INVASIVE SPECIES

Trophic niche overlap between native and non-native fishes

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Abstract In Mexico, non-native species are established in virtually every lake and represent one of the most important factors in species diversity loss. An iconic example is Lake Patzcuaro, which used to provide one of the most abundant fisheries of native species among freshwater systems in Mexico. But in the last decades, the relative abundance of non-native species has increased together with a reduction of native species populations. In this study, we analyze the trophic niche overlap between native and non-native species by using carbon and nitrogen stable isotopes. We did not found a spatial effect between physicochemical variables and isotopic signatures. The trophic niche area showed a small overlap among native species, but a substantial overlap of native species with non-native *C. carpio* and *O. aureus*. The non-native species *P. infans* presented almost no trophic overlap with other species. Non-native species have a trophic niche area two times larger than natives. The trophic niche overlap between native and non-native species was higher than among natives. The narrower trophic niche area and the high overlap with non-native species may explain the decline of native species populations. Alternative but untested explanations include altered water quality stemming from pollution and indirect effects of non-natives.

Keywords Patzcuaro · Native · Non-native · Carp · Tilapia · Isotopes

Introduction

Non-native species are one of the main causes of biodiversity loss in freshwater systems (Lodge, 1993; Dudgeon et al., 2006). The introduction of non-native species in Latin America has increased in the last few decades, mainly for aquaculture. However, there is little understanding of their effect on these systems, particularly on the population decline of native species (Canonico et al., 2005; Mitchell & Knouft, 2009). Nowadays, common carp (*Cyprinus carpio*) and tilapia (*Oreochromis* spp.) are the most widely distributed non-native fish in America, and they can have strong negative effects on native aquatic fauna, particularly in highly diverse regions such as Mexico (Zambrano et al., 2006). Non-native species are established virtually in every natural lake in Central Mexico, and represent one of the most important

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factors in species loss in these systems (Zambrano & Macías-García, 1999).

There are several ways in which non-natives can affect native species, but the effects throughout the food web seem to generate several changes on the native fish community structure. For example, non-native fish can compete directly for food resources (Zambrano et al., 2010a), which may result in diet shifts for native species (Ke et al., 2008; Sharma & Borgstrøm, 2008), affecting their fitness (Douglas et al., 1994). Similarly, non-native species can also have indirect effects on native fish populations. For instance, tilapia may cause trophic cascades by increasing nitrogen and phosphorus availability, promoting fast-growing algae (Figueredo & Giani, 2005). Also, the foraging behavior of common carp increases turbidity by re-suspending the sediment (Zambrano et al., 2001; Miller & Crowl, 2006). Turbidity reduces the capacity of macrophytes to survive, which may lead to a reduction of the trophic pathways from a multiple resources scenario (benthic, macrophytes, and pelagic) to only the prevalence of the pelagic pathway (Hargeby et al., 1994; Scheffer et al., 2006). In consequence, a good approach to understand the effect of non-native species on a native fish community is related to the understanding of the trophic structure.

The analysis of stable isotopes of carbon and nitrogen has been used as an effective tool to understand trophic positions of native and non-native species within a food web and to relate them to the conservation of native populations (Pilger et al., 2010). Isotopic signature of carbon ($\delta^{13}C$) provides information about the food source of organic carbon, and isotopic signature of nitrogen ($\delta^{15}N$) is associated with the trophic level (Peterson & Fry, 1987). This analysis has greatly increased the understanding of the trophic dynamics and the ecological effects of non-native species in aquatic ecosystems (Vander Zanden et al., 1999; Pilger et al., 2010; Cucherousset et al., 2012). For instance, the presence of non-native species can reduce the $\delta^{15}N$ values and narrow the range in $\delta^{13}C$ values of native species by constraining their diets (Marks et al., 2010; Pilger et al., 2010). Furthermore, stable isotopes can be used to analyze the trophic niche area of species (Mercado-Silva et al., 2008; Zambrano et al., 2010a). Previous studies suggest that trophic niche overlap between species can be interpreted as shared food source, and therefore

is a potential indicator of competitive interactions (Vander Zanden et al., 1999; Pilger et al., 2010).

