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Habitat characteristics and environmental parameters influencing fish assemblages of karstic pools in southern Mexico

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Fish assemblage structure was evaluated and compared among 36 karstic pools located within protected areas of the Calakmul Biosphere Reserve (southern Mexico) and unprotected adjacent areas beyond the Reserve. Nonmetric multidimensional scaling (MDS), indicator species analysis (ISA), and canonical correspondence analysis (CCA) were used to identify which environmental factors reflected local influences and to evaluate the correlation of these variables with fish assemblages structure. Thirty-one species were encountered in these karstic pools, some for the first time within the Reserve. These aquatic environments were separated into three groups based on physico-chemical characteristics. Although CCA identified significant associations between several fish species (based on their relative abundance) and environmental variables (K, NH4, NO3, and conductivity), the most abundant species (*Astyanax aeneus*, *Poecilia mexicana*, and *Gambusia sexradiata*) occur in most pools and under several environmental conditions. Baseline data on fish diversity along with a continued monitoring program are essential in order to evaluate the conservation status of fish assemblages and their habitats, as well as to measure the influence of anthropogenic impacts on pristine habitats such as the karstic pools of the Calakmul Biosphere Reserve.

A estrutura da assembleia de peixes foi avaliada e comparada entre 36 poços cársticos localizados dentro de áreas protegidas da Reserva da Biosfera Calakmul (sul do México) e nas áreas desprotegidas adjacentes à Reserva. A análise multidimensional não-métrica (MDS), a análise da espécies indicadora (ISA) e a análise de correspondência canônica (CCA) foram utilizadas para identificar as variáveis ambientais localmente mais importantes e para avaliar a correlação destas com a estrutura das assembleias de peixes. Trinta e uma espécies foram amostradas nos poços cársticos, algumas das quais representam o primeiro registro para a Reserva. Os poços foram separados em três grupos de acordo com as suas características físico-químicas. Embora a CCA tenha possibilitado a identificação de associações significativas entre várias espécies (baseado na abundância relativa das espécies) e as variáveis ambientais (K, NH4, NO3 e condutividade), as espécies mais abundantes (*Astyanax aeneus*, *Poecilia mexicana* e *Gambusia sexradiata*) ocorreram na maioria dos poços em diferentes condições ambientais. A obtenção de dados de base sobre padrões de diversidade, associado a implantação de programas de monitoramento, são essenciais para a avaliação do estado de conservação das assembleias de peixes e seus habitats, assim como para proporcionar informações sobre a influência de impactos antropogênicos sobre habitats prístinos, tais como os poços cársticos da Reserva da Biosfera Calakmul.

Key words: Biosphere Reserve, Exotic species, Freshwater fish, Habitat use, Hydrological conditions.

Introduction

An understanding of how bodies of water, stream habitats, and their surrounding environment shape the structure of fish assemblages is valuable in habitat assessment, stream restoration, and management and conservation of fish populations (Pease *et al*., 2011). Physico-chemical (*e.g.*, temperature, dissolved oxygen, conductivity, and pH) (Araújo *et al*., 2009), and other environmental variables such as landscape features (Angermeier & Winston, 1999), pool/riffle distribution and dimensions, and the amount of available cover can correlate strongly with fish assemblages (Schlosser, 1982; Brown, 2000; Fischer & Paukert, 2008; Rowe *et al*., 2009a). The concentration of dissolved oxygen, temperature, water velocity, and substrate composition have also been shown to deterministically affect fish assemblage structure in tropical floodplain systems (Daga *et al*., 2012). Karstic aquatic ecosystems resemble tropical floodplain lakes during dry conditions in that both show elevated temperatures and high fish densities during drought. These anoxic conditions and thermal stratification also strongly affect the survival of fishes (Anjos *et al*., 2008).

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Karst areas are shaped by the dissolution of layer(s) of limestone bedrock where cracks, fractures, and other solution channel irregularities are present. In Mexico karst topography prevails in the Yucatan Peninsula. These landscapes are similar to Florida in having thick sequences of relatively flat-lying Tertiary limestone; however, in Yucatan the lack of upper Tertiary clays and marls overlying the limestone, results in rapid infiltration of rainfall with no surface drainage (Back & Hanshaw, 1970; Southworth, 1984). The karstification of a landscape is the result of a complex interplay between geology, climate, topography, hydrology, and biological factors over long time scales which results in a variety of features consisting of cenotes (steep-walled sinks that usually penetrate the water table), bare limestone platforms, 'aguadas' (broad shallow solution basins), and 'resumideros' (funnelshaped conical depressions) (Liszkowski, 1975). The cenotes and aguadas are the two most important sources of water in the Yucatan Peninsula, and as a consequence, most of the Mayan cultural development and population centers are found to be closely associated with these karst features (Blair, 1986).

Although karstic environments have special hydrological properties and a characteristic native fauna, ichthyologic research is limited, fish databases are lacking, and little is known about spatial turnover in fish assemblages in these tropical ecosystems. Some of these environments are located within the protected forested areas making them inaccessible to humans. It has been observed that intact forest cover and undisturbed areas in the landscape surrounding streams are correlated with higher fish diversity (Rowe *et al*., 2009b); however, this generalization remains to be evaluated in karst environments.

Investigation of fish assemblages have the potential to increase the understanding of biological diversity, both through insights on how communities are structured, and by providing data that will help tease apart the different explanations for patterns of commonness and rarity (Magurran *et al*., 2011). In Mexico, aquatic ecosystems have been severely degraded since the beginning of the 20th century. Over-exploitation, habitat loss, pollution, and the introduction of exotic species are the main reasons for reductions in fish community richness and diversity (Contreras-Balderas & Escalante-Cavazos, 1984; Mercado-Silva *et al*., 2002). Out of 506 native freshwater fishes reported in Mexico, at least three have become extinct, 45 are endangered, and 50 are threatened (Espinosa *et al*., 1993). Moreover, basic ecological information such as geographic distribution, environmental requirements and population size is lacking for many of these species, thus preventing any kind of assessment of species conservation status (Miller *et al*., 2005). Limited understanding of very basic issues such as faunal diversity or distribution patterns makes it difficult to design and implement meaningful conservation and recovery plans, even when a decline is apparent (Norris *et al*., 2003). Moreover, habitats are being lost before their fish faunas have been thoroughly documented. This situation is certainly not unique to Mexican freshwater (Greenwood, 1991; Stiassny, 1996), and research efforts are necessary in order to understand these ecological systems and design effective conservation or restoration practices. By linking patterns at the local community level with the processes shaping those patterns, conservation biologists will be able to develop management strategies that contribute to the effective long-term conservation of biological diversity (Magurran *et al*., 2011).

