

# Distribution of fishes in the Río Guayalejo-Río Tamesí system and relationships with environmental factors in northeastern Mexico

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**Abstract** A priority issue in ecology and biogeography is understanding the patterns in species diversity and the causal factors of their distribution, which allows the generation of information for conservation strategies. The longitudinal distribution of fishes and their relationships with environmental variables were studied in the Guayalejo-Río Tamesí system (northeastern Mexico) from February 2000 to July 2001. A total of 5918 fish were caught in 27 collections along an altitudinal gradient in the main river course, from high mountain (1500 masl) to coastal plain near Tampico. Forty-three native and five exotic species, belonging to 35 genera in

23 families, were identified. Cluster analyses identified four major fish habitats in the river system. A distinctive euryhaline marine fish habitat (1) occurs near the mouth with native and two exotic species. Two other habitats consist essentially of freshwater fish species that are distributed along the longitudinal gradient. One of these habitats (habitat 4) shows greater diversity, as per the Shannon index value, and also includes amphidromous fish, in addition to two exotic freshwater fish; the other (habitat 2) includes freshwater, euryhaline and three exotic species. The changes in the frequency of occurrence and the abundance of *Gambusia vittata*, *Astyanax mexicanus*, and *Xiphophorus variatus* contribute to explaining differences between these habitats. Another habitat (3) is represented by two sampling sites located near the mouth and consist of freshwater and euryhaline fish and three exotic cyprinids with broad salinity tolerance. The low abundance and richness of exotic species suggest little impact on native fish fauna in this river. The fish assemblage of the Guayalejo-Tamesí river system species changes along a longitudinal gradient with the addition, replacement and presence of indicator species. Upstream fish fauna is mostly composed of freshwater species, some of them generalists that inhabit the entire longitudinal gradient, others that are restricted to certain sites, and the remainder of species is an assemblage composed of a mixture of euryhaline freshwater and marine species near the mouth.

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## Introduction

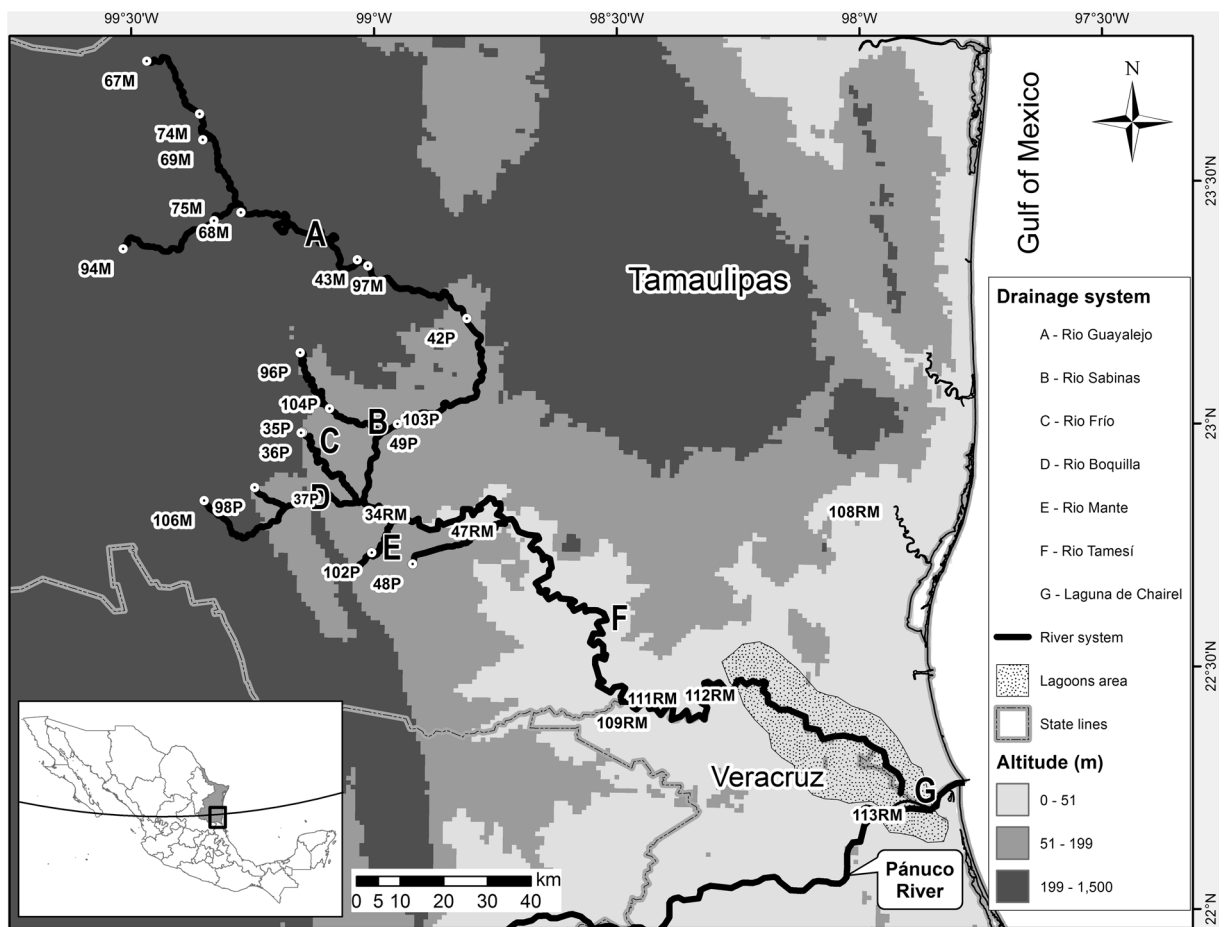
The mechanisms that explain changes in fish assemblage along a river have been well studied in both temperate and tropical rivers (Winemiller and Leslie 1992; Trujillo-Jiménez et al. 2002; Ibañez et al. 2009; Bhatt et al. 2012; Mercado-Silva et al. 2012; Mejía-Mojica et al. 2014; Carvajal-Quintero et al. 2015; Chea et al. 2016; Askeyev et al. 2017). Two hypotheses have been proposed to explain such changes: one that alludes to the concept of “biozonation”, and another that places emphasis on the addition of species. Both share the idea that environmental heterogeneity along the river is the main factor that drives changes in fish assemblage (Petry and Schulz 2006). As a result, the river continuum concept (*sensu* Vannote et al. 1980) was incorporated to explain the longitudinal changes in fish assemblages on temperate pristine rivers and streams, but have been strongly questioned (Statzner and Higler 1985; Miranda and Raborn 2000). However, this concept inspired theoretical and practical research in streams and rivers around the world (Statzner and Higler 1985; Ibañez et al. 2011). Previous work on freshwater fish assemblages reported diverse relationships between species diversity and the longitudinal gradient, such as inverse relationships (Jaramillo-Villa et al. 2010), unimodal (optimal in mid-elevations) or nonlinear (without correlation) patterns (Rahel and Hubert 1991; Grenouillet et al. 2004; Li et al. 2009; Askeyev et al. 2017), and even an increase in species diversity in high altitude zones (Carvajal-Quintero et al. 2015). Nonetheless, a case of ecological convergence has recently been found between species richness (assemblage) in four continents with comparable environmental conditions (i.e., assemblage position in the stream’s longitudinal continuum, Ibañez et al. 2011). It should be obvious that species richness in a river or stream depends on historical events (Ricklefs and Schluter 1993), but also on the constraints that environmental factors exert on them. For example, structural features of the rivers such as the width and depth of the channel, the diversity of the substrate, the order of the currents, etc., as well as biotic relationships such as predation, competition and disease, have been associated with different fish assemblage patterns (Matthews 1998; Tejerina-Garro et al. 2005). In the rivers of northeastern Mexico, such studies are rare, and it is important to know the changes in fish assemblage along the river due to human activity.

