Revista Mexicana de Biodiversidad 83: 117-128, 2012

Environmental factors associated with fish assemblage patterns in a high gradient river of the Gulf of Mexico slope

Factores ambientales asociados a los patrones en las comunidades de peces en un río de alta pendiente en la vertiente del golfo de México

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Abstract. Using multivariate analyses of fish community and environmental data, we explored associations among 13 fish species and 9 ecological guilds and identified ecological gradients that explain patterns in the fish community of the La Antigua River (Veracruz, Mexico). Altitude, distance to ocean, stream width, and water temperature were the most important variables explaining community composition. Sites with high altitudes (> 1 393 m), cold water (< 17ºC), located far from the ocean (> 100 km) and less than 5 m wide were dominated by non-native *Onchorhynchus mykiss*. Many sites exclusively inhabited by native poeciliids were also narrow (< 2 m), but were located at intermediate altitudes (1 039-1 400 m) and distances to the ocean (> 80 km, < 100 km) and had warmer water temperatures (> 20ºC). Because 7 guilds were exclusive to a single species, results from the guild analysis were very similar to species-specific analyses. Higher species and guild diversity were found in wider sites (> 5 m), sites with lower altitudes (< 600 m), and sites closer to the ocean (< 71 km). Variables related to human influence did not explain trends found in the fish communities.

Key words: Veracruz, fish community, Mexican rivers, La Antigua River, ecological gradients.

Resumen. Utilizamos datos de la comunidad de peces y de variables ambientales y análisis multivariados para explorar asociaciones entre 13 especies y 9 gremios ecológicos en el río La Antigua (Veracruz, México). Además, identificamos gradientes ecológicos que explicaron los patrones en las comunidades de peces. Las variables más importantes en la determinación de la composición de la comunidad fueron altitud, distancia al océano, ancho de río y temperatura del agua. Los sitios ubicados a gran altitud (> 1 393 m), con aguas frías (< 17°C), lejos del océano (> 100 km) y menos de 5 m de ancho estuvieron dominados por la especie no nativa *Onchorhynchus mykiss*. Muchos sitios habitados exclusivamente por poecílidos nativos también fueron angostos (< 2 m), pero se ubicaron a altitudes intermedias (1 039-1 400 m), tuvieron temperaturas más cálidas (> 20°C) y estuvieron a distancias intermedias al océano (> 80 km, < 100 km). Siete de los gremios ecológicos fueron exclusivos de una especie por lo que los resultados del análisis de gremios fueron similares a los análisis de las especies taxonómicas. La diversidad específica y de gremios fue mayor en sitios más anchos (> 5 m), con menor altitud (< 600 m) y más cercanos al océano (< 71 km). Las variables relacionadas con la influencia antropogénica no tuvieron relevancia en la explicación de las tendencias encontradas.

Palabras clave: Veracruz, comunidad de peces, ríos mexicanos, río La Antigua, gradientes ecológicos.

Introduction

Multiple geological, historical and ecological factors determine the composition and structure of riparian fish communities. These factors operate at a variety of spatial and temporal scales. Several models have proposed a hierarchy of factors that can help explain trends in the assemblage of fish communities (Angermeier and Karr, 1983; Lamoroux et al., 2002; Hoeinghaus et al., 2007; Ibanez et al., 2007). Atop these hierarchies, long-duration evolutionary and zoogeographical processes (i.e., volcanic events, stream capture) determine the species that can potentially be present in ecosystems within a

Recibido: 10 junio 2010; aceptado: 09 agosto 2011

region. At lower hierarchies, smaller scale factors (i.e., water temperature, channel depth, biological interactions) determine which species are actually capable of occupying a particular area of a river (Angermeier and Winston, 1998; Matthews and Robison, 1998; Lyons and Mercado-Silva, 1999; D'Ambrosio et al., 2009).

A number of fish community patterns in lotic systems are well studied in temperate areas. For example, an increase in species richness in an upstream-downstream gradient as a result of increased habitat size, diversity, or both, is a general attribute for most river systems (other general trends reviewed in Matthews, 1998). A growing body of literature has tested these patterns in tropical systems around the world (Cop Ferreira and Petrere, 2009; Ibañez et al., 2009) often finding support for general trends. Most of these studies have focused on taxonomic richness as the variable to test against biotic and abiotic determining factors. Fewer studies have tested the influence of these factors in structuring the functional assemblage of fish communities (e.g., Schlosser 1982, Higgins 2009, Higgins and Strauss 2008).

The information that can be obtained from carrying out community comparisons between areas based on taxonomic identities is valuable, but can be much improved by analyzing functional attributes of the recorded organisms (Welcomme et al., 2006; Elliot et al., 2007). Integration of species into guilds has been used to increase the information on functioning, hierarchical structure and connectivity, and to simplify complex ecosystem analysis (Elliot et al., 2007). Guilds are defined as a group of species that exploit the same class of environmental resources in a similar way (Root, 1967).

Multivariate analyses have been broadly used to estimate the relative importance of ecological and geographic variables that explain the composition and structure of fish communities in freshwater ecosystems. The use of these methods in Mexican tropical systems is incipient. At the national level, only a few studies have attempted to determine the relative importance of multiple habitat, ecological or geographic variables in structuring fish communities (Díaz-Pardo et al., 1993; Paulo-Maya and Ramírez-Enciso, 1997; Lyons and Mercado-Silva, 1999; Ruíz-Gómez et al., 2008). These studies are lacking in Mexican rivers draining into the Gulf of Mexico, systems that carry a rich and complex freshwater fish fauna in very diverse freshwater environments.

Species descriptions, their distribution, and their parasites have mostly been the focus of freshwater ichthyological studies in the State of Veracruz, Mexico, and the Gulf of Mexico coast in general (Obregón-Barbosa et al., 1994; Garrido-Olvera et al., 2006; McEachran and Dewitt, 2008; Mercado-Silva et al., 2011). Little is known about how various ecological parameters may be affecting the composition and structure of fish communities in this region. This information is of utmost importance not only for our understanding of the basic biology and ecology of species, but also for understanding how fish communities are affected by a wide array of anthropogenic factors present in this area of the country, and to better inform fish and freshwater ecosystem conservation and protection measures.