The aim of the present study is to understand how environmental variables may shape fish assemblages in karstic environments, and to evaluate the local attributes that influence fish species diversity. We hypothesize that pools located in areas with different levels of protection and with distinct habitat quality and physic-chemical conditions will present dissimilar fish assemblages. This research also contributes to a better understanding of the habitat attributes associated to species with restricted distributions and dominant species tolerant of a wide range of variation in environmental parameters.

Material and Methods

Study Area

Data were collected from 36 pools located in Calakmul Biosphere Reserve (CBR), located in the southeast of the Yucatan Peninsula, approximately > 300 km from the Gulf of Mexico (Fig. 1). This Reserve is the largest tropical protected area in Mexico and the largest forested area in the Americas (723,184 ha), second only the Amazon (Martínez, 2010). Climate is warm, and sub-humid with a marked precipitation gradient increasing from north to south (616-1194 mm) (García, 1981). In 1989, CBR was declared a protected area, and in 1993 it was included in the International UNESCO Man and the Biosphere Program (MAB). The Reserve is divided into two core areas, one where biological communities and ecosystems are protected (34.3% of its total surface), and a buffer zone (65.7% of the CBR's area) where human activities are allowed but monitored in order to detect impacts on biodiversity (Ek-Alcocer, 1997). Within the CBR, two biotic subprovinces are recognized: Yucateca, which includes the Reserve's northern portion, and Peten located to the south. Both areas are linked spatially by a biological corridor (Plan de Manejo, 2000), where a high level of endemism has been observed (Goldman & Moore, 1946; Barrera, 1962; Stuart, 1964).

A peculiarity of this region is the lack of surface water bodies and surface water flows. Most of the freshwater found in the CBR is confined to lowlands and natural pools (1354 freshwater bodies) surrounded by several types of tropical forest (defined by height and deciduousness), where the hydrology is influenced by precipitation and plant transpiration (García-Gil, 1991). These environments include 'aguadas' (ponds), creeks and seeps. 'Aguadas' are continental depressions which are either seasonally

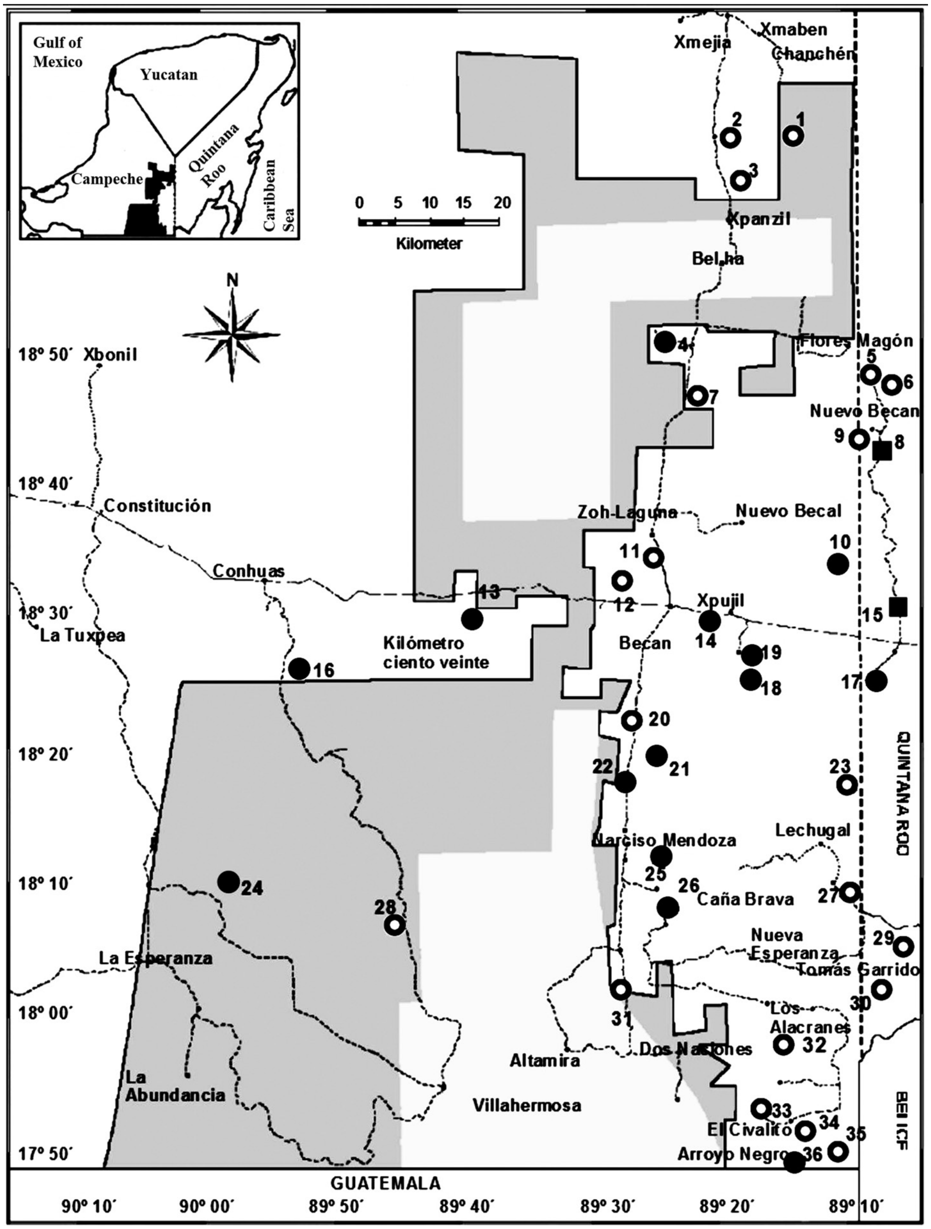

Fig. 1. Calakmul Biosphere Reserve in southern Mexico, showing the borderline of the core area, and buffer zone indicated by shaded polygons. The white circles denoted pools located in habitat A, black circles are pools in habitat B, and black squares in habitat C. Pool identification numbers are specified in Table 3.

