

Long-term changes in the fish assemblage of the Laja River, Guanajuato, central Mexico

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ABSTRACT

1. The structure and composition of fish communities in rivers of central Mexico have been altered as a result of water over-exploitation, habitat fragmentation, introduction of exotic species, and pollution. However, the specific pattern and degree of change are poorly documented.

2. Long-term information from the Laja River (Guanajuato, Mexico) in the Lerma River basin was used to explore trends in fish species richness and community composition (species origin, trophic niche, tolerance, and preferred habitat) from the 1960s to the present in both river and reservoir sites.

3. Declines in native, sensitive, benthic native and carnivore species ranging from 11% to 30% per decade, and increases in the number of tolerant and exotic species by 9–20% per decade, are documented. Repeated measures ANOVA and sign tests revealed significant declines in the number of benthic, native, carnivore and sensitive species. Species richness, number of exotics, tolerant species and omnivore species did not change statistically, though statistical power was low. Some important changes occurred in these variables, such as the expansion and establishment of exotics such as *Xiphophorus variatus* and *Micropterus salmoides*, which pose a serious potential threat to native species.

4. The changes in fish community composition for the Laja portray how the fish communities in other rivers in central Mexico, for which long-term data do not exist, have changed or could change if environmental deterioration continues.

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KEY WORDS: Lerma River; functional group; impact; environmental change; sensitive species; habitat deterioration; exotic species; habitat alteration

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INTRODUCTION

Species loss in Mexican freshwater ecosystems is considered among the most dramatic on the planet (Paxton and Eschmeyer, 2003). Freshwater fish extinctions and population declines have been caused by habitat deterioration, over-exploitation, and invasive species (Contreras-Balderas and Escalante-Cavazos, 1993; Contreras-Balderas and Lozano-Vilano, 1993; Lyons *et al.*, 1998). The high endemism of the freshwater fish fauna of Mexico makes it especially vulnerable to human impact. Approximately 70% of the freshwater fish species in the country are found nowhere else on earth, while numerous species have very limited geographic distributions and are located in highly sensitive regions where agriculture and industrial activities are intense (Lyons *et al.*, 1998; Soto-Galera *et al.*, 1999a).

The Lerma-Santiago River drains most of central Mexico, including the region known as the Bajío, and is considered one of the most degraded river basins in the country (Lyons *et al.*, 1998; Soto-Galera *et al.*, 1999a; Rosales-Hoz *et al.*, 2000; de Anda *et al.*, 2001). The fish in this basin have suffered significant declines (Díaz-Pardo *et al.* 1993). Lyons *et al.* (1998) identified at least three extinct species as of the 1990s and reported many sites that had been sampled prior to 1985 to be dry or too polluted to sustain fish. Only a few relatively isolated branches of this large system maintain environmental conditions required for the survival of a relatively intact fish fauna. The Laja River in the state of Guanajuato is one such tributary (Soto-Galera *et al.*, 1999a), but it is far from being considered pristine (Barbour, 2002) and has not escaped many of the impacts that the Bajío, one of the most productive and densely inhabited regions in Mexico, has imposed on its water resources. The Laja is unusual among Mexican rivers in that its fish fauna has been documented during several time periods since the 1960s, allowing the study of long-term changes in the composition and ecological structure of its fish community. Declines (or increases) in species richness or populations can be indicators of human-derived environmental change, but further information on the nature of the impact can be obtained from the consideration of the ecological attributes of individual species (Karr, 1981; Lyons *et al.*, 1995). Trophic role, habitat requirements, tolerance to pollution, and origin (exotic/native) are important factors to consider when analysing community change, especially when there is a need to understand biological impacts to the communities, such as those derived from the invasion of exotic species, one of the leading threats to biodiversity (Soulé, 1990).

This paper describes a long-term study of the changes in the composition and ecological attributes of the fish community of the Laja River. In addition, it provides a broader perspective on rivers of central Mexico, as the Laja is important for understanding general trends in the fish communities in rivers of the region.

STUDY AREA

The Laja basin (21° 33'–20° 58' N, 101° 28'–100° 30' W) covers 3476 km² of the State of Guanajuato in Central Mexico (Figure 1). The basin has numerous intermittent and semi-intermittent tributary streams draining into the Laja River. This semi-arid area is characterized by numerous mountain ranges and high plateaus (mean altitude > 1800 m) that have a relatively short rainy season during the summer (July–October) with total annual precipitation of 400–800 mm (CONABIO, 2000). Although much of the basin has been affected by agriculture, the typical natural vegetation types in the area include oak forests, chaparral and xerophyte vegetation. Riparian vegetation, where it occurs, consists of narrow strips of *Salix* sp. in small stretches of the river with rushes along river banks. Substrates in the main river channel are typically sand/silt-dominated with interspersed rocky segments. Practically all streams and rivers in the basin are truncated by reservoirs or other water extraction and storage structures. Two major reservoirs and a water-diversion dam have been built in the Laja River, but at least 12 more reservoirs are located on tributaries (CNA, 2002). The two major reservoirs, Ignacio Allende and Jesús María, were built in 1968 and 1982, respectively, to provide flood control and water for agriculture. The main stem of the Laja is 154 km

