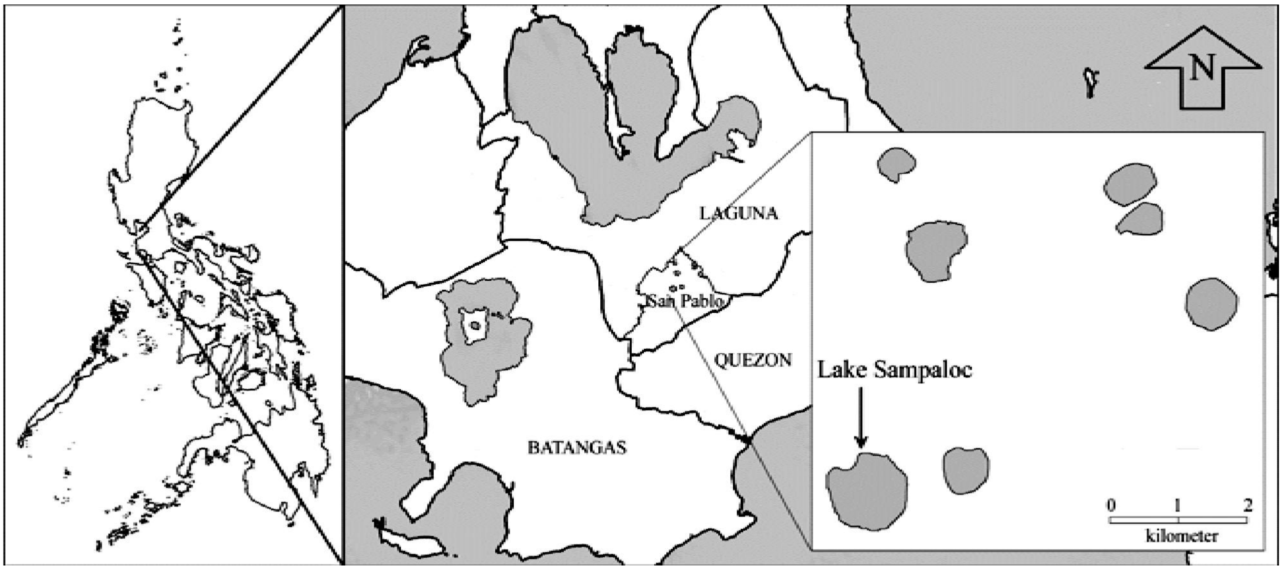

Fig. 1. Map of the Philippines highlighting the location of Lake Sampaloc in the city of San Pablo, located in the province of Laguna in the south of Luzon Island.

October), October to December 2013, and March 2014. Sampling was done once every month with the aid of local fishermen. We used two fine mesh gill nets with a 15 mm and 35 mm mesh size, respectively. Both nets were 20 m long and 3 m deep. These two gill nets were deployed in separate sub-sites that were oriented perpendicular from the shore and were left immersed from 6 pm until 6 am for a total of 12 h for every survey trip, with the location being randomized every sampling month to facilitate a comprehensive sampling of the lake. After retrieval, each fish specimen was photographed, identified, and measured for total length (cm). Catch per unit effort (CPUE) was computed as total fish caught per species divided by total number of gill nets used (n = 2) per survey trip. Mean CPUE was computed as CPUE divided by the total number of survey trips (n = 11).

Stable isotope analysis

We collected samples for stable isotope analysis in October 2013. We sampled for fish, floating macrophytes, and potential food items (leaf litter, periphyton, phytoplankton, and zooplankton) to get an overall view of the trophic structure of the lake. Fish flesh samples were isolated from the dorsal musculature of fish. Periphyton samples were retrieved by lightly brushing rocks in the lake's littoral areas, while leaf litter samples were recovered from the lake shoreline. Floating macrophyte samples were taken in the lake's littoral areas. We used a 50 μm plankton net towed vertically from a depth of 20 m to collect zoo- and phytoplankton samples from the limnetic areas of the lake. Oblique tows were used from the shore to collect samples from the littoral zone. Littoral and limnetic samples were integrated after collection. Plankton samples were separated by passing them through 57 μm and 75 μm mesh sieves. Phytoplankton samples were recovered from the 57 μm sieve, while zooplankton samples were sorted from the 75 μm sieve. Zoo- and phytoplankton samples were then vacuum-filtered into glass filters. All samples for isotope analysis were dried in 60 °C for at least 24 hours and grinded into fine powder prior to analysis. Dried and ground fish flesh samples were further immersed in chloroform : methanol (2:1) solution for 24 hours to remove lipids, and dried again in 60 °C for 24 hours. After processing, each sample was pre-weighed and wrapped in tin capsules. Isotope measurements were done using a continuous flow IRMS (Delta V Plus, Thermoscientific) coupled with an element analyzer (Flash EA, Thermoscientific) and were calculated as delta values using Pee Dee belemnite carbonate and atmospheric N_2 gas as the standards for carbon and nitrogen isotope ratios, respectively. IRMS data were reported as isotopic notations of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and expressed as permil (‰) deviation from the standard using the following equation:

$$\delta^{13}C, \delta^{15}N = [R_{sample}/R_{standard} - 1] \times 1000 \ (‰)$$

Table 1. Systematic list of fish species collected from Lake Sampaloc, Laguna, Philippines together with their relative size and abundance recorded from the duration of the study period. This checklist was produced from specimens recovered during fish surveys from 2012 - 2014 and constitutes the first provisional fish species list for Lake Sampaloc. N = total number of samples retrieved; SD = standard deviation.

Classification	Species	Occurrence	Common name	N	Mean total length (cm) ± SD	Mean CPUE
CYPRINIFORMES						
Cyprinidae	*Carassius gibelio*	non-native	Karpita	7	20.0 ± 4.0	0.3 ± 0.8
	Hypophthalmichthys nobilis	non-native	bighead carp	4	40.8 ± 11.0	0.1 ± 0.2
PERCIFORMES						
Channidae	*Channa striata*	non-native	Dalag	2	33.1 ± 6.6	0.1 ± 0.3
Cichlidae	*Oreochromis niloticus*	non-native	Tilapia	69	15.7 ± 4.1	3.1 ± 1.8
	Parachromis managuensis	non-native	Dugong	56	14.9 ± 4.3	2.5 ± 1.5
Eleotridae	*Giuris margaritacea*	native	Bakuli	22	12.6 ± 2.7	1.0 ± 1.1
Gobiidae	*Glossogobius aureus*	native	Biya	8	12.2 ± 3.0	0.4 ± 0.6
Terapontidae	*Leiopotherapon plumbeus*	endemic	Ayungin	39	10.8 ± 2.0	1.8 ± 1.7
SILURIFORMES						
Clariidae	*Clarias batrachus*	non-native	Hito	11	24.7 ± 8.8	0.5 ± 0.4
Pangasiidae	*Pangasianodon hypophthalmus*	non-native	Pangga	4	43.0 ± 3.1	0.2 ± 0.3
HYBRID CICHLIDS	*Oreochromis aureus* × *Oreochromis mossambicus*	non-native	red tilapia	1	12.2	0.05
	Cichlosoma × *Amphilophus* × *Paraneetroplus*	non-native	Flowerhorn	1	19.8	0.05