The objective of this study was to explore not only associations among species and ecological guilds, but also to identify ecological gradients that could explain patterns in the fish community in a river draining into the Gulf of Mexico. We used multivariate analyses of community and environmental data and other statistical analyses to test our specific expectations of higher taxonomic and functional group richness in an upstream-downstream gradient, and a relatively restricted distribution of specialized functional groups to upper areas of the basin.

Materials and methods

Study area. The La Antigua river is a high gradient piedmont river originating from the Cofre de Perote volcano and adjacent mountains (Sierra Madre Oriental) (altitude= 4 200 m) in the states of Puebla and Veracruz (Mexico) that runs approximately 100 km east into the Gulf of Mexico. The La Antigua River is the 6th largest system in the state of Veracruz and has a total basin area of 2 326 km^2 (Fig. 1) and an annual water discharge of 2.8 million m^3 (Tamayo, 1996; Miller et al., 2005). The La Antigua river watershed has been declared by the National Biodiversity Commission (Conabio) as one of high

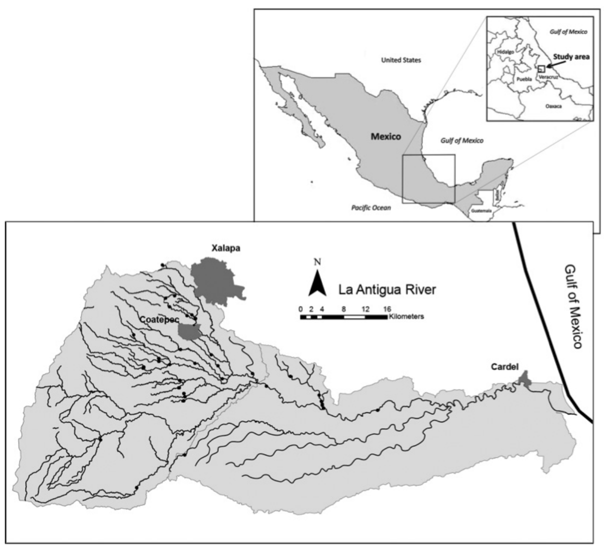

Figure 1. Map of the La Antigua River basin (Veracruz, Mexico). Sampling sites are indicated.

diversity and of great hydrological importance (Conabio, 2000). The river plays an important role supplying water to urban centers, agriculture, and supporting commercial and subsistence fisheries. Typical of rivers in hilly terrain, in La Antigua numerous headwater streams coalesce to form montane and piedmont canyons, before the river arrives at the coastal plain. The La Antigua runs through a variety of landscapes, ranging from relatively undisturbed fragments of alpine to deciduous tropical and riparian forests, to sugar cane plantations and urban areas. Cattle grazing, shade coffee and mango plantations are common in the area. Deforestation due to increased agriculture and animal husbandry practices is an ongoing problem in the region (Muñoz-Villers and López-Blanco, 2007; Martínez et al., 2009). Land use changes have resulted in reduced water quality in different areas of the basin (Martínez et al., 2009). The La Antigua region has 3 seasons: wet (Jun.-Oct.), cool dry (Nov.- Mar.) and warm dry (Mar. – May). Our sampling sites were located between 19º35' and 19º10' N, and 96º38' and 97º10' W at altitudes ranging approximately from 200 to 1 800 m (Fig. 1).

Data collection. Water and habitat quality, and fish community data were collected between February and September 2007 from 34 sites in the La Antigua river basin. Eleven sites were visited more than once, resulting in 56 total collections available for analysis. The 11 sites were visited during each season. The remaining 23 sites were visited during only 1 of the 3 seasons. Two of the 23 sites had no fish and were dropped from analyses. Specific collection information is located in the Appendix.

We used seines, DC backpack electroshockers, and dipnets, as required, to obtain representative samples of the fish community in all habitats at each sampling site. Sampling efforts were continued until we detected no changes in the number of species captured or their relative abundance. Collection effort (CPUE) was calculated as number of fish per minute of total sampling time across all collection methods. All fishes captured were identified and counted. Voucher specimens for some of the collections were deposited in the Colección de Peces of the Universidad Autónoma de Querétaro, in Querétaro, Mexico. Most of the fishes captured were released unharmed after processing.

Water, habitat and geographic information were obtained for each site via direct measurements in the field (indicated by [a]) or by analysis of existing ArcGis layers (indicated by [b]) (obtained from topographic maps of scale 1:50 000) and satellite images (Google Earth©) (indicated by [c]) for the following 16 variables: mean stream width[a], maximum depth[a], water velocity[a], habitat diversity[a], substrate diversity[a], cover for fishes[a], amount of erosion in land surrounding each site[a], landuse type[a], water clarity[a], quality of riparian forest at the site[a], site altitude[c], horizontal distance via stream channels to the Gulf of Mexico[c], basin area upstream from the sampling point[c], stream order (Strahler method)[b], distance via stream channels to nearest upstream urban area[c], and water temperature[a]. Units and categorical values for each variable are included in Table 1. Most of these variables are known as determinants of fish community composition in streams and rivers in North and Central America (Winemiller and Leslie, 1990; Rahel and Hubert, 1991; Lyons and Mercado-Silva, 1999).