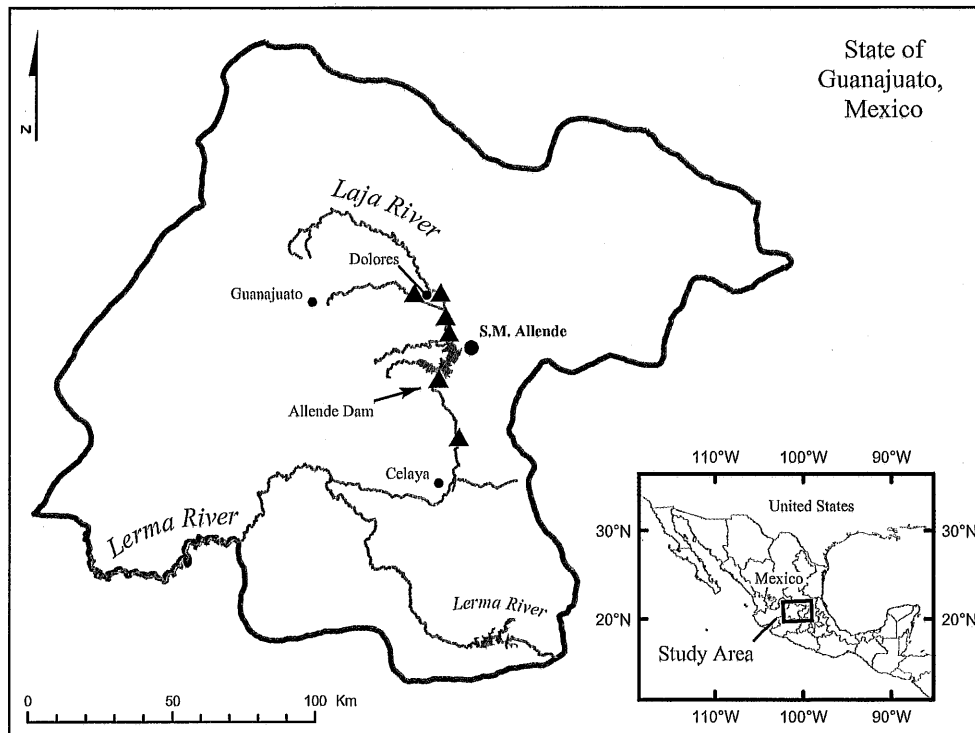


Figure 1. The Laja River (Guanajuato, Mexico). Triangles mark sites for which historical data were available (north to south: Presa el Gallinero, Arroyo San Gabriel, Atotonilco, El Xote, Presa Ignacio Allende, Empalme Escobedo).

in length, of which 124 km are located upstream from the Ignacio Allende Dam (Hernández-Javalera, 2002) and *ca.* 15 km are located above Jesús María. The water diversion dam was built in the 1970s in the lower Laja to divert water from the river into a series of irrigation canals in the agricultural valley of Celaya. Dry land and irrigated agriculture dictate water use in the basin; the number of deep wells in the area has increased significantly from 210 in 1971 ($145 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ water extracted), when the first hydrological studies were carried out in the region, to 781 in 1999 (*ca.* $210 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ water extracted) (CNA, 2002). Several other non-regulated water extraction operations are located along the river, usually in the form of pumps that extract water directly from the Laja. Numerous springs in the basin are used for recreation.

Except for the headwaters and a few canyons, the Laja has generally a low to moderate gradient with seasonal and dam-regulated flows. Water is stored in reservoirs during the rainy season, thus altering natural flow regimes. Especially during the later part of the rainy season, when dams release water, the flow in the river quickly fluctuates from isolated pools separated by dry river bed to fast runs exceeding 3 m in depth. Even though a large portion of the Laja is used for agriculture, its headwaters are considered as a priority area for conservation by CONABIO (2000) given their relatively high biodiversity.

METHODS

Historical collections

During 2003, museums and research institutions were searched for samples and scientific collection information from sites in the Laja River or any of its tributaries. Information was obtained from museum

records at the Laboratorio de Ictiología y Limnología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (ENCB-IPN), and the University of Michigan Museum of Zoology (UMMZ), which hold most of the records from the Laja system. Information from various independent fish collections in the Laja (Mercado-Silva *et al.*, 2002; Díaz-Pardo, 2004) and other unpublished data were also used. Records were examined to ensure that the location of the sampling sites was consistent among source institutions and individual collections. Sites with geographical descriptions too broad or inaccurate were discarded from the analysis. From each record, the number of species collected was obtained. For most historical accounts, no information on sampling effort or gear type was available. Museum records often lacked quantitative data; thus, only species presence/absence data was considered for analysis. For all museum records, it was assumed that fishing effort was comparable and that all species encountered were preserved or at least reported in field notes. It was also assumed that all collection events adequately sampled the fish community.