where, R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. These values were used to produce an isotope biplot to elucidate the potential trophic interactions in Lake Sampaloc. The standard deviation at 95 % confidence interval used was 0.6 and 0.4 for $\delta^{13}C$ and $\delta^{15}N$, respectively. To support these stable isotope results, we quantitatively estimated trophic position (production reliance and trophic level) for the analyzed fish species using isotope mixing models (Layman *et al.* 2012). We used MixSIR (version 1.0) to estimate production reliance assuming contributions from two major basal resources, periphyton and phytoplankton, for each analyzed fish species within Lake Sampaloc's littoral food web. MixSIR implements a stable isotope mixing model using a Bayesian analysis framework for the estimation of posterior probability distributions for the proportional contribution of a source to mixture of interest, through numerical integration by the use of sampling-importance-resampling (Semmens & Moore 2008). For each simulation (per fish species), we set at least 1,000,000 iterations to assure proper model function and assumed that the trophic enrichment factor for primary producers and subsequent consumers to be 3.4 ± 1 ‰ for $\delta^{15}N$ and 0.4 ± 1.3 ‰ for $\delta^{13}C$, respectively (Post 2002; Vander Zanden & Rasmussen 1999). With these, MixSIR was utilized to determine likelihood distributions and for plotting histograms of the posterior proportional contributions of each basal source to the mixture (production reliance on basal food sources of fish species). We also estimated the trophic level of each fish species utilizing a 2-source mixing model using the following equation:

$$TL_c = (TL_s + [\delta^{15}N_c - (\delta^{15}N_{phyto} \text{ x } contrib_{phyto} + \delta^{15}N_{peri} \text{ x } contrib_{peri})]\ ) / \delta^{15}N_{TEF}$$

where, TL_c is the trophic level of the consumer, TL_s is the trophic level of the basal source (assumed to be 1), $\delta^{15}N_c$ is the observed $\delta^{15}N$ value of the consumer, $\delta^{15}N_{phyto}$, $\delta^{15}N_{peri}$ and $contrib_{phyto}$, $contrib_{peri}$ represent the observed $\delta^{15}N$ and relative contribution (0 to 1) of phytoplankton and periphyton, respectively, while $\delta^{15}N_{TEF}$ represents the assumed trophic enrichment factor (3.4 ‰).

Univariate statistical analysis

CPUE data, length data, and trophic level data per fish species was tested for normality (Shapiro-Wilk W) and was determined to be all non-normally distributed for most fish species ($P < 0.05$ for all) even after attempts on data transformation. Non-parametric Kruskal-Wallis H test was then used to determine statistically plausible differences in CPUE data, length data, and trophic level across fish species with n > 1 specimens. Kruskall-Wallis H test determines if the probability that a random observation of one group data (*i* fish species CPUE or length) is greater than a random observation from other group data will be 0.5 (McDonald 2014). After which, Mann-Whitney U was used as a pair-wise comparison test to determine possible differences between specific pairs of groups. All univariate statistical tests were computed using PAST software (version 2.17) from Hammer *et al.* (2001). The level of significance for all tests was set at $\alpha = 0.05$.

Results

We collected 224 fish specimens for the duration of the study, which included twelve species belonging to three orders and eight families (Table 1). From the three orders, the order Perciformes was the most represented in number of species identified and collected (6 of 12 fish species, n = 194 of 224 specimens sampled). Fish size varied significantly among fish species (Kruskall-Wallis H test, H = 101.1, df = 11, $P < 0.01$) with the largest being *Pangasianodon hypophthalmus* (Siluriformes: Pangasiidae) with mean total length of 43.0 ± 3.1 cm, together with *Hypophthalmichthys nobilis* (Cypriniformes: Cyprinidae) with 40.8 ± 11.0 cm (Mann-Whitney U post-hoc test, pair-wise $P = 0.89$ between *P. hypophthalmus* and *H. nobilis* but $P < 0.01$ compared to other fish species). *Leiopotherapon plumbeus* (Terapontidae) was among the smallest fish species observed with mean total length of 10.8 ± 2 cm, together with *Glossogobius aureus* (Gobiidae) with 12.2 ± 3 cm (Mann-Whitney U post-hoc test, pair-wise $P = 0.08$ between *L. plumbeus* and *G. aureus* but $P < 0.05$ compared to other fish species). Relative abundance also varied significantly among fish species in the lake (Kruskall-Wallis H test, H = 61.56, df = 11, $P < 0.01$) with *Oreochromis niloticus* (Cichlidae) being the most abundantly collected (mean CPUE = 3.1 ± 1.8), followed only by *Parachromis managuensis* (Cichlidae) and *L. plumbeus*, with mean CPUE of 2.5 ± 1.5 and 1.8 ± 1.7, respectively (Mann-Whitney U post-hoc test, pairwise $P = 0.36$ comparing *O. niloticus* and *P. managuensis* CPUE, pairwise $P = 0.11$ comparing *O. niloticus* and *L. plumbeus* CPUE, pairwise $P < 0.01$ for all other fish species CPUE compared to *O. niloticus* CPUE).

We processed 37 specimens for stable isotope analysis comprising 4 samples of potential food items, 3 samples of floating macrophytes, and 30 flesh samples from eight fish species (Table 2). Leaf litter, phyto- and zooplankton $\delta^{13}C$ (8.5 ‰, 8.9 ‰, and 9.1 ‰) and $\delta^{15}N$ (-28.5 ‰, -29.2 ‰, and -30.8 ‰) were depleted among samples and represents the basal producers and a basal consumer in the lake's trophic chain (Fig. 2). Periphyton $\delta^{15}N$ (7.7) was similarly depleted but, in contrast, had the most enriched $\delta^{13}C$ signatures among basal producers.

The stable isotopic signatures of floating macrophytes are scattered and do not show any clear clustering patterns, hinting at their linkages to terrestrial food webs. *Nymphaea pubescens* was the most enriched in $\delta^{13}C$ (-24.7 ‰) among floating macrophytes, but was the most depleted in $\delta^{15}N$ (6.9 ‰), and may be associated with periphyton production. *Eichhornia crassipes* and *Pistia stratiotes,* in contrast, seemed to be associated with phytoplankton production, wherein *E. crassipes* was the most depleted in $\delta^{13}C$ (-29.9 ‰) among floating macrophytes while *P. stratiotes* was the most enriched in $\delta^{15}N$ (11.7 ‰). The stable isotopic signatures of most fish species were enriched in both $\delta^{13}C$ and $\delta^{15}N$ in most samples, and were inclined towards periphyton as a basal source. With the exception of flowerhorn ($\delta^{13}C$ = -27.0 ‰) which was associated with phytoplankton, and *O. niloticus* was strongly inclined towards periphyton but was depleted in $\delta^{15}N$ (7.7 ± 1.3 ‰) as compared to other fish species.

For the isotope mixing model, MixSIR produced more than 1000 posterior draws for the analysis of $\delta^{13}C$ and $\delta^{15}N$ data set of fish species, suggesting that the simulation will converge to the true posterior likelihood and produce an accurate model. In addition, no duplicate draws were made in the posterior chain, suggesting that the total number of iterations used were appropriate. The parameter vectors used by the resultant model did not sample multiple times, and the ratio between the posterior at the best draw and the total posterior density was 0 during all data set runs, suggesting that the model results have a plausible geometry. The resulting histogram from the isotope

Table 2. Description of the samples processed for stable isotope analysis, together with the computed trophic level estimate for consumers. All samples were taken from Lake Sampaloc during October 2013. The mean size of fish specimens processed for stable isotope analysis were within the size range of the overall samples collected for each species (refer to Table 1). N = total number of samples retrieved; SD = standard deviation.