The Río Pánuco is located between the Sierra Madre Oriental and the Gulf of Mexico in the Tamaulipean ecoregion of northeastern Mexico (Contreras-Balderas 1969; CONABIO 2000). The main tributary of this river is the Río Guayalejo-Tamesí system (hereinafter referred to as the river system), which drains an area of 15,257 km<sup>2</sup> (INEGI 1983). Darnell (1962) studied the fish community structure of this system; his inspection provided the first extensive inventory (60 species; 23 freshwater and 37 peripheral, of which 12 were exclusive or endemic). However, since this first inspection, no comprehensive studies are available on the fish along the river or their relationship with environmental variables. The basic knowledge of species composition contrasts with the deterioration of habitats, especially in the middle and lower parts of the basin (García-De León et al. 2005). Changes in water flow and the introduction of exotic species pose major threats to native fish assemblages (Hughes et al. 2005; Hermoso et al. 2011; Mendoza et al. 2014). Our study provides updated baseline information that may be useful for future conservation of fish fauna, land use planning and holistic watershed management. We are interested in knowing how the fish assemblage is determined by environmental factors along the channels’ longitudinal gradient and report the new species introduced in the system after Darnell’s (1962) inventory.

## Material and methods

### Study area

The Río Guayalejo-Río Tamesí system is located in east-central Mexico, in the northern part of the Tampico embayment. In the south, this embayment is drained by the lower section, the Río Pánuco, where these two branches join (22°13’N, 97°51’W) before entering the Gulf of Mexico (INEGI 1983). The northernmost tributary, the Río Guayalejo, originates in the Sierra Madre Oriental at 3400 m. The Sabinas, Frío, Boquilla, and Mante rivers join to form the Río Tamesí, which assumes a meandering course that borders the states of Tamaulipas and Veracruz (Fig. 1). Tributary rivers start as springs, large ponds or wetlands in shallow valleys in the foot-slopes of the Sierra Madre Oriental.



**Fig. 1** Sites along the Río Guayalejo-Río Tamesí system. See Table 1 for codes

**Fish collection**

Fish were collected in the river system from February 2000 through July 2001. The study area was divided into three elevation zones: *mountain and high elevations* (200–1500 m), *plains and low elevations* (50–200 m), and *river mouth* (0–50 m). The sampling sites are described in Table 1. Ejido Aldama, located ~60 km north of the main course of the river system, was included because it does not belong to any of the major basins of Tamaulipas. This study was conducted at the Technological Institute of Ciudad Victoria in Tamaulipas, where despite the lack of any animal care protocol, the animals were all collected under standard care procedures.

To collect fish, a combination of fishing gears was used, following standard fish-collecting procedures (Sooley et al. 1998). In the mountain zone, fish were collected with minnow seines, and supported with

electrofishing equipment for an average collecting time of 30 min for each sample. In the plains zone, we used electrofishing gear, a minnow seine, and experimental gillnets 180 m long and consisting of eight panels, each 23 m long with 1, 1.5, 2, 2.5, 3, 3.5, 4, and 5-in. meshes. At these sites, the experimental gillnets remained in place for 12 h. In the mouth zone, where the channels are deeper, we used a trammel net (180 m long with a 3-in. internal mesh) and the experimental gillnets described above, both of which were in place for 12 h. The elevation and coordinates of each site were measured with a GPS unit.

The fish were anesthetized and subsequently fixed in 10% formalin neutralized with sodium borate and then preserved in 50% isopropanol solution. The identification of each species was based on Álvarez del Villar (1969), Castro-Aguirre et al. (1999), Page and Burr (1991), McEachran and Fechhelm (1998), and Miller et al. (2005), as well as specific literature for some taxa.

