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Research Article

Long term changes in the fish fauna of Lago de Pátzcuaro in Central México

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ABSTRACT. Fish assemblages of lakes from central México have been altered as a result of water over-exploitation, pollution, habitat fragmentation, and introduction of exotic species. Patterns and the extent of change in most of these systems are poorly documented. This paper presents a long-term study of changes in the fish fauna of Lago de Pátzcuaro (State of Michoacán, México). Long-term information (years 1900-2010) of fish communities was used to explore trends in the composition of the fish community and their ecological attributes. Trends across time for each fish guild were evaluated through a multivariate analysis of variance. Native species dominated total species richness over the entire study period, but exotic fish comprised 46% of the community in the 2010s. During the last 110 years, there has been a decline in the number of carnivore species and an increase of omnivore species in the Lago de Pátzcuaro fish community. Sensitive species have disappeared from the lake and species tolerant to environmental degradation have increased from 13 to 61%. The data suggest that anthropic effects on the environmental condition of Lago de Pátzcuaro are associated with the loss of ecosystem elements (fish species) and ecosystem processes (species interactions). Ecological restoration and conservation programs must include information of these long term studies to be more effective in their efforts.

Keywords: shallow lake, environmental degradation, ecological guilds, historical analysis, exotic species, México.

Cambios a largo plazo en la fauna de peces del Lago de Pátzcuaro en México central

RESUMEN. El ensamble de las comunidades de peces en los lagos de México Central ha sido alterado como resultado de la sobre-explotación del agua, contaminación, fragmentación de hábitat y la introducción de especies exóticas. Los patrones y la extensión de los cambios en la mayoría de estos ecosistemas están escasamente documentados. Este artículo presenta un estudio a largo plazo de los cambios en la fauna de peces del Lago de Pátzcuaro (Estado de Michoacán, México). La información a largo plazo (años 1900-2010) de las comunidades de peces fue usada para explorar las tendencias en la composición específica y los atributos ecológicos de las especies en la comunidad. Las tendencias a través del tiempo para cada gremio de peces fueron evaluadas mediante análisis de varianza multivariado. Las especies nativas dominaron a través de todo el periodo de estudio, pero las especies exóticas alcanzaron 46% de la comunidad en la década del 2010. Durante los últimos 110 años, ha habido disminución en el número de especies carnívoras e incremento de las especies omnívoras en este ecosistema. Las especies intolerantes han desaparecido del lago y las especies tolerantes a la degradación ambiental han incrementado de 13 a 61%. Los datos sugieren que los efectos antrópicos sobre la condición ambiental del Lago de Pátzcuaro se asocian con la pérdida de elementos (especies de peces) y procesos (interacciones entre las especies) del ecosistema. Los programas de conservación y restauración ecológica deben incluir información proveniente de este tipo de estudios a largo plazo para ser más efectivos.

Palabras clave: lagos someros, degradación ambiental, gremios ecológicos, análisis históricos, especies exóticas, México.

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INTRODUCTION

Mexican freshwater ecosystems have been deteriorating since pre-Hispanic times, however this process has accelerated at the beginning of the 20th century, and worsened in the last 30 years (Lyons *et al*., 1998; Soto-Galera *et al*., 1999). The main causes of freshwater ecosystem degradation are deforestation, excessive sedimentation, the introduction of exotic species and discharge of urban and industrial waste water (Peters *et al*., 2005). These activities have altered the biotic community structure and function, decreased food web length, and favoured reduction of organism's maximum size and species diversity (Karr, 1981; Lyons *et al*., 1998). Other changes experienced by fish communities include the increase of exotic species, local extinction or near-extinction of several native species, and the collapse of many fisheries (Aloo, 2003).

Lago de Pátzcuaro is located in the highlands of central México and has been subjected to several hydrological modifications: erosion and runoff from deforested uplands, loss of surface area, reduction of the water column (approximately 6 m and 166 Mm^3 in the past 70 years), lower water transparency (approximately 2 m in the past 40 years), hyper-eutrophication, and point source contamination from local communities throughout the lake (Alvarado-Díaz *et al*., 1985; Chacón-Torres, 1993; Berry *et al*., 2011). Lago de Pátzcuaro supports one of the best-studied, for the last three decades, inland fisheries in México; many of its endemic species have been intensively fished since long before the colonial times (De Buen, 1941; Orbe-Mendoza & Acevedo-García, 1995; Orbe-Mendoza *et al*., 2002). However, fishery production from this lake has shown major fluctuations over the last 20 years and it is currently in sharp decline (Berry *et al*., 2011). Many of its fish populations are on the verge of collapse (Orbe-Mendoza *et al*., 2002).