or permanently flooded. These pools are swampy, with high levels of turbidity, variable in size and depth (1 to 10 m) and with wide variations in the abundance of aquatic vegetation (Duch, 1991).

Environmental parameters

Karstic pools located inside as well as outside (adjacent) of CBR were sampled over two years (February, 2000-March, 2001; May 2003-May 2004) (Fig. 1). It was not possible to sample all pools in both years owing to the perennial nature (lack of water) of some of them (33%). Each pool was selected in-situ based on accessibility and the location was recorded with a GPS Unit (Garming 12XL). The area of each pool was calculated using Google Earth Pro on digital photographic maps of the study area, enlarged over different scales according to the calibration limited by the geographic information system (up to 1:1600). The following habitat quality variables were estimated visually at five sites for each pool: percentage of grass, aquatic vegetation, and arboreal cover. Additional information on the use of pools for tilapia farming, and human use for water extraction and washing were obtained by field observations and interviews with local persons. Each pool was also categorized as located in the protected area of the Reserve (Protected) or in the zone that is not subject to any kind of protection (Unprotected). All these indicators were included as categorical variables.

At each sampling pool, and prior to fish collections, water temperature, specific conductivity and dissolved oxygen were measured during the daytime (07h00 to 18h00) with three replicates, at 50 cm sub-surface and between 2-3 m from the margins, using a multiparametric probe (Yellow Springs Instrument, model 85). Furthermore, pH, nitrate, ammonium, and potassium were measured using a multi-parameter water quality monitoring system (U-23 meter).

Ichhyofauna

Fishes were captured in each pool using two methods: a) a seine net (3.5 × 1.0 m, with 2 mm mesh) operated three times in non-overlapping areas, along 50 m reach which was extended from shore at *ca.* 1 m depth, and hauled directly toward the pond edge during a period of two hours, on average; b) a total of 10 cast net throws (1.5 m radius, 15 mm mesh) using a small boat (1.5 m long) at 15 minute intervals. Due to the harsh working conditions deep in the forest, with high temperatures (usually >35ºC) and long distances to sampling sites, fish were euthanized in ice slurry, and when the sampling was finished at the end of the day, the specimens were preserved in 15% formalin solution and subsequently transferred to 70% ethanol. Sampled fishes were identified, counted, measured (standard length to the nearest 0.01 cm), and weighed (to the nearest 0.1 g). Numerical abundance of each fish species was recorded for each pool (ind m^{-2}) for analysis of fish assemblage structure. Species identification was based on several taxonomic guides (Greenfield & Thomerson, 1997; Reis *et al*., 2003; Miller *et al*., 2005; Nelson, 2006; Schmitter-Soto, 2007). Voucher specimens of all species were deposited in the fish collection of Centro de Investigacion y de Estudios Avanzados del IPN, Merida (YUC.PEC 084-0999).

Data Analysis

A similarity matrix using Euclidean distance between pools, was computed using environmental parameters (temperature, dissolved oxygen, pH, conductivity, NO_3, NH_3, and K) as attributes (Clarke & Warwick, 2001), which were transformed (fourth root) to standardize data. Canonical variate analysis (CVA), also called Fisher's linear discriminant analysis, using Hill's scaling option with a focus on the pools distances, was conducted to evaluate which linear combination of environmental variable yields the highest F-ratio in a one-way analysis of variance and discriminate best between clusters of samples (selection 999 Monte Carlo permutations, $\alpha = 0.5$) (ter Braak & Smilauer, 2002).

Species composition and abundance were estimated by pooling specimens collected with both fishing methods per pool. We used a combination of multivariate analysis to compare fish assemblage composition and species distribution across the Reserve and in relation to environmental parameters. Separate ordinations were conducted with species presence/absence and abundance data. Presence/absence data give a greater weight to uncommon species, while abundance data reveal species assemblages patterns based on the most common species. The effect of extreme values was minimized by transforming the species abundance data by its fourth root. The resulting matrix of 30 species was used in the MDS ordination analyses. The Bray-Curtis and Sorensen similarity index were used as the distance measure for abundance and occurrence data, respectively. Non-metric multidimensional scaling is a distance based procedure that ordinates study units based on rank dissimilarities (Clarke & Warwick, 2001). Because it avoids assumptions of linearity and accurately maps sample units in ordination space in proportion to ecological distance, MDS is considered well suited for analysing patterns in assemblage structure. Stress values indicate how well the two-dimensional plot represent relationships among samples in the multidimensional space. Values < 0.15 indicate a good fit (Clarke & Warwick, 2001).

Analysis of variance (ANOVA) and t test were used to evaluate differences in species richness and diversity among the groups of karstic pools (obtained by CVA analysis) and between protected and unprotected pools, respectively. Differences in fish assemblage structure among the groups of karstic pools (obtained by CVA analysis), and among protected and unprotected pools, were tested with permutational multivariate ANOVA (PERMANOVA) using approaches described in Anderson (2001). This is a technique that uses label permutation to estimate the distribution of the test statistics under the hypothesis that within-group distances are not significantly different from between group distances.