**Table 1** Sampling sites for fishes and habitat assessment along the Río Guayalejo-Río Tamesí system, Tamaulipas, Mexico in 2000–2001

Zone	Code	Sampling sites	Altitude (mts)	River	Date (d/m/y)	Coordinates	
						Latitude N	Longitude W
Mountain	94 M	El Salto, Ej. La Florida, Jaumave	1418	Guayalejo	07/04/2000	23°21'33"	99°30'59"
	67 M	Ej. Carrizos, Jaumave	854	Guayalejo	18/11/2000	23°44'47"	99°28'04"
	74 M	Chihue, Jaumave	715	Guayalejo	09/12/2000	23°38'16"	99°21'32"
	69 M	Arroyo los Ángeles, Jaumave	690	Guayalejo	19/11/2000	23°35'04"	99°21'08"
	75 M	San Vicente, Jaumave	610	Guayalejo	09/12/2000	23°25'04"	99°19'45"
	68 M	Los Nogales, Jaumave	556	Guayalejo	18/11/2000	23°26'04"	99°16'25"
	106 M	Las Flores, Ocampo	296	Boquilla	12/05/2001	22°50'29"	99°20'58"
	97 M	Llera de Canales 1, Llera	244	Guayalejo	10/04/2001	23°19'28"	99°00'43"
	43 M	Llera de Canales 2, Llera	203	Guayalejo	21/03/2000	23°19'73"	99°01'61"
	Plain	98P	Ej. Coahuila, Ocampo	175	Boquilla	17/04/2001	22°52'06"
42P		Ej. I. Zaragoza, Llera	170	Guayalejo	21/03/2000	23°12'59"	98°48'29"
96P		Ej. Libertad, Gómez Farías	142	Sabinas	09/04/2001	23°08'46"	99°09'06"
49P		Ej. Brownsville 1, Xicoténcatl	92	Guayalejo	29/04/2001	22°59'57"	98°56'57"
103P		Ej. Brownsville 2, Xicoténcatl	90	Guayalejo	21/05/2000	22°59'56"	98°57'04"
104P		Ej. Sabinas y Saucillo, Gómez Farías	88	Sabinas	29/04/2001	23°01'51"	99°05'28"
37P		Rancho Nayarit, Gómez Farías 1	87	Frío	27/02/2000	22°58'56"	99°08'50"
35P		Rancho Nayarit, Gómez Farías 2	69	Frío	27/02/2000	22°58'52"	99°08'49"
36P		La Florida, Gómez Farías	69	Frío	27/02/2000	22°59'19"	99°08'49"
48P		Canal Ej. Emiliano Zapata, El Mante	63	Mante	20/05/2000	22°42'37"	98°55'11"
River Mouth	102P	Ciudad Mante, El Mante	52	Guayalejo	28/04/2001	22°44'03"	99°00'14"
	34RM	El Limón, El Mante	35	Guayalejo	26/02/2000	22°50'04"	99°01'08"
	47RM	Magiscatzin, González	35	Tamesí	20/05/2000	22°48'31"	98°44'20"
	112RM	Vuelta de las Yeguas, Altamira	26	Tamesí	08/07/2001	22°28'15"	98°14'29"
	111RM	Laguna La Culebra, González	21	Tamesí	07/07/2001	22°25'42"	98°21'40"
	108RM	Ej. Aldama, Aldama	14	Tigre	13/05/2001	22°50'55"	97°56'37"
	113RM	Puente Moralillo, Tampico	11	Tamesí	29/07/2001	22°13'26"	97°53'48"
	109RM	San Antonio Rayón, González	10	Tamesí	10/06/2001	22°24'51"	98°25'18"

Alkalinity, pH, dissolved carbon dioxide, hardness (amount of dissolved calcium and magnesium in the water, mg/l, Wetzel 2001), transparency, total dissolved solids, and temperature were measured at each site; conductivity ( $\mu\text{S}/\text{cm}$ ) and dissolved oxygen (mg/l) were measured with a conductivity meter and an oxygen meter, respectively. Salinity (ppt) was measured with a refractometer. Water samples collected in each site were fixed immediately in order to determine the quantity of nutrients (ppm) as nitrate, nitrite, and phosphate, all of which were measured with a spectrophotometer (SMART model, LaMotte, Chestertown, MD). To characterize environmental heterogeneity at each site, we considered 6 quantitative and 17 qualitative variables (Moyle and Nichols 1973; Table S1).