Lago de Pátzcuaro is one of the few lakes in México with a relatively long series of fish sampling records. Earliest data of the fish community from this lake are available from the 1900 decade and sampling efforts have continued to present times, allowing for a long-term study. To date there has not been an analysis of the long-term changes of the fish communities in the lake. Historical analyses of changes in fish communities offer information about the current conservation status of aquatic ecosystems and surrounding watershed conditions (Karr, 1981; Fausch *et al*., 1990). Analyses of this kind can detect the anthropic impacts that influence the fish community, and are useful to identify elements and ecosystem processes lost as a consequence of human activities (Scott & Hall, 1997; Lyons & Mercado-Silva, 1999). Further information on the nature of the impacts can be obtained from the ecological attributes of individual species (Karr, 1981; Lyons *et al*., 1995). Ecological studies on fish assemblages can integrate and evaluate a variety of impacts (water quality, habitat structure, species interactions) on biotic systems (Hobbie *et al*., 2003; Mercado-Silva *et al*., 2006). Species origin, feeding preferences and species tolerance to environmental degradation are fish attributes to consider when analysing community change and understanding cumulative anthropic impacts (Lyons & Mercado-Silva, 1999; Mercado-Silva *et al*., 2006).

This paper presents a long-term study of changes in the number of species (as indicators of the condition of ecosystem elements) and three ecological attributes (as indicators of the status of ecosystems processes) of the fish community of Lago de Pátzcuaro. The study provides a broad perspective that can help our understanding of general trends in fish communities of tropical lakes with similar conditions of environmental degradation.

MATERIALS AND METHODS

Study area

Lago de Pátzcuaro (Fig. 1) is part of an endorheic drainage basin in the highlands of central México (19°32′N-19°42′N, 101°32′W-101°42′W) in the State of Michoacán. With a maximum surface area of 116 km^2, Lago de Pátzcuaro is the third largest natural lake in México (Gomez-Tagle *et al*., 2002). It has a maximum depth of 12 m at maximum capacity and an average depth of 5 m. Water volume is determined by precipitation, evapotranspiration, and inflows from springs at the bottom of the lake and flows from small creeks in the watershed (Bernal-Brooks *et al*., 2002). The lake has experienced a 6 m water level decline since 1939 (Berry *et al*., 2011). Lago de Pátzcuaro is circadiomictic and is generally considered eutrophic

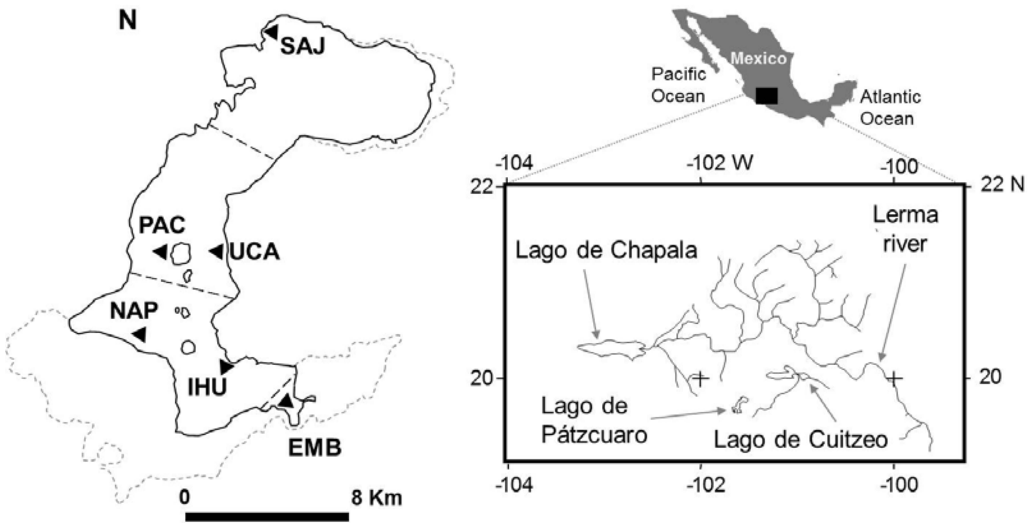

Figure 1. Location of Lago de Pátzcuaro and study sites. Limnological zones defined by Alcocer & Bernal-Brooks (2002) are indicated by dotted lines. An approximation of the surface loss is indicated by gray lines. Sampling sites locations are as follows: San Jerónimo (SAJ) (19°40′40.4″N, 101°36′16.9″W); La Pacanda (PAC) (19°36′38.1″N, 101°39′2.7″W); Ucasanastacua (UCA) (19°35′51.7″N, 101°37′58.5″); Napízaro (NAP) (19°35′20.8″N, 101°40′12.7″W); Ihuatzio (IHU) (19°35′35.1″N, 101°40′45.2″W); Embarcadero (EMB) (19°33′0.6″N, 101°37′30.7″W). Black triangles show each collection zone.

(Berry *et al.*, 2011). There are 26 urban areas surrounding the lake including one densely populated island (Isla Janitzio) in the southern part of the lake. The lake watershed covers 9,340 km^2 and includes land used for agriculture and livestock production (~40% of the watershed area), forestry (~30%), and urban activities (~22%) (Bravo-Espinosa *et al.*, 2006). Erosion caused by agriculture and ranching is high in some parts of the basin. High erosion rates are reflected in the rates of sedimentation (100,000 m^3 each year) in the lake (Gomez-Tagle *et al.*, 2002).

Study stages

This study was divided into two stages. First, we carried out a review of the historical data. Second, we made sampling efforts at the lake.