The study and management of non-native fish species in emergent economies like Mexico should be a priority due to the positive relationship between the number of non-native species and economic development (Leprieur et al., 2008). There is an urgent need for studies focused on areas that experience high homogenization of fish fauna such as Central Mexico (Villéger et al., 2011). Thus, our primary objective was to characterize trophic niches and position of native and non-native fishes in Lake Patzcuaro. In our study, we used the fish signatures of carbon and nitrogen isotopes to build a trophic niche analysis (Layman et al., 2007), compare the niche areas of native and non-native species (Mercado-Silva et al., 2008), and examining their trophic niche overlap (Zambrano et al., 2010a). The three non-native species in the lake are omnivorous; therefore, we hypothesize that trophic niche overlap between native and non-native species should be higher than among natives. This niche overlap can be one of the factors able to explain the reduction of native species populations in Lake Patzcuaro. Understanding the interactions among native and non-native fishes can lead to the implementation of effective plans for the restoration and management of Lake Patzcuaro.

Materials and methods

Study site

Lake Patzcuaro is a high altitude tropical lake (2,035 m above sea level) located in Central Mexico (19°32′–19°42′N and 101°32′–101°43′W) within an endorheic basin (Fig. 1) (Orbe-Mendoza & Acevedo-García, 2002). It is a eutrophic shallow lake (mean depth of 4 m) with a surface of 97.5 km². The predominant land uses in the basin are agriculture (45.4%) and forestry (37.5%) (Amador-García & Huerto-Delgadillo, 2011). Water quality has been decreasing during the last few decades. Some of the causes of this degradation are the input of untreated wastewater, bringing nutrient and bacterial pollution, urbanization of the surrounding areas, and agricultural activities. As a consequence, Lake Patzcuaro went from an oligo-mesotrophic and moderately polluted system (Chacón-Torres, 1993; Rosas et al., 1993) to a

Fig. 1 Map of Lake Patzcuaro's Basin with the eight sampling sites *1* Embarcadero; *2* Uranden; *3* Napizaro; *4* Pacanda (littoral zone of the island of Janitzio); *5* Cuello; *6* San Jerónimo; *7* Santa Fe; and *8* Tzintzuntzan
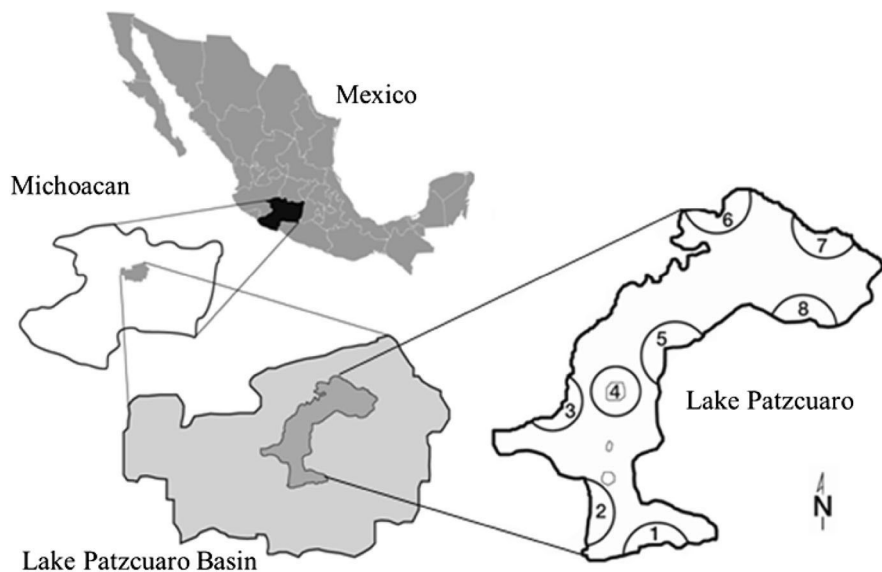
highly polluted and eutrophic system (Lyons et al., 2000; Sánchez-Chávez et al., 2011).