Indicator species analysis (ISA) was used to identify the species associated with groups of pools. Indicator species analysis assigns an indicator value (IV) to each taxon by calculating the product of the relative frequency (percent occurrence of a taxon among sample units in each group), and relative average abundance (percent of the total abundance of a taxon in each group) of each species in a group. The probability (p) of achieving an equal or larger IV value among groups (p) was estimated by using 999 random permutations of the original data (Dufrêne & Legendre, 1997). Species with significantly ($p \leq 0.10$) high IVs for a given group should be found mostly in a single group of a typology, and be present at most of the sites belonging to that type of habitat (Legendre & Legendre, 1998). The $p \leq = 0.10$ was selected because of the small sample size in pools from habitat C when comparing with the other types of habitat.

A canonical correspondence analysis (CCA) was used to evaluate the relationship of the fish species assemblages with environmental parameters, and habitat quality variables. This multivariate method is a direct gradient analysis that provides: (1) simultaneous representation of sampling sites, environmental variables and species centroids in a reduced ordination space of orthogonal axes, and (2) an integrated description of species-environment relationships by assuming a common response (as a unimodal distribution) of all species to a set of underlying environmental gradients (ter Braak, 1986). The significance of each environmental variable was tested by manual selection using 1000 Monte Carlo permutations ($\alpha = 0.05$). Species with abundances < 0.2% were removed from the analysis. In addition, environmental variables that exhibited collinearity, and variance inflation factors (VIF) > 20 were removed because such variables are strongly correlated with other variables and therefore do not make a unique contribution to the regression equation (ter Braak & Smilauer, 2002). PERMANOVA and PERMDISP multivariate analysis were performed using PRIMER statistical package (version 6; Clarke & Gorley, 2006) with the PERMANOVA add-on (Anderson *et al*., 2008), while CVA and CCA were run in the CANOCO v4.0 (ter Braak & Smilauer, 2002). Finally ISA was performed with the LABDSV package in R version 2.10.1 (R Development Core Team, 2008).

Results

Environmental parameters. Temperature records showed a range of values typical for the tropical water bodies studied (22.0 - 32.0 ºC), while conductivity, nitrate, ammonium, and potassium varied strongly across localities. The CVA identified three groups of pools based on environmental variables (Table 1). Among the environmental variables considered, potassium, nitrate, ammonium, and conductivity had the greatest influence defining such groups (Fig. 2). The habitat type A ($F = 5.39$; $p = 0.006$) was represented by 21 pools of which 13.5% were used by human populations for water extraction and 9.5% for tilapia farming. This habitat presented low aquatic vegetation, low potassium, and high ammonium concentrations. The habitat B ($F = 2.17$; $p = 0.008$) represented by 13 pools, showed moderate and sparse submersed vegetation and was characterized by high electrical conductivity (>1000.0 µS cm^{-1}). In habitat C, two sites with 100% of arboreal and aquatic vegetation were characterized by the highest potassium concentration, and lowest conductivity and ammonium levels ($F = 7.32$; $p = 0.008$) (Table 1).

Fish assemblage structure and composition. A total of 31 fish species distributed across six families were sampled during the study (Table 2). Of these species, three were identified at the genus level (*Astyanax* sp., *Poecilia* cf. *teresae* and *Atherinella* sp.), and are currently under taxonomic evaluation. The shortfin molly *Poecilia mexicana* Steindachner, 1863, exhibited high abundance (> 10%) and occurrence (> 70%) through the study region, with IVs (indicator species values) higher than 30% in habitats A and B. The teardrop mosquito *Gambusia sexradiata* Hubbs, 1936, showed high abundances in pools from habitat B (IVs > 50%), while the banded tetra *Astyanax aeneus* (Günther, 1860) and the bay snook *Petenia splendida* Günther, 1862 occurred in habitats A and B, but with significant importance in habitat A (IV > 30%). By contrast, some species occur preferentially in specific habitat types. Within these, mountain molly *Poecilia* cf. *teresae* Greenfield, 1990, and champoton gambusia *Carlhubbsia kidderi* (Hubbs, 1936) were collected at low abundances in pools located exclusively in habitat B, while yucatan gambusia *Gambusia yucatana* Regan, 1914 was restricted with high abundances to

Table 1. Mean environmental parameters (T: temperature, DO: dissolved oxygen, Cond.: conductivity, pH, NO$_3$: nitrates, NH$_4$: ammonium, K: potassium), habitat quality variables and descriptors of fish diversity for the groups of pools obtained by CVA analysis. Standard deviation is provided in parenthesis. Exclusive species and significant indicator value (IVs, p<0.10) from indicator species analysis are specified for each type of habitat (group).

Parameter	A	B	C
Number of pools	21	13	2
T (°C)	27.6 (2.3)	26.1 (1.6)	27.9 (0.8)
DO (mg.L^{-1})	6.7 (2.0)	5.9 (1.9)	6.8 (1.5)
Cond. (µS cm^{-1})	311.1 (81.2)	1970.3 (928.7)	237.6 (6.1)
pH	8.1 (0.5)	7.9 (0.4)	8.4 (0.6)
NO3 (mg L^{-1})	34.4 (22.0)	38.6 (21.5)	52.7 (22.4)
NH4 (mg L^{-1})	17.5 (26.3)	15.7 (19.6)	0.2 (0.1)
K (mg L^{-1})	0.6 (0.8)	11.0 (19.9)	65.8 (41.9)
Aquatic vegetation (%)	14.3	23.1	100
Arboreal cover (%)	85.7	92.3	100
Human use (%)	23.8	7.7	-
Tilapia farming (%)	9.5	-	-
Fish density (No. individuals m^{-2})	0.6 (1.6)	0.4 (1.0)	1.4 (4.9)
Species richness	8.8 (5.2)	11.0 (5.3)	8.0 (1.4)
Total species richness	26	28	14
Diversity	1.8	2.1	0.6
Indicator Species Analysis (p < 0.10)	*A. aeneus* 32.2 *P. mexicana* 37.6 *P. splendida* 47.7	*P. mexicana* 30.0 *G. sexradiata* 55.0	*G. yucatana* 23.5 *H. compressus* 23.3
Exclusive species	*O. mossambicus* *O. niloticus*	*P.cf. teresae* *C. kidderi*	*G. yucatana*