Long term data from collections

Historical fish collection information was obtained from scientific collection records at the University of Michigan Museum of Zoology (UMMZ), Universidad Michoacana de San Nicolás de Hidalgo (UMSNH), Instituto Politécnico Nacional (IPN) and data from personal collections by J. Lyons (University of Wisconsin-Madison Department of Zoology, *pers. comm.*). These sources comprise the majority of sampling records for Lago de Pátzcuaro. We also gathered information from records in Berlanga-Robles *et al*. (2002). We used species composition data for one year in the first decade of the 1900s (UMMZ) and for at least three years per decade from 1930s (UMMZ), 1950s (UMMZ), 1990s (J. Lyons' personal data, UMSNH, Berlanga-Robles *et al.* (2002)), 2000s (IPN, UMSNH) and 2010s (data collected as part of this study). No data was available for the decade of the 1920s, 1940s, 1960s, 1970s and 1980s. From each collection record, the taxonomic identity of the species and the number of species were obtained. Data from any location within the Lago de Pátzcuaro were considered. For most records no information on sampling effort or gear type was available, and we had to assume that sampling efforts adequately sampled the entire fish community. Because of this limitation, only presence/absence data were considered for analysis following Mercado-Silva *et al*. (2006).

We include the Lago de Pátzcuaro salamander *Ambystoma dumerilli* (Ambystomatidae) in the analysis because it is functionally equivalent to a fish in the ecosystem (Mercado-Silva *et al*., 2002). *A. dumerilli* is neotenic and completely aquatic throughout its life. It is an environmentally sensitive and a carnivorous species (Huacuz, 2002). The information about the long-term presence of this amphibian species in Lago de Pátzcuaro was taken from Huacuz (2002).

Recent sampling efforts

To assess the current condition of the fish community in Lago de Pátzcuaro we sampled six sites containing different types of fish habitat in four lake zones defined by Alcocer & Bernal-Brooks (2002): (1) San Jerónimo (SAJ) is a littoral zone (max. 10 m from the point of fish capture to the shore) located in the northern portion of the lake (mean depth = 1.4 m); (2) Pacanda Island (PAC) is a limnetic zone (more than 30 m from the point of fish capture to the closest shore) adjacent to an island in the center of the lake (mean depth = 6 m); (3) Ucasanastacua (UCA) is a littoral zone located halfway between the northern and southern most sections of the lake (mean depth = 2 m); (4) Napízaro (NAP) is a limnetic zone located in the southern portion of the lake (mean depth = 2.5 m); (5) Ihuatzio (IHU) is a littoral zone located in the southern portion of the lake (mean depth = 1.9 m); (6) Embarcadero (EMB) is a littoral zone located in the southern portion of the lake, adjacent to the Pátzcuaro City (mean depth = 1 m) (Fig. 1).

Samples from each site were collected in September and November 2009 (wet season), and February and June 2010 (dry season). Two different seines were used to obtain representative samples of the fish community, increasing the likelihood of collecting species of small and large size. Seining has been traditionally used by local fishermen to capture fish and *Ambystoma dumerilli* in the same sites used in this study (Huacuz, 2002; R. Quirino, Lago de Pátzcuaro fisherman, *pers. comm.*). A seine 150 m long, 9 m deep, with 4 cm mesh was used to capture relatively large fishes. A smaller seine 75 m length, 7 m deep, with 1 cm mesh was used to capture small fishes. Each net was launched three times at each site for a total of 144 sets in the study. Each seine launch was carried out in a different area in each site. Captured specimens were counted to assess the absolute abundance (number of individuals), the abundance per species, and frequency (percentage of sets where a species was encountered). Fish were identified to species except individuals in the genera *Oreochromis* and *Chirostoma* because of difficulties in their identification. At least two species of *Oreochromis* were introduced to Lago de Pátzcuaro, blue tilapia *O. aureus* and Nile tilapia *O. niloticus* (Berlanga-Robles *et al*., 1997, 2002; Gaspar-Dillanes *et al*., 2006). Hybridization has occurred between *Oreochromis* species, making positive identification at species level difficult. Among *Chirostoma*, taxonomic differences between four native species, bigeye silverside *Ch. grandocule*, Patzcuaro silverside *Ch. patzcuaro*, slender silverside *Ch. attenuatum*, and Pike silverside *Ch. estor* and one introduced species, shortfin silverside *Ch. humboldtianum* are currently in dispute (Barriga-Sosa *et al*., 2002; Bloom *et al*., 2009). Many studies argue that relatively recent hybridization among *Chirostoma* species has occurred in Lago de Pátzcuaro, making species identification difficult and obscuring taxonomic differences among the four native and one introduced species (Ledesma-Ayala & García de León, 1991; Oseguera-Figueroa & García de León, 1991; Soria-Barreto & Paulo-Maya, 2005). In the remainder of the text and analyses however, we consider all individuals in *Chirostoma* as native.