In Lake Patzcuaro, the fish community has been in constant change due to the introduction of multiple non-native species since 1933—the local extinction of two native species: *Skiffia lermae* (Meek) and *Allotoca dugesi* (Bean), and two unsuccessful species introductions: *Ctenopharyngodon idellus* (Valenciennes) and *Tilapia rendalli* (Boulenger) (Berlanga-Robles et al., 1997, 2002; Ramírez-Herrejón et al., 2014). Nowadays, there are 13 fish species reported in the lake, eight of them are native: *Chirostoma estor* (Jordan), *Chirostoma grandocule* (Steindachner), *Chirostoma patzcuaro* (Meek), *Chirostoma attenuatum* (Meek), *Algansea lacustris* (Steindachner), *Goodea atripinnis* (Jordan), *Alloophorus robustus* (Bean), *and Allotoca diazi* (Meek), and five non-native: *Oreochromis aureus* (Steindachner), *Cyprinus carpio* (Linnaeus), *Micropterus salmoides* (Lacepède), *Chirostoma humboldtianum* (Valenciennes), and *Poeciliopsis infans* (Woolman) (Galindo-Villegas & Sosa-Lima, 2002; Orbe-Mendoza et al., 2002; Ramírez-Herrejón et al., 2014). Approximately 40 years ago *C. carpio* and *O. aureus* were introduced as a part of a program that aimed to increase the fishery production in the lake (Berlanga-Robles et al., 2002). *Poeciliopsis infans* is a species native to Central Mexico, and it was first recorded as an introduced species in Lake Patzcuaro in 1997 (Galindo-Villegas & Sosa-Lima, 2002).

Lake Patzcuaro used to provide one of the most abundant fisheries in freshwater systems in Mexico. In particular, the multi-species catch in 1988 was 2,524 tons (Orbe-Mendoza et al., 2002), but since then, there has been an extraordinary reduction in fish captures. This depletion seems to be related to overfishing, non-native species introduction, and a decrease in water quality. However, even with this decline in fish abundance, native species still dominated the total fish biomass during the 1990s (Berlanga-Robles et al., 2002). In contrast, in the last decade, the relative abundance of carp and tilapia increased (Vargas-Velázquez, 2011), suggesting a reduction of native species populations. For fisheries, the most important species is the endangered endemic silverside *Chirostoma estor*, which is the highest-valued species in the lake (Ross et al., 2006). In recent years, total fish abundance has remained low, even though the fishery is now a secondary activity mainly for local consumption (Alaye et al., 2006; Vargas-Velázquez, 2011). In this context, our study was designed to understand the trophic relationship between native and non-native species. This knowledge will help to clarify whether non-native fish may play a role in the depletion of native species populations.

Sampling methods

During the wet season of 2009, we sampled eight sites distributed in the lake to evaluate spatial differences in

Table 1 Mean and standard deviation of physicochemical variables at each site

Site	Depth (m)	Secchi (cm)	Temp (°C)	pH	DO (mg/l)	Cond (μS/cm)	TDS (ppt)
Embarcadero	1.2 ± 0.1	18.0 ± 1.4	21.5 ± 0.6	7.6 ± 1.4	3.9 ± 1.2	933.5 ± 3.5	0.40 ± 0.095
Uranden	2.1 ± 0.2	22.3 ± 2.1	20.9 ± 0.1	8.9 ± 0.2	4.5 ± 0.2	967.7 ± 3.5	0.48 ± 0.045
Napizaro	2.2 ± 0.4	13.0 ± 1.7	20.7 ± 0.1	8.3 ± 0.2	5.1 ± 0.0	1,028.5 ± 6.1	0.51 ± 0.003
Pacanda	5.3 ± 0.5	24.8 ± 2.8	22.4 ± 0.6	8.1 ± 0.3	5.1 ± 0.8	1,066.3 ± 5.2	0.53 ± 0.002
Cuello	5.5 ± 2.3	27.0 ± 3.5	21.6 ± 0.2	8.7 ± 0.4	4.7 ± 0.2	1,079.3 ± 2.3	0.54 ± 0.001
San Jerónimo	6.3 ± 1.9	26.3 ± 1.7	21.4 ± 1.1	8.5 ± 0.2	5.6 ± 2.8	1,065.0 ± 1.2	0.53 ± 0.003
Santa Fe	7.1 ± 1.4	24.0 ± 2.6	21.0 ± 0.2	8.5 ± 0.3	3.7 ± 0.8	1,079.3 ± 1.2	0.54 ± 0.001
Tzintzuntzan	2.9 ± 1.1	21.8 ± 2.4	22.4 ± 0.8	8.5 ± 0.2	3.5 ± 1.2	1,085.0 ± 3.9	0.54 ± 0.002

