

# Fishes from Lachuá Lake, Upper Usumacinta Basin, Guatemala

Pablo Granados-Dieseldorff<sup>1,2\*</sup>, Måds F. Christensen<sup>3</sup> and P. Herman Kihn-Pineda<sup>4</sup>

- 1 Universidad de San Carlos de Guatemala, Escuela de Biología. Edificio T10, segundo nivel, Ciudad Universitaria zona 12. 01012. Guatemala Ciudad, Guatemala.
  - 2 Texas A&M University, Marine and Coastal Geography, Department of Geography. 810 Eller Oceanography & Meteorology Bldg. 77843-3147. College Station, TX, USA.
  - 3 Danish Association of International Cooperation (MS-Guatemala) – Fundación Solar. 15 avenida 18-78 zona 13. 01013. Guatemala Ciudad, Guatemala.
  - 4 Universidad de San Carlos de Guatemala, Museo de Historia Natural. Calle Mariscal Cruz 0-56 zona 10. 01010. Guatemala Ciudad, Guatemala.
- \* Corresponding author. E-mail: [pablogd@tamu.edu](mailto:pablogd@tamu.edu)

**ABSTRACT:** Guatemala's Maya Lowlands constitute one of the most biodiverse regions in Mesoamerica and include 35% of the total number of continental fish species estimated for the nation. From May 2000 through February 2001, we conducted the first long-term ichthyological survey of Lachuá Lake, a 4 km<sup>2</sup>, 195 m deep, karstic sinkhole located in the middle of Guatemala's Laguna Lachuá National Park (LLNP), southern Maya Lowlands. Thirty-six native fish species were identified and *Gobiomorus dormitor* Lacepède, 1800 was collected for the first time in northern Guatemala. Greater number of species occurred in the rocky shore of the lake's littoral zone, especially around the mouths of Lachuá's tributary and effluent rivers, and close to the visitor center of LLNP. A hierarchical cluster analysis for classifying ichthyogeographically regional fish assemblages placed Lachuá Lake in the upper Usumacinta River drainage basin shared by Guatemala and Mexico, stressing the need for regional conservation and management strategies.

## INTRODUCTION

The continental ichthyofauna of Guatemala is highly diverse (Rosen and Bailey 1963; Miller 1966, 1976; 1982; Bussing 1976, 1985; Rosen 1979; Kihn-Pineda *et al.* 2006). Lachuá Lake is an oligotrophic, karstic, and deep sinkhole located in Guatemala's Laguna Lachuá National Park (LLNP), Department of Alta Verapaz, southern Maya Lowlands. Surrounded by southeastern Mexico, Guatemala's Maya Lowlands concentrate the largest national terrestrial natural reserves, include 35.2% of the total number of freshwater fish species estimated for the country, and constitute one of the most preserved and important biodiversity regions in Mesoamerica (Valdez-Moreno *et al.* 2005; 2009).

Biological inventories of regions with minimal habitat degeneration are crucial in the planning and establishment of conservation and management strategies by governmental and nongovernmental agencies (Schmitter-Soto 1998; Valdez-Moreno *et al.* 2005). Although Guatemala's freshwater ichthyofauna has been relatively well described (Miller 1976; Willink *et al.* 2000), studies are generally old and sparse, many lack of exact collection localities, and most fail to synthesize and update the available information (Miller 1982; Valdez-Moreno *et al.* 2005). In particular, the extensive ichthyological surveys and collections in Guatemala during the last century did not include LLNP and no specimens from Lachuá Lake are recorded in interinstitutional databases of fish biodiversity in the neotropics (*e.g.*, NEODAT 2001).

Considering Lachuá Lake's regional and internationally-shared biodiversity, and faced with the potential anthropogenic threats to its unknown ichthyofauna, we conducted the first long-term ichthyological survey of this

limnological system from May 2000 through February 2001. The overall objective was to present a taxonomic list of Lachuá's ichthyofauna and a general description of its associated habitats, in order to provide a baseline for local managers to develop conservation strategies for LLNP aquatic systems.

## MATERIALS AND METHODS

Guatemala's Maya Lowlands extend south of the Yucatan Peninsula (Leyden 2002) across a low limestone platform with an average altitude of 200 m above sea level (asl). Their karst topography hosts numerous lakes and small depressions, particularly in the Departments of El Petén and Alta Verapaz. Lachuá is an oligotrophic and meromictic karstic lake in the Department of Alta Verapaz and it belongs to the southern upper reaches of the Usumacinta River drainage basin (Granados-Dieseldorff *unpublished data*). The lake is located in the center of the Laguna Lachuá National Park (LLNP, 15°53' N, 90°40' W), south of El Petén and the southeastern Mexico border (Figure 1).

Located at 173 m altitude, Lachuá Lake has a circular surface area of 4 km<sup>2</sup>, a pool-shaped basin of approximately 620 million m<sup>3</sup>, a maximum depth of 195 m, and an anoxic hypolimnion residing below a 40 m deep thermocline and a 60 m oxycline (Granados-Dieseldorff *unpublished data*). On the western side of its basin, a permanent river (Peyán) and an intermittent stream (Escondido) flow into Lachuá Lake (Figure 1). On the eastern side, Lachuá Lake drains into an intermittent stream (Altar) and two permanent rivers (Lachuá and Tzetoc), which then flow into the Icbolay River, an affluent of the Chixoy-Salinas River, upper reach of the Usumacinta River.