Criteria for the construction of ecological guilds. We categorized each species into ecological guilds based on their reproduction, size, diet, position in the water column, and migratory tendencies. All of these guild attributes have been reported as useful for understanding the functional attributes of a fish community (Welcomme et al., 2006). Information for each species was obtained from literature (Table 2). Based on their reproductive strategies, fishes were categorized as having simple, complex or viviparous reproductive strategies. Simple reproduction refers to an oviparous strategy without nest building or parental care; complex reproduction refers to an oviparous strategy with either nest building or parental care. Fishes with a typical maximum adult total length (ATL) < 100 mm were categorized as *small*, fishes with ATL between 100 mm and 200 mm were categorized as *medium*, and fishes with ATL > 200 mm were categorized as *large*. Diet categories were *herbivore* (> 75% of diet dominated by plant materials), *omnivore* (with ≥ 25% animal material and ≥ 25% plant material or detritus) and *carnivore* (> 75% of diet dominated by animals). Fishes that are normally in constant contact with substrates were categorized as benthic, whereas those that occupy positions between the stream bottom and the water surface were categorized as *water column* fishes. Fishes that require migrations to brackish/salt water environments to complete their life cycles were categorized as *migratory*, while those that can complete their life cycles within their immediate habitat were categorized as *local*. We further identified species native and exotic to the Antigua basin, but did not include this information as part of our analyses.

Analysis. We built separate databases that contained geographic variables, habitat variables, and fish collection information. Separate fish collection databases were built using CPUE for species and CPUE for ecological guilds found at a site. We carried out preliminary analyses of species richness and species' relative abundances among samples from each site taken in different seasons; no relevant differences at any of the sites for either richness or relative abundance were related to season. Thus, for

Table 1. Habitat and geographic variables for sites in La Antigua basin, Veracruz, Mexico. Categorical and quantitative variables are included. Categorical variables: width, depth, water velocity, habitat variability, substrate diversity, cover for fish, bank erosion, landuse, water clarity, riparian vegetation. Each categorical variable was examined in NMDS using the "Score" given at each site, except for those with specific quantitative units (n/a)

Variable	*Score*	*River atributes, variable units, or notes.*
Width	1	Mean river width < 2 m
	2	Mean river width 2-5 m
	3	Mean river width > 5 m
Depth	1	Maximum depth <0.5 m
	2	Maximum depth 0.5 - 1 m
	3	Maximum depth > 1 m
Water velocity	1	High: Higher than 20 $cm*s^{-1}$
	2	Moderate: Approximately 10-20 $cm*s^{-1}$
	3	Low: No flow to ~10 $cm*s^{-1}$
Habitat diversity	1	Single habitat type (i.e., runs, riffles, pools) covering ≥ 90% of sampling reach.
	2	Two or more habitat types covering ≥ 90% of sampling reach.
	3	Three or more habitat types present in the sampling reach.
Substrate diversity	1	Soft sediments covering ≥ 90% of the sampling reach.
	2	Rocky substrates covering ≥ 90% of the sampling reach or a mixture of 2 substrate types (> 10% of each).
	3	A mixture of 3 or more substrates types.
Cover for fish	1	≤ 5% of the sampling reach with structures or areas for fish cover (i.e., boulders, logs, macrophytes, undercuts).
	2	5-10% of the sampling reach with structures or areas for fish cover.
	3	> 10% of the sampling reach with structures or areas for fish cover.
Bank erosion	1	Erosion is evident in river banks. Denuded soil is present in the banks. < 50% of the bank is protected by vegetation.
	2	Erosion is present along banks in the sampling reach. 50 – 90% of banks are protected by vegetation.
	3	No erosion present in the bank along the entire sampling reach. >90% of the bank is protected by vegetation.
Landuse	1	Urban or pasture surrounding the sampling reach
	2	Agriculture interspersed with natural vegetation surrounding the sampling reach.
	3	Completely natural vegetation surrounding the sampling reach.
Water clarity	1	Turbid, contaminated water in the sampling reach.
	2	Moderately turbid water in the sampling reach.
	3	Transparent or naturally tainted water in the sampling reach
Riparian vegetation	1	Denuded soil or pasture in river banks. No riparian vegetation present
	2	Only fragments of riparian vegetation interspersed with agriculture present in river banks.
	3	Completely natural riparian forest present in river banks. No apparent effect of agriculture or other anthropogenic activities along river banks.
Site Altitude	n/a	Meters above sea level
Distance to the Gulf of Mexico	n/a	Kilometers along the river
Basin area upstream from sampling point	n/a	Hectares
Stream Order	n/a	Determined using the Strahler technique and ArcGis maps of scale 1:50 000
Distance to nearest upstream town	n/a	Kilometers
Water Temperature at sampling	n/a	Degrees Centigrades

those sites sampled more than once, we retained only the sample from May 2007 (the year when most of the other collections were made) resulting in a total of 31 samples, 1 from each of the 31 sites, in the final dataset used for analyses.

We used Non Metric Multidimensional Scaling (NMDS), implemented through PC-ORD software (Version 5.18; McCune and Mefford 2006), to ordinate sites based on the 13 species, and separately on the 9 guilds, and then correlated site scores for NMDS results with values for the environmental variables, in order to identify ecological gradients. Our use of NMDS follows from the inclusion of non-linear and categorical data in our analysis; NMDS is an appropriate ordination

Table 2. Ecological attributes and guilds for fishes captured in La Antigua river Basin, Veracruz, Mexico. Please refer to methods section for considerations in species classification. Under guild, the combination of ecological attributes creates the ecological guild to which a species belongs; this combination is identified by a specific letter (in superscript)

Family *Species name (acronym)*	*Rep.*	*Size*	*Diet*	*Position*	*Mobility*	*Guild (group)*	*Source*
Characidae							
Astyanax mexicanus(ASME)	S	S	O	P	L	SSOPL(g)	B
Pimelodidae							
Rhamdia guatemalensis(RHGU)	S	L	C	B	L	SLCBL(e)	A
Salmonidae							
Onchorhynchus mykiss(ONMY)	S	L	C	P	L	SLCPL(d)	B
Mugilidae							
Agonostomus monticola(AGMO)	S	L	O	P	M	SLOPM(f)	B
Poecilidae							
Poecilia sphenops(POSP)	V	S	O	P	L	VSOPL(h)	B, D
Poecilia mexicana(POME)	V	S	O	P	L	VSOPL(h)	B, E
Xiphophorus helleri(XIHE)	V	S	O	P	L	VSOPL(h)	B, F
Poeciliopsis gracilis(POGR)	V	S	O	P	L	VSOPL(h)	B
Heterandria bimaculata(HEBI)	V	S	C	P	L	VSCPL(i)	B,D
Symbranchidae							
Ophisternon aenigmaticum(OPAE)	S	L	C	B	L	SLCBL(e)	A
Gobidae							
Sycidium gymnogaster(SYGY)	C	M	H	B	M	CMHBM (c)	B
Cichlidae							
Vieja fenestrata (VIFE)	C	L	O	P	L	CLOPL(a)	A
Thorichthys ellioti (THEL)	C	M	C	P	L	CMCPL(b)	A, C