DO dissolved oxygen, *Cond* conductivity, *TDS* total dissolved solids

biotic and abiotic variables, and maximize catch probabilities of each fish species (Fig. 1). We sampled only in wet season, because in nutrient-enriched shallow lakes resources are limited as phytoplankton biomass is lower (Osborne, 2007). At each sampling site, three measurements of physicochemical variables (depth, water transparency, temperature, pH, dissolved oxygen, conductivity, and total dissolved solids) were obtained with a Secchi disk and a portable water quality meter (HANNA HI-9828; Table 1), and two samples of particulate organic matter (POM, 63–150 μm) were obtained from the surface water. Fish were collected at each site three times, using two different seine nets: 75×5 m², mesh size: 1 cm to collect: *Chirostoma* spp*., P. infans, A. robustus*; and 150×9 m², mesh size: 4 cm, to collect: *C. carpio, C. estor, G. atripinnis,* and *O. aureus.*

Isotope analysis

Throughout the entire system, 16 samples of particulate organic matter (POM) were collected to be used as a baseline. Stable isotope analysis was performed on the muscle tissue of the most abundant fish species in the lake (capture frequency ≥10%) according to Ramírez-Herrejón et al. (2014). A total of 182 tissues (Table 2) were collected from adults of the following species: *Goodea atripinnis*, *Allophorus robustus*, *Chirostoma* spp., *Chirostoma estor*, *Poeciliopsis infans*, *Cyprinus carpio*, and *Oreochromis aureus*. Adults were classified according to size (Orbe-Mendoza et al., 2002). All isotope samples were frozen at −4°C after collection, dried at 50°C for 48 h, ground into fine powder, packed in tin capsules, and analyzed for the carbon and nitrogen signature using continuous

flow isotope ratio mass spectrometry (UC Davis, 20-20 mass spectrometer: Europa Scientific). The isotopic ratios were expressed in standard delta "δ" notation. The mean standard deviation between samples and UC Davis laboratory standards was 0.069‰ for $\delta^{13}C$ and 0.129‰ for $\delta^{15}N$.

Data analysis

We grouped all silversides (*Chirostoma*) smaller than 10 cm into a single taxon because species of this genus are challenging for taxonomic identification (Barbour, 1973), and tend to hybridize under natural conditions, having a high degree of trophic, reproductive, and habitat niche overlap (Jiménez-Badillo & Gracia, 1995). Organisms larger than 15 cm were identified as *Chirostoma estor,* as no other species can reach that size (Barbour, 1973). We did not catch any organism between 10 and 15 cm, probably because the two seine nets used had a poor performance on that length class.

The spatial heterogeneity of limnetic variables can influence the isotopic signatures (Zambrano et al., 2010b). Therefore, we tested a potential relationship between the $\delta^{13}C$ and $\delta^{15}N$ of each species with physicochemical variables using individual Spearman correlations and applying the Bonferroni correction. We evaluated the differences in carbon and nitrogen among fish species by using a non-parametric Kruskal–Wallis, Mann–Whitney post hoc test and applying the Bonferroni correction. To evaluate the differences of both the carbon and nitrogen signatures between species, we used a one-way non-parametric MANOVA based on Euclidean distance (Anderson, 2001).

Trophic position of fish species was estimated assuming a trophic level increase of 3.4‰ and

Table 2 Fish species characteristics: standard length, isotopic signature, frequency of capture, trophic position, trophic guild, and common food items

	n	SL (cm)	δ^{13}C	δ^{15}C	Freq. (%)[a]	TP	Trophic guild†	Food items [b]
Native								
G. atripinniis	41	10.6 ± 1.5	−23.11 ± 1.58 a	12.83 ± 1.75 d	56	2.5	Omnivore	A, D, Z, BI
A. robustus	10	5.7 ± 1.2	−22.96 ± 0.45 a	16.4 ± 0.81 e	10	3.6	Carnivore	Z, BI, F
Chirostoma spp.	40	6.4 ± 0.7	−24.23 ± 0.35 a,c	18.09 ± 1.28 f	100	4.1	Zooplanktivore	Z, BI
C. estor	15	16.6 ± 2.3	−23.74 ± 0.72 c	18.56 ± 1.02 f	–	4.2	Carnivore	Z, C, F
Non-native								
P. infans	9	3.2 ± 0.4	−19.2 ± 0.74 b	14.45 ± 1.44 d,e	83	3	Omnivore	D, ED, TI
O. aureus	17	10.9 ± 3.1	−22.92 ± 2.21 ac	13.29 ± 1.46 d	49	2.7	Omnivore	A, P
C. carpio	50	25.2 ± 5.2	−24.57 ± 1.56 c	15.4 ± 1.46 e	68	3.3	Omnivore	D, P, BI, Z