To eliminate potential effect of seasonality on the results, *t*-tests were carried out between collections made in dry versus wet seasons for each historical site to test for differences in the number of species captured. The same was done for samples from 2003–2004. In addition, samples were examined to detect whether a species presence was restricted to a given season.

Historical information was found for six sites (four river and two reservoir) along the Laja River. Table 1 presents the sources of data for each sampling included in the analyses. Two river sites (Arroyo San Gabriel and Atotonilco) had been sampled only once in the past. All other sites had been sampled three or more times in the period 1966–2003 (including authors' samples). The most historical information was available for the Ignacio Allende Reservoir and the Empalme Escobedo sites (Table 1).

Recent sampling efforts

During 2003–2004, as part of a more general survey of the Laja system, four of the sites that had been reported in museum records together with 13 additional sites in reservoirs, main-stem and effluent streams in the Laja River basin were intensively sampled (Figure 1). Sampling occurred during January, June, August and November 2003, and January 2004, but not all sites were sampled on every occasion. Seines, DC backpack electroshockers, and gillnets, as required, were used to obtain representative samples of the fish community in all habitats at each sampling site. Sampling continued until no changes were detected in the number of species captured or their relative abundance. All fish captured were identified and counted.

Table 1. Source of information on fish collections in the Laja River. There may be more than one sample per year. Sources for each of the collections are given as footnotes (UMMZ = University of Michigan Museum of Zoology, ENCB-IPN = Escuela Nacional de Ciencias Biológicas — Instituto Politécnico Nacional)

Site	Site type	Time range
(1) Arroyo San Gabriel	River	1966 ^e , 2003 ^a
(2) Ignacio Allende Dam	Reservoir	1969 ^c , 1986–1992 ^e , 1996–1997 ^e , 2003 ^a
(3) Gallinero Dam	Reservoir	1966 ^e , 1978 ^e , 1986 ^e
(4) Empalme Escobedo	River	1969 ^e , 1977 ^d , 1986 ^e , 1997 ^{e,f} , 2003 ^a
(5) Atotonilco	River	1986 ^e , 2003 ^a
(6) El Xote	River	1997–1999 ^b

Sources: ^aMercado-Silva (original data);

^bMercado-Silva *et al.* (2002);

^cBarbour and Douglass (UMMZ);

^dSmith and Baker (UMMZ);

^eENCB-IPN;

^fDíaz-Pardo, 2004.

Voucher specimens for some of the collections were deposited in the Colección Nacional de Peces of the Institute of Biology (Universidad Nacional Autónoma de México) in Mexico City. Most of the fish captured were released unharmed after processing.

Analysis

For each year represented in museum collections and other sampling occasions an analysis was made of the number of species collected in each year and the ecological attributes of each species. Ecological attributes comprised origin (native versus exotic), feeding habits (carnivore, herbivore or omnivore), habitat use (pelagic versus benthic) and tolerance to pollution or habitat deterioration, and were established based on the criteria of Lyons *et al.* (1995), Mercado-Silva *et al.* (2002) and Medina-Nava (2003) (Table 2).

Annual information for each site was summarized to give an average value for each fish attribute for each decade between 1960 and 2000. Trends across decades for each fish attribute were analysed for river and reservoir sites separately and for the river as a whole. Repeated measures analysis of variance (RMANOVA) (SAS V8 SAS Institute) with autoregressive type 1 model for covariance structure, was used to test for trends. Given the sparseness of the data in time series, and to increase confidence in the interpretation of the *p*-values generated from the RMANOVA, a Sign Test (Zar, 1999) for the slopes (positive or negative) of the change of each fish community variable through time was applied for each site independently. The overall percentage change (per decade) for each of the fish community variables was calculated as the mean of the percentage change estimated from each decadal interval, excluding zero values to prevent bias from extreme values. Standard errors were estimated based on the individual decadal changes for each fish community variable.