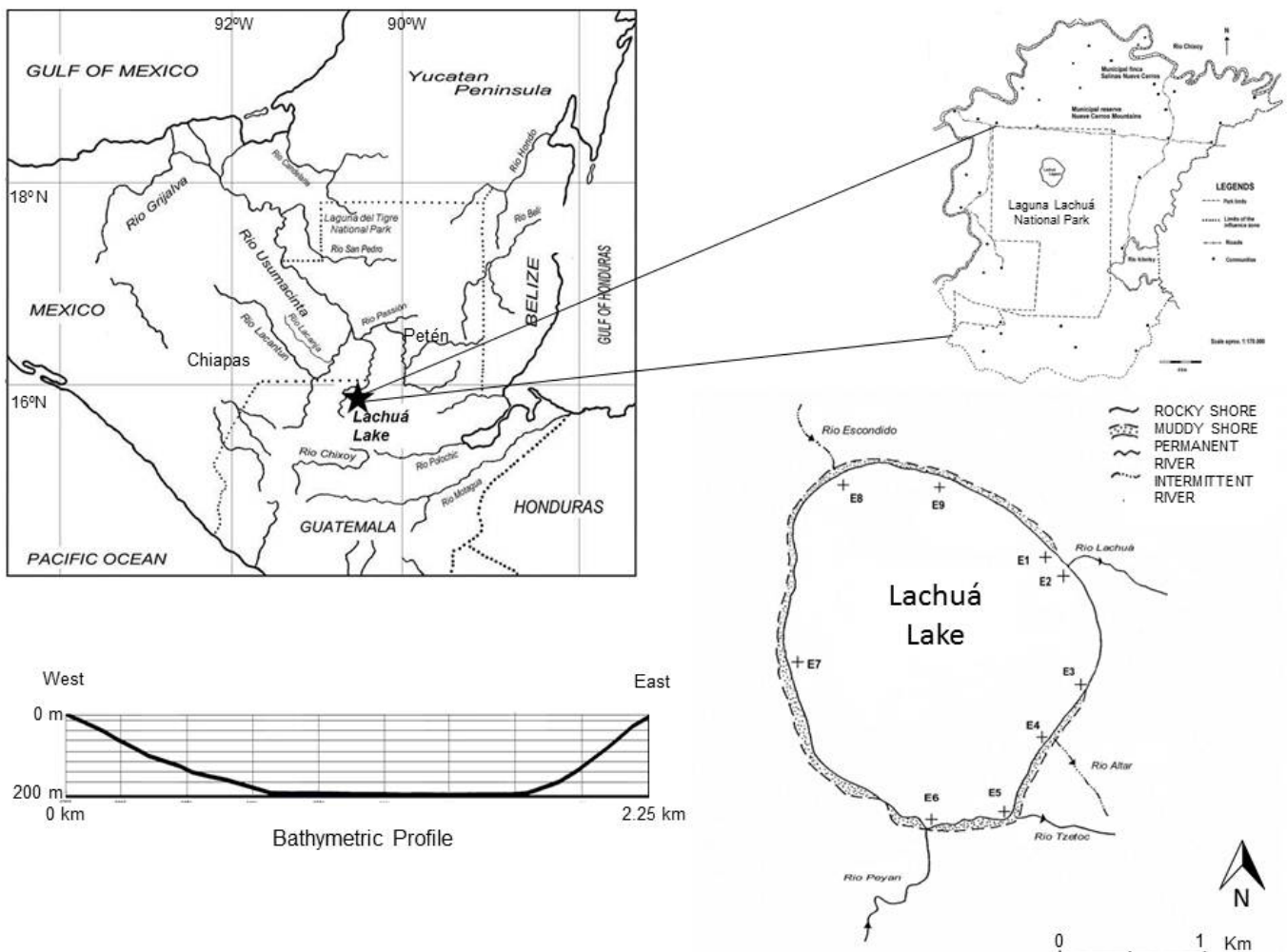
The value of Lachuá Lake and the surrounding 14,500 ha of tropical rainforest as an important biodiversity refuge and recreational center was recognized in 1996, when the area became fully protected as a national park of Guatemala (Avendaño-Mendoza *et al.* 2005). In 2006, Lachuá Lake was included in the Annotated Ramsar List of Wetlands of International Importance (Ramsar 2007). Access to Lachuá Lake is very limited (*i.e.*, a 4-km hike through the forest connects the lake to the closest access road) and fishing and hunting are totally prohibited in the natural reserve. Besides two small piers, a visitor center for seasonal tourists, and a biological station for park rangers and researchers, the area lacks modern infrastructure and facilities.

The national park and its buffer zone (Figure 1) belong to Guatemala's northern tropical rainforest remnants, which represent the last and northernmost forest mass after Amazonia in South America (Mendoza and Dirzo 1999). The region has a dominant seasonal climate with a mean annual temperature ranging between 25°C and 28°C, a precipitation of 3000 mm/yr, and differentiated wet (May through November) and dry seasons (December through April) (Granados-Dieseldorff *unpublished data*; Leyden 2002). Currently, the Q'eqchi' ethnic group represents most of the surrounding population, with approximately 11,000 inhabitants from 38 local communities. Land registration and road building was established in the

region in an attempt to create infrastructure and social services for local repatriated communities after the end of the civil war in 1996 (Avendaño-Mendoza *et al.* 2005).