Lower case letters in δ^{13}C (a, b, c) and in δ^{15}N (d, e, f) show significant differences ($P < 0.01$)

SL standard length, *TP* trophic position based on δ^{15}N, *A* filamentous algae, *P* plant material, *D* detritus, *ED* epiphytic diatoms, *Z* zooplankton, *BI* benthic invertebrates, *C* crustacean, *TI* terrestrial insect, *F* small fish

[a] Frequency of capture in 2009–2010 according to Ramírez-Herréjon et al. (2014)

[b] Trophic guild and principal food items were independent of size classes based on Jiménez-Badillo & Gracia (1995), Orbe-Mendoza et al. (2002), Ramírez-Herréjon et al. (2013)

following the equation of Cabana and Rasmussen (1996):

$$TP_{isotope} = \left[\left(\delta^{15}N_{fish} - \delta^{15}N_{MOP} \right)/3.4 \right] + 2$$

We assumed POM is composed mainly of phytoplankton (Gu, 2009) and defined the trophic baseline as the mean of POḾs δ^{15}N values of all sites. Trophic niche analysis was performed adapting the community niche analysis using δ^{13}C–δ^{15}N bi-plot to assess the trophic niche of species (Layman et al., 2007; Mercado-Silva et al., 2008; Zambrano et al., 2010a). Trophic niche analysis evaluates the trophic niche area of a single species based on the total niche area (TA), carbon range (CR), and nitrogen range (NR). These three parameters evaluate the occupied trophic niche of each species, the broad range of food sources a species can consume, and the capacity of a species to consume organisms from different trophic levels (Layman et al., 2007). The same bi-plots were used to analyze trophic niche overlap using MatLab. We calculated the trophic niche overlap for each pair of species and expressed each one as a percentage of the total niche area (TA). The total overlap of each species was analyzed to determine the relative proportion represented by native and non-native species.

We used a Monte Carlo method to bootstrap the same number of samples for each species. We sampled randomly nine individuals (comparable minimum)

from each species. The procedure was repeated 1,000 times for each species, and then, we calculated the mean of each value of the trophic niche analysis and the trophic niche overlap. We analyzed trophic niche overlap between every pair of species. Afterwards, we grouped the overlap values in native and non-native species and looked for differences using a Mann–Whitney U test. In this analysis, we did not consider the trophic niche overlap between *Chirostoma* spp. and *C. estor* due to their taxonomic and ecological similarities (Jiménez-Badillo & Gracia, 1995).

Results

We did not find a spatial effect between physicochemical variables and fish isotopic signatures (Table 3). With this information, we decided to analyze the trophic niche areas of each organism without considering the sampling location. The mean isotopic values of δ^{13}C in all species were within the range −24.5 ± 1.4‰ and −22.9 ± 2.2‰, except for *P. infans,* which had a higher δ^{13}C value (−19.2 ± 0.7‰) (Table 2). Particularly, *P. infans* presented significant differences in δ^{13}C with the rest of the species (*G. atripinnis*: U(48) = 0, $P < 0.01$; *A. robustus*: U(17) = 0, $P < 0.01$; *Chirostoma* spp.: U(47) = 0, $P < 0.01$; *C. estor*: U(22) = 0,

Table 3 Spearman's correlation coefficient (r_s) between isotopic signatures of each species and physicochemical variables

n	Depth	Secchi	Temp	pH	DO	Cond	TDS
G. atripinnis							
41							
$\delta^{13}C$	0.14	0.13	0.05	0.08	−0.003	0.08	0.08
$\delta^{15}N$	0.05	0.005	0.04	−0.13	0.09	−0.01	−0.01
A. robustus							
10							
$\delta^{13}C$	0.59	0.45	0.06	0.59	−0.54	0.54	0.54
$\delta^{15}N$	−0.33	−0.36	−0.69	0.29	0.14	−0.33	−0.33
Chirostoma spp.							
40							
$\delta^{13}C$	0.45	0.14	0.33	−0.05	−0.23	0.46	0.45
$\delta^{15}N$	−0.09	0.09	−0.002	−0.19	0.36	−0.18	−0.17
C. estor							
15							
$\delta^{13}C$	−0.11	−0.19	0.10	0.27	−0.22	0.22	0.22
$\delta^{15}N$	0.30	0.61	−0.31	−0.33	0.62	−0.59	−0.56
P. infans							
9							
$\delta^{13}C$	0.34	0.22	0.02	−0.10	0.02	0.15	0.14
$\delta^{15}N$	−0.03	0.11	−0.08	−0.04	0.25	−0.16	−0.15
O. aureus							
17							
$\delta^{13}C$	0.14	0.13	0.05	0.08	−0.003	0.08	0.08
$\delta^{15}N$	0.05	0.005	0.04	−0.13	0.09	−0.01	−0.01
C. carpio							
50							
$\delta^{13}C$	0.28	0.12	−0.19	−0.22	0.13	−0.03	−0.04
$\delta^{15}N$	−0.17	−0.08	−0.17	−0.54	0.27	−0.48	−0.48