#### Statistical analysis

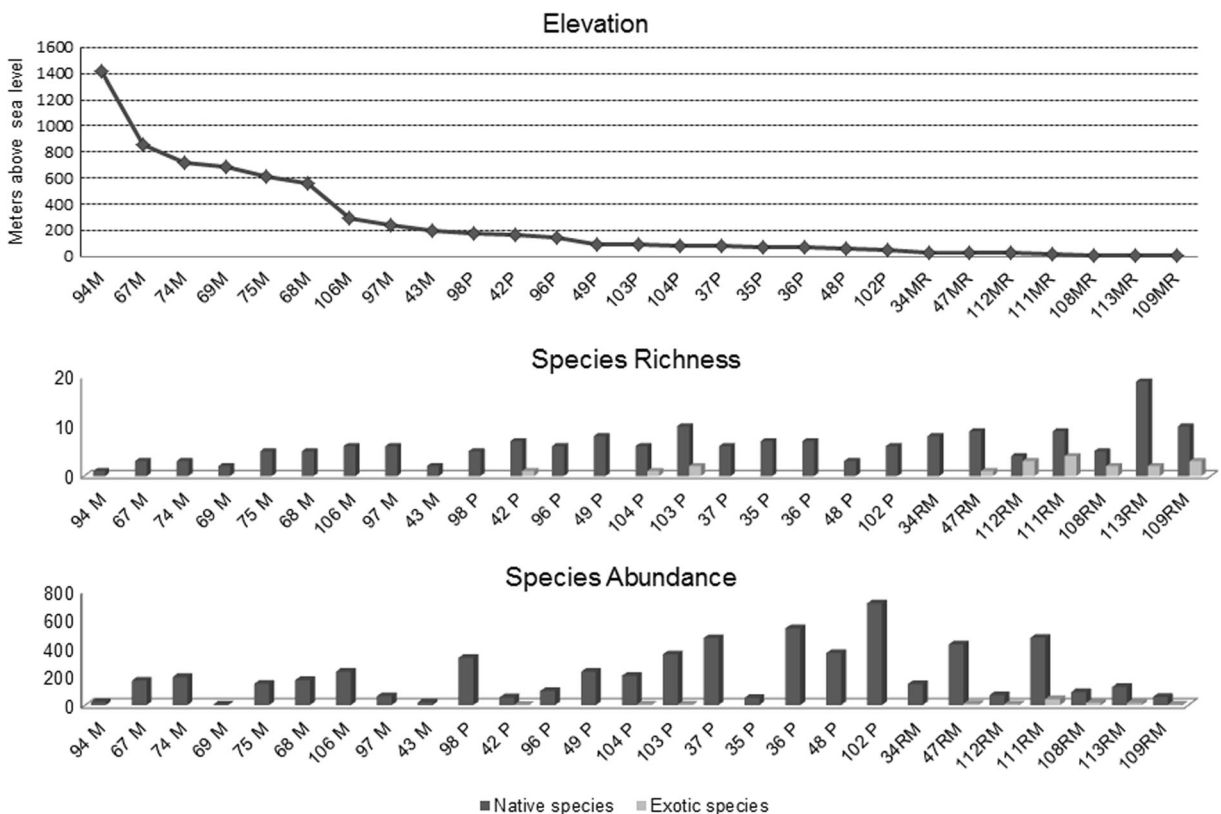
To describe fish habitats, the presence-absence of each species was recorded (Table S2) and used to quantify the similarity in species composition between sampling sites, using an agglomerative hierarchical two-way cluster analysis. For this analysis, we determined the Euclidian distances between sampling sites and a complete linkage-clustering algorithm, using PRIMER6 software (Clarke 1993; Clarke and Warwick 2001, 2005). The significance of the clusters was tested by similarity profile analysis (SIMPROF, PRIMER6). To detect significant differences in the dissimilarity values between fish habitats, we applied a one-way analysis of similarity of the significance of the habitats defined a

priori (ANOSIM). The average similarity and percentage of contribution of each species to the identity of each habitat were determined using the similarity percentage routine (SIMPER) in PRIMER 6 (Clarke and Warwick 2001).

A canonical correspondence analysis (CCA) was performed to define the relationships between each type of habitat and environmental variables. The environmental matrix contained the average of the physicochemical parameters and qualitative variables of the environment that had the highest value in explaining the variables at the 95% confidence level, in an initial CCA (Table 2a). These variables were the maximum depth of the channel, the percentage of water riffles, hardness, the average depth, the percentage of backwater, channel width, and the percentage of floating macrophytes. Diversity (Shannon index), dominance, and evenness of species in each habitat were calculated using PAST 2.07 diversity software (Hammer et al. 2001).

### Results

We collected 5918 fish belonging to 23 families, 35 genera, and 48 species, taken at 27 collection sites in the study area (Tables 1 and S2). Of 48 species, 43 were native and five were exotic (*Cyprinus carpio*, *Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *Micropterus salmoides*, and *Oreochromis aureus*). Exotic species were only present in some places of lower elevation (*Micropterus salmoides* and *Oreochromis aureus*) and in virtually all the sites of the mouth region (five species). Exotic species were more numerous in the mouth area, but none was important in terms of abundance with respect to native species (Fig. 2). Globally, four species accounted for 75.9% of abundance (*Astyanax mexicanus*, *Gambusia vittata*, *Poecilia mexicana*, and *Herichthys labridens*, Table S2). Most river species were restricted in distribution along the longitudinal gradient; 43 species were found at fewer than six sites. Five species were found at many locations along the river: *Astyanax mexicanus* (24 sites), *Poecilia*



**Fig. 2** Species richness and abundance along the Río Guayalejo–Río Tamesí system in northeastern Mexico. The upper figure represents the elevation of each sampling site