Classification	Description	Occurrence	Common name	N	Mean total length (cm) ± SD	Estimated trophic level
FOOD ITEM						
Phytoplankton	aggregated sample < 57 µm size	--	--	1	--	1*
Zooplankton	aggregated sample < 75 µm size, mostly Cladocera	--	--	1	--	1.73
leaf litter	from littoral areas	--	--	1	--	
Periphyton	*Cladophora* spp.	--	lumot	1	--	1*
MACROPHYTE						
Pontederiaceae	*Eichhornia crassipes*	non-native	water hyacinth	1	--	
Nymphaeaceae	*Nymphaea pubescens*	non-native	pink lotus	1	--	
Araceae	*Pistia stratiotes*	non-native	quiapo	1	--	
FISH						
Cichlidae	*Oreochromis niloticus*	non-native	tilapia	4	15.8 ± 1.8*	1.0 ± 0.4***
	Parachromis managuensis	non-native	dugong	5	14.3 ± 2.9*	2. 5 ± 0.2
Eleotridae	*Giuris margaritacea*	native	bakuli	5	11.5 ± 2.9*	2.1 ± 0.3
Gobiidae	*Glossogobius aureus*	native	biya	4	10.3 ± 2.9*	2.9 ± 0.1
Terapontidae	*Leiopotherapon plumbeus*	endemic	ayungin	9	9.6 ± 0.8*	2.4 ± 0.5
Clariidae	*Clarias batrachus*	non-native	hito	1	22.3*	2.0
HYBRID CICHLIDS	*Oreochromis aureus* × *Oreochromis mossambicus*	non-native	red tilapia	1	12.2*	0.8***
	Cichlosoma × *Amphilophus* × *Paraneetroplus*	non-native	flowerhorn	1	19.8*	2.5

*within the size range of the overall samples collected for each species.

**assumed to be the basal producers and assigned the trophic level of 1.

***lower trophic level values assumed to be from the accumulation of unaccounted temporal turn-over rate of stable isotopes in periphyton.

mixing model supports the clustering patterns in the isotope biplot, confirming that many fish species rely heavily in periphyton production in the lake's littoral food web (Fig. 3). The contribution of periphyton production ranged from 95 % to 98 % (50th percentile of the posterior proportional contribution of each source) in *O. niloticus*, red tilapia, *G. margaritacea*, *G. aureus*, and *L. plumbeus*. Periphyton contribution in *C. batrachus* and *P. managuensis* was slightly lower (85 % and 88 %). In contrast, the contribution of phytoplankton production was only higher in flowerhorn (57 %) as compared to all other fish species examined.

Trophic level (TL) estimates varied significantly among some fish species (Kruskall-Wallis H test, H = 16.28, df = 7, $P < 0.01$). *G. aureus* recorded the highest trophic level estimate (n = 4, mean TL = 2.9 ± 0.1), hinting at the step-wise contributions of at least two or three trophic groups reliant on periphyton production (Mann-Whitney U post-hoc test, pair-wise $P < 0.05$ across analyzed fish species). On the other hand, the two tilapiid species (*O. niloticus,* n = 4; and red tilapia, n = 1) registered unusually low trophic level estimates (mean TL = 1.0 ± 0.4), suggesting a very strong reliance on only periphyton and other possibly unaccounted sources such as algal detritus (Mann-Whitney U post-hoc test, pair-wise $P < 0.05$ across analyzed fish species). The trophic level estimate of *P. managuensis* (n = 5, mean TL = 2.5 ± 0.2) was significantly lower than *G. aureus* TL and significantly higher than *O. niloticus* TL, but overlapped with that of *L. plumbeus* (n = 9, mean

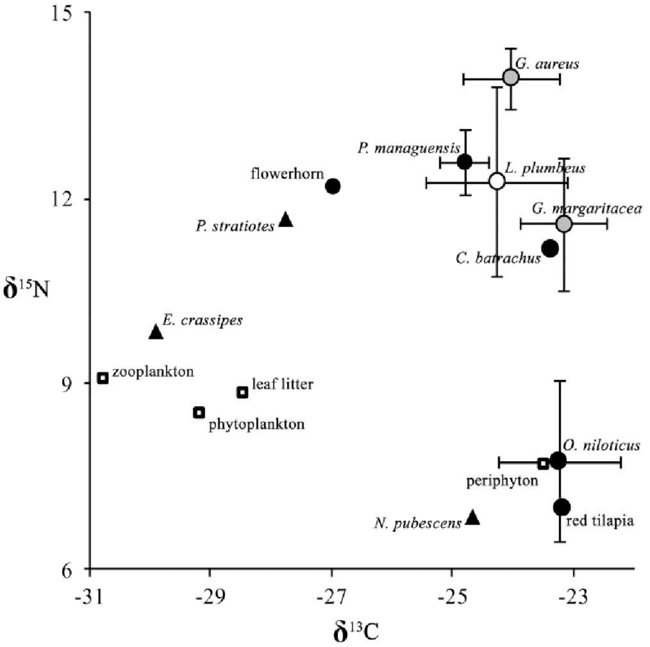

Fig. 2. Biplot of $\delta^{13}C$ and $\delta^{15}N$ isotope values for selected fish species (circles), floating macrophytes (triangles) and potential basal food items for fish (squares) in the Lake Sampaloc ecosystem. Grey circles indicate native species; black circles represent non-native species; and white circles correspond to Philippine endemic species.

TL = 2.4 ± 0.2) and *G. margaritacea* (n = 5, TL = 2.1 ± 0.3) (Mann-Whitney U post-hoc test, pairwise $P = 0.4$ and 0.06, respectively), suggesting potential niche overlaps with a strong production reliance on periphyton.

Discussion

Native fish populations are still present in Lake Sampaloc, but the high relative abundance of non-native species and their potential niche overlap with native fish should be a cause for concern. Our CPUE data suggest that the Philippine endemic *L. plumbeus* still comprises a significant proportion of the fish community, but lags in number compared to non-native fish species. Throughout the Philippines, populations of *L. plumbeus* have been consistently declining through the years (Guerrero 1996; Palma *et al.* 2002), with current conservation efforts directed towards artificial spawning to produce brood stocks (Agron 2009; Denusta *et al.* 2014). A similar pattern of native fish population decline has been observed in many Philippine inland water bodies and is attributed to overfishing, mismanagement of aquaculture practices, and establishment of invasive fish (Bagarinao 2001; Papa & Mamaril 2011). Apart from *L. plumbeus*, *Giuris margaritacea* and *Glossogobius aureus* were the only other native fish species identified from the lake. These benthic fish species do not have high relative abundance, but have higher CPUE compared to other non-native fish, such as *H. nobilis* and *P. hypophthalmus*. The two species are documented from disturbed environments and are widely distributed in the Indo-Pacific region (Larson 2013a, b) with *G. aureus* often misidentified as *Glossogobius giuris* because of their exceptionally similar morpho-logical features (Akihito & Meguro 1975). This may also be the case in many accounts of *G. giuris* in the Philippines (Aquilino *et al.* 2011; Aquino *et al.* 2011). The other nine species we recovered from the lake are all non-indigenous, and are among ~170 non-native fish species that are reported to have been introduced to Philippine inland waters since the 1900s (Cagauan 2007). It is important to assess if these non-native species have established self-sustaining populations in Lake Sampaloc, since this will be a pre-requisite in determining their potential impacts to the lake.