DO dissolved oxygen, *Cond* conductivity, *TDS* total dissolved solids, No significant correlations were found

$P < 0.01$; *O. aureus*: $U(24) = 2$, $P < 0.01$; *C. carpio*: $U(57) = 8$, $P < 0.01$). The native *Chirostoma* spp. and *C. estor* were the species with the highest trophic level and were significantly different from the rest of the species in $\delta^{15}N$ (Table 2), but did not present significant difference between them ($U(53) = 258$, $P = 0.43$). A one-way non-parametric MANOVA based on Euclidean distance showed significant differences between every pair of fish species ($F(348) = 62.07$, $P < 0.01$), except between *Chirostoma* spp. versus *C. estor* ($F(52) = 1.83$, $P = 0.34$) and *O. aureus* versus *G. atripinnis* ($F(55) = 0.506$, $P = 0.61$).

Omnivorous non-native species had a trophic position between 2.7 and 3.3 (Table 2) and were located in the lower and middle range of the food web (Fig. 2). The trophic niche area bi-plot showed a high overlap among the non-native *C. carpio* and *O. aureus* with the rest of the species. In contrast, non-native *P. infans* presented no overlap with any native species. Each native species showed a trophic niche overlap with at least one non-native species. The only substantial overlap among native species was between *Chirostoma* spp. and *C. estor*.

The trophic niche analysis revealed that *G. atripinnis* had the highest nitrogen range (NR), while *O. aureus* had the greatest carbon range (CR) and total niche area (TA) (Table 4). In particular, the native species with the widest trophic niche was *G. atripinnis* with a trophic niche 2.8 times wider than *C. estor* (the native species with the second widest trophic niche) and 5.6 times wider than *A. robustus* (the species with the narrowest niche area). In contrast, the invasive *O. aureus* had a trophic niche 1.3 times wider than *G.*
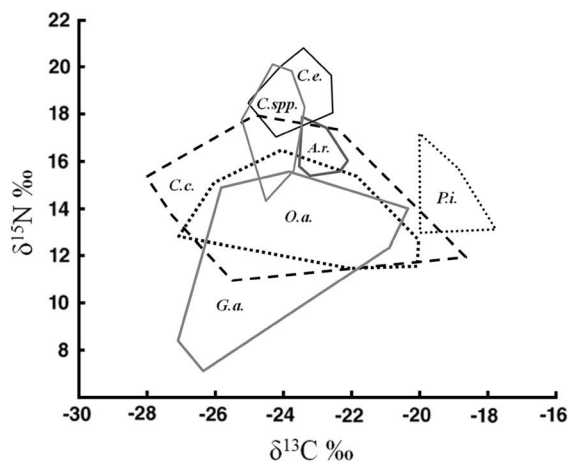
Fig. 2 Trophic niche area of each species. Polygons encompass the convex hull area of all individuals. *G.a.*: *G. atripinnis*; *P.i.*: *P. infans*; *A.r.*: *A. robustus*; *C.*spp.: *Chirostoma* spp.; *C.e.*: *C. estor; O.a.*: *O.aureus; C.c.*: *C. carpio.* Non-native species are represented with *dashed lines*

atripinnis and 7.2 times wider than *A. robustus*. On average, non-native species presented a trophic niche area two times wider than native species.

C. carpio had a trophic niche overlap with all other species (Table 4). In contrast, *P. infans* was the species with the fewest number of overlaps. The highest overlap values were shown between *G. atripinnis* and *O. aureus*, and between *C. carpio* and *O. aureus*. In general, non-natives presented a similar trophic niche overlap with natives and with the other non-natives (U(16) = 34.5, *P* = 0.92). In contrast,

trophic niche overlap between native and non-native species was higher than among natives (U(16) = 9, *P* < 0.01).