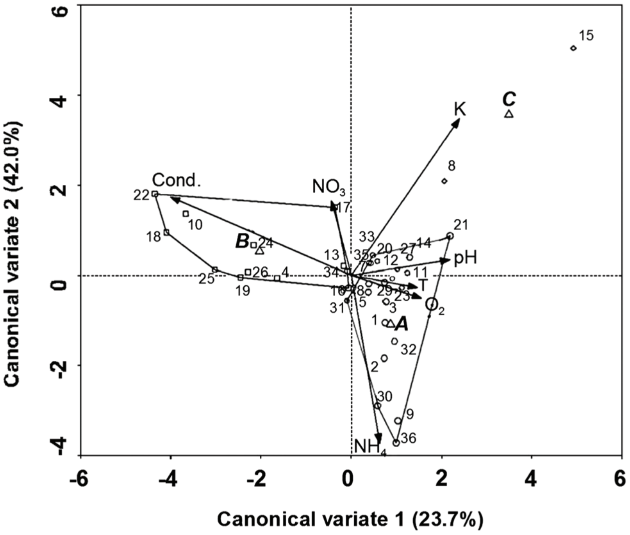

Fig. 2. Biplot of the scores for the environmental variables (36 pools) using canonical variate analysis (CVA) based by Euclidean distance (Hill's scaling option). Environmental vector showed the direction along which each variable changes most: temperature (T), dissolved oxygen (DO), conductivity (Cond), pH, nitrates (NO_3), ammonium (NH_4), and potassium (K). Polygons: group locations (pools) with similar hydrological characteristics (Table 1). Group A: pools characterized by high ammonium concentration, B: pools with high electrical conductivity, and C: pools with high phosphorous concentrations.

habitat C, and together with the mayan tetra *Hyphessobrycon compressus* (Meek, 1904), showed significant IV for habitat C (Table 1). Nonnative fish species sampled in our study included Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852) and Nile tilapia *O. niloticus* (Linnaeus, 1758), which were brought to the Reserve for cultivation by local people, and registered only in habitat A (Fig. 3).

Richness per site varied from one to 23 species, with some pools exhibiting low evenness (Table 3). When comparing habitats, species richness didn't showed significant differences (ANOVA: $p = 0.51$), while diversity differed among the habitats B and C (ANOVA: $p = 0.02$ Tukey's post-hoc test: $p = 0.02$), being similar among the other combination of habitats (Tukey's post-hoc test: $p>0.09$). The highest diversity values were recorded at habitat B and the lowest in habitat C. Fish assemblage structure showed significant differences among habitat types (PERMANOVA: $F = 2.70, p = 0.020$). Differences were between habitats A and B with habitat type C (PERMANOVA A-C: $p = 0.04$; B-C: $p = 0.009$). By contrast, patterns of species composition based on presence/absence of species did not differ among habitats (PERMANOVA: $F = 1.21$, $p = 0.29$). Considering the level of protection, there were significant differences in the fish assemblages between protected and unprotected pools, when considering abundance data (PERMANOVA, $F = 1.832, p = 0.05$). Species richness and diversity were similar between both categories (t test: $p>0.92$; Protected: 35 species, 2.9 bits; Unprotected: 36 species, 3.0 bits, respectively) (Table 3). However, rare species (*Poecilia* cf. *teresae* and *Carlhubsia kidderi*), were registered exclusively and with moderate abundances in protected pools.

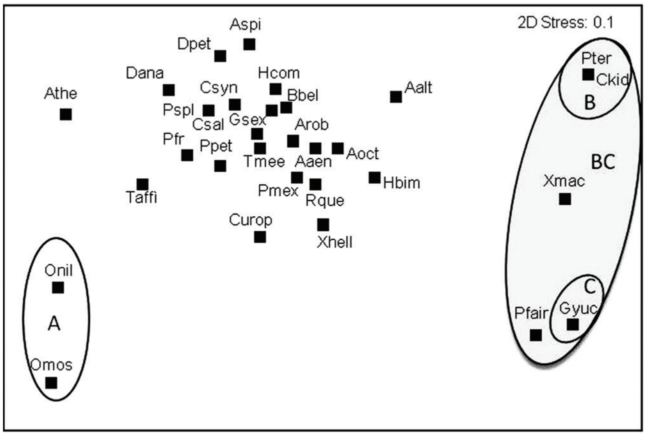

Fig. 3. Non-metric multi-dimensional scaling ordination of fish assemblage structure in karstic pools from Calakmul Biosphere Reserve. Habitat type obtained by CVA analysis s specified for the exclusive species.

Associations between environmental parameters and species abundance are displayed in the CCA biplot (Fig. 4). The variables were statistically significant ($F = 6.09$, $p = 0.026$), and the first two axes explained 57.5% of the variation of data. Potassium and dissolved oxygen were the most important variables which were significantly related to the ichthyofaunal composition. Most of the species located at the center of the CCA diagram were eurytopic, extremely tolerant to a wide range of hydrological conditions (dissolved oxygen: 1.5-11.4 mg l^{-1}, electrical conductivity: 110-2800 µ S cm^{-1}) and widely spread across the study area (>30% of the samples) from the total of pools (Fig. 4). Another group of species were found with moderate abundances in habitats where arboreal cover and stagnant water co-occurred. Within this assemblage, *Atherinella* sp. and yellow meeki *Thorichthys affinis* (Günther, 1862) showed lower abundances (density < 1.0%) and a limited distribution. *Gambusia yucatana* was recorded at only one locality and *Phallichthys fairweatheri* was restricted to two pools, which showed a strong relationship with potassium concentration and pH values, respectively. Most of the poeciliids (swordtail *Xiphophorus hellerii* and spottail killifish *Heterandria bimaculata*), pale catfish *Rhamdia quelen*, and *Astyanax* species were associated with aquatic grass and greater conductivity values, while cichlids and clupeids were more related to urban activities, high ammonium concentrations, and a lack of aquatic vegetation. The threadfin shad *Dorosoma petenense* (Günther, 1867), showed a higher abundance compared to the mexican river gizzard shad *Dorosoma anale* Meek, 1904, although both species co-occurred in 50% of the localities where they were recorded.