For reproduction (Rep.) C= complex, S= simple, V= viviparous; for size, L= large, M= medium, S= small; for diet O= omnivore, H= herbivore, C= carnivore; for position in water column (Position) P= pelagic, B= benthic; for mobility L= local, M= migratory. Sources of information: A= Miller et al., 2005; B= Mercado-Silva et al., 2002; C= Hulsey, 2006; D= Trujillo-Jimenez and Toledo-Beto, 2006; E= Tobler, 2008; F= Dawes, 1991.

technique for community analyses (Kenkel, 2006). For each ordination, we calculated 2 ordination axes, and the statistical significance of similarity in species' distributions among sites on each axis and for the overall ordination was determined by a Monte Carlo re-sampling procedure. For each ordination, bi-plots (sites and either species or guilds) were generated showing their relationships in multivariate space.

In the plots, samples that fell close to each other had similar species or guild composition, whereas those far apart had different fish assemblages. Similarly, species or guilds that were close in the plot had similar distribution patterns among sites, whereas those far apart had different distribution patterns. We used the results from the NMDS to interpret possible relationships among the sites and either species or guilds to our geographical and habitat variables for the following characteristics: altitude, temperature, stream width at site, basin area at site, and distance to the ocean. These relationships were studied using correlation analysis (Kendall's τ). Environmental variables were then added to the bi-plot (based on correlations with sample scores) to reveal these additional relationships within the context of the original bi-plot.

Results

We collected 5 412 individuals of 13 species in 8 families (Table 2). Two exotic species, *Onchorhynchus mykiss* and *Xiphophorus helleri*, were captured. Among all species collected, *Heterandria bimaculata*, *Poecilia sphenops* and *Xiphophorus helleri* (Table 3) were most numerous and widespread. We found 9 ecological guilds (Table 2). Seven guilds each comprised a unique species. Guilds VSOPL and VSCPL were the most abundant and widely distributed (Table 3).

Sites located at higher altitudes had lower water temperatures ($r= -0.831$, $p < 0.001$), smaller stream width ($r= -0.392$, $p= 0.029$), smaller basin area ($r= -0.367$, $p= 0.042$) and a larger distance to the ocean ($r= 0.908$, $p > 0.001$). Sites farther from the ocean also had lower water temperature ($r= -0.768$, $p > 0.001$), smaller stream width ($r= -0.411$, $p= 0.024$), and smaller basin area ($r= -0.393$,

$p < 0.029$). Sites with greater basin area had higher water temperature ($r = 0.411$, $p = 0.024$).

Both of the NMDS ordinations and axes accounted for significantly more of the patterns in similarity among species distributions among sites than would be expected by chance. For the fish species ordination, the first 2 axes accounted for 62% of the similarity in fish distribution and abundance among sites, with each of the axis explaining 31%. For the first axis, *H. bimaculata, Xiphophorus helleri* and *A. monticola* had negative loadings and the remaining 11 species had positive loadings, which were relatively strong for 8 species (Table 3). Thus, sites with low scores on this axis were most likely to have relatively high abundance of either *H. bimaculata* or *A. monticola* and low abundance of most of the remaining species, whereas the opposite was true for sites with high scores. For the second axis, 11 species had negative loadings, with the largest magnitude for *A. monticola*, whereas *H. bimaculata* and *X. helleri* had relatively small magnitude and positive loadings. Sites with low scores on the second axis had relatively high numbers of many species, whereas sites with high scores would tend to have mainly *H. bimaculata* and *X. helleri*. For the fish guild ordination, the first 2 axis explained 86% of the variation in guild distribution and abundance among sites, with the first axis explaining 63% and the second 23%. For the first axis, 3 guilds had positive loadings, with VSCPL (i) having the greatest magnitude. The remaining 8 guilds in the first axis had negative scores, with SLCPL (d) having the greatest magnitude (Table 3). For the second axis, only 1 guild, SLCPL, had a positive loading, and the rest were negative, with the greatest magnitude for SLPOM (f) and CLOPL (a). For both axes in the guild ordination, sites with lower scores were more likely to comprise fish of several guilds, whereas sites with higher scores had fewer guilds present.

Patterns in the distribution of species and guilds were evident from the ordination plots. For the species ordination, sites dominated by *H. bimaculata* were distinctive from other sites and tended to have low scores on axis 1 and high scores on axis 2 (Fig. 2a). All other sites, including those dominated by *O. mykiss*, were not distinctive from one another, and clustered together with sites that had higher species richness. No sites had high scores on both axis 1 and axis 2. For the guild analysis, sites dominated by guild SLCPL (d, uniquely *O. mykiss*) were distinctive, with high scores on axis 2 and low scores on axis 1 (Fig. 2b). Sites dominated by guild VSCPL (i, uniquely *H. bimaculata*) had high scores on both axis 1 and axis 2. Other sites contained several different guilds, had low to intermediate scores on axis 1, and intermediate to high scores on axis 2.

