

Genetic diversity and structure of largemouth bass (*Micropterus spp.*) populations in reservoirs of northeastern Mexico

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ABSTRACT. The largemouth bass (belonging to the genus *Micropterus*) is one of the most important freshwater fish for sport fishing; the native range of Micropterus salmoides extends into the northeastern Mexican drainages, providing important economic benefits for communities with thriving bass populations. However, the genetic diversity of this species is progressively declining due to various factors, including direct human impacts and alteration of natural ecosystems. In this study, the genetic diversity and structure of largemouth bass from the main reservoirs of northeastern Mexico were assessed. A total of 350 Micropterus spp. dorsal fin samples collected from seven reservoirs were genotyped using a panel of 10 microsatellite markers. The individual samples were genotyped and the different genetic diversity parameters and population structure analysis were evaluated. The microsatellite markers used in this study were highly informative. All the populations exhibited Hardy Weinberg disequilibrium, with some degree of inbreeding within populations. The populations showed moderate genetic differentiation, allowing the establishment of three genetic clusters. Structure analysis indicated that four ancestral populations is most likely. The populations are characterized by low genetic diversity, reduced effective population sizes and a high probability of inbreeding. This study highlights the importance of genetic diversity studies to manage native largemouth bass in the main reservoirs of northeastern Mexico.

Key words: *Micropterus spp.*; Diversity; Genetic structure; México; Microsatellites

INTRODUCTION

The largemouth bass (*Micropterus salmoides*) is the largest member of the Centrarchidae family and is one of the most important freshwater fish for sport fishing (Barthel et al., 2010). Although sometimes unrecognized by anglers, in the scientific community largemouth bass are considered to have two distinct subspecies: the Florida largemouth bass (*M. s. floridanus*) and the northern largemouth bass (*M. s. salmoides*). These subspecies occupy habitats from peninsular Florida to northeastern Mexico, southeastern Canada, and the U.S. corridor in between (MacCrimmon and Robbins, 1975). The northern largemouth bass *Micropterus s. salmoides* has native habitat in Mexico, ranging from the binational Rio Grande basin, including the Cuatro Ciénegas valley in the state of Coahuila, southward and eastward through two adjacent Gulf Coast drainages, the Río San Fernando and Río Soto La Marina in Nuevo León and Tamaulipas (García de León et al., 2015).

Due to the growing popularity of sport fishing, fingerlings and juveniles of this subspecies are widely reared in public and private hatcheries to supply recreational fishing waters. Largemouth bass of uncertain lineages have also been introduced worldwide (MacCrimmon and Robbins, 1975; Philipp and Whitt, 1991; Gratwicke et al., 2001; Near et al., 2003; Ribeiro et al., 2008). However, the *M. s. floridanus* subspecies has been introduced more frequently, even within the native range of *M. s. salmoides*, due to its apparent rapid growth (Addison and Spencer, 1971).

Currently, the two subspecies are sympatric in some regions of the southern U. S. and introgression is thought to have occurred as *M. s. floridanus* genes have been found in the *M. s. salmoides* genome (Fields et al., 1987; Philipp and Whitt, 1991; Johnson and Fulton, 2004; García de León et al., 2015). Philipp et al. (1983) revealed that genetic distinctions among some largemouth bass populations are diluted by introgression. Johnson and Fulton (2004) further reported that alleles from *M. s. floridanus* persist in *M. s. salmoides* across many generations.

Within Mexico, extensive translocations of *Micropterus spp*. have been performed both within the native range of *M. s. salmoides* and throughout the country since 1960 (Arredondo Figueroa, 1983; Contreras-Balderas and Escalante-Cavazos, 1984; NOM-034-PESC-2003; García de León et al., 2005). García de León et al. (2015) indicated that largemouth bass in northeastern Mexico generally exhibit low nuclear diversity but high mitochondrial diversity; however, no posterior analysis has been documented.

Since the genetic diversity of largemouth bass can be impacted by human activity, especially aquaculture and recreational fishing (Wang et al., 2019), the estimation of the genetic diversity and structure of the genus *Micropterus* in Mexico might provide valuable information on its current conditions and future management and conservation of these populations. Thus, the objective of this study was to assess the genetic diversity and structure of largemouth bass populations in the main reservoirs of northeastern Mexico.