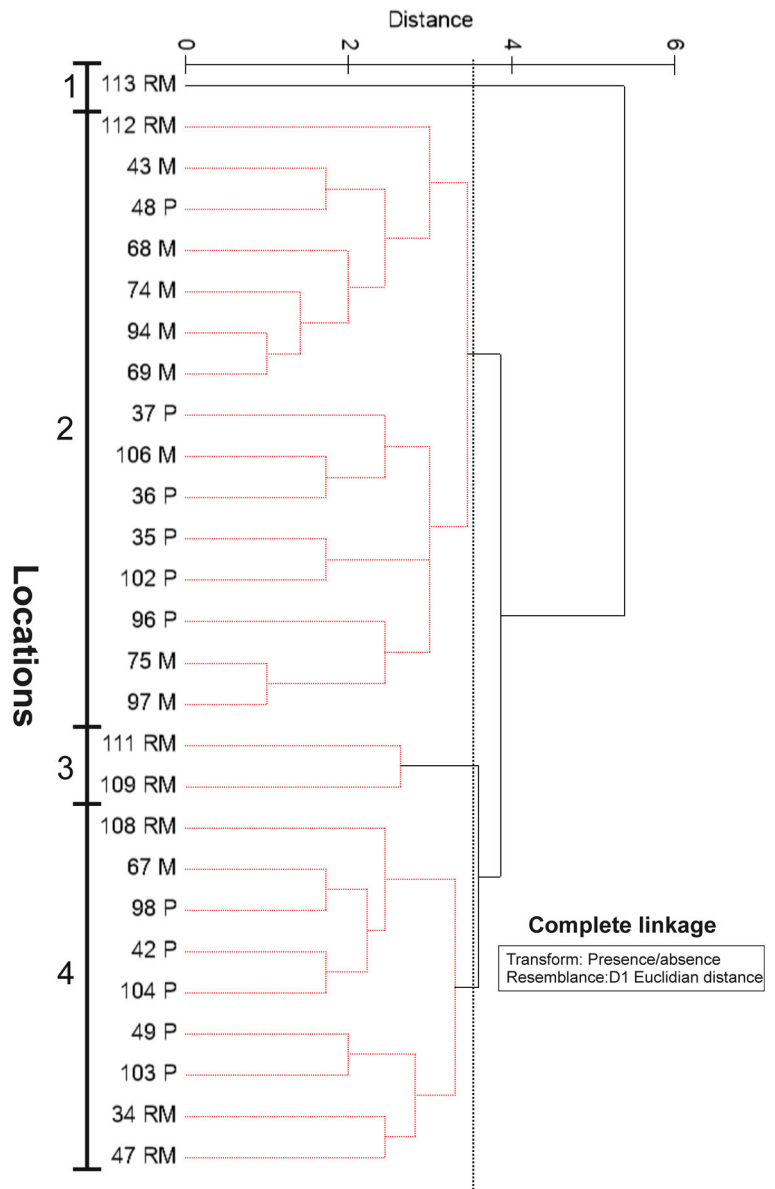


*mexicana* (19 sites), *Herichthys labridens* (16 sites), *Gambusia vittata* (11 sites), and *Poecilia formosa* (11 sites) (Table S2).

### Fish habitats

The dendrogram of fish species similarity defined four fish habitats (groups of sampling sites) with a separation of 3.6% distance (Fig. 3). These groupings were statistically significant (ANOSIM:  $R = 0.519$ ,  $P < 0.05$ ); all pairwise comparisons were also statistically significant (Table S3).

**Fig. 3** Dendrogram of fish species similarity (presence-absence) based on Euclidian distances between sampling sites in the Río Guayalejo-Río Tamesí system. Red clades indicate significant clusters using the SIMPROF permutation test (5% significance level, 999 permutations) of all specimens



**Table 2** Relative contribution of each variable by the canonical correspondence analysis (a) and percentage of variance explained by each axis (b)

(a)			
Variable	Explained %		
Maximum depth of channel	9.7		
Average depth	9.7		
Channel width	7.1		
Percentage of riffles	6.9		
Percentage of backwater	6.9		
Hardness	5.9		
Percentage of floating macrophytes	1.1		
(b)			
	Axis 1	Axis 2	Axis 3
Eigenvalues	0.2398	0.1917	0.1105
Explained variation (cumulative)	23.98	43.15	54.2

five sites in the plains, three at the mouth, and one in the mountain zone, and was essentially characterized by freshwater fish (Fig. 3; Tables 1 and 3).

Since habitat 1 was characterized by high salinity and dominated by marine species, and some of them (euryhaline species) were distributed upstream, it was not included in the CCA. The CCA had three components that accounted for 54.2% of the total variation, considering seven assessed environmental variables (Table 2b). Variation in hardness and percentage of riffles were positively correlated, and channel (width and depth) with percentage of backwater were negative on the first axis. This axis shows no separation between the three habitats (Fig. 4).

On the second axis, the percentage of floating macrophytes was positively correlated, while maximum depth and average depth were negatively correlated (Fig. 4). This axis shows a better separation between the sites of habitat 4 (correlated with a greater presence of macrophytes) and those of habitat 2, which show greater correlation with maximum depth. Sites in habitat 2 show a higher average maximum depth (2.9 m) in relation to habitat 4 (average 1.27 m). Habitat 3 had sites with broader channels and high percentages of backwaters.

The highest diversity (average Shannon index;  $H' = 2.19$ ) and the lowest dominance (average  $D = 0.17$ ) and evenness (average  $E = 0.47$ ) were found at sites near the mouth of the river (Table 4); habitat 1 at Puente Moralillo, Table 1). In contrast, the highest

**Table 3** Similarity percentages–species contribution (SIMPER) estimated from Euclidean distances and abundance data

Species	Habitats			
	1	2	3	4
<i>Gambusia vittata</i>		91.09		61.59
<i>Astyanax mexicanus</i>		3.01	90.30	11.93
<i>Gambusia</i> sp		0.57	7.78	
<i>Poecilia mexicana</i>		3.82	0.23	4.33
<i>Xiphophorus variatus</i>				8.53
<i>Poecilia formosa</i>		0.46		6.74
<i>Gambusia aurata</i>		0.04		5.56
<i>Oreochromis aureus</i>			1.56	0.16
<i>Herichthys cyanoguttatus</i>			0.03	0.47
<i>Herichthys labridens</i>		0.31	0.01	0.45
<i>Notropis</i> sp		0.22		
<i>Dionda erimyzonops</i>		0.17		
<i>Gambusia regani</i>		0.13		0.09
<i>Gambusia panuco</i>				0.09
<i>Poecilia latipunctata</i>		0.07		0.04
<i>Xiphophorus pigmaeus</i>		0.07		
<i>Dorosoma petenense</i>		0.02	0.05	
<i>Ariopsis felis</i>			0.03	
<i>Dorosoma cepedianum</i>			0.01	
<i>Gobiomorus dormitor</i>			0.01	0.01
<i>Micropterus salmoides</i>				0.01
<i>Elops saurus</i>	49.02			
<i>Bairdiella chrysoura</i>	31.37			
<i>Brevoortia gunteri</i>	17.65			
<i>Dasyatis americana</i>	1.96			