Many of the non-native species in Lake Sampaloc were introduced to the country to create diversified commercial fishery opportunities (see Herre 1953), but unfortunately are also documented globally as successful invaders and contributors to habitat and fish community alteration outside their native range (Table 3). In the Philippines, *Clarias batrachus* has already displaced the native catfish *Clarias macrocephalus* in Luzon Island (Juliano *et al.* 1989). Similarly, *Channa striata* has since been found inhabiting various large lakes and lowland rivers in the country (Conlu 1986; Umali 1950) after its introduction before the 1990s (see Seale 1908). *C. striata* spawns throughout the year (Herre 1924), with both parents aggressively protecting the nest (Lowe-McConnell 1987). *Parachromis mana-guensis* was introduced to the country primarily for aquarium trade but was first reported to be spreading in Lake Taal where it is now considered established and invasive, displacing local *Leiopotherapon plumbeus* populations (Agasen 2005). An increase in the market demand of *Hypophthalmichthys nobilis* and *Pangasianodon hypophthalmus* resulted in the intensive and widespread aquaculture of these two species in the Philippines within the last decade (Fernandez 2002; Valencia 2012). However, research on the

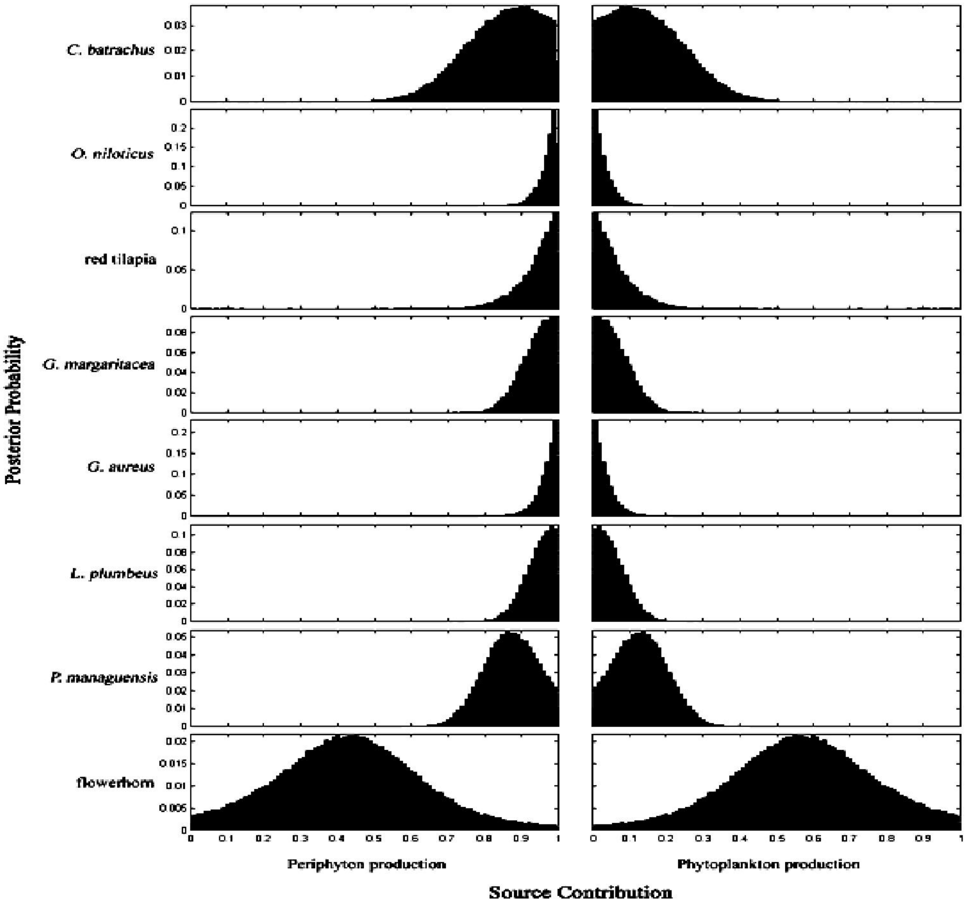

Fig. 3. Histogram of the distribution of posterior proportional contributions of periphyton and phytoplankton to the production reliance of fish species in Lake Sampaloc's littoral food web.

establishment and potential negative impact of these two species is still wanting. Among all the species mentioned, *Oreochromis niloticus* is the most cage-cultured freshwater fish in the country, to date (BFAR 2011; PCAMRD 1998; Smith *et al.* 1985). *O. niloticus* is prolific in establishing self-sustaining feral populations in Philippine inland waters where aquaculture had been introduced (Santiago 2001). The presence of two hybrid cichlids in Lake Sampaloc, namely flowerhorn and red tilapia, poses a legitimate conservation threat since these may contribute to irreversible genetic impacts to the native fish community (see Arthington 1991; also Ferguson 1990), notwithstanding the fact that hybrid cichlids are becoming relatively successful invasive freshwater fish in many Asian countries (Ng & Tan 2010; Nico *et al.* 2007). We argue that many of the non-native species listed have the capacity to establish self-sustaining populations in Lake Sampaloc, in light of the lake's size and current eutrophic state. This raises legitimate concerns about the detrimental impacts of the interactions between native and non-native fish populations in the lake, which may be initially assessed by determining the trophic niche of these fish species in the lake ecosystem.

The total number of fish specimens retrieved in the study may seem low due to predetermined gear and logistical limitations, but our consistent use of the same sampling design for the duration of the study supports our relative abundance comparisons and taxa richness estimates (see Portt *et al.* 2006) even if potential underestimates of the actual population size are likely. Even though gill nets are known to be strongly selective of active and medium- to large-bodied fish species, it is notable that we were able to sample a wide range of fish lengths (smallest was *L. plumbeus* = 9.6 ± 0.8 cm; largest was *P. hypophthalmus* = 43.0 ± 3.1) using two mesh sizes. We were also able to sample relatively stationary ambush predators like *C. striata* by employing a 12 h soak time that

Table 3. Summary of information regarding the native range and prominent characteristics of non-native fish species found in Lake Sampaloc in the duration of the study period.