MATERIAL AND METHODS

Sample origin and management

A total of 350 *Micropterus spp*. dorsal fin samples were collected from seven reservoirs (n = 50 samples per site) from the state of Tamaulipas: Falcon International (FI), Las Blancas (LB), Marte R. Gómez (MR), Vicente Guerrero (VG), Republica Española (RE), Emilio Portes Gil (EP), and Pedro J. Méndez (PJ). They came from banks of specimens collected during fishing tournaments; as such our institutional Animal Care Ethics committee did not consider

that ethics approval was necessary for this research. The samples were preserved in 96% ethanol and stored at 4°C until processing. Genomic DNA was extracted using the GenElute Mammalian Genomic DNA Miniprep Kit (G1N70; Sigma–Aldrich®, St. Louis, MO, USA) following the manufacturer's instructions.

PCR and genotyping

The samples were genotyped using a panel of 10 microsatellite markers (Table 1), as reported by Lutz-Carrillo et al. (2008). PCR was performed using a Thermocycler DNA Engine TETRAD 2 Peltier thermal cycler (MJ Research, Inc., Waltham, MA, USA) in a total volume of 10 μl, including 50 ng of DNA, 1x PCR Buffer (Promega®), 1.5 to 2 mM MgCl₂, 0.2 mM dNTPs and 0.125 U of GoTaq® DNA Polymerase. The amplified PCR products were separated by capillary electrophoresis under denaturing conditions on ABI PRISM® 3130 automated sequencing equipment (Applied Biosystems). The individual samples were genotyped with GeneMapper Software v4.0 (Applied Biosystems) using the GeneScanTM 500 ROXTM molecular weight marker (Applied Biosystems, Waltham, MA, USA) as a reference.

Table 1. PCR conditions and microsatellite markers used to assess the genetic diversity and structure of *Micropterus spp.* in northeastern Mexico.

Locus	Primer 5′-3'	Allelic range (bp)	Temperature (°C)	Number of cycles	MgCl ₂ mM
MiSaTPW090	F: TGCCAGAGATCCTGAGCTAC R: CCACTTACCTGAATAACCAGAGACA	164-233	55	29	1.5
MiSaTPW068	F: CAACTTTAATGCAAATACAGA R: CAGGCAGGCTTAAGTAA	168-204	55	28	1.5
MiSaTPW011	F: CAACATGGACGCTACTAT R: CAACCATCACATGCTTCT	170-194	60	27	1.5
MiSaTPW070	F: ACTTCGCAAAGGTATAAC R: CCTCATGCAGAAGATGTAA	171-494	55	30	1.5
MiSaTPW062	F: ATGCTTTCTGCTGAAGTGC R: TCCCTTTTGGAAGTAGAAGT	190-222	55	29	1.5
MiSaTPW173	F: CCACACAGTGACACAAACTGTGC R: GCCATTGTGCTGCTGCAGAG	209-277	60	32	2.0
MiSaTPW190	F: TCAGTGAAGCAGAGCAGCCTTCT R: GTACATATCAGTGCCAGTCCAGGCA	228-286	60	32	1.5
MiSaTPW184	F: TTGTATACCAAGTGACCTGTGG R: GGGAGTGCATCTTTCTGAAGTGCC	247-272	60	32	1.5
MiSaTPW012	F: CGGTTGCAAATTAGTCATGGCT R: CAGGGTGCTCGCTGTCT	290-361	60	29	1.5
MiSaTPW060	F: TATAGTTTGGTCCAGCAGGTGGCGT R: TGTGGAATGACATTTAGCCGAGGCC	294-561	60	29	1.5

Genetic diversity and structure analyses

The observed heterozygosity (Ho), expected heterozygosity (He), and polymorphic information content (PIC) were estimated using Cervus 3.0 (Kalinowski et al., 2007). Deviations from Hardy-Weinberg (HW) genetic equilibrium were evaluated using Genepop 4.2 software (Raymond, 2008). The fixation index (F_{IS}) was calculated using Arlequin 3.11 (Excoffer et al., 2005).

The effective population size (Ne) was analyzed with the LD method implemented in Ne estimator software (Do et al., 2014). Since only one reliable estimation was obtained, an

alternative temporal method (Pollak, 1983) was used. Under this method, VG data served as the reference population, except for VG reservoir data, in which case was used EP reservoir data.