Table 3. Distribution, number of individuals, and non-metric multidimensional scaling ordination results of fish species and guilds in the La Antigua River basin, Veracruz, Mexico. Results for 2 axes of ordination are shown. For guild definitions please see Table 2

Species	*No. Sites*	*No. individuals*	*Axis 1*	*Axis 2*
Heterandria bimaculata	24	2 222	-0.60161	0.15783
Poecilia sphenops	9	1 066	0.87765	-0.63091
Xiphophorus helleri	14	876	-0.06195	0.08277
Poeciliopsis gracilis	7	380	0.77193	-0.76565
Thorichthys ellioti	7	236	0.86781	-0.62686
Poecilia mexicana	7	167	0.8122	-0.68132
Onchorhynchus mykiss	7	138	0.33422	-0.79939
Vieja fenestrata	7	133	0.73105	-0.74519
Sycidium gymnogaster	8	82	0.1618	-0.81585
Ophisternon aenigmaticum	9	51	0.74534	-0.25617
Astyanax mexicanus	9	29	0.68883	-0.32352
Rhamdia guatemalensis	8	27	0.75454	-0.32479
Agonostomus monticola	1	5	-0.49789	-1.21425
Guild (No. of species in guild)				
VSOPL (4)	15	2 489	0.02359	-0.7441
VSCPL (1)	24	2 222	0.59726	-0.01972
CMCPL (1)	7	236	-0.06574	-0.82815
SLCPL (1)	7	138	-1.38736	0.75337
CLOPL (1)	7	133	-0.15618	-0.86157
CMHBM (1)	8	82	-0.26403	-0.8347
SLCBL (2)	7	78	0.00971	-0.72663
SSOPL (1)	7	29	-0.01968	-0.73813
SLOPM (1)	1	5	-0.6739	-0.98043

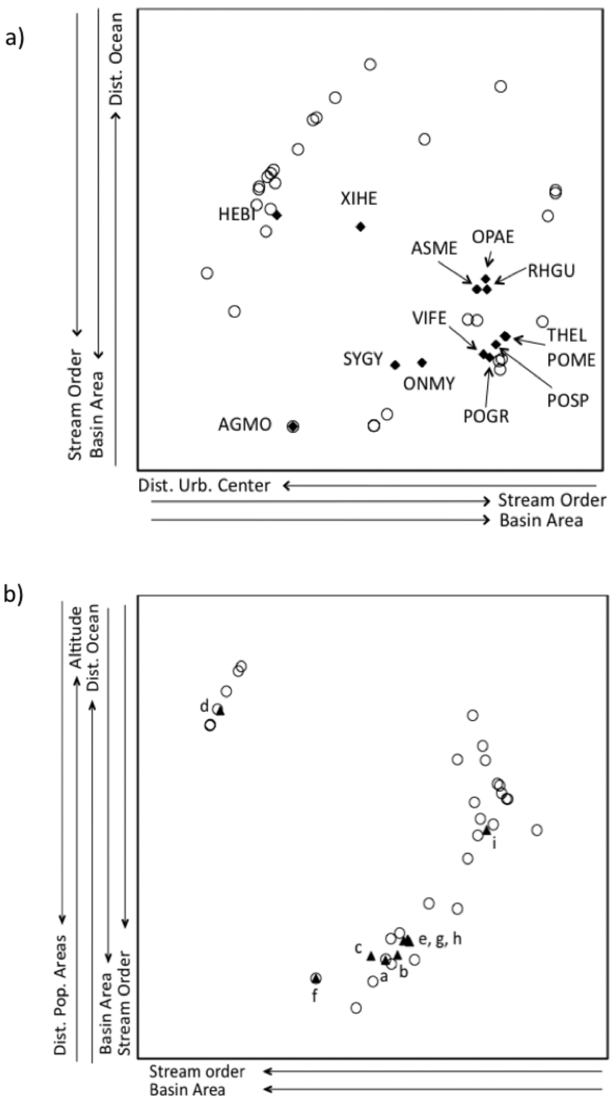

Figure 2. Non-metric multidimensional scaling plots for the analysis of fish communities and environmental data: a) upper plot for all 31 sites (open circles) and 13 species (closed diamonds), b) lower plot for all 31 sites and 9 ecological guilds. Text indicates either species or guilds as in Table 2. In both figures, environmental variables responsible for clustering are shown; the direction of arrow identifies greater dimensions for the variable.

Site scores from the 2 ordinations were significantly related to environmental variables. For the species ordination, the first axis was negatively correlated with distance from urban centers (Kendall's tau [τ]= -0.268) and positively correlated with stream order (τ= 0.180) and basin area (τ= 0.172). In other words, sites with higher (magnitude) scores on this axis tended to be of higher stream order and greater basin area (i.e., larger streams) and were located relatively close to population centers, whereas the opposite was true of sites with lower scores. The second axis was negatively correlated with stream order (τ= -0.408) and basin area (τ= -0.353), and positively correlated with distance to the ocean (τ= 0.233). Sites with higher scores on this axis were relatively smaller and located relatively farther from the ocean. For the guild ordination, the first axis was significantly negatively correlated with stream order (τ= -0.372) and basin area (τ= -0.177). Sites with higher scores on this axis tended to occur in smaller streams. The second axis had strong positive correlations with altitude (τ= 0.646) and distance from the ocean (τ= 0.547) and negative correlations with basin area (τ= -0.366), stream order (τ= -0.342), and distance from population centers (τ= -0.268). Sites with higher scores on this axis were mainly found on relatively smaller streams located at higher altitudes and farther from the ocean, but relatively closer to population centers.

Discussion

Abiotic and biotic variables are important in structuring stream fish assemblages (Gilliam and Fraser 2001; Higgins and Wilde 2005). The physical structure of a stream channel, along with flow regimes and energy inputs produce a consistent pattern of structure along a stream (Vannote et al. 1980). This pattern has been widely used to explain the spatial and temporal structure of fish assemblages (Hoeinghaus et al. 2003; Higgins 2009, Ibañez et al., 2009) in many lotic systems around the globe. Stream size and geographic attributes are associated with differences in the species composition and guild structure of fish communities in the La Antigua river system. Longitudinal zonation in species diversity and composition is common in stream-fish assemblages (Oberdorff et al., 1993; Ostrand and Wilde, 2002). Stream order, related to altitudinal position and stream size, has been linked to changes in species diversity (Hawkes, 1975; Godinho et al., 2000). Especially in large scale studies such as this, abiotic (e.g., climatic, geographic) factors often appear as drivers of community composition and assemblage structure and become more important than biotic factors (Jackson et al., 2001). The sharp inclination of the terrain and high altitudinal gradient of the La Antigua system may be the most important factors determining which species can be found in different areas of the river. High river slopes are known to affect upstream fish movement, impeding the passage of many species from lower to higher portions of the river (Lyons and Navarro-Pérez, 1990; Lyons et al., 1998; Rodiles-Hernández et al., 1999). In addition, along its short course from the high altitude volcanoes to the coastal plateau the La Antigua river has numerous falls >10m in altitude that likely block fish movement.