Classification	Native range	Remarks
CYPRINIFORMES		
Carassius gibelio	Europe, Central and East Asia	- strongly tolerates low O_2 concentrations and pollution (Kottelat & Freyhof 2007) - contributed to significant decline of native fish, invertebrates and plant populations (Japoshvili *et al.* 2013; Karakus *et al.* 2013; Verreycken *et al.* 2007)
Hypophthalmichthys nobilis	Southern and Central China	- may disrupt natural ontogenic patterns of native fish (Conover *et al.* 2007)
PERCIFORMES		
Channa striata	most parts of Asia, but reports considered "species complex"	- highly invasive and territorial, with no natural predators (Courtenay & Williams 2004) - able to move on land, tolerates polluted waters (Lee & Ng 1991)
Oreochromis niloticus	tropical and sub-tropical Africa	- attributed to population decline of native haplochromine cichlids in Lake Victoria (Goldschmidt *et al.* 1993; Nijiru *et al.* 2005)
Parachromis managuensis	tropical America	- flourishes in the mud substrata of highly eutrophic lakes (Conkel 1993)
SILURIFORMES		
Clarias batrachus	certain parts of Southeast Asia	- strong survivability in disturbed environments , competes for food (Lowe *et al.* 2000)
Pangasianodon hypophthalmus	Cambodia, Laos, Vietnam, Thailand	- endangered in native range due to overfishing (Vidthayanon & Hogan 2011)
HYBRID CICHLIDS		
Red tilapia	--	- first strain is genetic mutant produced in Taiwan from the crossing of *O. niloticus* and *O. mossambicus*, and introduced to Philippines in 1979 (Galman & Avtalion 1983) - tolerates a wider range of salinities as compared to *O. niloticus* (Smith *et al.* 1985)
Flowerhorn	--	- genetic cross from from the genera *Cichlosoma*, *Amphilopus*, and *Paraneetroplus* (McMahan *et al.* 2010) - omnivorous and may quickly establish proliferating populations when introduced to tropical inland water bodies (Herder *et al.* 2012; Knight 2010)

may have helped maximize catch efficiency, since net visibility is high when too many fish are captured and the net becomes saturated. We understand that using such a sampling scheme, temporal comparisons of population structure is not advisable due to the fact that catch efficiency varies also with fish condition and gravidity, even within similar size classes. But we maintain that such a sampling design is adequate for our purpose of detecting fish taxa and comparing their relative abundances.

The trophic structure of Lake Sampaloc's fish community is represented mainly by littoral fish assemblages whose abundance seems to be regulated mainly by periphyton production. The lake has been consistently recorded as turbid and eutrophic in the last decade, with a recorded high density of phytoplankton standing biomass in the water column and periphyton in littoral areas (LLDA 2005, 2008). The minimal presence of native macrophytes in the lake may be due to the high density of phytoplankton, resulting to high turbidity and the suppression of macrophyte growth (Phillips *et al.* 1978). From our stable isotope analysis, we could infer that tilapine cichlids, such as *O. niloticus* and red tilapia, primarily graze and exploit the littoral periphyton in the lake, while other fish species may depend indirectly on the increase of abundance of potential prey items that are reliant of periphyton production. The observed wide variations in the isotope ratios of *O. niloticus* may possibly reflect the unaccounted temporal variations in nutrient uptake of periphyton resulting from its growth and development in the lake, which may cause varied temporal turn-over rates of isotopic values (Hill & Middleton 2006; O'Reilly 2006). In light of this, we suspect that the observed abundance of *O. niloticus* in Lake Sampaloc may be attributed to the absence of competitive interactions, and also the bottom-up effects of nutrient-mediated increase in periphyton density thru sustained organic input of aquaculture feeding practices.

In addition to the similar proportional reliance on periphyton production by fish species in the lake, it should be a concern that highly abundant non-native fish species, such *as P. managuensis,* interact within the same trophic niche with endemic or native fish, such as *L. plumbeus* and *G. margaritacea.* An important aspect for future research will be to determine if the high abundance of *P. managuensis* in Lake Sampaloc is linked to its exploitation of these similar niche interactions, whether it is through the undesired effects of competition, or as the result of density-mediated or trait-mediated predation (Preisser *et al.* 2005; Schmitz *et al.* 2004). This is because *P. managuensis* juveniles have been recorded to feed mainly on benthic invertebrates and potentially shift to feeding on both benthos and fish when they mature and breed (Gestring & Shafland 1997). In Lake Taal, *P. managuensis* spawns throughout the year with one breeding female having the capacity to lay 3,000 eggs at a time (Agasen 2006). In addition, high numbers of *P. managuensis* were attributed to the decrease in the catch of *L. plumbeus, G. aureus* and other fish species in Lake Taal (Rosana *et al.* 2006). With this in mind, it is possible that the resiliency of *L. plumbeus* may be the only reason why its population still comprises a significant portion of the Lake Sampaloc's fish community. In Laguna de Bay, *L. plumbeus* populations are known to feed on a variety of food items: phyto- and zooplankton, zoobenthos, periphyton, and even fish, depending on what is most available in their immediate habitat (Kock *et al.* 2000). But overall, our results suggest that Lake Sampaloc's trophic structure is concentrated on a majority of potentially invasive fish species that are high trophic level consumers being supported by the lake's present eutrophic state. This pattern of trophic dynamics has time and again resulted to either local biotic extinction or catastrophic habitat alteration (Witte *et al.* 1992; Zambrano *et al.* 2001). We, therefore, suggest that the direction the lake's continued rehabilitation should be focused on is addressing both the abundance of non-native species and the lake's eutrophic state.

Lake restoration encompasses many important aspects of rehabilitation, but focusing on central point source factors will have longer lasting implications. We recognize and commend the efforts of the local and national government units, local stakeholders and lake shore residents in their continuous advocacy in rehabilitating Lake Sampaloc (Bondad 2013; Mallari Jr. 2000). To support this, we would like to point out possible directions for future research that may facilitate lake rehabilitation. In tandem with the stricter regulations on nutrient input, we believe that the reestablishment of native macrophyte assemblages may be a good central theme in future lake conservation plans. The presence of native macrophyte assemblages has always been regarded as a good indicator of the ecological quality of a lake ecosystem, since such aquatic vegetation can stabilize clear water conditions up to certain nutrient loadings (Sondergaard *et al.* 2010). Increasing the abundance of native submerged macrophyte fauna may help in reducing phytoplankton standing biomass and improve water turbidity, since phytoplankton cannot increase significantly in density when submerged macrophyte biomass is relatively high (Balls *et al.* 1989). Such an intervention must involve a rigid selection process of potential native macrophyte candidates to avoid undesired and irreversible ecological changes. This will require the characterization of both native and alien aquatic flora already present in freshwater ecosystems in the country, which will be guided by policies pertaining to the implications of invasive flora and fauna management (see Shah & Reshi 2014). In addition, the removal of certain non-native fish species that cause habitat alteration may also benefit the lake. Removal of *Carassius gibelio* may aid in reducing water turbidity since this species is notorious in disrupting benthic food webs by its habit of stirring up bottom sediments during feeding (Richardson & Whoriskey 1992; Richardson *et al.* 1995). Also, the nonpartisan removal of hybridized fish should be a priority, since these may produce irreversible genetic impacts to the fish community. To determine the potential effects of such interventions, extensive mesocosm experiments may be attempted within a framework that mimics the present ecological state of Lake Sampaloc, wherein the effects of the introduction and/or expulsion of certain factors could be tested. We believe that well-researched and carefully planned biomanipulation (Jeppesen *et al.* 2005a) and rigorous policy implementation on nutrient or fisheries input (Jeppesen *et al.* 2005b) in Lake Sampaloc could increase the functional micro-habitats of fish assemblages and reduce the pressure of potential detrimental density- or behavior-mediated trophic interactions. We think this could possibly be achieved if native submerged vegetation is allowed to thrive and colonize the deeper areas of the lake, subsequently widening the range of benthic invertebrate grazers that may act as prey for littoral fish assemblages, and also provide refugia for smaller fish species (Jeppesen *et al.* 1997). Although most biomanipulation studies related to macrophyte population in lakes have been performed in temperate countries (Jeppesen *et al.* 1997, 2005a), studies on tropical lakes also confirm that macrophyte assemblages significantly contribute to primary productivity in lake ecosystems by utilizing nutrients in lake sediments (see Tamire & Mengistou 2014). A change to a clear water system due to macrophyte biomass increase may result in a wider habitat use by the lake fish community, and may also aid in releasing potential negative interactions between native and non-native fish species because of trophic niche overlaps.