Table 2. Families, species, relative density and (occurrence frequency) at each type of habitat in karstic pools of the Calakmul Biosphere Reserve, southern Mexico.

Family	Species	Code	Relative density (Frequency)		
			A	B	C
Clupeidae	*Dorosoma anale*	Dana	0.14(14.3)	0.5(23.1)	-
	Dorosoma petenense	Dpet	1.2(33.3)	1.6(30.8)	-
Characidae	*Astyanax aeneus*	Aaen	15.1(90.5)	39.5(100)	-
	Astyanax altior	Aalt	0.01(4.8)	0.9(53.8)	-
	Astyanax sp.	Ast	0.1(19.0)	4.4(15.4)	-
	Hyphessobrycon compressus	Hcom	2.5(38.1)	1.5(30.8)	8.9 (50.0)
Atherinopsidae	*Atherinella* sp.	Athe	0.4(4.8)	0.8(7.7)	-
Poeciliidae	*Belonesox belizanus*	Bbel	0.6(33.3)	2.0(69.2)	-
	Poecilia mexicana	Pmex	12.2(76.2)	16.0(100)	1.4(100)
	Poecilia petenensis	Ppet	2.1(33.3)	1.6(30.8)	-
	Poecilia cf. teresae	Pter	-	1.9(7.7)	-
	Gambusia sexradiata	Gsex	47.5(66.7)	17.6(53.8)	1.0(100)
	Gambusia yucatana	Gyuc	-	-	86.0(50.0)
	Heterandria bimaculata	Hbim	8.1(23.8)	2.3(46.2)	0.1(50.0)
	Xiphophorus maculatus	Xmac	-	0.4(7.7)	0.2(50.0)
	Xiphophorus hellerii	Xhell	2.6(38.1)	1.3(61.5)	0.2(50.0)
	Carlhubbsia kidderi	Ckid	-	0.4(7.7)	-
	Phallichthys fairweatheri	Pfair	-	0.02(7.7)	0.1(50.0)
Heptapteridae	*Rhamdia quelen*	Rque	0.6(47.6)	9.5(61.5)	-
Cichlidae	*Thorichthys affinis*	Taff	0.3(23.8)	0.4(15.4)	-
	Thorichthys meeki	Tmee	2.3(57.1)	3.8(69.2)	0.1(50.0)
	Cichlasoma salvini	Csal	0.4(38.1)	1.0(38.5)	0.1(50.0)
	Cichlasoma urophthalmus	Curo	0.2(23.8)	0.1(23.1)	0.3(50.0)
	Paraneetroplus synspilus	Psyn	0.3(33.3)	0.4(38.5)	-
	Amphilophus robertsoni	Arob	0.3(38.1)	0.5(53.8)	0.1(50.0)
	Cryptoheros spilurus	Cspi	0.2(28.5)	0.3(30.8)	-
	Rocio octofasciata	Roct	1.9(42.9)	1.3(69.2)	1.6(50.0)
	Parachromis friedrichsthalii	Pfri	0.1(23.8)	0.1(15.4)	-
	Petenia splendida	Pspl	0.3(28.6)	0.4(23.1)	0.1(50.0)
	Oreochromis niloticus	Onil	0.3(14.3)	-	-
	Oreochromis mossambicus	Omos	0.1(4.8)	-	-

Discussion

Fish assemblages and linkages to environmental variables

Physico-chemical conditions (electrical conductivity, dissolved oxygen, nutrient concentration), and habitat quality factors (aquatic vegetation, surrounding grass), had a significant effect on fish species composition and abundance in the karstic environments studied. Conductivity values and nutrient concentrations (NO_3, K) displayed great variations from one pool to another. High conductivity values were related to decomposed organic matter (and low DO), suggesting the presence of large amounts of total dissolved salts (TDS) (Moore *et al*., 2008). We observed high conductivity values in some of the pools, which showed greater species richness compared to those with low values. Similar results were found in Amazonian forest streams (Bührnheim & Fernandes, 2001), and floodplain lakes (Petry *et al*., 2003).

The study of the ecology of fishes in these karstic environments and little explored areas has been a difficult task that was complicated by the presence of little morphological differentiation among the fishes, thus making accurate identification difficult. Given the limited knowledge of fish diversity in freshwater systems of south-east Mexico, this study represents a relevant contribution to the field. A previous study in the Grijalva Usumacinta province revealed 27 freshwater species, with some of these also reported in this

Table 3. Average fish density (individuals per m^{-2}) and biomass (g per m^{-2}), total species richness (S), diversity (H') and watershed area (km^2) obtained at each pool in the Calakmul Biosphere Reserve, southern Mexico. Categorization (Cat) of protected (Pr) and not protected (NP) is specified for each pool. Pool identification numbers (ID) follow those in Fig. 1. Group (habitat) designation corresponds to CVA analysis.