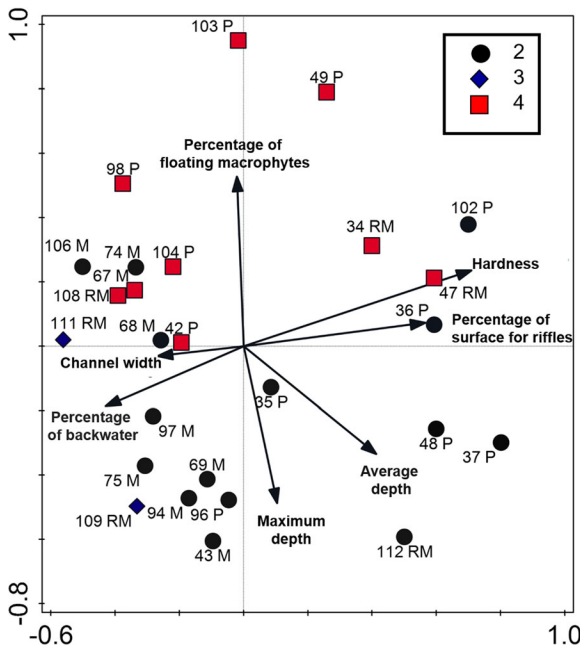
dominance (average  $D = 0.58$ ) and evenness (average  $E = 0.58$ ), and the lowest diversity (average  $H' = 0.82$ ), were recorded in habitat 2 at higher elevations (average 349 m), where *Gambusia vittata* and *Astyanax mexicanus* were the most abundant species (Table 4).

## Discussion

Darnell’s (1962) ground-breaking study of fishes from Río Guayalejo and its tributaries was carried out by field collections and complemented with previous records from Jordan and Dickerson (1908). However, Darnell’s study did not assess the component of brackish and marine fishes entering coastal lagoons and near river







**Fig. 4** Canonical correspondence analysis showing the effect of the environmental variables on the abundance of fish habitats. Black arrows indicate the environmental variables. Symbols are fish habitats

mouths, or their seasonal variation. Furthermore, Darnell lacked taxonomic revisions for some freshwater fish taxa, mainly in the families Cyprinidae and Poeciliidae. All these reasons account for the differences observed between our study and that of Darnell. Indeed, one notorious change is the occurrence of exotic species in the system (Table S5). The higher abundance and richness of exotic species occurred in sections of the river near the mouth with warmer waters and greater maximum depths and channel width (Table S2). It is important to mention that Darnell (1962) did not record the presence of exotic fish species in the study area due to the high levels of introduction of exotic fishes in Mexico during the 1970s and 1980s (Contreras-Balderas and Escalante 1984; Contreras-Balderas et al. 2004, 2008). We believe that exotic species may have been introduced in the river system in the 1970s, which means that these species have already been interacting with native species for at least 30 years – long enough to disperse throughout the system. However, invasion of the whole river system did not seem to have occurred, at least during sampling. At higher elevations, no exotic species was observed. It is possible that species of tropical origin, such as tilapia, show low yields in northern areas of Mexico with low temperature during winter

**Table 5** Abundance and frequency of occurrence of fish species in the Río Guayalejo-Río Tamesí system in 2000–2001. Absolute abundance (AA) and relative abundance (RA), standard deviation (SD), frequency of occurrence (F). H1, H2, H3, and H4 were determined by cluster analysis (dendrogram)

H1				
Species	AA	RA	SD	F
<i>Brevoortia gunteri</i>	3	2.1	–	–
<i>Cyprinus carpio</i>	1	0.7	–	–
<i>Hypophthalmichthys molitrix</i>	14	9.9	–	–
<i>Ariopsis felis</i>	10	7.0	–	–
<i>Bairdiella chrysoura</i>	4	2.8	–	–
<i>Pomadasis crocro</i>	1	0.7	–	–
<i>Dasyatis americana</i>	1	0.7	–	–
<i>Elops saurus</i>	5	3.5	–	–
<i>Opsanus beta</i>	1	0.7	–	–
<i>Mugil cephalus</i>	26	18.3	–	–
<i>Centropomus undecimalis</i>	4	2.8	–	–
<i>Caranx crysos</i>	3	2.1	–	–
<i>Eucinostomus argenteus</i>	48	33.8	–	–
<i>Awaous banana</i>	3	2.1	–	–
<i>Chaetodipterus faber</i>	1	0.7	–	–
<i>Trichiurus lepturus</i>	1	0.7	–	–
<i>Etropus crossotus</i>	1	0.7	–	–
<i>Eugerres plumieri</i>	12	8.5	–	–
<i>Gerres cinereus</i>	3	2.1	–	–
H2				
Species	AA	RA	SD	F
<i>Dorosoma petenense</i>	13.0	0.4	4.4	6.7
<i>Astyanax mexicanus</i>	531.0	16.7	129.0	93.3
<i>Notropis sp</i>	58.0	1.8	16.6	26.7
<i>Cyprinus carpio</i>	4.0	0.1	1.4	6.7
<i>Dionda erimyzonops</i>	34.0	1.1	11.6	6.7
<i>Ctenopharyngodon idella</i>	2.0	0.1	0.7	6.7
<i>Ictalurus cf. australis</i>	4.0	0.1	1.1	20.0
<i>Ictalurus mexicanus</i>	6.0	0.2	1.9	13.3
<i>Gambusia sp</i>	63.0	2.0	21.5	6.7
<i>Gambusia vittata</i>	1810.0	57.0	466.5	46.7
<i>Gambusia aurata</i>	19.0	0.6	6.0	13.3
<i>Gambusia regani</i>	30.0	0.9	10.2	6.7
<i>Gambusia affinis</i>	2.0	0.1	0.7	6.7
<i>Xiphophorus pigmaeus</i>	22.0	0.7	7.5	6.7
<i>Xiphophorus variatus</i>	9.0	0.3	2.5	20.0
<i>Xiphophorus nezahualcoyotl</i>	7.0	0.2	2.0	13.3
<i>Poecilia mexicana</i>	332.0	10.5	87.5	60.0
<i>Poecilia formosa</i>	65.0	2.0	20.7	33.3
<i>Poecilia latipunctata</i>	32.0	1.0	9.2	13.3
<i>Micropterus salmoides</i>	1.0	0.0	0.3	6.7