From May 2000 through February 2001, 10-day surveys of Lachuá's ichthyofauna were conducted monthly. Three major habitat types were identified *a priori* in the lake's littoral zone (7.4 km total perimeter): a muddy shore (calcareous silt, 85% of the littoral zone), a rocky shore (calcareous rocks, 14%), and the mouths of four rivers (< 1%, two affluents –Peyán and Escondido, and two effluents –Lachuá and Tzetoc) (Figures 1 and 2). In an attempt to cover the three major habitat types, a total of nine sampling sites were selected and marked using a GPS Garmin II Plus (Figure 1). Three sites were situated in the muddy shore (MS – E1, E7, and E9), two in the rocky shore (RS – E3 and E4), and four distributed among each of the four river mouths (RM – E2, E5, E6, and E8). Each site was sampled for ichthyofauna and associated physiochemical parameters (water temperature, pH, conductivity, hardness, transparency, and nutrients concentration), on a daily basis, every month (*i.e.*, a 10-day sampling effort per site, per month), and surveys covered the wet (May–November) and dry (December–February) seasons.

A bathymetric map and profile of Lachuá Lake were produced using an Apelco ecosounder that measured depths at 50 randomly georeferenced sites (Figure 1). Data were geoprocessed in ArcView 2.x. Water samples



**FIGURE 1.** Map of study area, showing geographic location of Lachuá Lake within the Lachuá Lake National Park (15°53' N, 90°40' W), Alta Verapaz, Guatemala. Sampling sites (E1-E9), geomorphology, and bathymetry of Lachuá Lake are indicated.

were collected at each sampling site with a 2-L vertical Van Dorn hydrographic bottle and physiochemical analyses were made with a portable LaMotte Smart Water Analysis Laboratory, which included thermometer, pH meter, conductivity meter, Secchi disk, reactants, and colorimeter (Table 1).

Fish were collected during dark and light hours using standard ichthyological gear, including an experimental gill net (3 m deep, 40 m long, with 5 different panels of 8 m long each, and 2.5-, 3.75-, 5-, 6.75-, and 7.5-cm mesh size, respectively), a fine mesh dipnet (20 cm deep, 40x40 cm frame, 0.5-cm mesh size), a seine (1.30 m deep, 10 m long, 0.6-cm mesh size), a hook line (30 m long, 12 fish hooks of different sizes), four double-cone traps (50 cm long with 2.5-, 3.75-, 5-, and 6.75-cm interior opening, respectively), a cast net (2-m radius, 0.63-cm mesh size), and a spear gun. Bait for traps and hooks included a combination of different meats and vegetables. Fishing effort was equally distributed in each sampling site, although seining was extremely difficult in the muddy shore and in the river mouths.

Research and collecting permits were provided by the Instituto Nacional de Bosques (INAB) and Fundación Solar (institutional co-managers of the LLNP) to the Escuela de Biología, Universidad de San Carlos de Guatemala (USAC) (Convenio y Permiso de Investigación 2000-2001/Componente Limnológico Proyecto Lachuá/Escuela de Biología USAC/Fundación Solar/ INAB). In order to comply with the LLNP management regulations and research permits, no intensive collections of ichthyofauna were performed and fish collections were very limited in quantity. Organisms were preferably identified in the field and those with appropriate size, photographed inside an arranged 30x15x20 cm tank before being released alive back to the lake. Specimens of uncertain field identification were retained and were first preserved in 10% formalin for at least 48 hours, and then transferred to 70° GL ethanol for transportation and laboratory identification. Ichthyofauna data were recorded as presence-absence of individual fish species in sampling sites. Voucher specimens were deposited in the fish collection of the Museo de Historia Natural (MUSHNAT), Universidad de

**TABLE 1.** Description of the habitat types surveyed for ichthyofauna in Lachuá Lake, Alta Verapaz, Guatemala. Habitat types are ordered by sampling sites and are denoted by MS (muddy shore), RM (river mouth), and RS (rocky shore). Affluent (aff) and effluent (eff) rivers are marked, physiochemical parameters (water temperature [T], pH, conductivity [C], hardness [H], and concentrations of sulfates [S], and nitrates and phosphates [NP]) averaged for the total study period, and observations on bottom structure and microhabitat complexity presented. Geographic location of sampling sites is indicated in Figure 1 and examples of localities in Figure 2.