RESULTS

Twenty-three fish species are known from the Laja River, based on historical accounts and authors' sampling efforts (Table 2). Historical records for the river accounted for 22 species. The exotic *Ctenopharyngodon idella* (Cyprinidae) (one individual) was the only species reported in 2003 that had not been previously reported. Fifteen species of fish from the 17 sites sampled in the Laja River were collected in 2003–2004. *Chirostoma jordani* (Atherinopsidae), *Yuriria alta* (Cyprinidae), *Xenotoca variata* and *Goodea atripinnis* (Goodeidae), all native species, were the most prevalent and abundant species in the basin (Table 3). Seven exotic species were captured in the Laja in 2003–2004. The most widely distributed exotics were *Oreochromis aureus* (11/17 sites) and *Carassius auratus* (10 sites). Of all sites sampled, only one (Rio San Juan) lacked exotic species. *Notropis calientis* and *Algansea tincella* were the most restricted natives and were found in one and four river sites respectively. Six native and two exotic species that had been historically collected in the Laja were not found in 2003: *Scartomyzon austrinus* (Catostomidae), *Ictalurus dugesi* (Ictaluridae), *Skiffia lermæ* and *Alloophorus robustus* (Goodeidae), *Aztecula sallaei* (Cyprinidae), *Chirostoma humboldtianum* (Atherinopsidae) and the exotics *Poecilia sphenops* (Poeciliidae) and *Lepomis cyanellus* (Centrarchidae). These are for the most part categorized as carnivores, and as sensitive or medium tolerance species (Table 2).

Species tolerant to environmental degradation comprised most of the catch for the samples collected during 2003. *Notropis calientis* was the only sensitive species captured in 2003 from a single river site. *A. tincella*, *Chirostoma arge*, and the exotics *Lepomis macrochirus*, and *Micropterus salmoides* were the few species with medium tolerance captured in 2003. *A. tincella* was captured at two sites located immediately below the Ignacio Allende reservoir and in the headwaters of the Laja (Arroyo Cantera). *C. arge* was captured from six river sites throughout the Laja, though it was present in low relative abundance at

Table 2. Fish of the Laja River, their ecological attributes, and collection sites. For trophic position (T.P.): O = omnivore, C = carnivore, H = herbivore. For origin: N = native, E = exotic. For tolerance: S = sensitive, M = medium tolerance, T = tolerant. For habitat: W = water column, B = benthic, EB = exotic benthic. Classification modified from Mercado-Silva *et al.* (2002). Sites where the species was collected in the 1966–2003 period are indicated (Ri = river site; Re = reservoir site). Asterisk identifies species reported for the Laja but not captured in the 2002–2003 collections or the sites studied here. Species collected in 2003 intensive samples are identified

Family and species	T.P.	Origin	Tolerance	Habitat	Site where collected		Collected in 2003
					Ri	Re	
Cyprinidae							
<i>Algansea tincella</i>	O	N	M	W	X		X
<i>Carassius auratus</i>	O	E	T	EB	X	X	X
<i>Cyprinus carpio</i>	O	E	T	EB	X	X	X
<i>Notropis calientis</i>	C	N	S	W	X		X
<i>Aztecula sallaei</i>	C?	N	S?	W	X	X	
<i>Yuriria alta</i>	O	N	T	W	X	X	X
<i>Ctenopharyngodon idella</i>	H	E	T	W		X	X
Catostomidae							
<i>Scartomyzon austrinus</i>	C	N	S	B	X		
Ictaluridae							
<i>Ictalurus dugesi</i>	C	N	M	B	X		
Atherinopsidae							
<i>Chirostoma jordani</i>	C	N	T	W	X	X	X
<i>Chirostoma arge</i>	C	N	M	W	X	X	X
<i>Chirostoma humboldtianum</i> *	C	N	S?	W			
Poeciliidae							
<i>Poecilia sphenops</i>	H/O	E	T	W	X	X	
<i>Poeciliopsis infans</i>	O	N	T	W	X	X	X
<i>Xiphophorus variatus</i>	O	E	T	W	X	X	X
Goodeidae							
<i>Goodea atripinnis</i>	O	N	T	W	X	X	X
<i>Xenotoca variata</i>	O	N	T	W	X	X	X
<i>Alloophorus robustus</i> *	C	N	M	W			
<i>Skiffia lernae</i> *	O	N	S	W			
Centrarchidae							
<i>Lepomis macrochirus</i>	C	E	M	W	X	X	X
<i>Lepomis cyanellus</i> *	C	E	T	W			
<i>Micropterus salmoides</i>	C	E	M	W	X	X	X
Cichlidae							
<i>Oreochromis mossambicus</i>	O	E	T	W	X	X	X

each site. No native benthic species were found in the 2003–2004 samples. The only benthic species collected were the exotics *C. auratus* and *C. carpio*. All other species were ‘water column’ species. Four carnivore species were found in the Laja in 2003–2004, but only two were native: *C. jordani* (found at most sites) and *C. arge* (6/17 sites). The exotic carnivore *L. macrochirus* was well represented throughout the Laja, but the exotic *M. salmoides* was not widely distributed. The rest of the species collected were omnivores.