Analysis

According to historical records and after identification in the field (for our field efforts), each fish and amphibian were assigned to their correspondent guild based on their origin (native or exotic to the basin), feeding habits (carnivorous, omnivorous) and tolerance to pollution or habitat deterioration (tolerant, sensitive), following published classifications (Lyons *et al*., 2000; Mercado-Silva *et al*., 2002) (Table 1). These attributes were selected because they can inform about several aspects of the conservation of freshwater ecosystems. The persistence of natives and the presence of exotics are related with the conservation status of geologic, biogeographic and evolutionary processes (Harig & Bain, 1998; Aparicio *et al*., 2000; Olden & Poff, 2005). The maintenance of certain proportions of carnivores and omnivorous over a long term indicates that ecological processes associated with ecosystems functional conditions are preserved (Karr, 1993; Scott & Hall, 1997; Dobson *et al*., 2006). The proportion of tolerant and sensitive species can be related to the levels of degradation in a lake (Karr, 1981; Whittier & Hughes, 1998; Meador & Goldstein, 2003; Seilheimer & Chow-Fraser, 2006).

Long term data samples (1900-2000) often had relatively vague geographical descriptions. We were able to identify that they were obtained within the lake, but rarely was there a within-lake specific location established. Therefore, samples were assumed to be representative of the entire lake. Information from collections taken in any year within a decade (regardless of the specific site) was summarized to produce an average value for each fish guild per decade between 1900 and 2010. To explore the variation of fish guilds over time, we used the number of species and average value for each guild gathered in a decade. The analysis combines species information for each of the six guilds for the following decades: 1900s, 1930s, 1950s, 1990s, 2000s and 2010s. Data were standardized using a square-root transformation ($\sqrt{n}$) following (Clarke & Gorley, 2006), to balance the contributions of dominant and rare groups. Trends across decades for each fish guild were analysed through a multivariate analysis of variance. A

Table 1. Fish guilds, collection decades and presence-absence of each taxon in Lago de Pátzcuaro. For trophic guild (TG): O: omnivore, C: carnivore, H: herbivore. For origin (OR): N: native, E: exotic. For tolerance (TOL): S: sensitive, M: moderately tolerant, T: tolerant, *Amphibian included in the study, 1: presence, 0: absence.

Family	Species	OR	TG	TOL	1900s	1930s	1950s	1990s	2000s	2010s
Cyprinidae	*Algansea lacustris*	N	C	M	1	1	1	1	1	1
	Cyprinus carpio	E	O	T	0	0	0	1	1	1
	Ctenopharyngodon idella	E	H	T	0	0	0	1	1	0
Goodeidae	*Allotoca dugesii*	N	C	S	1	1	1	1	1	0
	Allotoca diazi	N	C	M	1	1	1	1	1	1
	Alloophorus robustus	N	C	M	1	1	1	1	1	1
	Goodea atripinnis	N	O	T	1	1	1	1	1	1
	Skiffia lermae	N	H	S	1	1	1	1	0	0
Atherinopsidae	*Chirostoma* spp.	N	C	M	1	1	1	1	1	1
Poecilliidae	*Poeciliopsis infans*	E	O	T	0	0	0	1	1	1
Cichlidae	*Oreochromis* spp.	E	O	T	0	0	0	1	1	1
Centrarchidae	*Micropterus salmoides*	E	C	M	0	1	1	1	0	1
Ambystomatidae	*Ambystoma dumerilii**	N	C	S	1	1	1	1	0	0

posteriori pairwise comparison analysis was used to search for differences among decades. Because our data do not fulfill the assumptions of normality, homogeneity of variance, or independence, we decided to use an analysis based on permutation techniques in PERMANOVA (Anderson, 2001) from PRIMER 6 (Clarke & Warwick, 2001).

RESULTS

Recent sampling

Nine fish taxa were collected in 2009-2010, five were considered native and four exotic. The native *Chirostoma* spp. was the most abundant in the lake (83,209 individuals and 100% of frequency), followed by the blackfin goodea *Goodea atripinnis* (252 individuals and 56% of frequency). The most abundant exotics were the lerma livebearer *Poeciliopsis infans* (3,679 individuals and 83% of frequency), common carp *Cyprinus carpio* (1,721 individuals and 68% of frequency), and tilapiine cichlids *Oreochromis* spp. (3,174 individuals and 49% of frequency). The uncommon natives were the bulldog goodeid *Alloophorus robustus* (10 individuals and 10% of frequency), Pátzcuaro chub *Algansea lacustris* (7 individuals and 8% of frequency), and the Pátzcuaro allotoca *Allotoca diazi* (2 individuals and 1% of frequency), the latter was found only at one site. The uncommon exotic was the largemouth bass *Micropterus salmoides* (2 individuals and 1% of frequency). Three native (*Ambystoma dumerilii,* the bumblebee allotoca *Allotoca dugesii* and the olive skiffia *Skiffia lermae)* and one exotic (grass carp *Ctenopharyngodon idella)* species that had been historically collected were not found.

Species tolerant to environmental degradation comprised most of the samples; no sensitive species were captured. Moderately tolerant fish captured include *A. lacustris*, *A. diazi*, *Chirostoma* spp., *A. robustus*, and the exotic *M. salmoides*. Five species were carnivorous: four native (*A. lacustris*, *A. robustus, A. diazi, Chirostoma* spp.) and one exotic (*M. salmoides*). All other species were omnivorous (Table 1).