Acknowledgments

This study was funded by the Commission on Higher Education of the Philippines under the Philippine Higher Education Research Network grant (CHED-PHERNet UST Project A-1) to RDSP and GAC, as one of the projects of the University of Santo Tomas as a member institution. Likewise, this research was partly supported by the Research Institute for Humanity and Nature (RIHN). The stable isotope analysis was conducted with the aid of Cooperative Research Facilities of the Center for Ecological Research of Kyoto University. JCB is grateful for the funding provided by the Science Education Institute of the Department of Science and Technology (DOST-SEI) of the Philippines, as part of his scholarship grant under the Accelerated Science and Technology Human Resource Development Program (ASTHRDP). We are thankful to our two anonymous reviewers and to DM Bilkovic for providing excellent reviews that have definitely improved the paper.

References

Agasen, E. V. 2005. *Report on the Preliminary Investigation on the Presence of the Jaguar Guapote.* Publication of the National Fisheries Research and Development Institute, Quezon City, Philippines.

Agasen, E. V., J. P. Clemente, Jr., M. R. Rosana & N. S. Kawit. 2006. Biological investigation of Jaguar Guapote *Parachromis managuensis* (Gunther) in Taal Lake, Philippines. *Journal of Environmental Science and Management* **9**: 20-30.

Agron, E. B. 2009. BAR highlights promising UPLB technology to save endangered fish species. *BAR Chronicle* **10**. Official Publication of the Bureau of Agricultural Research, Philippines.

Akihito, P & K. Meguro. 1975. Description of a new gobiid fish, *Glossogobius aureus*, with notes on related species of the genus. *Japanese Journal of Ichthyology* **22**: 127-142.

Aquilino, S. V. L., J. M. Tango, I. K. Fontanilla, R. C. Pagulayan, Z. U. Basiao, P. S. Ong & J. P. Quilang. 2011. DNA barcoding of the icthyofauna of Taal Lake, Philippines. *Molecular Ecology Resources* **11**: 612-619.

Aquino, L. M., J. M. Tango, R. J. Canoy, I. K. Fontanilla, Z. U. Basiao, P. S. Ong & J. P. Quilang. 2011. DNA barcoding of fishes of Laguna de Bay, Philippines. *Mitochondrial DNA* **22**: 143-153.

Arthington, A. H. 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **48**(Supplement 1): 33-43.

Bagarinao, T. U. 2001. The decline of native fishes and fisheries and the rise of aquaculture in lakes and rivers in the Philippines (abstract only). *In*: C. B. Santiago, M. L. Cuvin-Aralar & Z. U. Basiao (eds.) *Conservation and Ecological Management of Philippine Lakes in Relation to Fisheries and Aquaculture.* Southeast Asian Fisheries Development Center, Aquaculture Department, Iloilo, Philippines; Philippine Council for Aquatic and Marine Research and Development, Los Baños, Laguna Philippines; Bureau of Fisheries and Aquatic Resources, Quezon City, Philippines.

Balls, H., B. Moss & K. Irvine. 1989. The loss of submerged plants with eutrophication. I. Experimental design, water chemistry, aquatic plant and phytoplankton biomass in experiments carried out in ponds in the Norfolk Broadland. *Freshwater Biology* **22**: 71-87.

Bondad, I. L. 2013. *Fish Farmers Coop Lead Sampaloc Lake Cleanup*. Article in the News Feature of the Los Baños Times, Published in September 11, 2013 in the Philippines.

Bureau of Fisheries and Aquatic Resources (BFAR). 2011. *Philippine Fisheries Profile*. Yearly Report of BFAR of the Department of Agriculture, Philippines.

Cagauan, A. 2007. Exotic aquatic species: Introduction in the Philippines for aquaculture – a threat to biodiversity or a boon to the economy? *Journal of Environmental Science and Management* **10**: 48-62.

Cariño, J. K. I. 2003. *Integrated Water Resources Management: The Experience of Laguna Lake Development Authority (LLDA) Philippines*. Proceedings of the National Congress on Philippine Lakes. Los Baños, Laguna, Philippines.

Carpenter, S. R. & J. F. Kitchell. 1993. *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.

Conkel, D. 1993. *Cichlids of North and Central America*. T.F.H. Publications, Inc., USA.

Conlu, P. V. 1986. *Guide to Philippine Flora and Fauna. Vol. IX of Fishes.* Natural Resources Management Center. Ministry of Natural Resources and University of the Philippines.

Conover, G., R. Simmonds & M. Whalen (eds.). 2007. *Management and Control Plan for Bighead, Black, Grass, and Silver Carps in the United States*. Asian Carp Working Group, Aquatic Nuisance Species Task Force, Washington, D.C.

Courtenay, W. R. & J. D. Williams. 2004. *Snakeheads (Pisces: Clariidae) - A Biological Synopsis and Risk Assessment*. U.S. Geological Survey Circular **1251:** 115-120.

Denusta, P. J., E. G. de Jesus-Ayson, M. A. Laron & L. M. Garcia. 2014. Effects of human chorionic gonadotropin (hCG) and handling stress on spemiation of silver perch *Leiopotheraponplumbeus* (Knerr, 1864). *Journal of Applied Ichthyology* **30**: 448-453.

Ferguson, M. M. 1990. Genetic impact of introduced fishes on native species. *Canadian Journal of Zoology* **68**: 1053-1057.

Fernandez, R. A. 2002. *Bighead Carp Edges out Milkfish in Laguna Lake*. Article in the Business Features of the Philippine Star, Published November 17, 2002 in the Philippines.

Galman, O. R. & R. R. Avtalion. 1983. A preliminary investigation of the characteristics of red Tilapias from the Philippines and Taiwan. pp. 291-301. *In:* L. Fishelson & Z. Yaron. *International Symposium on Tilapia in Aquaculture*. Tel Aviv University Publisher, Tel Aviv, Israel.

Gestring, K. B. & P. L. Shafland. 1997. Status and selected life history attributes of the exotic jaguar guapote (*Cichlasoma managuense*) in Florida. *Florida Scientist* **60**: 137-142.

Global Nature Fund. 2014. *Intensive Fish Farming Threatens Philippine Crater Lake - Lake Sampaloc is "Threatened Lake of the Year 2014".* Press Release of Global Nature Fund for World Wetlands Day on 2nd February 2014. pp.1-2.

Goldschmidt, T., F. Witte & J. Wanink. 1993. Cascading effects of the introduced Nile Perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* **7**: 686-700.

Guerrero III, R. D. 1996. Human impacts on Laguna de Bay, Philippines and management strategies for their mitigation. *GeoJournal* **40**: 69-72.

Hammer, Ø., D. A. T. Harper, P. D. Ryan. 2001. Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4**: 9.