Table 3. Percentage occurrence (percentage of sites where encountered) and number of individuals collected for species from the Laja River in 2003–2004 (17 sites sampled)

Species	Percentage occurrence (%)	Number of individuals collected
<i>Chirostoma jordani</i>	94	3833
<i>Yuriria alta</i>	88	1032
<i>Xenotoca variata</i>	82	913
<i>Goodea atripinnis</i>	82	2156
<i>Oreochromis mossambicus</i>	64	187
<i>Poeciliopsis infans</i>	64	1043
<i>Carassius auratus</i>	58	108
<i>Xiphophorus variatus</i>	52	1418
<i>Cyprinus carpio</i>	52	26
<i>Chirostoma arge</i>	35	44
<i>Lepomis macrochirus</i>	35	154
<i>Micropterus salmoides</i>	23	238
<i>Algansea tincella</i>	23	19
<i>Notropis calientis</i>	5	3
<i>Ctenopharyngodon idella</i>	5	1

HISTORICAL COMPARISONS

Seasonality of historical collections had no influence on the historical trends observed; species richness in dry versus wet season collections were similar ($p > 0.05$). When all sites (river and reservoir) were analysed together, the number of sensitive species and the number of native benthic species showed significant declines over time ($F = 9.56$, $P > F = 0.005$; $F = 12.86$, $P > F = 0.0024$; respectively) (Figure 2) based on RMANOVA. Three other fish community variables — number of exotic, medium tolerance, and carnivore species — showed marked, though not statistically significant, changes through time (Figure 2).

When analysed separately, neither river nor reservoir sites showed significant trends in any of the community variables for the period 1960–2000. The numbers of sensitive and benthic species in river sites were the only variables that showed a near-significant result based on RMANOVA ($F = 12.38$; $P > F = 0.076$ and $F = 11.32$; $P > F = 0.082$, respectively). All other variables had p -values ≥ 0.1 . No variables were close to significance in reservoir sites (All p -values ≥ 0.1) when analysed independently, indicating that changes in the fish community are greater for river than reservoir sites.

The sign test analysis generally supported the results from the RMANOVA. The decline in sensitive species through time at all six sites examined was significant ($p = 0.031$). However, the decline in the number of benthic species was not significant in the sign test ($p = 0.125$), even when all four sites where this variable was applicable showed a decline. The scarcity of data for the Laja limited the power of the statistical methods. Some fish community variables that did not change significantly through time using RMANOVA showed significant trends using sign test analysis. The decline in carnivore and native species at all six sites was statistically significant ($p = 0.031$ for both). The decline of medium tolerance fish through time was not statistically significant even when all five sites showed a decline through time ($p = 0.062$). All other aspects of the fish assemblage did not change significantly through time.

Fish community variables showed strong declines in the number of sensitive species (30% per decade), species of medium tolerance (33%), benthic species (18%), carnivore species (18%), and native species (13%). There was virtually no change in the total number of species (2.5%) and the number of omnivore