Comparisons along time

All taxa encountered in samples taken in the decade of 1900s were native to Lago de Pátzcuaro. By the 1930s one species, *Micropterus salmoides,* had been introduced. By the 1990s, four other fish taxa were introduced (*Cyprinus carpio, Ctenopharyngodon idella, Poeciliopsis infans,* and *Orechromis* spp.). By the 2000s, two native species – one fish (*Skiffia lermae*) and one amphibian (*Ambystoma dumerilii*), and one exotic species (*Micropterus salmoides*) were not recorded (Table 1).

MANOVA indicated differences among fish collections related to the decline in the number of native and carnivorous species over time (Pseudo-F = 7.99, $P < 0.004$; Pseudo-F = 12.64, $P < 0.001$, respectively). The number of sensitive species declined (Pseudo-F = 0.81, P = 0.087) and the number of exotic, omnivorous, and tolerant species increased over time (Pseudo-F = 174, $P < 0.001$; Pseudo-F = 186.79, $P < 0.001$; Pseudo-F = 198.3, $P < 0.001$, respectively).

From 1900 to 2010, the number of native species changed from 8 to 3.3 ± 1.5, a reduction of 46% in native species richness. Exotic species increased from 0 to 3.6 ± 1.1 in the same period. During the same time frame, the number of carnivorous species went from 6 to 2.6 ± 1.2, a decrease from 75 to 39% of the total number of collected species. The number of omnivorous species increased from 1 to 4 (13 to 61% of the total number of collected species) and sensitive species disappeared (38 to 0% of the total number of collected species). The number of tolerant species increased from 1 to 4 (13 to 61% of the total number of collected species) in the same period (Fig. 2).

DISCUSSION

Shallow lakes are considered the most threatened ecosystems as a consequence of human fragmentation of habitats, introduction of exotic species, and changes in land use (Miller *et al*., 1989; Dudgeon *et al*., 2006). Historical research on changes in ecosystem elements and processes help understand the effects of anthropogenic threats and provide specific information that can be used to reduce further ecosystem degradation (Karr, 1981; Mercado-Silva *et al*., 2006). Data about long-term changes can aid in developing monitoring strategies and future conservation efforts (Olden & Poff, 2005; Mercado-Silva *et al*., 2006). Although anthropic effects on the watershed and the water quality of Lago de Pátzcuaro are relatively well documented, this study represents the first effort to understand the long-term changes of the fish assemblages in this lake.

The origin of fish fauna of Lago de Pátzcuaro is biogeographically associated with tectonic and volcanic events that occurred in the late Tertiary and begining of the Pleistocene in Central region of México, during which a great number of endemic species were generated in families such as Petromizontidae, Cyprinidae, Ictaluridae, Poecilidae, Goodeidae and Atherinopsidae (De Buen, 1947; Barbour, 1973a, 1973b; Barbour & Miller, 1976). The fish fauna and ecosystem of Lago de Pátzcuaro have experienced changes in their ecological characteristics coinci-dentally with the increase of cumulative and combined human exploitation of the lake and the surrounding drainage basin. Native, sensitive carnivorous species have decreased and the number of exotic, tolerant, omnivorous species has increased. These changes suggest that Lago de Pátzcuaro has lost ecosystem elements (fish species), ecosystems processes (species interactions), and perhaps habitat diversity.

Lago de Pátzcuaro, like many others in Central México, shows ecosystem changes related to long period of cumulative anthropic effects. The surface area of the lake has decreased by more than 30 km^2 since 1970s. Water depth has decreased >5 m, water volume has lost >150 Mm^3 and water transparency has decreased >3 m over the same period (Bernal-Brooks *et al*., 2002; Orbe-Mendoza *et al*., 2002). Fisheries were one of the most important economic activities during the earlier (1900s to 1960s) decades (Berry *et al*., 2011) but can no longer sustain fishermen livelihood. Currently there are no full time active fishing communities in the lake. Most local fishermen now occasionally fish for supplemental food during certain seasons and complement their diets with farm animals (R. Quirino, Lago de Pátzcuaro fisherman, *pers. comm.*). These landscape and human dimension changes in the history of Lago de Pátzcuaro fishery reflect our description of decline in the fish communities over 110 years, between 1900 and 2010. The yield of all fisheries in the lake have declined from ~2500 ton in 1988 to <50 ton in 2007 (Diario Oficial de la Federación, 2010).