Genetic structures between populations were analyzed, and the fixation rates (F_{ST}) were estimated using FSTAT version 1.2 (Goudet, 1995). A correspondence factorial analysis was performed using GENETIX 4.05 (Belkhir et al., 2004) to graphically depict the determined structures. Additionally, a population inference analysis was performed using STRUCTURE 2.3.4 (Pritchard et al., 2000) using a burning period of 50,000 iterations and a run length of 200,000 Markov chain Monte Carlo replicates. STRUCTURE HARVESTER software (Earl and vonHoldt, 2012) was subsequently used to infer Delta K.

RESULTS

For microsatellite genotyping, the MisaTPW070 marker showed the highest number of alleles, followed by MisaTPW173, with means of 21.7 and 18.4 alleles per locus, respectively. In contrast, the MisaTPW068 marker showed fewer polymorphisms in all populations. High Ho levels were observed for the MisaTPW011, MisaTPW060, MisaTPW090 and MisaTPW070 loci, with values of 1.000, 0.960, 0.880 and 0.860 in the RE, FI, PJ and MR reservoirs, respectively. Additionally, the average PIC of the microsatellite panel used for each reservoir could be considered highly informative. All loci were analyzed using the HW equilibrium test, which revealed that most of the loci were imbalanced (Table 2), with the exceptions of MisaTPW062 and MisaTPW184 in MR and PJ, respectively. However, all reservoirs showed HW deviations (p<0.05). Additionally, the test to determine deficient or excess heterozygosity revealed that the loci were deficient in heterozygosity in the populations; similarly, the F_{IS} statistic indicated inbreeding within the reservoirs.

Table 2. The main indicators of largemouth bass (*Micropterus spp.*) genetic diversity in populations in the Tamaulipas reservoirs.

		Mean					
Reservoir	Но	Не	PIC	HW	F_{IS}	LD Ne (95 % C.I)	Temporal Ne (95% C.I.)
LB	0.67	0.81	0.773	*	0.166		9.5 (5.4-15.8)
MR	0.59	0.79	0.749	*	0.252		7.7 (4.3-12.8)
FI	0.75	0.77	0.729	*	0.016		15.4 (9.3-25.0)
VG	0.62	0.76	0.720	*	0.181		12.0 (7.9-17.9)
PJ	0.68	0.73	0.687	*	0.077	65.1 (51-87.3)	8.7 (4.9-14.6)
RE	0.63	0.69	0.641	*	0.089	, ,	12.6 (6.4-23.5)
EP	0.66	0.74	0.695	*	0.108		12.0 (7.9-17.9)

Ho: observed heterozygosity, He: expected heterozygosity, PIC: polymorphic information content, FIS: inbreeding coefficients, HW: Hardy-Weinberg equilibrium (*P< 0.05). LD: Linkage disequilibrium, Ne: effective population size, C.I.: Confidence Intervals. The reported values represent the mean of individual values for the 10 markers.

The paired analysis of the F_{ST} statistic based on the Weir and Cockerman (1984) method (Table 3) revealed moderate genetic differentiation between the largemouth bass populations. The PJ population was the most different from the other populations; in contrast, the LB and MR populations exhibited the least amount of genetic differentiation.

The correspondence factorial analysis (Figure 1) revealed three organized groups. Group 1 included the LB and MR populations, which showed little genetic differentiation ($F_{ST}=0.04244$). Group 2 included the FI, VG, EP and RE populations, and Group 3 was formed by the PJ population. Moderate genetic differentiation was found between the FI and VG populations

 $(F_{ST}=0.05860)$ and between the FI and EP populations $(F_{ST}=0.08544)$. The genetic differentiation among the RE, VG, and FI populations was low $(F_{ST}=0.04169)$, and moderate differentiation was found between the RE and EP populations (FST=0.06848) and 0.09407, respectively). Finally, the third group was formed by the PJ population, with F_{ST} values of 0.07731, 0.09547, 0.10190 and 0.12119 when compared with the FI, EP, VG and RE populations, respectively.

Table 3. Pairwise F_{ST} statistic values of largemouth bass (*Micropterus spp.*) populations in the Tamaulipas reservoirs.