SITE	HABITAT TYPE	DESCRIPTION
E1	RS	Calcareous rocky bank, with attached crusty algae patches of pale, greyish color. Riparian vegetation absent, with submerged aquatic vegetation only apparent during the wet season (highest Lake water level). Dominant bottom sediments with gravel texture, pale, whitish color. Few submerged tree trunks observed. Littoral zone only 5-6 m wide, with a 3-m maximum depth, extending quickly into the steep pelagic slope. Water very clear. T=29.1°C, pH=8.5, C=926.5 µS, H=1181 mg/l, S=360 mg/l, NP=0.21 mg/l. Infrastructure of the park present: bathing pier and visitor facilities.
E2	RM, Río Lachuá (eff)	Permanent effluent river mouth. Calcareous rocky shore, with attached crusty algae patches of pale, greyish color. Riparian vegetation composed mainly of trees, palms, and submerged grasses. Canopies of shading trees contiguously down into water surface. Dominant bottom sediments with gravel texture, pale, whitish color. Tree trunks and roots present. Littoral zone only 5-6 m wide, with a 3-m maximum depth, extending quickly into the steep pelagic slope. Water clear, with strong current from the mouth area toward the river, and with increasing flow during the wet season. T=28.8°C, pH=8.5, C=932.0 µS, H=1074 mg/l, S=440 mg/l, NP=0.21 mg/l.
E3	RS	Calcareous rocky bank, with attached crusty algae patches of pale, greyish color. Riparian vegetation composed mainly of trees, shrubs and submerged grasses. Dominant bottom sediments with gravel texture, pale, whitish color. Tree trunks and roots present. Littoral zone only 5-6 m wide, with a 3-m maximum depth, extending quickly into the steep pelagic slope. Water very clear. T=28.6°C, pH=8.3, C=904.5 µS, H=1074 mg/l, S=390 mg/l, NP=0.20 mg/l.
E4	MS	Calcareous muddy bank. Vegetation predominantly of submerged grasses, with fringing forest towards the firm, dry ground. Canopies of some shading trees contiguously down into water surface. Dominant bottom sediments with silt texture, whitish color. Tree trunks absent. Littoral zone wide (20-30 m) and shallow (< 1 m deep), extending into the steep pelagic slope. Water clear. T=28.8°C, pH=8.3, C=922.0 µS, H=1074 mg/l, S=380 mg/l, NP=0.21 mg/l.
E5	RM, Río Tzetoc (eff)	Permanent effluent river mouth. Calcareous muddy bank. Riparian vegetation of medium size, predominantly composed of submerged grasses. Dominant bottom sediments with silt texture, whitish color. Few trunks present. Littoral zone wide (20-30 m) and shallow (< 1 m deep), extending into the steep pelagic slope. Water very clear. Strong currents from the mouth area towards the river, with increasing flow during the wet season. T=28.6°C, pH=8.3, C=931.5 µS, H=1074 mg/l, S=470 mg/l, NP=0.21 mg/l.
E6	RM, Río Peyan (aff)	Permanent affluent river mouth. Calcareous rocky bank. Vegetation riparian composed of mainly trees, palms and submerged grasses. Riparian vegetation composed mainly of trees, palms, and submerged grasses. Canopies of shading trees contiguously down into water surface. Dominant bottom sediments with gravel texture, pale, whitish color. Tree trunks and roots present. Littoral zone only 5-6 m wide, yet deep, with a 20-m maximum depth, extending quickly into the steep pelagic slope. Water very clear, with the lowest surveyed temperatures, with a strong current into the lake, and with increasing flow during the wet season. T=28.2°C, pH=8.0, C=960.5 µS, H=1081 mg/l, S=390 mg/l, NP=0.21 mg/l.
E7	MS	Calcareous muddy bank. Vegetation predominantly of submerged grasses, with fringing forest towards the firm, dry ground. Canopies of some shading trees contiguously down into water surface. Dominant bottom sediments with silt texture, whitish color. Tree trunks absent. Littoral zone wide (20-30 m) and shallow (< 1 m deep), extending into the steep pelagic slope. Water clear. T=28.5°C, pH=8.0, C=926.5 µS, H=1074 mg/l, S=470 mg/l, NP=0.20 mg/l.
E8	RM, Río Escondido (aff)	Intermittent river mouth. Riparian vegetation riparian of medium size, predominantly of submerged grasses. Dominant bottom sediments with silt texture, grey/brownish color due to deposition of organic matter. Some tree trunks and roots present. Littoral zone wide (20-30 m) and shallow (< 1 m deep), extending into the steep pelagic slope. Water clear. Very weak water flow, only during the wet season. T=28.9°C, pH=8.1, C=936.0 µS, H=1038 mg/l, S=300 mg/l, NP=0.21 mg/l.
E9	MS	Calcareous muddy bank. Vegetation predominantly of submerged grasses, with fringing forest towards the firm, dry ground. Canopies of some shading trees contiguously down into water surface. Dominant bottom sediments with silt texture, whitish color. Tree trunks absent. Littoral zone wide (10-20 m) and shallow (< 1 m deep), extending into the steep pelagic slope. Water very clear. T=28.9°C, pH=8.1, C=919.5 µS, H=1074 mg/l, S=390 mg/l, NP=0.20 mg/l.

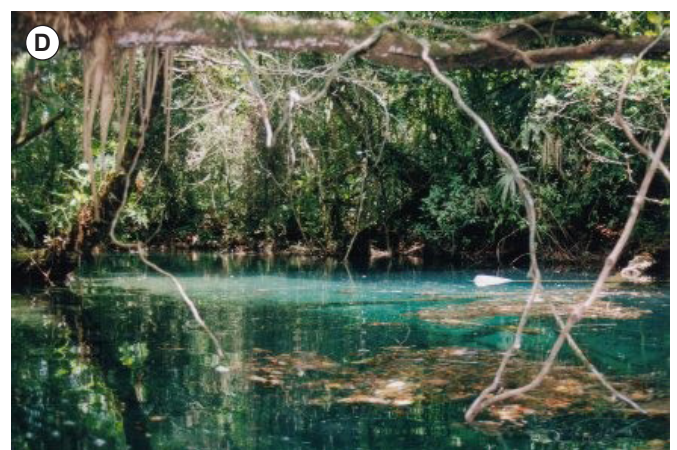
San Carlos de Guatemala (USAC), Guatemala City. Families in the taxonomic list (Table 2) were arranged according to Eschmeyer and Fong (2012).

Two hierarchical, agglomerative cluster analyses, using PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6.1.6 (Clarke and Gorley 2006) were performed in order to classify arrangements of fish assemblages across sampling sites (E1-E9) and explore patterns of similarity among fish assemblages of four limnological systems of the biogeographic Usumacinta Province (Bussing 1976; Miller 1982; Abell *et al.* 2008). Data for the second analysis included the fish species lists of the Usumacinta River (112 species, Miller 1976; Willink *et al.* 2000), Laguna del Tigre National Park (55 species, Willink *et al.* 2000), Lacanjá River (44 species, Rodiles-Hernández *et al.* 1999), and Lachuá Lake (36 species, this study) (Figure 1). Bray-Curtis distance similarities were based on presence-absence of fish species and clustering groups were weighted using the group average method.