Locality	ID	No. m^{-2}	g. m^{-2}	S	H'	km^2	Cat	Group
Xcan-Ha1	1	0.13	0.57	6	0.93	192.76	Pr	A
Xcan-Ha	2	1.14	1.46	11	0.50	1.934	NP	A
Xcan-Ha2	3	0.20	1.10	13	1.80	2.67	NP	A
San Roman	4	0.85	2.12	14	1.48	5.87	Pr	B
Flores Magon	5	0.19	1.22	19	2.12	39.67	NP	A
Flores Magon 2	6	0.39	2.04	7	0.62	4.62	NP	A
El Refugio	7	3.04	0.77	10	0.75	11.57	Pr	A
Dos Banderas	8	0.32	0.30	7	0.34	71.21	NP	C
Chuma-hil	9	0.33	1.29	4	0.12	93.07	NP	A
El Chorro	10	0.16	0.68	16	1.87	812.36	NP	B
Zoh-Laguna	11	0.30	0.68	13	1.47	40.47	NP	A
El Porvenir	12	0.63	1.66	7	1.05	81.05	NP	A
P. Tanyucan	13	0.14	1.13	7	1.03	8.23	Pr	B
Gravera	14	0.07	0.59	9	1.72	2.18	NP	B
Gasolinera Xpujil	15	2.31	0.80	9	0.29	10.0	NP	C
Regueña	16	0.40	1.85	23	2.19	2.33	Pr	B
S. Antonio S. 2	17	0.89	0.37	7	0.63	47.42	NP	B
El Chorro Sur	18	0.07	0.44	7	1.30	25.83	NP	B
20 noviembre	19	0.05	0.20	10	1.39	7.52	NP	B
La Lucha	20	1.70	1.20	5	1.10	9.78	Pr	A
Manuel Castilla	21	0.23	0.96	10	1.79	16.87	NP	B
La Guadalupe	22	0.13	0.39	4	0.95	5.31	Pr	B
San. Francisco	23	2.24	2.57	8	1.25	2.73	NP	A
Manantial	24	0.16	0.32	7	1.44	10.31	Pr	B
Crist. Colon	25	0.47	0.81	17	1.48	40.90	NP	B
Carmelitas	26	0.45	2.14	11	1.09	55.35	NP	B
Tesoro 2	27	0.29	0.41	8	1.18	22.56	NP	A
Lag. Calakmul	28	0.21	0.71	14	1.09	28.99	Pr	A
P. dos aguas	29	0.64	0.11	4	0.92	4.47	NP	A
Nuevo San Jose	30	0.92	1.60	1	0.00	2.80	NP	A
3 Km 11 de mayo	31	0.15	0.60	6	0.66	5.10	Pr	A
Alvarado	32	1.31	0.72	6	1.20	318.14	NP	A
Cam. A. Negro	33	0.45	1.86	7	1.27	5.63	NP	A
Justo Sierra	34	0.21	0.62	11	1.68	103.18	NP	A
Arroyo Negro	35	0.32	1.31	21	1.85	63.77	NP	A
Río Negro	36	0.08	0.57	10	1.78	469.44	NP	A

research (López-López *et al*., 2009). However for some of these species, it is the first time that they have been recorded for the region (*Atherinella* sp., *Poecilia* cf. *teresae*, *X. helleri*, and *Phallichthys fairweatheri*).

Species diversity of fish assemblages in isolated karstic pools is positively influenced by aquatic vegetation, roots and arboreal cover. Higher and significant values of this ecological parameter were recorded at habitat B, where 23% and 92%

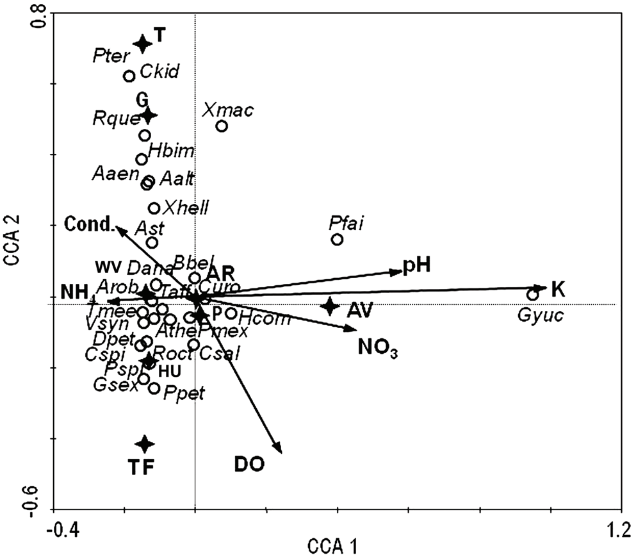

Fig. 4. CCA ordination diagram based on species abundances (closed circles), with habitat quality variables designed by a star: G = grass, T= ephemeral, P = perennial, WV = without vegetation, AR = arboreal cover, AV = aquatic vegetation, HU = human use, TF = tilapia farming. Environmental parameters represented by vectors: O_2 = dissolved oxygen, Cond. = conductivity, pH, NO_3 = nitrates, NH_4 = ammonium, and K = potassium. See Table 2 for species abbreviations. The first canonical axes: (F = 6.09, P = 0.026) and for all canonical axes (F = 1.879, P = 0.040).

of the total pools presented aquatic vegetation and arboreal cover. Similar results were found by Montaña *et al.* (2008) and Silva *et al.* (2010) in lowlands streams from Venezuela and the Amazonas, respectively. A high degree of structural complexity in the karstic pools increased the number of ecological niches, supporting rare and endemic species. A similar relationship was observed by Engman & Ramírez (2012) in watersheds of Puerto Rico, where more heterogeneous habitats were numerical dominated by native species.

Human activity may have influenced the ecological structure of the pools in the habitat type A through an increase in ammonium concentration, and a decrease in aquatic vegetation (lower habitat heterogeneity). Tilapia farming, water extraction, and other uses by local people, may have also contributed to the deterioration of water conditions, which can have a relevant effect on the biological patterns and ecosystem-level process (Snyder *et al.*, 2003; Rodríguez-Olarte *et al.*, 2006). Furthermore, the fragmentation of adjacent forests may have an impact on the adjacent fish community. For example, Bührnheim & Fernandes (2001) reported that cutting and burning riparian vegetation in Amazonia can indirectly influence fish community structure. Although most of the pools in the CBR are well preserved, previous studies have reported that sites which are disturbed by human activities, including the introduction of exotic species, have fish assemblage structures characterized by a few dominant species and low species richness (López-López *et al.*, 2009).

This pattern of lower specific richness associated with human activity was not observed in unprotected karstic pools, which suggests the pristine nature of these environments. The same has been reported by Alexandre *et al.* (2010), where fish communities in stream within cane fields supported a diverse fish assemblage with relatively little disturbance because of the presence of riparian forest. The occurrence of rare (*P. teresae*) species in protected areas demonstrated how these pools act as buffer regions that permit the persistence of diverse communities.