Herder, F., U. K. Schliewen, M. F. Geiger, R. K. Hadiaty, S. M. Gray, J. S. McKinnon, R. P. Walter & J. Pfaender. 2012. Alien invasion in Wallace's Dreamponds: records of the hybridogenic "flowerhorn" cichlid in Lake Matano, with an annotated checklist of fish species introduced to the Malili Lakes system in Sulawesi. *Aquatic Invasions* **7**: 521-535.

Herre, A. W. 1924. Distribution of the true fresh-water fishes in the Philippines, Vol. II of The Philippine Labyrinthici, Clariidae, and Siluridae. *Philippine Journal of Science* **24**: 683-709.

Herre, A. W. 1953. *Checklist of Philippine Fishes*. A Federal Government Series Publication by the U. S. Fish and Wildlife Service. United States of America.

Hill, W. R. & R. G. Middleton. 2006. Changes in carbon stable isotope ratios during periphyton development. *Limnology and Oceanography* **51**: 2360-2369.

Japoshvili, V., L. Mumladze & F. Kucuk. 2013. Invasive *Carassius* carp in Georgia: Current state of knowledge and future perspectives. *Current Zoology* **59**: 732-739.

Juliano, R. O., R. D. Guerrero III & I. Ronquillo. 1989. The introduction of exotic aquatic species in the Philippines. pp. 83-90. *In:* S. S. De Silva (ed.) 1989. *Exotic Aquatic Organisms in Asia.* Proceedings of the workshop of the Asian Fisheries Society. Manila, Philippines.

Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen, L. J. Pedersen & L. Jensen. 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* **342/343**: 151-164.

Jeppesen, E. M. Sondergaard, N. Mazzeo, M. Meerhoff, C. C. Branco, V. Huszar, F. Scasso & M. V. Reddy. 2005b. Lake restoration and biomanipulation in temperate lakes: Relevance for subtropical and tropical lakes. (book chapter) *In:* M. V. Reddy. *Restoration and Management of Tropical Eutrophic Lakes.* CRC Press, Taylor and Francis Group Publishing.

Jeppesen, E., M. Sondergaard, J. P. Jensen, K. E. Havens, O. Anneville, L. Carvalho, M. F. Coveney, R. Deneke, M. T. Dokulil, B. Foy, D. Gerdeaux, S. E. Hampton, S. Hilt, K. Kangkur, J. Kohler, E. Lammens, T. L. Lauridsen, M. Manca, M. R. Miracle, B. Moss, P. Noges, G. Persson, G. Phillips, R. Portielje, S. Romo, C. L. Schelske, D. Straile, I. Tatrai, E. Willeni & M. Winder. 2005b. Lake responses to reduced nutrient loading - an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology* **50**: 1747-1771.

Karakus, U., S. Agdamar, A. S. Tarkan & N. Ozdemir. 2013. Range extension of the invasive freshwater fish species, gibel carp *Carassius gibelio* (Bloch, 1782) in western Turkey. *BioInvasion Records* **2**: 153-157.

Knight, J. D. 2010. Invasive ornamental fish: a potential threat to aquatic biodiversity in peninsular India. *Journal of Threatened Taxa* **2**: 700-704.

Kock, M., U. Focken, H. Richter, K. Becker & C. B. Santiago. 2000. Feeding ecology of silverperch, *Terapon plumbeus* Kner, and the impact of fish-pens in Laguna de Bay, Philippines. *Journal of Applied Ichthyology* **16**: 240-246.

Kottelat, M. & J. Freyhof. 2007. *Handbook of European Freshwater Fishes*. Publications Kottelat, Cornol, Switzerland.

Laguna Lake Development Authority (LLDA). 2005. *Water Quality Report on Sampaloc Lake 1996-2005*. Terminal Report of the LLDA Environmental Quality Management Division, Philippines.

Laguna Lake Development Authority (LLDA). 2008. *Water Quality Report of the Seven Crater Lakes 2006-2008*. Terminal Report of the LLDA Environmental Quality Management Division, Philippines.

Lake, J. L., R. A. McKinney, F. A. Osterman, R. J. Pruell, J. Kiddon, S. A. Ryba & A. D. Libby. 2001. Stable nitrogen isotopes as indicators of anthropogenic activities in small freshwater systems. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 870-878.

Larson, H. 2013a. *Giuris margaritacea. In*: International Union for Conservation of Nature. 2013. *IUCN Red List of Threatened Species*. Version 2013.2. www.iucnredlist.org (accessed on 01 May 2014).

Larson, H. 2013b. *Glossogobius giuris. In:* International Union for Conservation of Nature. 2013. *IUCN Red List of Threatened Species*. Version 2013.2. www.iucnredlist.org (accessed on 01 May 2014).

Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, A. E. Rosenblatt, J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop. 2012. Applying stable isotopes to examine food-webstructure: an overview of analytical tools. *Biological Reviews* **87**: 545-562.

Lee, P. G. & P. K. Ng. 1991. The snakehead fishes of the Indo-Malayan Region. *Nature Malaysiana* **16**: 113-129.

Lowe, S., M. Brown, S. Boudjelas & M. De Poorter. 2000. *100 of the World's Worst Invasive Alien Species: a Selection from the Global Invasive Species Database.* Published by The Invasive Specialist Group (ISSG) of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). Auckland, New Zealand.

Lowe-McConnell, R. H. 1987. *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, England.

Mallari, Jr., D. T. 2000. *Sampaloc Lake Clean-up Drive Marred in Controversy*. Article in the Across the Nation Section of the Philippine Daily Inquirer, published in March 3, 2000 in the Philippines.

McDonald, J. 2014. *Handbook of Biological Statistics.* 3rd edn. Sparky House Publishing, Maryland, USA.

McMahan, C. D., A. D. Geheber & K. R. Piller. 2010. Molecular systematics of the enigmatic Middle American genus *Vieja* (Teleostei: Cichlidae). *Molecular Phylogenetics and Evolution* **57**: 1293-1300.

National Research Council (NRC). 1992. *Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy*. National Academy Press, Washington, D.C., USA.

Ng, H. H. & H. H. Tan. 2010. An annotated checklist of the non-native freshwater fish species in the reservoirs of Singapore. *Cosmos* **6**: 95-116.

Nico, L. G., W. H. Beamish & P. Musikasinthorn. 2007. Discovery of the invasive Mayan Cichlid fish *Cichlasoma urophthalmus* (Gunther 1862) in Thailand, with comments on other introductions and potential impacts. *Aquatic Invasions* **2**: 197-214.

Nijiru, M., E. Waithaka, M. Muchiri, M. van Knaap & I. G. Cowx. 2005. Exotic introductions to the fishery of Lake Victoria: What are the management options? *Lakes and Reservoirs: Research and Management* **10**: 147-155.

O'Reilly, C. M. 2006. Seasonal dynamics of periphyton in a large tropical lake. *Hydrobiologia* **553**: 293-301.

Oertli, B., D. A. Joyer, E. Catella, R. Juge, D. Cambin & J. B. Lachavanne. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation* **104**: 59-70.

Palma, A. L., A. S. Diamante & R. M. Pol. 2002. An assessment of fishery resources of Laguna de Bay. *Aquatic Ecosystem Health Management* **5**: 139-146.