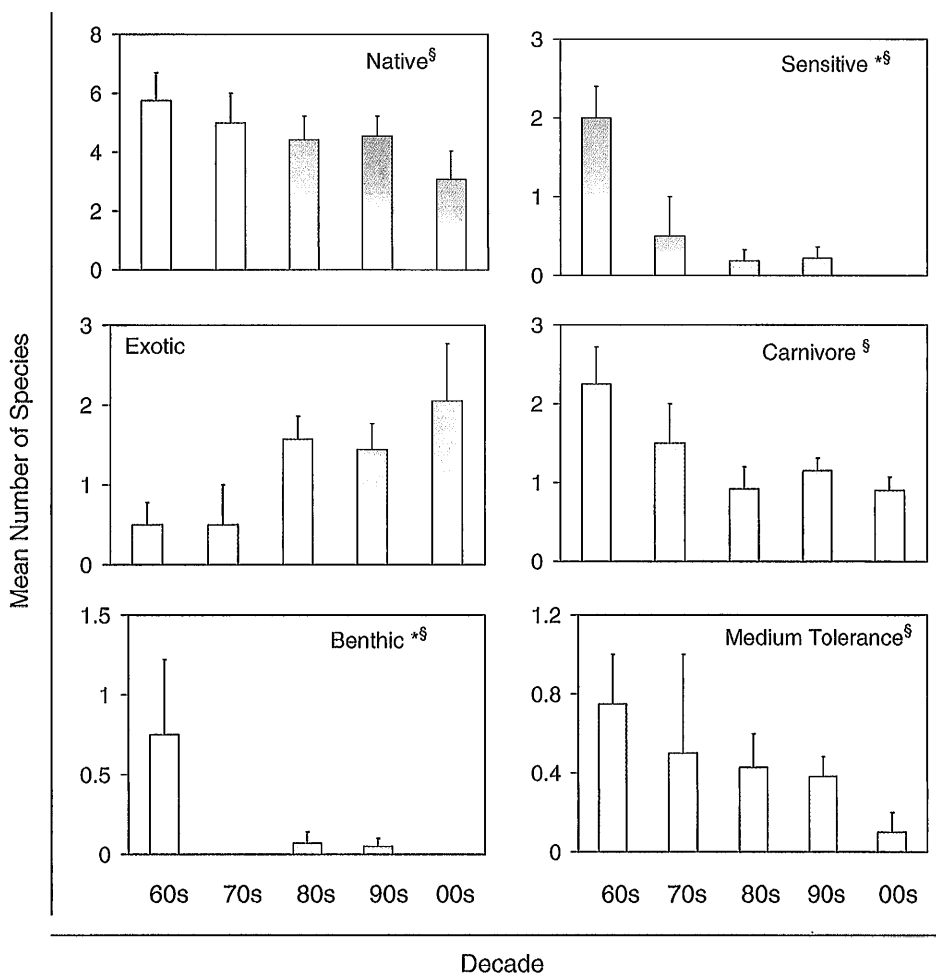


Figure 2. Trends (1960–present) for selected variables of the fish community in the Laja River. All river and reservoir sites are considered in these plots. Variables that showed a significant change ($\alpha = 0.05$) through time using RMANOVA are indicated with an asterisk. Variables showing significance with Sign Test analysis indicated by a 'section' sign (§).

species (2.7%). There were overall increases in the number of tolerant (9.7% per decade), exotic (22%) and exotic benthic species (20%) (Figure 3).

DISCUSSION

Rivers and lakes are considered the most threatened ecosystems because of human impacts such as flow alteration, habitat fragmentation and degradation, introduced species, and land-use change (Miller *et al.*, 1989; Moyle, 1994). Fish communities of the Laja River have changed significantly as a consequence of human impacts, resulting in a fish community characterized by species that are tolerant and omnivorous, and in which exotics are very common.

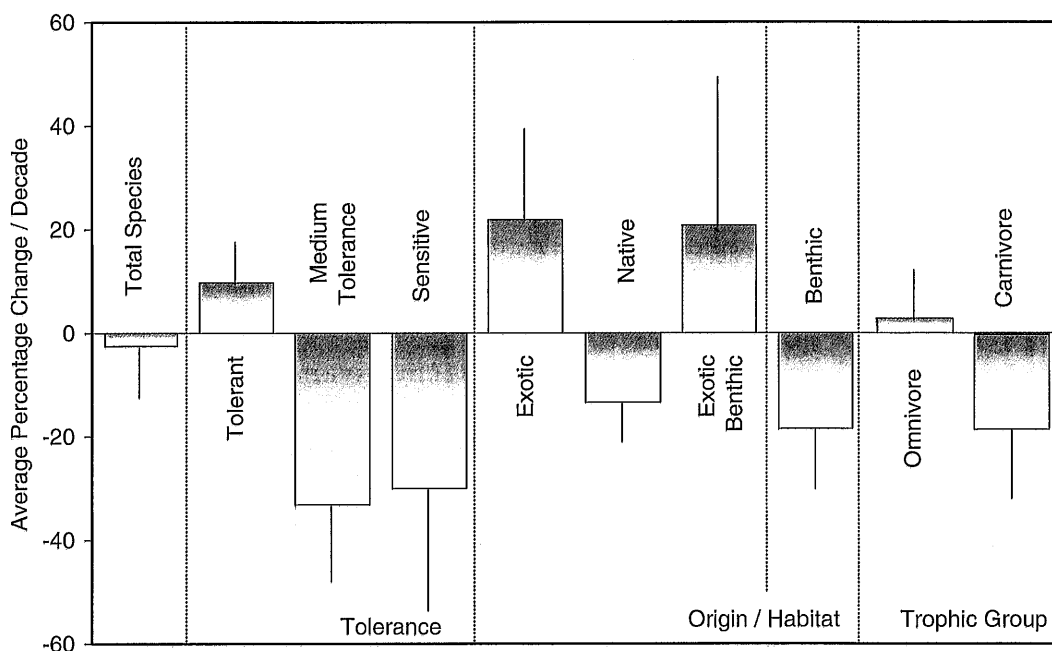


Figure 3. Average percentage change per decade for the attributes of the fish community of the Laja River. Positive value indicates increase, negative values indicate decline.

The disappearance of *S. austrinus* and *I. dugesi*, two native benthivore species requiring good water and habitat quality, parallels their loss in other rivers in Central Mexico (Soto-Galera *et al.* 1999a; López-López and Paulo-Maya, 2001). *S. austrinus*, like most suckers, is a species commonly found in rocky areas of streams where water flow is medium to low, albeit constant (Walsh *et al.*, 1998). In the Laja, the main channel remains dry for extensive periods as a consequence of closure of the various dams on the river. In addition, unsustainable agriculture is widespread and promotes soil erosion that results in the siltation of the rocky and gravel substrate required by the species. *I. dugesi* is moderately sensitive to habitat degradation and was important to local fisheries which may have caused their decline through over-exploitation (Lyons *et al.*, 1998). Local fishermen report not having seen catfish in recent years.