Several environmental variables used in our analysis are correlated with altitude and distance from the ocean. Water temperature is lower in higher elevation montane areas influenced by snowmelt from nearby volcanoes. In the La Antigua river, such low temperatures (10-20ºC) can only be tolerated by *O. mykiss*, an introduced species from aquaculture activities. As the river descends, increasing temperatures allow for higher species richness, including species accustomed to warmer waters (for example, the families Cichlidae and Pimelodidae), and those which carry out seasonal reproductive migrations (*S. gymnogaster* and *A. monticola*) between fresh and saline waters. Distance to the ocean thus has an important effect on the composition of the fish communities.

The native fish fauna in the La Antigua basin is neotropical and includes most elements of the Papaloapan-Usumacinta division of Miller et al. (2005). We only found 2 non-native species in the area we sampled, *O. mykiss* (rainbow trout) and *X. helleri*. Numerous trout farming operations exist in the higher elevation areas of the La Antigua basin and adjacent basins, and trout are widely used in the restaurant industry of the region. Trout are commonly raised in artificial tanks that extract water from the numerous rivers in the basin. During the rainy season, it is common that the water-holding capacity of the tanks is surpassed and trout escape to the main stream. It is unknown if trout have established self-sustained, naturalized populations in the river. *Xiphophorus helleri* have most likely been introduced to the La Antigua river basin as escapees from the aquarium industry which is prevalent in the region. However, the status of *X. helleri* as a non-native species in high elevation areas of the basin is uncertain because native populations may exist in lower portions of the La Antigua basin (Rosen, 1960). Our collections failed to produce other non-native fishes that are known from several coastal systems in Veracruz: *Oreochromis* spp., *Carassius auratus and Cyprinus carpio*. It is likely that these species utilize low-flow, turbid-water habitats located lower areas in the basin than those we sampled.

Only 1 of the species we captured, *Rhamdia guatemalensis*, is listed as a species with special protection by the Mexican federal government (NOM-059-SEMARNAT-2001). However, it is important to note that the fish fauna in the La Antigua river is facing several conservation issues. A few samples, particularly those near sugar processing plants, in areas with intensive agriculture, and near urban centers, produced no fish. In some of these collection efforts low water quality (i.e., high turbidity, presence of detergents and other contaminants, or excess nutrients) was evident. An active commercial and subsistence fishery is present in the lower portions of the La Antigua basin. It is unknown if fishing activities are having adverse effects on fish populations in these areas.

Aside from variables like stream width, altitude, water temperature, distance to the ocean, and basin area, other variables did not help to explain the variability found in our fish collections. This may stem from the strong correlations that exist among the most explanatory variables on these 2 axes, which may obscure the effects of any other non-correlated variables. Alternatively, variables measured in our samples may not reflect the diverse habitat conditions that can be found throughout the basin. We expected that some variables related to habitat quality (i.e., cover for fish, bank erosion, quality of riparian vegetation) would help determine some of the trends we found in the communities. The absence of these may reflect some or all of several factors, such as insufficient sampling across the entire continuum of habitat quality existing in the basin, little effect of habitat quality on the viability of fish communities, or as stated above, the strong influence that geographic variables have in structuring the communities of the La Antigua river. Similarly, we may have insufficiently sampled higher order systems in the basin. Increased geographical coverage of sampling efforts could help in providing a better description of environmental factors that determine fish assemblage in the basin.

Similar to other studies in Mexican systems (Lyons and Mercado-Silva, 1999), the relatively high number of ecological guilds found in the fish community of the La Antigua river reflects that ecological differences follow taxonomical differences in these fish assemblages. This result may be a product of the criteria chosen for the definition of the guilds. These criteria were chosen since they may reflect the diversity of habitats that species can use within an ecosystem and may allow our understanding of a species' function in the community. Other criteria, based on other aspects of the life history of the species (Winemiller, 2005), could group more species into fewer guilds, which could change some of the interpretation of our results. The use of these criteria however could be hampered by the lack of information on the basic biology of many of the species in the La Antigua basin. Guild-based analyses of fish communities will benefit from further study of species life histories, especially those that can help in determining whether a species does or does not change its ecological function in the community as a result of ontogeny or opportunity (Jackson et al., 2001). We encourage future studies to consider other guilds that might be more responsive to the same or different environmental variables. Additionally, we suggest that future studies attempt to represent an entire study region or basin in a more balanced way in their sampling efforts. In our results, some overlap among ecological guilds may result simply from an unbalanced distribution of sampling sites.

It is important to note that other native species are known from the La Antigua basin and were not captured in our efforts. Especially in areas located near the Gulf of Mexico at lower altitudes, Eleotrids, Ictalurids, other species of Cichlids, and Gobiids are present. In locations near some of our sampling sites, *Parachromis friedrichstalli* (Cichlidae), *Poecilia latipinna*, and *Poeciliopsis catemaconis* (Poeciliidae) have also been collected (EDP – unpublished data). The fish fauna of the lower La Antigua river, remains largely unstudied.

To our knowledge, this is one of the first community-level studies of the fish assemblages in Mexican rivers of the Gulf Coast, especially for the numerous rivers that originate from the Neovolcanic Axis in Central Mexico. In addition to providing information on the composition and ecological attributes of the fish communities in this region, we believe the information presented herein could be important for future investigations and management decisions as to the conservation of the fish fauna of the State of Veracruz.