Reservoir	LB	MR	FI	VG	PJ	RE	EP
LB	0.00000						
MR	0.04244	0.00000					
FI	0.07135	0.07698	0.00000				
VG	0.07320	0.08388	0.05860	0.00000			
PJ	0.10069	0.07306	0.07731	0.10190	0.00000		
RE	0.10586	0.09783	0.09407	0.06848	0.12119	0.00000	
EP	0.08387	0.08272	0.08544	0.06165	0.09547	0.04169	0.00000

(*P< 0.05). Falcon International (FI), Las Blancas (LB), Marte R. Gómez (MR), Vicente Guerrero (VG), Republica Española (RE), Emilio Portes Gil (EP), and Pedro J. Méndez (PJ).

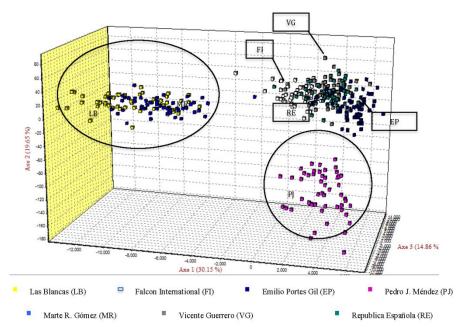


Figure 1. Correspondence factorial analysis of seven largemouth bass populations in the Tamaulipas reservoirs.

Population structure analysis showed that the largest Delta K was K = 4, partially coinciding with the results found in the correspondence factorial analysis. A graphical depiction of the population structure is shown in Figure 2. The following clusters were found in the population structure of the analyzed reservoirs: cluster 1 (the LB and MR populations); cluster 2 (the FI and VG populations); and cluster 3 (the PJ, RE, and EP populations).

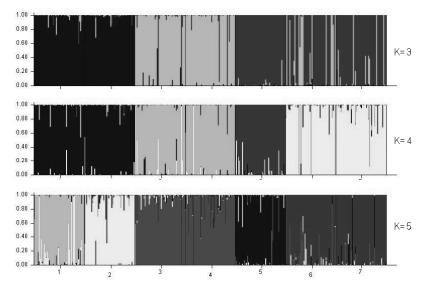


Figure 2. Population structure inferred between K = 3 and K = 5 of *Micropterus spp.* populations in Tamaulipas reservoirs. 1 = MR, 2 = LB, 3 = FI, 4 = VG, 5 = RE, 6 = EP, 7 = PJ.

DISCUSSION

To the best of our knowledge, this is the first study to widely assess the genetic diversity and structure of largemouth bass (*Micropterus spp.*) populations in fishing reservoirs in Tamaulipas, Mexico. The microsatellite markers used in the present study (with the exception of MisaTPW068 in all reservoirs) were highly informative (Botstein et al., 1980) and provided sufficient PIC to determine the genetic variability in largemouth bass (*Micropterus spp.*) populations.

The highest value of observed heterozygosity was observed in the FI population (Ho=0.75), which had an expected heterozygosity of 0.77; which is likely to indicate the presence of a previous population bottleneck, crossover or new specimen introduction. This general pattern of genetic variation is similar to that reported by Johnson and Fulton (2004), and Lutz-Carrillo (2006 and 2008).

The reservoirs are characterized by low genetic diversity, possibly due to reduced effective population sizes that led to inbreeding; alternatively, the populations may be subjected to selection forces or result from a previous population bottleneck. In these reservoirs, sport fishing is regularly conducted. Neal et al. (2001) estimated that tournament mortality removed 6% of the adult largemouth bass population, but mortality rates of up to 16% have been reported due to fishing competitions (Driscoll and Smith, 2007). These high fishing mortality rates substantially truncate the range of ages and sizes in the structure of bass populations (Allen et al. 2008). Moreover, in sport fishing tournaments, the capture of the largest "trophy" largemouth bass is rewarded with strong economic incentives. The ages of trophy bass range from 5 to 13 years (Horton and Gilliland 1993), and the trophy size of largemouth bass exceeds 5.4 kg (Hughes and Wood 1995). The largemouth bass spawning season starts in April and may last until January. However, northeastern Mexico sport fishing tournaments commence during largemouth bass spawning, leading to the loss of nests and the capture of females that have not yet spawned; reportedly: "the females are heavy and large because they're full of eggs and ready

to spawn". In areas with heavy recreational fishing pressure during spawning, 94.4% of caught males abandon their nests due to stress, leading to brood loss. This anthropogenic impact on breeding may reduce the future reproductive success of largemouth bass (Twardek et al., 2017).