Discussion

The lack of relation between physicochemical variables and fish isotopic signatures suggests a constant movement of individuals among locations (Syväranta et al., 2006), or little variation of feeding habits (Jennings et al., 1997) and food sources on the base of the food web (Vizzini et al., 2005). Similarly, Ramírez-Herrejón et al. (2014) analyzed the trophic position based on δ^{15}N of Lake Patzcuaro ichthyofauna and did not found a strong spatial pattern in the lake.

Fish isotopic signatures coincide with previous records of feeding habits (Jiménez-Badillo & Gracia, 1995; Orbe-Mendoza et al., 2002; Ramírez-Herrejón et al., 2013). For example, native *Chirostoma* spp. is principally zooplanktivorous, and *C. estor* is both zooplanktivourous and piscivorous (Jiménez-Badillo & Gracia, 1995; Ross et al., 2006). The difference in their diets can explain their trophic niche overlap and the enrichment in δ^{15}N of *C. estor*. Also, the relation between the two native species, the predator *A. robustus* and the prey *G. atripinnis* (Berlanga-Robles et al., 2002) is consistent with their isotopic signatures. Low δ^{15}N values are correlated with greater isotopic variation (Gu et al., 1997), thus a wider trophic niche area. In Lake Patzcuaro, the native *G. atripinnis* and

Table 4 Trophic niche analysis and trophic niche overlap between species

Specie	Status	Niche analysis			Trophic niche overlap (%)							Overlap percentage		
		NR	CR	TA	*G.a.*	*A.r.*	*C.*spp.	*C. e.*	*P.i.*	*O.a.*	*C.c.*	T	N	NN
G. atripinnis	Native	5.2	4.8	11.1	–	0	2	0	0	53.7	11	64.8	0	100
A. robustus	Native	2.3	1.3	2	0	–	0	1	0	3.8	32.7	37.5	3	97
Chirostoma spp.	Native	3.8	1.1	2.3	0.2	0	–	47.7	0	3.7	21.7	73.3	65	35
C. estor	Native	3.2	2.2	4	0	0.5	27.4	–	0	0	0.7	28.7	97	3
P. infans	Non-native	4.2	2.2	5.3	0	0	0	0	–	0	0.3	0.3	0	100
O. aureus	Non-native	3.9	6.3	14.4	41.4	0.5	0.6	0	0	–	23.5	66.1	64	36
C. carpio	Non-native	4.1	4.4	9.7	12.6	6.7	5.1	0.3	0.2	34.9	–	59.9	41	59

Trophic niche overlap is read row by row, it represents the overlap in percentage of the total area (TA)

NR nitrogen range, *CR* carbon range, *TA* total area, *G.a. G. atripinnis*, *A.r. A. robustus*, *C.spp. Chirostoma* spp., *C.e. C. estor*, *P.i. P. infans*, *O.a. O. aureus*, *C.c. C. carpio*, *T* total trophic niche overlap, *N* trophic niche overlap represented by native species, *NN* trophic niche overlap represented by non-native species

the non-natives *C. carpio* and *O. aureus* presented low values of δ^{15}N and the widest trophic niche areas. These three species are omnivorous and display a high trophic niche overlap among them. In particular, *G. atripinnis* and *C. carpio* share food sources as organic detritus and benthic invertebrates (Orbe-Mendoza et al., 2002). Similarly, *G. atripinnis* and *O. aureus* share filamentous algae as a food source (Orbe-Mendoza et al., 2002).

Previous studies suggest that isotopic niche overlap between species can be interpreted as a shared food source (Vander Zanden et al., 1999; Pilger et al., 2010) and, therefore, as an indicator of potential competition (Kelly & Jellyman, 2007; Zambrano et al., 2010a). The non-native *O. aureus* and *C. carpio* exhibited a high trophic niche overlap between them. However, their wider trophic niche area suggests that these non-native species are opportunistic and can overcome possible changes in trophic structure or competition (Kondoh, 2003), which may explain their coexistence. In contrast, native species presented narrower trophic niche areas. For example, although *Chirostoma* spp. might include five species, the isotopic signatures framed a narrow trophic niche area, suggesting all these species are specialists.