## RESULTS AND DISCUSSION

A total of 36 different species, distributed in 26 genera, 15 families, and 10 orders were identified for the first time in Lachuá Lake (Table 2). *Gobiomorus dormitor* Lacepède 1800 was collected for the first time in northern Guatemala in 2001 (Granados-Dieseldorff *unpublished data*) and later recorded by Valdez-Moreno *et al.* (2005). The species list comprises almost half of the combined total number of species found in the Departments of El Petén and Alta Verapaz. Although Alta Verapaz is a region characterized by a high degree of endemism as a result of local karst topography combined with tectonic activity (Valdez-Moreno *et al.* 2005), none of the species are endemic solely to the lake, none are listed as threatened or endangered in Guatemala, and most of them are distributed along the central region of the Usumacinta province, which consists of northern Guatemala, Belize and southern Mexico (Miller 1966, 1976, 1982; Bussing 1976; Abell *et al.* 2008). However, the species *Atherinella schultzi* (Álvarez and Carranza, 1952), *Batrachoides goldmani* (Evermann and Goldsborough, 1902), *Hyporhamphus mexicanus* Álvarez, 1959, *Paraneetroplus bifasciatus* (Steindachner, 1864), *Paraneetroplus synspilus* (Hubbs, 1935), *Petenia splendida* Günther, 1862, *Potamarius nelsoni* (Evermann and Goldsborough, 1902), *Theraps heterospilus* (Hubbs, 1936), *Theraps lentiginosus* (Steindachner, 1864), *Theraps pearsei* (Hubbs, 1936), *Thorichthys helleri* (Steindachner, 1864), *Thorichthys meeki* Brind, 1918, and *Thorichthys passionis* (Rivas, 1962) are endemic to the Usumacinta River Basin (Miller 1976, 1982; Willink *et al.* 2000), the main binational collecting system to which Lachuá Lake is hydrologically connected (Granados-Dieseldorff *unpublished data*).

According to Myers' (1966) phylogenetic classification, which is based on historical salinity tolerance of freshwater fish families, 11% of the Lachuá's fish species are primary, 57% secondary, and 32% peripheral. In agreement with the typical fish species composition of the Usumacinta Province (Miller 1966; 1982), cichlids (40% of the total fish species) and poeciliids (14%) constituted together more than half of the fish species collected in Lachuá Lake.



**FIGURE 2.** Examples of sampled localities in Lachuá Lake, Alta Verapaz, Guatemala. A. Visitor pier located between sampling sites E1 and E2. B. Rocky bank (E1). C. Mouth of Río Lachuá (E2). D. Mouth of Río Peyán (E6).

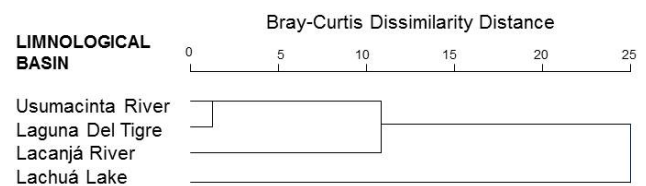
Although no exotic species were collected, the presence of two introduced species to the region (Miller 1976; Valdez-Moreno *et al.* 2005), the grass carp *Ctenopharyngodon idella* (Valenciennes, 1844) and blue tilapia, *Oreochromis aureus* (Steindachner, 1864), has been reported in surrounding river basins (Granados-Dieseldorff *unpublished data*). Considering their competitive and invasive behavior (Morales-Román and Rodiles-Hernández 2000), these exotic species would constitute an eminent threat to Lachuá's native fish fauna if their presence is confirmed by posterior surveys.

Based on species composition, the similarity between the ichthyofaunas of the Usumacinta River and the adjacent Laguna del Tigre National Park (LTNP) was the greatest (Figure 3). Together, these ichthyofaunas were similar to Lacanjá River's in the southwest Usumacinta River drainage basin (Figure 1). In the southernmost, upper reaches of this system, the ichthyofauna of Lachuá Lake was the most dissimilar. This is in agreement with observations from other drainage basins around the world where ecosystem processes and biological community structure change along fluvial gradients within drainage basins (*e.g.*, Hynes 1970; Bussing and López 1977; Lowe-McConnell 1987; Winemiller *et al.* 2011). Moreover, lotic systems, such as the Usumacinta River, Lacanjá River, and the streams network of LTNP, differ in ecological attributes (*sensu* Lowe-McConnell 1987) from lentic systems, such as Lachuá Lake. Productivity of ecosystems, organismal responses to variations in fluvial discharge, and species interactions all vary along gradients of limnological and morphometric factors that transition from headwaters into downstream reaches (Hynes 1970; Lowe-McConnell 1987; Winemiller *et al.* 2011).