Commercial and subsistence fishing of species such as *Oreochromis aureus*, *Astyanax mexicanus*, *Carpiodes carpio*, *Ictalurus punctatus*, *Cichlasoma cyanoguttatum*, and *Macrobrachium acanthurus* occur in the studied reservoirs. Even when the catch of *Micropterus spp*. is regulated and prohibited (PROY-NOM-033-PESC2001; NOM-034-PESC-2003; NOM-043-PESC-2003; NOM-060-SAG/PESC-2016), no strict supervision is guaranteed. Thus, both activities can be considered indirect selection factors that affect the effective population sizes.

On the other hand, these studies suggested that this pattern may be influenced by the continual release of *M. s. floridanus* specimens into the reservoirs, indicating that the populations are in a state of genetic change or that *M. s. floridanus* alleles have a selective advantage in warm temperatures. Moreover, a reduction in genetic variation has been reported in populations of several species that inhabit northern latitudes (Bernatchez and Dodson 1991; Bernatchez and Wilson 1998).

Additionally, the lack of available information on the actual origin and species identity of released or introduced individuals to repopulate the studied reservoirs limits our understanding of the population dynamics. The only published public reports are that the Texas Parks and Wildlife Department (TPWD) exported *Micropterus s. floridanus* fingerlings to Mexico for introduction into VG. Introductions began in 1982 with 207,000 fingerlings; in 1988, 91,000 fingerlings were introduced; and in 1992 and 1993, 97,000 offspring and 203,000 fingerlings, respectively, were introduced (Rodriguez, 2004). On the other hand, the Mexican National Standard NOM-034-PESC-2003 indicates that largemouth bass and Florida bass species were introduced to the EP reservoir in 1985. These results indicate a need to identify the incidence of *Micropterus s. salmoides* and *Micropterus s. floridanus* in fishing reservoirs in Tamaulipas, Mexico.

The populations showed moderate genetic differentiation, indicating three genetic groups, and could indicate that the recorded releases of fingerlings originated from the same location. These results may also be attributable to the continuous exchange of specimens of outstanding sizes between reservoirs as a result of the preference of the fishing location and the proximity to the home of the fishermen.

The formation of the first cluster could be explained by the following hypothesis: since both of these reservoirs are interconnected through an irrigation channel, a continuous exchange of genetic material between them is possible. Additionally, the river mouths of both reservoirs independently meet in the waters of the Rio Grande. The second cluster included the FI and VG populations; FI is located on the Rio Grande, upstream of LB and MR (Figure 1). Similar results were found by García de León et al. (2015) for the El Tigre (ET) and Graciano Sánchez (GS) tributaries that converge in the Corona River, which is the main tributary of VG (VGR-ET $F_{ST} = 0.42$ and VGR-GS $F_{ST} = 0.30$).

The third cluster was formed by the PJ, RE and EP populations; the RE and EP populations mostly shared common ancestors with the populations in cluster two, possibly because VG and EP empty into the Guayalejo River. The PJ population in the Soto la Marina-RE River shared the fewest common ancestors with the aforementioned populations, including those of cluster two, likely because the PJ waters join the small streams of the Bermegos, whose waters join the San Juan River downstream and then empty into the waters of VG.

Several factors, such as a lack of government support, arbitrary and uncontrolled releases of fingerlings in the native range of *M. s. salmoides*, and environmental stress, make it difficult to determine the current genetic diversity of largemouth bass populations in reservoirs

in Tamaulipas. However, these data provide fishery managers with a means for understanding and predicting variations in stocking populations for regulation and management of one of the most important native species in northeastern Mexico. Our study emphasizes the need to establish management plans for the introduced species *M. s. floridanus*.

CONCLUSIONS

The largemouth bass (*Micropterus spp.*) in fishing reservoirs of Tamaulipas, Mexico are characterized by low genetic diversity, reduced effective population sizes and a high probability of inbreeding. These findings support the development of programs to maintain the genetic diversity of this species and to determine the management of introduction programs and reproduction to improve genetics and/or conservation. Likewise, the coexistence of *M. s. salmoides* and *M. s. floridanus* should be explored in these reservoirs.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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