Acknowledgements

We are thankful to Emanuel Mimila, Miguel Rubio, Lyssette Muñóz-Villers, Gabriela Vázquez, David Escandón, Enrique Meza, Guillermo Salgado, Rosario Landgrave, Javier Tolome, Ariadna Martínez, I. Chacón, A. Barrera and two anonymous reviewers for their assistance with field work, technical support, and in the preparation of this manuscript. A portion of the work for this project was part of NMS postdoctoral research at the Instituto de Ecología, A.C. Funding for this research was provided by CONACYT project No. 43082 and FOMIX project No. 32679.

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Appendix. Collection details for sites in La Antigua basin, Veracruz, Mexico. Data are presented in the following sequence: Site number / UTM Coordinates X, Y (UTM Region 14 for all sites); Altitude (m) / Mean stream width, maximum depth, water velocity, habitat diversity, substrate diversity, cover for fish, bank erosion, land use, water clarity, riparian vegetation, basin area, stream order at site, distance to ocean, distance to nearest human population upstream / Sampling date (month in year 2007) (species code-individuals captured, species 2 code-individuals captured, etc.) / Time sampled (minutes) in sample 1, sample 2, etc. / Temperature (ºC) sample 1, sample 2, etc. For species codes see Table 2.

Site 1 / UTM 2146077, 705656; Alt. 1393 / 2, 1, 2, 2, 3, 2, 1, 1, 3, 2, 407, 2, 92.68, 0 / 02 (HEBI-8); 03 (HEBI-10, ONMY-4); 05 (HEBI-33, ONMY-1) / 14, 26, 18 / 18.4, 18.7, 21.

Site 2 / UTM 2147646, 708438: Alt. 1299 / 2, 2, 2, 3, 3, 1, 2, 1, 2, 1, 196, 1, 88.8, 0 / 02 (HEBI-94); 03 (HEBI-39); 05 (HEBI-151) / 20, 14, 14 / 21, 18.3, 20.5.

Site 3 / UTM 2147057, 708476; Alt. 1278 / 1, 2, 2, 3, 3, 2, 2, 2, 3, 2, 443, 2, 88.79, 0 / 02 (HEBI-77); 03 (HEBI-47); 05 (HEBI-74) / 36, 10, 20 / 18.8, 19.2, 22.4.

Site 4 / UTM 2139820, 713020; Alt. 1145 / 1, 1, 2, 2, 2, 3, 2, 2, 1, 2, 82, 1, 99.64, 1435 / 02 (HEBI-37); 03 (HEBI-47); 05 (HEBI-31) / 21, 20, 18 / 17.6, 19.5, 18.

Site 5 / UTM 2140567, 713260; Alt. 1039 / 2, 2, 2, 3, 3, 3, 2, 2, 3, 2, 1500, 3, 98, 2471 / 02 (HEBI-83, XIHE-26); 03 (HEBI-30, XIHE-24, SYGY-4), 05 (HEBI-107, XIHE-30, SYGY-5) / 25, 27, 20 / 22, 20.4, 20.8.

Site 6 / UTM 2142182, 712154; Alt. 1105 / 2, 2, 2, 3, 1, 2, 2, 2, 1, 2, 2169, 2, 101, 0 / 02 (HEBI-40); 03 (HEBI-16); 05 (HEBI-68) / 19, 21, 15 / 23.7, 19.6, 23.1.

Site 7 / UTM 2143528, 712324; Alt. 1097 / 2, 2, 2, 2, 3, 2, 2, 2, 2, 2, 1568, 3, 97, 0 / 02 (HEBI-71); 03 (HEBI-55); 05 (HEBI-47) / 17, 22, 15 / 20.6, 21.3, 23.5.

Site 8 / UTM 2138472, 738880; Alt. 308 / 2, 3, 3, 3, 3, 3, 2, 2, 3, 2, 6993, 3, 62.3, 0 / 02 (HEBI-21, XIHE-14, THEL-46, VIFE-18, ASME-1, SYGY-1, POGR-56, RHGU-5, POSP-173, POME-47); 03 (HEBI-10, XIHE-12, THEL-23, VIFE-9, OPAE-7, POGR-35, RHGU-1, POSP-147, POME-9); 05 (HEBI-26, XIHE-3, THEL-27, VIFE-8, OPAE-7, ASME-4, SYGY-3, POGR-12, RHGU-3, POSP-159, POME-34); 07 (HEBI-46, XIHE-9, THEL-34, VIFE-17, OPAE-5, ASME-4, SYGY-2, POGR-30, RHGU-3, POSP-175, POME-13) / 27, 28, 23, 44 / 21.7, 20.9, 23.4, 24.6.

Site 9 / UTM 2145817, 705542; Alt. 1401 / 2, 2, 1, 2, 2, 3, 2, 2, 3, 2, 3800, 3, 92.56, 0 / 02 (ONMY-7) / 17 / 16.5.

Site 10 / UTM 2141135, 713071; Alt. 1051 / 1, 1, 2, 2, 2, 3, 2, 2, 1, 2, 124, 1, 97.9, 0 / 02 (HEBI-11); 03 (HEBI-22); 05 (HEBI-15) / 15, 17, 19 / 18.7, 18.6, 20.8.

Site 11 / UTM 2142217, 712211; Alt. 1115 / 1, 1, 2, 2, 2, 2, 2, 2, 1, 2, 457, 1, 102, 0 / 02 (HEBI-14); 03 (HEBI-6); 05 (HEBI-19) / 18, 10, 14 / 22.1, 20.5, 21.

Site 12 / UTM 2154984, 715207; Alt. 1245 / 3, 3, 2, 2, 3, 3, 2, 1, 3, 2, 7268, 4, 101.41, 0 / 05 (HEBI-92, XIHE-13); 06 (HEBI-61).

Site 13 / UTM 2164912, 709102; Alt. 1862 / 2, 2, 2, 3, 2, 3, 1, 1, 3, 1, 1578, 3, 120, 0 / 05 (ONMY-23) / 16 / 14.