The processes that regulate fish assemblage structure vary across spatial and temporal scales, and range from local biotic interactions to large-scale biogeographic history (Poff, 1997). Several studies have suggested that tropical fish assemblages that do not exhibit a clear organizational pattern are being stochastically assembled (Goulding *et al.*, 1988; Saint-Paul *et al.*, 2000). However, this study does not support the concept of unpredictability in the organization of fish assemblages in pools of CBR. Canonical correlation analysis revealed that environmental parameters (electrical conductivity and nutrients), and habitat quality variables (grass and human use), deterministically affect fish assemblage structure. We found three habitat-specialist species which were restricted to only one or a few localities in environments with abundant aquatic vegetation and high potassium concentration (*Gambusia yucatana* and *Phallichthys fairweatheri*), and strongly dependent on grass presence and high conductivity values (*P.* cf. *teresae*). Of the 31 species recorded in the CBR, only five are primary freshwater species, *i.e.*, those which have evolved in freshwater and cannot cross saltwater boundaries (Lowe-McConnell, 1987), such as the characins (*Hyphessobrycon compressus*, *Astianax altior*, *Astyanax aeneus*, and *Astyanax* sp.), and the catfish family Heptapteridae (*Rhamdia quelen*). The remaining 26 are secondary freshwater species (those that have evolved in freshwater but originated from marine groups and are able to cross at least short saltwater regions). Previous studies conducted on other major land masses (except Australia) have reported that primary freshwater fishes are more numerous, both in terms of species number and abundance. For instance, Garcia *et al.* (2003) found that characids and siluriforms were the most abundant freshwater fishes in Patos Lagoon, Brazil. In the present study the characids (Characidae) included three species of South American origin, their ancestor having moved north after the uplift of the Isthmus of Panama (Greenfield & Thomerson, 1997), as well as several populations of an apparent hybrid (*A. aeneus vs. A. altior*), which was listed as *Astyanax* sp. Such co-occurring *Astyanax* populations have been documented for several water bodies and caves south of Campeche and Quintana Roo (Mexico) (Schmitter- Soto, 1998). It is interesting to note that at all sampled localities where *A. altior* was recorded (13 sites in total), it co-occurred with *A. aeneus* in environments characterized by low dissolved oxygen and conductivity values greater than 300 µS cm^{-1}.

Regional Fish Biogeography

It is possible that peripheral and secondary freshwater fishes evolved in this area during the Neocene, and once they arrived, underwent speciation and filled most of the available niches in the absence of primary freshwater species which arrived in the late Tertiary (Briggs, 1984). Cichlids for instance, which are tolerant to saltwater, may have spread from South America to Central America in the early Miocene (or before), and have since undergone spectacular adaptive radiations (*e.g.*, over 70 species of *Cichlasoma* have evolved in Central America; Miller, 1966) before the Pleistocene land bridge was formed (Lowe-McConnell, 1987). Less numerous in species but more diverse in Central American genera than the cichlids, evolution of poeciliids in Central America probably began in the Oligocene (33.9 MYA). Apparently limited to rather small physical size by heredity, the poeciliids nevertheless evolved a rapacious predator such as *Belonesox* in middle Central America (Myers, 1966). At the end of the Pliocene (3.6 MYA), the closing of the Panama sea gap permitted an influx of South American primary ostariophysans (Myers, 1966). Speciation events of freshwater fish in the Yucatan Peninsula have taken place relatively recently, probably following periods of repopulation after the original fauna was wiped out by some catastrophic event such as a marine transgression during the Cenozoic, which kept the Yucatan Peninsula under water during most of that time. It seems clear, that freshwater fish species which have reached the Yucatan Peninsula have done so via dispersal from southern regions (Briggs, 1984).

In the case of CBR, we recorded four families of secondary freshwater fishes which could have crossed the seawater barrier and reached south-east Mexico following the emergence of the Panama Isthmus during the Pleistocene (2-5 MYA) (Hulsey *et al*., 2004). Poeciliidae (live bearers) were represented by seven genera and eleven species, compared to nine genera and twelve species for the Cichlidae Family. Similar results were found by López-López *et al*. (2009), where the most diverse families were Cichlidae and Poeciliidae with 12 and eight species, respectively. The observed patterns of occurrence for poeciliids and cichlids suggest an active migration process from nearby freshwater areas which drain into this region, as well as from groundwater discharges. The three most abundant species at the CBR (*A. aeneus*, *P. mexicana*, and *G. sexradiata*) were associated with both stagnant and running water and occurred under most environmental conditions. The high abundance of these species can also be explained by the absence of predators and competitors (Winemiller, 1989; Bührnheim & Fernandes, 2001).

Conservation of biodiversity

We document, native and endemic fishes with a restricted distribution, but also the occurrence of exotic species in these karstic pools, which is a risk to biodiversity conservation. Even though these aquatic ecosystems are patchy and isolated, they are flooded during the rainy season, allowing the displacement of the tilapias to other pools, and thus endangering native and endemic species that have a restricted distribution. As a result, it is important to control tilapia farming, and promote farming of native cichlids (*e.g.*, *P. splendida*).

We detected a high species richness and diversity in pools located in the unprotected area of the Reserve, suggesting a healthy environment with little alterations. The pristine nature of these pools could be the reason for these results. The high conservation value of the buffer zone, stress the importance of the these areas for the maintenance of local fish diversity. Furthermore, findings from the present study emphasize the importance of habitat horizontal heterogeneity for fish conservation at local scale.

Knowledge of fish assemblage structure in these systems should be incorporated into decision-making related to fish species conservation. Understanding factors that influence fish assemblage structure is important not only for accumulating basic ecological information, but also to predict the effects of environmental change on the integrity of these communities. This information will help in planning future conservation activities and maintain the biodiversity in these karstic pools.

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