The other non-native species (*P. infans*) was first reported in the lake in 1997 (Galindo-Villegas & Sosa-Lima, 2002), and nowadays it represents one of the most abundant species in the lake (Ramírez-Herrejón et al., 2014). However, little is known about the possible impacts of this establishment on the native species populations (Ramírez-Herrejón et al., 2013). The almost null trophic niche overlap with other species is consistent with gut content analysis as no other species in the lake consume epiphytic diatoms or terrestrial insects (Ramírez-Herrejón et al., 2013; Table 2). Also, terrestrial insects represent an allochthonous food source for *P. infans* that could contribute to the enrichment of δ^{13}C. In addition, the recent establishment of *P. infans* could be explained by the use of trophic resources not exploited by other species.

Algansea lacustris and *Allotoca diazi* are two native species that were not caught during this study. Both species are omnivorous, feeding mainly on filamentous algae, benthic invertebrates, and zooplankton (Orbe-Mendoza et al., 2002). Thus, these species might present a high trophic niche overlap in the base of the trophic food web with *O. aureus*, *C. carpio*, and

G. atripinnis. Nowadays, these native species are two of the less abundant species in the lake (Ramírez-Herrejón et al., 2014). However, *Algansea lacustris* once represented the 25% of the total fish biomass (Berlanga-Robles et al., 2002). Similarly, non-native *Micropterus salmoides* population has greatly decreased in the last decades, and no fish were recorded during this study. *Micropterus salmoides* is a pelagic carnivore, it feeds mainly on fish and invertebrates, which suggest a potential trophic niche overlap with *C. estor* (Contreras & Escalante, 1984).

Niche differentiation can explain species coexistence, but empirical support has been sparse (Mason et al., 2008). However, niche specialization has been considered as a common phenomenon in fish community assemblages (Ross, 1986; Pilger et al., 2010). In Lake Patzcuaro, there seems to be a trophic niche specialization within the native species, supported by their slight trophic niche overlap. The only substantial overlap among native species was between *Chirostoma* spp. and *C. estor*, which are taxonomically and ecologically related (Jiménez-Badillo & Gracia, 1995). Also, *Chirostoma* spp. may include juvenile organisms of *C. estor*. In contrast, the high trophic niche overlap between native and non-native species (*C. carpio* and *O. aureus*) suggests potential competition for food resources (Kelly & Jellyman, 2007; Zambrano et al., 2010a).

The presence of both *C. carpio* and *O. aureus* can also affect the population of native species by indirect effects. In several studies, *C. carpio* has been related to an increase in turbidity, total phosphorus, suspended solids, and phytoplankton biomass; and negatively related to macrophyte and macroinvertebrate abundances (Breukelaar et al., 1994; Zambrano et al., 2006; Parkos et al., 2011). In a North Carolina, power plant cooling reservoir, *Tilapia zilli* (redbelly tilapia) became the most abundant species within three years of their introduction and eliminated all floating and submerged aquatic macrophytes within two years, coinciding with significant declines of four abundant native species populations (Crutchfield et al., 1992). Furthermore, the presence of these two species simultaneously can create additive or synergistic effects on turbidity (Rowe, 2007).

In addition to the effects of non-native species, changes in water quality are also possibly affecting the trophic structure of the lake. In the last 20 years, Lake Patzcuaro went from an oligo-mesotrophic to a

eutrophic system (Chacón-Torres, 1993; Sánchez-Chávez et al., 2011), which can be related to a switch from a benthic to a pelagic dominance of primary productivity and be linked through the food web (Vadeboncoeur & Jeppesen, 2003). The indirect effects of non-native species can generate a positive feedback with water quality by increasing turbidity, total phosphorus, and suspended solids (Scheffer, 1998). In this scenario, the wider trophic niche area of non-native species and their biological attributes (fast reproductive and growing rates) can be an advantage over the native species in this altered system (Kondoh, 2003; Vadeboncoeur et al., 2005; Winemiller, 2005).

The narrow trophic niche area of native species suggests that a small change in the food sources abundance would generate a big change in the native species populations. This can contribute to the depletion of the native species, because the system has been changing rapidly in the last decades. Another factor is the trophic niche overlap between native and non-native species, suggesting shared resource use among species and potential competition. However, with a wider trophic niche, non-natives are able to switch food sources depending on their abundance, while natives that only feed in a small range of food sources are more susceptible to these changes.

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