**Table 5** (continued)

<i>Herichthys labridens</i>	122.0	3.8	30.7	46.7
<i>Megalops atlanticus</i>	3.0	0.1	1.0	6.7
<i>Agonostomus monticola</i>	5.0	0.2	1.5	13.3
<i>Gobiomorus dormitor</i>	2.0	0.1	0.7	6.7
<b>H3</b>				
Species	AA	RA	SD	F
<i>Dorosoma petenense</i>	40.0	7.3	4.2	100.0
<i>Dorosoma cepedianum</i>	2.0	0.4	1.4	50.0
<i>Astyanax mexicanus</i>	317.0	58.2	183.1	100.0
<i>Cyprinus carpio</i>	5.0	0.9	2.1	100.0
<i>Ctenopharyngodon idella</i>	1.0	0.2	0.7	50.0
<i>Hypophthalmichthys molitrix</i>	3.0	0.6	0.7	100.0
<i>Ictalurus cf. australis</i>	1.0	0.2	0.7	50.0
<i>Ariopsis felis</i>	7.0	1.3	3.5	100.0
<i>Gambusia sp</i>	108.0	19.8	53.7	100.0
<i>Poecilia mexicana</i>	13.0	2.4	9.2	50.0
<i>Herichthys cyanoguttatus</i>	5.0	0.9	3.5	50.0
<i>Herichthys labridens</i>	4.0	0.7	1.4	100.0
<i>Oreochromis aureus</i>	36.0	6.6	24.0	100.0
<i>Centropomus undecimalis</i>	1.0	0.2	0.7	50.0
<i>Gobiomorus dormitor</i>	2.0	0.4	1.4	50.0
<b>H4</b>				
Species	AA	RA	SD	F
<i>Astyanax mexicanus</i>	470.0	23.31	22.9	100.0
<i>Notropis tropicus</i>	1.0	0.05	0.0	11.1
<i>Pylodictis olivaris</i>	1.0	0.05	0.0	11.1
<i>Gambusia sp</i>	4.0	0.20	0.2	33.3
<i>Gambusia vittata</i>	444.0	22.02	21.6	44.4
<i>Gambusia aurata</i>	192.0	9.52	9.3	55.6
<i>Gambusia panuco</i>	13.0	0.64	0.6	11.1
<i>Gambusia regani</i>	13.0	0.64	0.6	11.1
<i>Xiphophorus variatus</i>	130.0	6.45	6.3	22.2
<i>Poecilia mexicana</i>	354.0	17.56	17.2	100.0
<i>Poecilia formosa</i>	189.0	9.38	9.2	66.7
<i>Poecilia latipunctata</i>	12.0	0.60	0.6	22.2
<i>Micropterus salmoides</i>	10.0	0.50	0.5	44.4
<i>Herichthys cyanoguttatus</i>	95.0	4.71	4.6	88.9
<i>Herichthys labridens</i>	95.0	4.71	4.6	77.8
<i>Oreochromis aureus</i>	26.0	1.29	1.3	33.3
<i>Agonostomus monticola</i>	2.0	0.10	0.1	11.1
<i>Gobiomorus dormitor</i>	4.0	0.20	0.2	22.2

(Kapetsky 1997), which limits the breeding activity of this African cichlid fish.

#### Fish habitats and their relationship with environmental factors

Cluster analyses identified four major fish habitats in the river basin. A very different euryhaline marine fish habitat (habitat 1) occurs downstream near the mouth of the river with interchange of flows between the sea and river. Three species (*Elops saurus*, *Bairdiella chrysoura* and *Brevoortia gunteri*) distinguish this type

of habitat located in Puente Moralillo, all of which are of euryhaline marine origin and penetrate to coastal lagoons or rivers with sandy bottoms to feed and reproduce (Table S6). *Elops saurus* and *Bairdiella chrysoura* feed on small fish and crustaceans, and *Brevoortia gunteri* feeds on plankton. This habitat also contains two exotic cyprinids in low abundance (*Cyprinus carpio* and *Hypophthalmichthys molitrix*). These are related to benthos and are tolerant, over brief periods, to backwaters and low concentrations of oxygen. The former is omnivore and the latter feeds on phytoplankton and zooplankton (Freyhof and Kottelat 2008; Zhao 2011).

Two other habitats (2 and 4) consist essentially of freshwater fish that are distributed along the longitudinal gradient of the channel, but are distinguished by the greater or lesser percentage of floating macrophytes, and the depth of the channel (Fig. 4). Both habitats include generalist species (*Astyanax mexicanus*, *Poecilia mexicana* and *Herichthys* sp.) of neotropical origin as well as species typical to all Atlantic basins, with a high dispersion capacity (Miller and Smith 1986; Miller et al. 2005). This last fish species inhabits practically all the environments along the longitudinal gradient of the river; other species such as *Gambusia vittata* show more restricted distribution upstream, in an area characterized by high levels of hardness and presence of riffles or *Xiphophorus variatus* confined to shallower environments with floating macrophytes (Fig. S1). However, downstream, habitat 4 includes amphidromous species, in which adults are strictly freshwater (*Agonostomus monticola* and *Gobiomorus dormitor*, McDowall 1997; Ribeiro and Villalobos 2010), and exotic species with low abundance (*Micropterus salmoides* and *Oreochromis aureus*), while habitat 2 has a clear influence of euryhaline marine fish (*Dorosoma petenense* and *Megalops atlanticus*) (Table S6). The frequency of occurrence and abundance of some species (*Gambusia vittata*, *Astyanax mexicanus* and *Xiphophorus variatus*) also contributed to the differences between the two habitats (Table 5). Habitat 3 is also composed of generalist freshwater species (*Astyanax mexicanus*), but shows a large proportion of euryhaline marine species (*Dorosoma petenense*, *Ariopsis felis*, *Centropomus undecimalis*, and *Gobiomorus dormitor*) and three exotic cyprinids in sites close to the mouth of the river (*Cyprinus carpio*, *Ctenopharyngodon idella*, and *Hypophthalmichthys molitrix*) with tolerance to the