N. calientis is a sensitive, carnivorous cyprinid that was present at only one site in 2003. The species has declined throughout much of its range, which encompasses much of the Bajío (Lyons *et al.*, 1998; Soto-Galera *et al.*, 1999a). It was found in a site unaffected by reservoir management located in a tributary to the Laja, where immediate impacts from pollution or agricultural activities were not evident. However, *N. calientis* is now absent from sites where the species had historically been captured but which are now polluted, dry or otherwise severely degraded. A similar situation arises with three sensitive species previously known from the Laja basin: *S. lermae*, *A. robustus* and *C. humboldtianum* are no longer found at the few sites where they were present historically (López-López and Díaz-Pardo, 1991). These sites are located in the lowermost areas of the Laja, near the confluence of the Laja with the Lerma River, which has suffered extensive alteration from agriculture and urban development in the cities of Celaya and Apaseo el Grande (Guanajuato). In all, the number of species that are sensitive or moderately tolerant to pollution or environmental degradation in the Laja has been reduced by 66% (calculated for all species known for the Laja in these categories), and today only three such species (out of nine) are still present in the river. The average 30% and 33% decadal declines observed for sensitive and medium tolerance fish species highlights the strong declines for those fish requiring pristine or relatively pristine habitats.

The lack of a significant trend in the increase in the number of exotic species in the Laja could be explained by the relatively long history of the presence of exotic species in the system. The introduction of exotic species into rivers in Central Mexico accompanied the construction of reservoirs. The available data do not cover a sufficiently long period for a pre-reservoir–post-reservoir (pre-exotic–post-exotic) comparison. Essentially all exotic species accounted for in the 2003 samples were present in the 1960–1990 period, except for four species, *C. idella*, *P. sphenops*, *L. macrochirus* and *Xiphophorus variatus*, that had not been reported in the Laja prior to the 1990s and this study. Exotics were deliberately introduced as food resources in reservoirs or as accidental aquarium releases throughout the river and have consistently increased in the river after the 1970s. The increase of exotics and the concurrent loss of natives appear to be the trend throughout Mexico (Contreras-Balderas and Escalante-Cavazos, 1993; Contreras-MacBeath *et al.*, 1998). The exotics *L. macrochirus* and *X. variatus* are now widespread in the river. We stress that *X. variatus* can cause severe impacts in the Laja and several other river systems in central Mexico. Evidence of the impact of this poeciliid on other species is anecdotal, but observations show that its abundance is overwhelmingly higher than that of other livebearers at several sites. The species is known to prey on larval fish (Borowsky, 1978) and can interbreed with native livebearers (Hems, 1977; Wischnath, 1993), resulting in gene pool deterioration. *M. salmoides*, although previously known in the Laja, is now widespread in the headwaters of the system, where it could pose a serious threat to native fish. This species has been responsible for the extirpation of some species of pupfish in the United States (Minckley *et al.*, 1991) and has been reported as a grave threat to natives in other aquatic ecosystems (Simberloff, 1999; Velázquez-Velázquez and Schmitter-Soto, 2004). The biological significance of the introduction of a new species that can cause broadscale changes for the rest of the community supersedes the lack of statistical significance found for this variable.

It is not surprising that the community of fish in the reservoirs remains unchanged through time relative to lotic sites. 'Exotic' ecosystems, such as a reservoir, offer habitat for only those river species that could adapt to them (Craig 2000). If anything, an increase in the number of exotic species stocked in these reservoirs would be expected; yet it is not evident. However, dams and other forms of habitat degradation have isolated populations of the native *A. tincella*. Once relatively widespread in the Laja, this species can only be found in a relatively short reach of the river downstream from the Ignacio Allende reservoir and at the uppermost sites sampled in 2003.

The lack of change in species richness through time may be a function of the combined loss of native species and gain of exotic species. However, the number of native species showed significant decline that accelerates after the 1990s (Figure 2). Those species that remain tend to be tolerant of extremes in temperature, habitat degradation and water quality (see Table 2). López-López and Díaz-Pardo (1991) reported three additional native, sensitive species for the Laja, *A. robustus*, *C. humboldtianum* and *S. lermæ* that were not captured in 2003–2004, thus increasing the significance of the decline of native species in the Laja beyond what is shown in the present analysis. The sites where these species were found had only been sampled once in the time-frame presented here.