At the species level, current changes have been dramatic. The pike silverside *Chirostoma estor* fishery registered >130 ton in 1981, <5 ton in 1999 (Hernández-Montaño, 2006) and has currently collapsed. Small-size silverside fisheries (<150 mm SL) declined from >500 ton in 1985 to <50 ton in 1999 (Hernández-Montaño, 2006) and has currently also collapsed, with only a few fishermen using it as an infrequent self-consumption fishery. The *Algansea lacustris* fishery changed from >650 ton in 1988 to <50 ton in 1999 (Hernández-Montaño, 2006) and is currently a rare self-consumption fishery (R. Quirino, Lago de Pátzcuaro fisherman, *pers. comm.*). The *Goodea atripinnis fishery* registered 258 ton in 1989 and 13.5 ton in 1999 and is currently also a rare self-consumption fishery (Hernández-Montaño, 2006). There have also been declines of the Lago de Pátzcuaro salamander *Ambystoma dumerilii*; its fishery registered 6 ton in 1987, <3 ton in 1998 and <0.3 ton in 1999. Their exploitation has currently collapsed and the salamander is possibly extinct (Huacuz, 2002). The exotic largemouth bass *Micropterus salmoides* fishery registered 1988 ton in 1981, 0.4 ton in 1999 (Hernández-Montaño, 2006) and has currently collapsed. Even the most recent fishery on the exotic common carp *Cyprinus carpio* has decreased, catches declined from >600 ton in 1988 (Gaspar-Dillanes *et al.,* 2006) to <40 ton in 1999 (Hernández-Montaño, 2006), <20 to in 2007 (Diario Oficial de la Federación 2010) and <10 to in 2009 (Zambrano *et al*., 2011). The exotic Nile tilapia

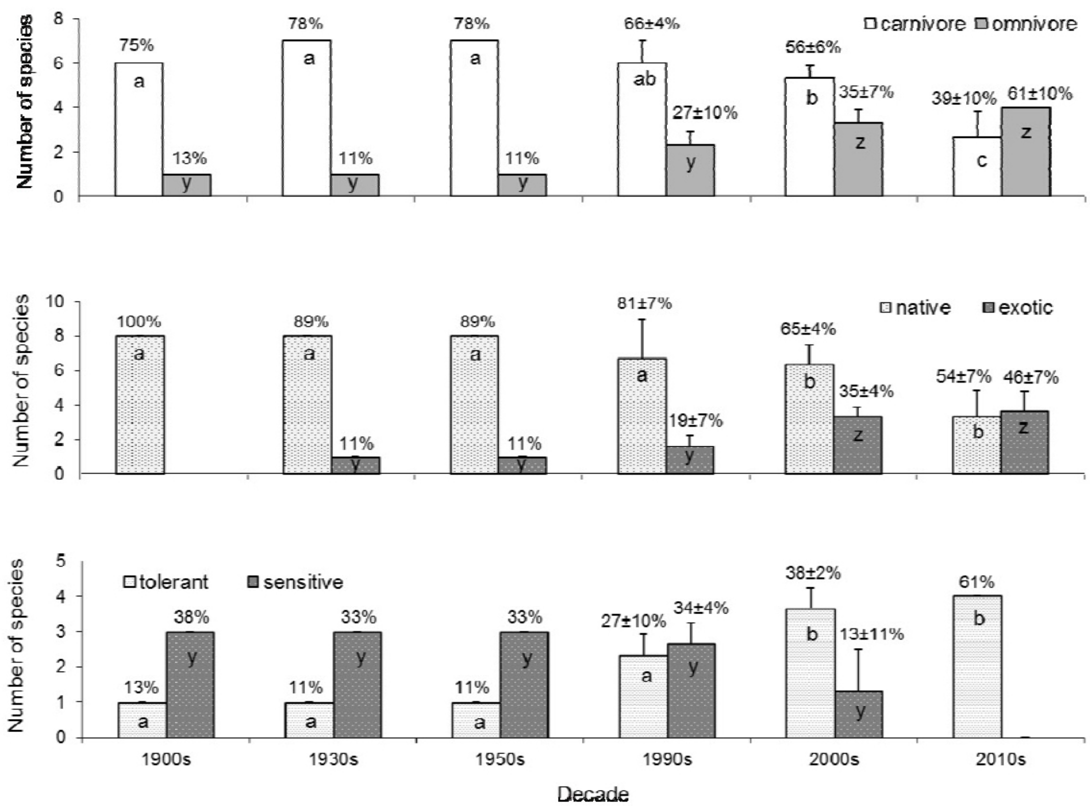

Figure 2. Long-term trends (1900-2010) of fish guilds in Lago de Pátzcuaro. Columns show mean and standard deviation. Average percentage change of each fish guilds by decade is presented above each bar. Letters a, b, c, and y, z indicate groups of decades for which no difference in the number of species was found in *a posteriori* pairwise comparisons obtained by MANOVA.

(*Oreochromis* spp.) fishery has decreased from 243 ton in 1988 to 34 ton in 1999 (Hernández-Montaño, 2006). Non-commercial fish populations have also declined. These include *Skiffia lermae*, *Allotoca dugesii*, *Allotoca diazi*, *Alloophorus robustus* and *Algansea lacustris* (Berlanga-Robles *et al*., 2002; Huacuz, 2002; Orbe-Mendoza *et al*., 2002).