Papa, R. D. & A. C. Mamaril, Sr. 2011. History of the biodiversity and limno-ecologal studies on Lake Taal with notes on the current state of Philippine limnology. *Philippine Science Letters* **4**: 1-10.

Philippine Council for Aquatic and Marine Research and

Development (PCAMRD). 1998. *Tilapia culture.* PCAMRD Currents **3**(1), Publication of the Department of Science and Technology, Philippines.

Phillips, G. L., D. Eminson & B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany* **4**: 103-126.

Portt, C. B., G. A. Coker, D. L. Ming & R. G. Randall. 2006. *A Review of Fish Sampling Methods Commonly Used in Canadian Freshwater Habitats.* Canadian Technical Report of Fisheries and Aquatic Sciences 2604.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**: 703-718.

Preisser, E. L., D. Bolnick & M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **86**: 501-509.

Quilang, J. P., Z. U. Basiao, R. C. Pagulayan, R. R. Roderos & E. B. Barrios. 2007. Meristic and morphometric variation in the silver perch, *Leiopotherapon plumbeus* (Kner, 1864), from three lakes in the Philippines. *Journal of Applied Ichthyology* **23**: 561-567.

Richardson, M. J. & F. G. Whoriskey. 1992. Factors influencing the production of turbidity by goldfish. *Canadian Journal of Zoology* **70**: 1585-1589.

Richardson, M. J., F. G. Whoriskey & L. H. Roy. 1995. Turbidity generation and biological impacts of an exotic fish *Carassius auratus*, introduced into shallow seasonally anoxic ponds. *Journal of Fish Biology* **47**: 576-585.

Rosana, M. R., E. V. Agasen, L. S. Villanueva, J. P. Clemente & J. T. de la Vega. 2006. Status and economic impact of *Parachromis managuensis* in Taal Lake, Philippines. *Journal of Environmental Science and Management* **9**: 1-19.

Santiago, A. 2001. Pen and cage culture in Philippine lakes. pp. 372-376. *In:* IIRR, IDRC, FAO, NACA and ICLARM. 2001. *Utilizing Different Aquatic Resources for Livelihoods in Asia: a Resource Book.* International Institute of Rural Reconstruction, International Development Research Centre, Food and Agriculture Organization of the United Nations, Network of Aquaculture Centers in Asia-Pacific and International Center for Living Aquatic Resources Management. Published in the Philippines.

Santiago, A. & R. P Arcilla. 1993. Tilapia cage culture and the dissolved oxygen trends in Sampaloc Lake, the Philippines. *Environmental Monitoring and Assessment* **24**: 243-255.

Santiago, C. B., M. L. Cuvin-Aralar & Z. U. Basiao (eds.). 2001. *Conservation and Ecological Management of Philippine Lakes in Relation to Fisheries and Aquaculture.* Southeast Asian Fisheries Development Center, Iloilo; Philippine Council for Aquatic and Marine Research and Development, Quezon City, Philippines.

Santos, B. S., I. K. Fontanilla & J. P. Quilang. 2010. Geo-metric morphometric analysis and gill raker count variation of populations of the endemic Philippine silver perch, *Leiopothera ponplumbeus* (Perciformes: Terapontidae). *Philippine Agricultural Scientist* **93**: 406-419.

Scheffer, M., G. J. Van Geest, K. Zimmer, E. Jeppesen, M. Søndergaard, M. G. Butler, M. A. Hanson, S. Declerck & L. De Meester. 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* **112**: 227-231.

Schmitz, O. J., V. Krivan & O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**: 153-163.

Seale, A. 1908. The fishery resources of the Philippine Islands. Part I: Commercial fishes. *Philippine Journal of Science* **3**: 513-531.

Semmens, B. X. & J. W. Moore. 2008. MixSIR: A Bayesian stable isotope mixing model, Version 1.0. http://www.ecologybox.org. Date of Download: October 2014.

Smith, I. R., E. B. Torres & E. O. Tan. 1985. *Philippine Tilapia Economics.* Proceedings of a PCARRD-ICLARM Workshop in Los Baños, Laguna, Philippines last 10 - 13 August 1983. Phili-ppine Council for Agriculture and Resources Research and Development; International Center for Living Aquatic Resource Management. Manila, Philippines.

Shah, M. A. & Z. A. Reshi. 2014. Characterization of alien aquatic flora of Kashmir Himalaya: implications for invasion management. *Tropical Ecology* **55**: 143-157.

Sondergaard, M., L. S. Johansson, T. L. Lauridsen, T. B. Jorgensen, L. Liboriussen & E. Jeppesen. 2010. Submerged macrophytes as indicators of the ecological quality of lakes. *Freshwater Biology* **55**: 893-908.

Tamire, G. & S. Mengistou. 2014. Biomass and net aboveground primary productivity of macrophytes in relation to physico-chemical factors in the littoral zone of Lake Ziway, Ethiopia. *Tropical Ecology* **55**: 313-326.

Tan, R. L., T. Higuchi, & T. Honma. 1994. Estimating inefficiency in fish cage culture operation via stochastic frontier total cost function: the case of Sampaloc Lake, Philippines. *The Developing Economies* **32**: 86-106.

Umali, A. F. 1950. *Key to the Families of Common*

Commercial Fishes in the Philippines. U. S. Fish and Wildlife Service Research Report **21**, USA.

Vadeboncoeur, Y., M. J. Vander Zanden & D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food webs. *BioScience* **52**: 44-54.

Valencia, C. 2012. *Department of Trade and Industry Eyes More Local Pangasius Production*. Article in the Business Features of the Philippine Star, Published April 15, 2012. Philippines.

Vander Zanden, M. J., J. M. Casselman & J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**: 464-467.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter & C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. *Ecosystems* **6**: 274-288.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, N. E. Mandrak. 2004. Predicting occurrences and impacts of small mouth bass introductions in North temperate lakes. *Ecological Applications* **14**: 132-148.

Vander Zanden, M. J. & J. B. Rasmussen. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. *Ecology* **80**: 1395-1404.

Vander Zanden, M. J. & Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* **83**: 2152-2161.

Verreycken, H., D. Anseeuw, G. Van Thuyne, P. Quartaert & C. Belpaire. 2007. The non-indigenous freshwater fishes of Flanders (Belgium): review, status, and trends in the last decade. *Journal of Fish Biology* **71**: 160-172.

Vidthayanon, C. & Z. Hogan. 2011. *Pangasianodon hypophthalmus*. *In: International Union for Conservation of Nature*. 2013. *IUCN Red List of Threatened Species*. Version 2013.2. www.iucnredlist.org (accessed on 01 May 2014).

Wetzel, R. G. 2001. *Limnology - Lake and River Ecosystems*. 3rd edn. Academic Press.

William, P., M. Whitfield, J. Biggs, B. Bray, G. Fox, P. Nicolet & D. Sear. 2003. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation* **115**: 329-341.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas & N. Bouton. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* **34**: 1-28.

Zalewski, M. & R. Welcomme. 2001. Restoration of physically degraded fish habitats - the model of intermediate restoration. *Ecohydrology and Hydrobiology* **1**: 279-282.

Zambrano, L., M. Scheffer & M. Martinez-Ramos. 2001. Catastrophic response of lakes to benthivorous fish introduction. *Oikos* **94**: 344-350.

(Received on 13.06.2014 and accepted after revisions, on 10.02.2015)