The number of omnivore species in the Laja has also remained relatively constant. Again, the majority of the native species in the Laja are omnivores, and the introduction of exotic species has not resulted in a significant change in this variable. Native carnivores remain common in the Laja, although the number of carnivore species has declined by an average 18% per decade. Today, instead of relatively large-sized and benthic carnivores such as *S. austrinum* and *I. dugesi*, or the sensitive *N. calientis*, carnivores are relatively small-sized atherinopsids (*C. arge* and *C. jordani*) which are generally considered zooplanktivores. *C. arge* was mostly absent in reservoir sites, whereas *C. jordani* was abundant throughout the basin where it plays an important role in food webs (Soto-Galera, 1993). This species was observed in great numbers below dams and in pools throughout the river where it is subject to high mortality when dams are abruptly closed and downstream pools dry out. There is no regulatory water management in the Laja that prescribes a minimum flow to sustain biological communities or attempts to mimic the natural flow regime.

The fish attributes analysed here allow examination of community changes from the perspective of ecological functioning. These have been used as indicators of biological integrity (Fausch *et al.*, 1990; Lyons *et al.*, 1995; Frenzel, 1996; Lyons *et al.*, 2000; Vázquez and Simberloff, 2002; Wang *et al.*, 2003) and are valuable for understanding functional changes resulting from environmental deterioration. In the Laja, they help portray the loss of ecological specialists and their replacement by generalists that can survive in adverse conditions.

Datasets necessary for long-term studies of biological communities in freshwater systems in Mexico are rare. Most of the information is dispersed in museum records, and published and unpublished material from taxonomic, biogeographic and/or phylogenetic studies. The Laja is one of few rivers in Mexico with a relatively long series of sampling records. This study, and independent observations, along with Soto-Galera *et al.* (1999b) in the Río Grande de Morelia (Michoacán, Mexico), and Contreras-MacBeath *et al.* (1998) in the Río Balsas (Central Mexico), characterizes fish community changes resulting from environmental degradation, and is the basis for predicting how fish communities will change if regional environmental impacts continue (Table 4). These predictions apply to a situation where human impact is intermediate, not inconsequential, but also not as bad as it could be. With severe degradation, as observed in the Lerma River in areas near the cities of Celaya, La Piedad (Mestre, 1997), and Toluca (Esteller and Díaz-Delgado 2002), fish decline would be dramatic and only a few of the most tolerant species (probably exotics) would remain. In extreme cases no fish would survive.

Table 4. Changes perceived in the fish assemblage of the Laja River. These changes are considered hypothesized predictions for other systems in central Mexico when exposed to similar human impacts (see text)

Community attributes	Response	Hypothesized causes
Total species	No change	Exotic additions offset natives loss. Potential for increased richness exists as more exotics become established in the systems.
Tolerant	Small increase	Tolerant native species remain and exotic species (usually tolerant) are added to the community.
Omnivores	Small increase	This guild dominates fish communities but there is an addition of exotic omnivore species. Omnivory could also increase among other species as their preferred food items disappear (e.g. macroinvertebrates, other fish) from the channel.
Exotics	Increase	New habitats, aquarium releases, fishery introductions contribute to an increase. In addition, species can be translocated from other basins in the region through channelization and connection of streams belonging to different basins.
Natives	Decline	Mainly sensitive and benthic native species are extirpated. Decline related to habitat loss, pollution, channel desiccation, and potentially from predation or competition interactions with exotics.
Sensitive and medium-tolerance species	Decline	Distribution reduced to isolated areas where water availability is permanent and human impacts are relatively low.
Carnivores	Decline	Prey habitat has been destroyed. Refuge areas disappear owing to regulated flows and habitat destruction. Perhaps associated with fishery over-exploitation. Remaining native carnivores are essentially zooplanktivores and exotics dominate this category. Benthivores sensitive to pollutants in sediments are extirpated.
Native benthic species	Decline	Habitat change from rocky and gravel bottoms to silt and sand as a consequence of erosion. Lack of water in channels reduces availability of pools.

Protecting the fish communities of the Laja will require significant changes at the river basin scale. Definition of priority conservation and restoration areas using morphological stream attributes (*sensu* Rosgen, 1994) (Hernández-Javalera, 2002) has begun, and there are similar efforts from local non-governmental organizations (e.g. Salvemos al Laja A.C.) in headwater areas. However, it remains unclear whether these efforts will have an effect elsewhere in the river. Attempts to identify other priority areas, implementation of sewage treatment facilities in larger cities (e.g. San Miguel de Allende and Dolores Hidalgo), erosion control strategies, and restoration of natural flow regimes are incipient in the basin and need to be further expanded as part of a basin-scale management plan. Other measures, such as impeding further expansion of exotics throughout the river basin and restoring riparian vegetation, would also prevent further degradation of the Laja. Eradication of exotics does not seem likely in this river. However, in secondary channels where morphological barriers (e.g. large step pools) could help prevent exotics' invasion of areas where sensitive natives still occur, deliberate introductions of exotic species should be prevented. These recommendations are made locally for the Laja basin, but are applicable to aquatic ecosystems throughout the country, since the changes that have occurred in the Laja are emblematic of the declining state of aquatic biodiversity across Mexico.

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