Species richness is widely employed as a tool in ecological assessments because it has positive correlations with measurements of habitat and water quality (Scott & Hall, 1997; Gotelli & Colwell, 2001). In Lago de Pátzcuaro several native species have declined in numbers and this could be associated with alterations to the ecosystem. The absence of *Ambystoma dumerilli*, *Skiffia lermae* and *Allotoca dugesii* in our collections and the few individuals captured of *Allotoca diazi*, *Algansea lacustris* and *Allophoorus robustus* may indicate ecosystem degradation via the loss of their reproductive habitat and alterations to their food resources. This coincides with Soto-Galera *et al*. (1999) and Lyons *et al*. (2000) who argued that species of subfamily Goodeinae are sensitive to changes in trophic webs and habitat degradation. According to Anderson (1972) species of *Ambystoma* genus are also highly sensitive to habitat loss. Some authors argue that *Skiffia lermae* and *Allotoca dugesii* are locally extinct in this lake (Berlanga-Robles *et al*., 2002). The trends we found in Lago de Pátzcuaro resemble those found by Mercado-Silva *et al*. (2006) who showed that, after serious degradation, the number of native species declined greatly in lentic and lotic aquatic ecosystems of the Lerma-Chapala Basin in central México, over a period of approximately 50 years.

Untreated sewage inputs to the lake and water hyacinth trituration in parts of Lago de Pátzcuaro have caused tremendous input of oxygen-demanding wastes that degrade water quality, changing productivity (Xie *et al*., 2004). This productivity changes affect biotic interactions, which in turn provides advantages to omnivorous fishes (Karr, 1993; Vanni *et al*., 2005). For example, exotic, small-sized, and short-lived species (*Oreochromis* spp.) were introduced to Lago de Pátzcuaro in the 1970s (Rosas, 1976), and their persistence through the years is due in part to its capacity to resist alterations of aquatic habitats and water quality (Harig & Bain, 1998). Additionally, the common carp (*C. carpio*) was introduced in 1974 for commercial aquaculture (Rosas, 1976) and has subsisted in the lake probably because it can use highly diverse sources of food (Zambrano & Macías-García, 2000). In addition, these two fish taxa (*Oreochromis* spp. and *C. carpio*) can modify entire habitats and compete for feeding resources with native fish species (Zambrano *et al*., 2006).

A somewhat different situation has occurred with another exotic species, *M. salmoides*, which requires relatively good water and habitat quality and can be useful as an indicator of environmental degradation. *Micropterus salmoides* is a top predator in Lago de Pátzcuaro. Before 1990, the lake contained two pelagic piscivores, one native (*Ch. estor*) and one exotic (*M. salmoides*) (Solorzano-Preciado, 1963; García de León & Pérez-Velazco, 1996). Today, fisheries of both species have collapsed as a consequence of habitat degradation and overfishing (Gaspar-Dillanes *et al*., 2006; Berlanga-Robles *et al*., 2002). Fish at the top of the food chain are usually the first to disappear since they depend on a stable food web (Domínguez-Domínguez *et al*., 2008), and relatively high water transparency for selecting food (Fausch *et al*., 1900; Simon & Lyons, 1995; Lyons *et al*., 2000) and abundant fish and benthic invertebrates as feeding resources (Godinho & Ferreira, 1994). Both species also use the littoral zone as reproductive habitat in Lago de Pátzcuaro (García de León, 1984), and these areas have been lost in more than 70% (Alcocer-Durand & Bernal-Brooks, 2002).

Chirostoma estor is not currently extinct in this lake possibly because there are still remnant wetland areas where this fish species can breed and the contribution of terrestrial insects that may result from agriculture or livestock in areas surrounding the lake. Terrestrial insects are part of the current diet of *Chirostoma* spp. (Vital-Rodríguez, 2011).

In the past, top predators used to be large sized (>170 mm SL) ichthyophagous fish (García de León & Pérez-Velazco, 1996) and now they are smaller in size (<120 mm SL) planktivorous fish (*Chirostoma* spp.). The decrease in the sizes of large carnivores has occurred also in Lake Chapala (Moncayo-Estrada *et al*., 2012). According to Seilheimer & Chow-Fraser (2006), top predators (typically long-lived species) are susceptible to long-term physical and chemical habitat alterations. Other studies have argued that lakes with high clay turbidity are more beneficial to planktivorous fish than piscivorous predators for successful feeding (De Robertis *et al*., 2003; Moncayo-Estrada *et al*., 2010). In our study, small silversides (*Chirostoma* spp.) were captured in every seine pull and at all collection sites. Small silversides are typically open water fish using pelagic zones as feeding and reproductive habitat (Lyons *et al*., 1995; Mercado-Silva *et al*., 2002). These small fishes feed mainly on pelagic zooplankton and use a variety of reproductive substrates (gill nets, buoys, floating branches) that can be located far from the littoral zone (Rojas-Carrillo, 2006; Moncayo-Estrada *et al*., 2010). Silverside fishes represented more than 90% of the fish collected in our sampling efforts, which could indicate that species able to utilize non-littoral habitats have an advantage over species requiring now degraded littoral zones. These results are similar to those reported by Domínguez-Domínguez *et al*. (2008), where carnivorous species, such as *A. robustus* and *A. dugesii* declined in the drainage basins of the Río Morelia and Río Laja, two rivers located in central México, associated with changes in the trophic web or destruction of the habitat of prey.