Site 14 / UTM 2159228, 711353; Alt. 1433 / 2, 2, 3, 3, 3, 3, 2, 1, 3, 2, 1406, 3, 109.66, 0 / 05 (ONMY-24) / 23 / 14.7.

Site 15 / UTM 2158742, 709688; Alt. 1573 / 2, 2, 2, 3, 3, 3, 3, 2, 3, 3, 959, 3, 111.78, 0 / 05 (ONMY-51) / 34 / 15.

Site 16 / UTM 2146240, 719366; Alt. 664 / 2, 2, 1, 2, 2, 3, 1, 1, 1, 1, 1454, 2, 89.99, 1743 / 06 (No fish collected) / 16 / 23.

Site 17 / UTM 2148299, 718132; Alt. 1041 / 2, 2, 2, 3, 3, 3, 3, 2, 2, 2, 1046, 2, 91.84, 4601 / 06 (HEBI-54, POSP-6) / 22 / 24.9.

Site 18 / UTM 2143911, 720170; Alt. 830 / 3, 3, 1, 3, 3, 3, 2, 2, 1, 2, 8958, 4, 87.62, 10526 / 06 (HEBI-127, XIHE-27) / 30 / 18.7.

Site 19 / UTM 2146684, 715112; Alt. 1075 / 1, 1, 3, 1, 1, 1, 3, 3, 3, 3, 7, 1, 95.59, 0 / 06 (No fish collected) / 2 / 20.8.

Site 20 / UTM 2149295, 712447; Alt. 1147 / 3, 3, 1, 3, 3, 3, 2, 1, 1, 2, 2727, 4, 99.07, 1601 / 06 (XIHE-146) / 28 / 19.4.

Site 21 / UTM 2138046, 748841; Alt. 222 / 3, 3, 1, 3, 2, 3, 1, 1, 1, 1, 157495, 5, 57, 13501 / 07 (HEBI-1, XIHE-4, THEL-1, VIFE-8, ASME-1, SYGY-30, POGR-13, POSP-11, AGMO-5, POME-12) / 38 / n/a.

Site 22 / UTM 2151983, 703802; Alt. 1749 / 3, 3, 1, 2, 2, 2, 3, 2, 1, 1, 2068, 3, 96.17, 0 / 08 (ONMY-17) / 27 / 14.2

Site 23 / UTM 2153608, 714914; Alt. 1180 / 2, 1, 1, 2, 2, 2, 1, 1, 2, 1, 2386, 3, 107.43, 100 / 08 (HEBI-106, XIHE-9) / 22 / 16.9.

Appendix. Continues.

Site 24 / UTM 2144873, 725752; Alt. 617 / 2, 3, 3, 1, 2, 2, 3, 2, 3, 2, 806, 2, 81.74, 2085 / 08 (HEBI-126; XIHE-183) / 19 / 23.
Site 25 / UTM 2138954, 738611; Alt. 306 / 3, 3, 2, 3, 3, 2, 3, 2, 3, 2, 6474, 3, 62.93, 0 / 07 (HEBI-16, XIHE-10, THEL-15, VIFE-23, OPAE-1, SYGY-9, POGR-58, POSP-63, POME-8) / 34 / 23.
Site 26 / UTM 2139186, 738631; Alt. 316 / 3, 2, 2, 3, 2, 2, 3, 2, 3, 2, 6469, 3, 63.15, 0 / 08 (HEBI-8, XIHE-22, THEL-9, VIFE-7, OPAE-1, ASME-1, SYGY-9, POGR-56, POSP-92, POME-12) / 34 / 26.2.
Site 27 / UTM 2138954, 738611; Alt. 306 / 3, 3, 2, 3, 2, 2, 3, 2, 3, 2, 6474, 3, 62.93, 0 / 07 (HEBI-19, XIHE-14, THEL-20, VIFE-20, OPAE-3, ASME-1, SYGY-9, POGR-69, RHGU-1, POSP-81, POME-11) / 38 / 27.
Site 28 / UTM 2139737, 738436; Alt. 328 / 3, 2, 2, 3, 3, 2, 3, 2, 3, 2, 6438, 3, 63.82, 0 / 08 (HEBI-44, XIHE-68, THEL-38, VIFE-11, OPAE-5, ASME-7, SYGY-6, POGR-27, RHGU-5, POSP-85, POME-11) / 60 / 24.8.
Site 29 / UTM 2140846, 738053; Alt. 345 / 3, 3, 2, 2, 3, 2, 2, 2, 3, 3, 5968, 3, 65.12, 0 / 08 (HEBI-33, XIHE-60, THEL-31, VIFE-12, OPAE-12, ASME-5, SYGY-4, POGR-24, RHGU-6, POSP-73, POME-10) / 55 / 24.5.
Site 30 / UTM 2144308, 732737; Alt. 600 / 3, 2, 2, 3, 3, 2, 2, 2, 3, 3, 142, 2, 71.12, 0 / 08 (HEBI-74, XIHE-202, OPAE-10, ASME-5, RHGU-3, POSP-1) / 38 / 22.1.
Site 31 / UTM 2129846, 713226; Alt. 1230 / 2, 3, 3, 2, 2, 2, 3, 2, 1, 2, 308, 2, 85.75, 0 / 09 (HEBI-67) / 16 / 19.
Site 32 / UTM 2155647, 714556; Alt. 1235 / 2, 3, 2, 2, 2, 2, 2, 2, 2, 2, 351, 1, 102.66, 0 / 09 (No fish collected) / 17 / 19.1.
Site 33 / UTM 2157133, 710433; Alt. 1522 / 3, 3, 1, 2, 3, 3, 2, 2, 3, 2, 31.56, 1, 114.86, 0 / 09 (ONMY-11) / 30 / 17.2.
Site 34 / UTM 2155493, 713651; Alt. 1254 / 2, 1, 3, 2, 1, 2, 2, 2, 3, 2, 90.85, 1, 103, 0 / 09 (HEBI-41) / 12 / 19.3.