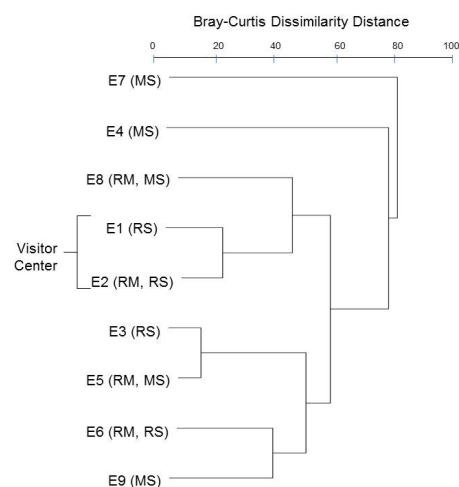
Greater numbers of fish species occurred in the rocky shore of the littoral zone (*i.e.*, 15% of the Lake's littoral), especially around the mouths of Lachuá's tributary and effluent rivers, and close to the piers and visitor center. The sampling sites closest to Lachuá's visitor center (E1 and E2), which combined a rocky and river-influenced littoral (Figures 1 and 2; Table 2), remarkably accounted for more than 90% of the total species identified for the lake. Their assemblage structure, based on the number of recorded fish species during the total study period, was different from the other sampling sites (Figure 4). The anthropogenic input of nutrients (*i.e.*, organic contamination from an estimated visitation rate of 50 visitors/m<sup>2</sup>/yr) may be driving the aggregation of fishes around the visitors' area. This has also been suggested in other ichthyological studies of karstic lakes in southern Mexico (Schmitter-Soto and Gamboa-Pérez 1996; Gamboa-Pérez and Schmitter-Soto 1999). Similarly to other studies in the region (Rodiles-Hernández *et al.* 1996, 1999; Schmitter-Soto and Gamboa-Pérez 1996; Gamboa-Pérez and Schmitter-Soto 1999) and characteristic of tropical fish communities of lentic systems (*c.f.*, Lowe-McConnell 1987), the distribution of fish species in Lachuá Lake is mainly driven by the structural and spatial configuration of habitats and microhabitats in the littoral zone of Lachuá

Lake (*c.f.*, Tables 1 and 2). The distribution and complexity of suitable habitat available to neotropical freshwater fish species (*e.g.*, presence of periphyton in the substrate, submerged aquatic vegetation, type of bank vegetation, presence of submerged stems and tree trunks) influence the distribution, abundance, and community structure of Lachuá's ichthyofauna by providing individuals with refuge, food, and reproduction areas.

Lachuá's high number of species, its composition in secondary and peripheral species, the presence of species endemic to the Usumacinta River, and the seasonal presence of highly migratory diadromous fishes such as *Megalops atlanticus* Valenciennes, 1847, portrayed this karst lake as an important open system in the uppermost Usumacinta River drainage basin. The disclosure of Lachuá Lake as a tributary of the surrounding binational hydrological system stresses the importance of addressing conservation issues at a broader regional scale. Future sustainability of Lachuá's ichthyofauna is dependent upon a continued healthy exchange of gene pools with the surrounding environment, as well as an open passage for migratory species. In order to preserve Lachuá's ichthyofauna and its associated habitats, we advocate for binational (Mexico-Guatemala) and multiagency efforts in the regulation, conservation, and management of the shared aquatic resources of the Usumacinta River drainage basin.



**FIGURE 3.** Dendrogram of the hierarchical cluster analysis classifying fish assemblages from four limnological systems of the biogeographic Usumacinta Province: Usumacinta River, Laguna del Tigre National Park, Lacanjá River, and Lachuá Lake, south towards the upper reaches of the drainage system.



**FIGURE 4.** Dendrogram of the hierarchical cluster analysis classifying the fish assemblages determined across the sampling sites (E1-E9) from May 2000 through February 2001.

**TABLE 2.** Taxonomic list of the 36 fish species identified in Lachuá Lake, Laguna Lachuá National Park, Alta Verapaz, Guatemala, from May 2000 through February 2001. Families are listed according to Eschmeyer and Fong (2012), genera and epithet in alphabetical order (Eschmeyer and Fricke 2012). Habitat types where taxa were identified are denoted by MS (muddy shore), RM (river mouth), and RS (rocky shore). Institutional (USAC) catalogue numbers for available vouchers are indicated in brackets.

<b>CLASS ACTINOPTERYGII</b>
<b>ORDER ELOPIFORMES</b>
<b>Family Megalopidae</b>
<i>Megalops atlanticus</i> Valenciennes, 1847; RS, RM.
<b>ORDER CLUPEIFORMES</b>
<b>Family Clupeidae</b>
<i>Dorosoma anale</i> Meek, 1904; RM.
<i>Dorosoma petenense</i> (Günther, 1867); RM.
<b>ORDER CHARACIFORMES</b>
<b>Family Characidae</b>
Astyanax clade
<i>Astyanax aeneus</i> (Günther, 1860); RS, RM, MS. [USAC 1730]
Hemigrammus clade
<i>Hypessobrycon compressus</i> (Meek, 1904); RM. [USAC 1731]
<b>Family Bryconidae</b>
Subfamily Bryconinae
<i>Brycon guatemalensis</i> Regan, 1908; RS, RM, MS. [USAC 1751]
<b>ORDER SILURIFORMES</b>
<b>Family Ariidae</b>
<i>Ariopsis assimilis</i> (Günther, 1864); RS, MS. [USAC 530]
<i>Potamarius nelsoni</i> (Evermann and Goldsborough, 1902); RS, RM.
<b>Family Heptapteridae</b>
<i>Rhamdia quelen</i> (Quoy and Gaimard, 1824); RS, RM. [USAC 1729]
<b>ORDER BATRACHOIDIFORMES</b>
<b>Family Batrachoididae</b>
Subfamily Batrachoidinae
<i>Batrachoides goldmani</i> (Evermann and Goldsborough, 1902); RM.
<b>ORDER ATHERINIFORMES</b>
<b>Family Atherinopsidae</b>
Subfamily Menidiinae
<i>Atherinella schultzi</i> (Álvarez and Carranza, 1952); RS, RM. [USAC 1737]
<b>ORDER CYPRINODONTIFORMES</b>
<b>Family Poeciliidae</b>
Subfamily Poeciliinae
<i>Belonesox belizanus</i> Kner, 1860; RS, RM. [USAC 1733]
<i>Gambusia yucatanana</i> Regan, 1914; RS, RM. [USAC 1734]
<i>Heterandria bimaculata</i> (Heckel, 1848); RS, RM. [USAC 1736]
<i>Poecilia mexicana</i> Steindachner, 1863; RS, RM. [USAC 1735]
<i>Xiphophorus hellerii</i> Heckel, 1848; RM.
<b>ORDER BELONIFORMES</b>
<b>Family Belonidae</b>
<i>Strongylura hubbsi</i> Collette, 1974; RS, RM.
<b>Family Hemiramphidae</b>
Subfamily Hemiramphinae
<i>Hyporhamphus mexicanus</i> Álvarez, 1959; RS, RM. [USAC 1728]
<b>ORDER SYNBRANCHIFORMES</b>
<b>Family Synbranchidae</b>
<i>Ophisternon aenigmaticum</i> Rosen and Greenwood, 1976; RS, RM.
<b>ORDER PERCIFORMES</b>
<b>Family Gerreidae</b>
<i>Eugerres mexicanus</i> (Steindachner, 1863); RM.
<b>Family Cichlidae</b>
Subfamily Cichlinae
<i>Amphilophus robertsoni</i> (Regan, 1905); RS, RM.