Some studies have argued that it is possible to distinguish different functional groups of *Chirostoma* spp. by separating them into at least two different sizes: small silversides (<170 mm SL) and large silversides (from >170 mm to 340 mm SL) (Hernández-Montaño, 2006; Moncayo-Estrada *et al*., 2012). Further, it has been argued that small and large silversides can been classified in different trophic categories, where small silversides are secondary consumers and big silversides tertiary consumers and top predators (Moncayo-Estrada *et al.*, 2012). In Lago de Pátzcuaro, silversides could be classified into small and large fishes before the decade of 2000s. However, in the present study, the largest captured silversides showed <130 mm SL, rendering the differentiation between large and small-sized fish ineffective. It is possible that this size reduction has resulted from intensive fishing efforts. Interestingly there is no diet variation among *Chirostoma* spp. 30-90 mm SL, and some small silversides (<90 mm SL) can feed on juvenile silversides (Vital-Rodriguez, 2011).

Some fishes in the Goodeidae family and the achoque (*Ambystoma dumerilli*) are known to live only in conserved lakes because they are extremely sensitive to water quality, vulnerable to predation, and have narrow habitat requirements (Huacuz, 2002; Domínguez-Domínguez *et al*., 2008). The presence of some goodeid fishes and achoque serve as indicators of water quality and relatively pristine habitats (Harig & Bain, 1998; Domiguez-Domínguez *et al*., 2008). We did not collect typically sensitive goodeid species, such as *Skiffia lermae* and *Allotoca dugesii*, or any amphibians, such as *Ambystoma dumerilli*. Their absence could indicate considerable degradation in water and habitat quality in the lake (Anderson, 1972; Soto-Galera *et al*., 1999; Lyons *et al*., 2000).

The native and carnivore fishes *Allotoca dugesii*, *Allotoca diazi*, *Alloophorus robustus*, big *Chirostoma* (*C. estor* >150 mm SL), *Algansea lacustris* and the exotic *Micropterus salmoides* depend on littoral zones for reproductive habitat in the lake (Gaspar-Dillanes *et al*., 2006). Severe alteration of the littoral zone could explain the decrease or absence of these species. We hypothesize that, if environmental degradation in Lago de Pátzcuaro continues, the fish community will in the future be dominated by four species: *Chirostoma* spp. (mostly native, carnivorous, tolerant) and *Cyprinus carpio*, *Oreochromis* spp. and *Poeciliopsis infans* (exotic, omnivorous, tolerant), with perhaps just a few areas of the lake where other species may persist. Since habitat structure plays an essential role in the maintenance of fish assemblages, and fish ecological guilds change when loss of habitat complexity ocurrs (Jones & Sayer, 2003; Bond & Lake, 2005), restoration of the littoral zone of Lago de Pátzcuaro will need to be a priority to achieve survival of its historical fish fauna. The loss or extinction of endemic species in the lake would represent alarming changes in the elements and ecological processes and also in geologic and biogeographic processes that allowed the origin of this fauna, and it would represent a greater chance of losing ecosystem services in the future.

Our study is based on a review of the historical collections recorded at zoological museums at a variety of institutions. We recognize that sampling equipment, time, location and objectives among many other variables may have changed from one sampling event to another. While these sampling inconsistencies certainly throw uncertainty into our analysis and forced our analyses to be relatively basic, the described trends on the fish community are strong and give a gross picture of the changes that have ocurred throughout the lake. The long period (1900-2010) covered by the analysis represents an advantage difficult to find in similar studies. We also recognize that "species-lumping" may have reduced the specificity of our findings. As stated above, we could not consistently separate the numerous individuals of *Chirostoma* we captured, and we analyzed all individuals as single taxa. This undoubtedly reduced the number of elements (species) that we could use in our comparisons. We believe however, that this aspect of data management does not obscure the overall trends we found in the Lago de Pátzcuaro fish community.

This study is a first attempt to characterize the long-term changes in the fish community associated with environmental degradation at Lago de Pátzcuaro. It could be used to predict the future status of the fish community and ecological processes of this ecosystem (Soto-Galera *et al*., 1999; Contreras-MacBeath *et al*., 1998). It could further offer the base-line to create new indices for environmental quality such as the index of biotic integrity (Karr, 1981) and other ecosystem monitoring protocols. Currently, the conservation activities have focused on improving water quality, the eradication of exotic species and the cultivation of some native species to enhance their populations. However, the dramatic changes in the ecological processes of the lake cannot ensure a successful species re-introduction. Our results suggest that the restoration of littoral habitat (wetland zones) represent a key management need to preserve ecosystem processes in Lago de Pátzcuaro. This would support the recommendations that the restoration of vegetated littoral zones could provide habitat regeneration for native small fish species and improve water quality in Lake Chapala (Moncayo-Estrada *et al*., 2010). We support the suggestion made by Orbe-Mendoza *et al.* (2002) that it is urgent to implement practices that offer fishermen a subsistence and sustainable fishery in the short term.

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