salinities of the estuarine environment (Cudmore and Mandrak 2004; Freyhof and Kottelat 2008; Zhao 2011); however, the habitat also exhibits low species richness and abundance.

Various environmental, geographic and topographic features are often described as determinants of patterns of species richness along longitudinal gradients (Ricklefs and Schluter 1993; Matthews 1998; Tejerina-Garro et al. 2005). How these factors impact the richness of species has been debated (Benke et al. 2011). Our study, the fish species diversity decreases with high elevations, a pattern commonly reported by other authors (Edwards and Contreras-Balderas 1991; Jaramillo-Villa et al. 2010). In order to understand this, we evaluated abiotic factors and found that factors on an intra-basin scale such as salinity, depth, percentage of riffles and backwaters, hardness, channel width and percentage of floating macrophytes could prevent colonization and limit upstream and downstream dispersion, which could act as ecological barriers or filters (Contreras-Balderas 1969; Ruiz-Campos et al. 1985; Contreras-Balderas et al. 2002). For example, *Astyanax mexicanus* and *Herichthys cyanoguttatus* are generalist species with dietary habits related to the availability and diversity of food in the particular habitat (Miller 1966; Mitchell et al. 1977). These characteristics allowed them to have an extensive distribution and high abundance, in particular for *Astyanax mexicanus*, what could be interpreted as species with high tolerance to different environmental conditions, while other species with less environmental tolerance, such as *Gambusia affinis* and *G. regani*, are restricted to lentic biotopes or weedy backwater conditions with virtually no current (Darnell 1962; Miller et al. 2005, Table S6). In addition, many freshwater fish species are benthopelagic but have different food requirements; for example, the most representative species of habitat 2, *Astyanax mexicanus*, feeds on insects, crustaceans and worms; others, such as *Gambusia vitatta* and *Herichthys labridens*, are omnivores, and *Poecilia mexicana* feeds mainly on detritus; this feeding partitioning exhibited by all these species enables them to avoid competition and allows stability in the fish community along the river (Miller and Smith 1986; Tejerina-Garro et al. 2005; Hoeinghaus et al. 2007; Winemiller et al. 2008). The same situation occurs in species of marine origin that enter the river for feeding (Table S6).

In summary, the structure of the fish community of the Guayalejo-Tamesí river system is represented by one

upstream fauna composed of mostly freshwater species – some of them generalists that inhabit the entire longitudinal gradient, and others that inhabit more restricted areas – and a downstream assemblage composed of a mixture of the more abundant upstream elements and species of marine origin, both of which are tolerant to brackish water near the mouth. The low abundance of exotic species and the richness of upstream and downstream freshwater species may indicate few changes in this type of rivers in the region (Ruiz-Campos et al. 1985; Edwards and Contreras-Balderas 1991).

The river continuum concept establishes that physical conditions of streams or rivers from upstream to downstream areas create strong constraints on assemblage structure linked to food availability (Vannote et al. 1980). However, the original concept was modified to make it flexible and more applicable (Statzner and Higler 1985). One modification that emerged with studies of modern ecology is that physical connectivity may account for differences in freshwater assemblages between sites (Miranda and Raborn 2000). Recently, Ibañez et al. (2009) provided evidence, from the comparative study of headwater streams in four continents, that the richness of fish assemblage and trophic structure converged along the continuous river to a substantial degree. The Guayalejo-Tamesí river system seems to be consistent with this principle, in particular with regard to species addition and replacement and the occurrence of indicator species along a longitudinal gradient. These findings have been reported by other studies (Grenouillet et al. 2004; Petry and Schulz 2006; Grosman et al. 2010; Bhatt et al. 2012; Carvajal-Quintero et al. 2015; Chea et al. 2016; Silva et al. 2016; Askeyev et al. 2017).

In terms of conservation, the least disturbed area is the upper part of the river system (habitats 2 and 3); however, without proper regulation and enforcement, tourism and mining could seriously affect fish diversity (García-De León et al. 2005). In the plains and mouth (habitats 1, part of 2, and 3), fish diversity has been heavily affected by several dams, exotic species, pollution with agricultural fertilizers and pesticides, ranching, siltation, and pollution associated with petroleum operations (García-De León et al. 2005; Rodríguez Rodríguez et al. 2012).

The Mexican government continues to deliver programs aimed at introducing exotic fish (Ibañez et al. 2011). According to our results, exotic species might have a lower impact; however, the effects of exotic

species on freshwater ecosystems are widely known (Moyle and Nichols 1973; Contreras-Balderas and Escalante 1984; Mendoza et al. 2014), so it is advisable to continue to monitor the system, since other factors may emerge with long-term ecological data (Grosmann et al. 2010). Unfortunately, at both the federal and state level, the programs that exist in this region for conserving natural resources and maintaining the biodiversity of fish are practically nonexistent (Gobierno de Tamaulipas 2011). Extensive work on the part of the Mexican government is necessary to promote comprehensive strategies in using and managing aquatic resources. This should begin with establishing a baseline of information on the biological diversity and environmental services provided by balanced riverine ecosystems.

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