<i>Cichlasoma salvini</i> (Günther, 1862); RS, RM. [USAC 1741]
<i>Paraneetroplus argenteus</i> (Allgayer, 1991); RM. [USAC 1750]
<i>Paraneetroplus bifasciatus</i> (Steindachner, 1864); RM. [USAC 1742]
<i>Paraneetroplus synspilus</i> (Hubbs, 1935); RS, RM, MS. [USAC 528; 531; 1745]
<i>Petenia splendida</i> Günther, 1862; RS, RM. [USAC 526]
<i>Theraps heterospilus</i> (Hubbs, 1936); RS, RM. [USAC 1738; 1743; 1744]
<i>Theraps heterospilus</i> (Hubbs, 1936); RS, RM. [USAC 1738; 1743; 1744]
<i>Theraps intermedius</i> (Günther, 1862); RM.
<i>Theraps lentiginosus</i> (Steindachner, 1864); RM.
<i>Theraps pearsei</i> (Hubbs, 1936); RS, RM. [USAC 1739]
<i>Thorichthys aureus</i> (Günther, 1862); RS [USAC 1748]
<i>Thorichthys friedrichsthalii</i> (Heckel, 1840); RM. [USAC 1740; 1746]
<i>Thorichthys helleri</i> (Steindachner, 1864); RS, RM. [USAC 1651]
<i>Thorichthys meeki</i> Brind, 1918; RS.
<i>Thorichthys pasionis</i> (Rivas, 1962); RS, RM. [USAC 1747; 1749]
<b>Family Eleotridae</b>
Subfamily Eleotrinae
<i>Gobiomorus dormitor</i> Lacepède, 1800; RM.

**ACKNOWLEDGMENTS:** This study was conducted under a research agreement between the Instituto Nacional de Bosques (INAB) - Fundación Solar (co-managers of the LLNP) and the Escuela de Biología de la Universidad de San Carlos de Guatemala (EB-USAC). The project was supported by research grants from the IUCN-Mesoamerica Ecoregión Lachuá Project, the USAID-Conservation International-Mexico “Mayan Biosphere” Program, and the Danish Association of International Co-operation (MS). We thank L. Cornel-Caal, F. Ayala, and the park rangers of the LLNP for field support and A. Morales and L. Prado for assistance in the ichthyological collections of the MUSHNAT, USAC. We also appreciate valuable feedback from C. Avendaño-Mendoza, A. Baumgarten, E.B. Cano, R. Monzón, M.R. Rodiles-Hernández, P. Rockstroh, J.J. Schmitter-Soto, M.E. Valdez-Moreno, and two anonymous reviewers.

#### LITERATURE CITED

- Abell, R., M.L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N. Mandrak, S. Contreras-Balderas, W. Bussing, M.L.J. Stiassny, P. Skelton, G.R. Allen, P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J.V. Higgins, T.J. Heibel, E. Wikramanayake, D. Olson, H. L. López, R.E. Reis, J.G. Lundberg, M.H. Sabaj Pérez and P. Petry. 2008. Freshwater ecoregions of the World: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* 58(5):403-414.
- Avendaño-Mendoza, C., A. Morón-Ríos, E.B. Cano and J. León-Cortés. 2005. Dung beetle community (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical landscape at the Lachuá Region, Guatemala. *Biodiversity and Conservation* 14(4): 801-822.
- Bussing, W.A. 1976. Geographic distribution of the San Juan Ichthyofauna of Central America with remarks on its origin and ecology; p. 157-175. In T.B. Thorson (ed.). *Investigations of the Ichthyofauna of Nicaraguan Lakes*. Lincoln: University of Nebraska Press.
- Bussing, W.A. 1985. Patterns of distribution of the Central American Ichthyofauna; p. 453-473. In F.G. Stehli and S.D. Webb (ed.). *The Great American Biotic Interchange*. New York: Plenum Press, Geobiology Series.
- Bussing, W.A. and M.I. López. 1977. Distribución y aspectos ecológicos de los peces de las cuencas hidrográficas de Arenal, Bebedero y Tempisque, Costa Rica. *Revista de Biología Tropical* 25(1):13-37.
- Clarke, K.R. and R.N. Gorley, 2006. *PRIMER v6: User Manual/Tutorial*. Plymouth: PRIMER-E.
- Eschmeyer, W.N. and J.D. Fong. 2012. *Species of fishes by family/subfamily*. Online version dated 12 JAN 2012. Electronic Database accessible at <http://research.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>. Captured on 18 January 2012.
- Eschmeyer, W.N. and R. Fricke (ed.). 2012. *Catalog of fishes electronic version (12 JAN 2012)*. Electronic Database accessible at <http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Captured on 18 January 2012.
- Gamboa-Pérez, H.C. and J.J. Schmitter-Soto. 1999. Distribution of cichlid fishes in the littoral of Lake Bacalar, Yucatan Peninsula. *Environmental Biology of Fishes* 54 (1): 35-43.
- Hynes, H.B.N. 1970. *The ecology of running waters*. Toronto: University of Toronto Press. 555 p.
- Kihn-Pineda, P.H., E.B. Cano and A. Morales. 2006. Peces de las aguas

- interiores de Guatemala; p. 457–486 In E.B. Cano (ed.). *Biodiversidad de Guatemala*. Guatemala Ciudad: Editorial de la Universidad del Valle de Guatemala.
- Leyden, B.W. 2002. Pollen evidence for climatic variability and cultural disturbance in the Maya Lowlands. *Ancient Mesoamerica* 13: 85-101.
- Lowe-McConnell, R.H. 1987. *Ecological studies in tropical fish communities*. Great Britain: Cambridge University Press. 391 p.
- Mendoza, E. and R. Dirzo. 1999. Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. *Biodiversity and Conservation* 8(12): 1621-1641.
- Miller, R.R. 1966. Geographical distribution of Central American freshwater fishes. *Copeia* 4: 773-802.
- Miller, R.R. 1976. Geographical distribution of Central American freshwater fishes; p. 125- 156 In T.B. Thorson (ed.). *Investigations of the Ichthyofauna of Nicaraguan Lakes*. Lincoln: University of Nebraska Press.
- Miller, R.R. 1982. Pisces; p. 486-501 In S.H. Hurlbert and A. Villalobos-Figueroa (ed.), *Aquatic biota of Mexico, Central America and the West Indies*. San Diego: San Diego State University.
- Morales-Román, M. and R. Rodiles-Hernández. 2000. Implicaciones de *Ctenopharyngodon idella* en la comunidad de peces del río Lacanjá, Chiapas. *Hidrobiológica* 10(1): 13-24.
- Myers, G.S. 1966. Derivation of the freshwater fish fauna of Central America. *Copeia* 4: 766-773.
- NEODAT. 2001. *Inter-Institutional Database of fish biodiversity in the Neotropics*. University of Michigan, University of New Orleans, and American Museum of Natural History. Electronic Database accessible at <http://www.neodat.org>. Captured on 2 July 2007.
- Ramsar. 2007. Electronic database accessible at [http://www.ramsar.org/cda/en/ramsar-documents-list/main/ramsar/1-31-218\\_4000\\_0](http://www.ramsar.org/cda/en/ramsar-documents-list/main/ramsar/1-31-218_4000_0). Captured on 2 July 2007.
- Rodiles-Hernández, R., E. Díaz-Pardo and J. Lyons. 1999. Patterns in the species diversity and composition of the fish community of Lacanja River, Chiapas, México. *Journal of Freshwater Ecology* 14(4): 455-468.
- Rodiles-Hernández, R., S. Domínguez-Cisneros and E. Velásquez-Velásquez. 1996. Diversidad íctica del Río Lacanjá, Selva Lacandona, Chiapas, México. *Zoología informa* 34: 3-18.
- Rosen, D.E. 1979. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History* 162(5): 268-375.
- Rosen, D.E. and R.M. Bailey. 1963. The Poeciliid fishes (Cyprinodontiformes), their structure, zoogeography, and systematics. *Bulletin of the American Museum of Natural History*, 126(1):1-176.
- Schmitter-Soto, J.J. 1998. *Catálogo de los peces continentales de Quintana Roo*. Quintana Roo: Guías científicas de ECOSUR. 283 p.
- Schmitter-Soto, J.J. and H.C. Gamboa-Pérez. 1996. Composición y distribución de peces continentales en el sur de Quintana Roo, Península de Yucatán, México. *Revista de Biología Tropical* 44(1):199-212.
- Valdez-Moreno, M., N.V. Ivanova, M. Elías-Gutiérrez, S. Contreras-Balderas, and P.D.N. Hebert. 2009. Probing diversity in freshwater fishes from Mexico and Guatemala with DNA barcodes. *Journal of Fish Biology* 74(2):377-402.
- Valdez-Moreno, M.E., J. Pool-Canul and S. Contreras-Balderas. 2005. A checklist of the freshwater ichthyofauna from El Petén and Alta Verapaz, Guatemala, with notes for its conservation and management. *Zootaxa* 1072: 43-60.
- Willink, P.W., C. Barrientos, H.A. Kihn and B. Chernoff. 2000. Un estudio ictiológico del Parque Nacional Laguna del Tigre, Petén, Guatemala; p. 134-142 In B. Bestelmeyer and L.E. Alonso (ed.). *Evaluación biológica de los sistemas acuáticos del Parque Nacional Laguna del Tigre, Petén, Guatemala*. Washington D.C.: Conservation International, Boletín RAP de Evaluación Biológica 16.
- Winemiller, K.O., D.J. Hoeninghaus, A.A. Pease, P.C. Esselman, R.L. Honeycutt, D. Gbanaador, E. Carrera and J. Payne. 2011. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. *River Research and Applications*, 791-803.

RECEIVED: October 2011

ACCEPTED: February 2012

PUBLISHED ONLINE: February 2012

EDITORIAL RESPONSIBILITY: Javier Maldonado