

Fish community structure in freshwater karstic water bodies of the Sian Ka'an Reserve in the Yucatan peninsula, Mexico

Luis Zambrano*, Ella Vázquez-Domínguez**, Daniel García-Bedoya*,
 William F. Loftus*** and Joel C. Trexler****

We evaluated the relationship between limnetic characteristics and fish community structure (based on species richness, abundance and individual size) in contrasting but interconnected inland aquatic habitats of freshwater karstic wetlands in the Yucatan peninsula, Mexico. In the western hemisphere, freshwater karstic wetlands are found in south-eastern Mexico, northern Belize, western Cuba, Andros Island, Bahamas and the Everglades of southern Florida. Only in the Everglades have fish communities been well described. Karstic wetlands are typically oligotrophic because calcium carbonate binds phosphorus, making it relatively unavailable for plants. Fourteen permanent and seasonally flooded water bodies were sampled in both wet and dry seasons in Sian Ka'an Biosphere Reserve, in the Mexican state of Quintana Roo. Water systems were divided by morphology in four groups: cenotes with vegetation (CWV), cenotes without vegetation (CNV), wetlands (WTL), and temporal cenotes (TPC). Discriminant analysis based on physical characteristics such as turbidity, temperature, depth and oxygen confirmed that these habitats differed in characteristics known to influence fish communities. A sample-based rarefaction test showed that species richness was significantly different between water systems groups, showing that WTL and CWV had higher richness values than CNV and TPC. The most abundant fish families, Poeciliidae, Cichlidae and Characidae, differed significantly in average size among habitats and seasons. Seasonal and inter-annual variation, reflecting temporal variation in rainfall, strongly influenced the environmental differences between shallow and deep habitats, which could be linked to fish size and life cycles. Five new records of species were found for the reserve, and one new record for Quintana Roo state.

Introduction

Fish species richness in tropical freshwater systems is often higher than in comparable temperate systems (Shiel & Williams, 1990). This pattern has been explained by physical factors like spatial

heterogeneity, nutrient state, solar radiation or temperature (Emery, 1978) that markedly differ among aquatic systems at different latitudes (Lewis, 1987), as well as by interactions of those factors with historical biogeographic conditions (e.g., Miller, 1966). The role of physical factors

* Instituto de Biología, UNAM, Ciudad Universitaria, Apdo. Postal 70-153, México, DF, 04510, Mexico. E-mail: zambrano@ibiologia.unam.mx

** Instituto de Ecología, UNAM, Ciudad Universitaria, Apdo. Postal 70-275, México, DF, 04510, Mexico.

*** USGS-Florida Integrated Science Center, 40001 State Road 9336, Homestead, FL 33034, U.S.A.

**** Florida International University, Dept. of Biological Sciences, Miami, FL 33199, U.S.A.

has been widely studied in temperate fish communities (Matthews & Heins, 1987; Matthews, 1998), while fewer studies have been done aimed at understanding their significance in influencing freshwater-fish community structure in tropical systems (Lowe-McConnell, 1987; Lévêque et al., 1988; Winemiller, 1990; Jackson et al., 2001). Even the description of the origin and geomorphology of aquatic systems is still lacking in much of the tropics, and this is particularly true for southern Mexico.

Karstic wetlands of the Caribbean region have not been well described, though they form major aquatic habitats in south-eastern Mexico, northern Belize, areas of western Cuba (peninsula de Zapata and Guanahacabibes) and south-western Jamaica (Black River Morass), Andros Island of the Bahamas and the Everglades in southern Florida. Only in the Everglades have the wetlands been extensively studied (Davis & Ogden, 1994; Porter & Porter, 2002). The limestone geology of these regions yields oligotrophic wetlands because calcium carbonate binds with phosphorus, rendering it relatively unavailable to plants (Noe et al., 2001). These oligotrophic conditions play an important role in shaping food webs of aquatic ecosystems on karst (Turner et al., 1999), in addition to seasonal hydrological conditions in the western Caribbean that yield marked fluctuations in habitat area between wet and dry seasons. Seasonal drying causes extensive mortality of fishes that fail to locate aquatic refuges, leading to disturbance-dominated population dynamics (Loftus & Kushlan, 1987; Trexler et al., 2005).

The Yucatan peninsula of south-eastern Mexico, a low, relatively flat plain of porous limestone, emerged above sea level in relatively recent geological times (Lugo-Hubp et al., 1992). Because of its geomorphology, rainwater rapidly infiltrates into the ground, yielding few surface-water drainages and extensive subsurface drainage. Combined with dissolution processes, this subterranean drainage network has produced karstic aquatic habitats called 'cenotes' (sinkholes) that are typically deep, well-like holes with a variety of shapes and depths that contact the underground aquifer (Hall, 1936; Schmitter-Soto et al., 2002). In poorly drained regions of the peninsula, particularly near the coasts, there are extensive areas of seasonally flooded, fresh- and brackish-water wetlands (Pearse, 1936). One of these wetland systems, in the Sian Ka'an Biosphere

Reserve of Quintana Roo State, was the focus of our study (Fig. 1).

Despite the wide distribution and large area of wetlands and cenotes in southern Mexico, these systems have received little study (Alcocer et al., 2000). Pearse (1936) mentioned that the word 'cenote' was loosely applied in Yucatan to various types of water bodies formed by cavities in the limestone. Hall (1936) distinguished four types of cenotes based on their morphology to encompass most of the water bodies in the northern part of the peninsula: jug-shaped, vertical-walled, aguada (pond-like) and cave-like cenotes. Recent studies have classified in more detail the peninsula's water bodies (Wilkins, 1982; Iliffe, 1992; Schmitter-Soto et al., 2002), like inland cenotes (deep sinkholes), lagoons (fault-formed and coastal) and wetlands that include seasonally flooded freshwater marshes, tidal brackish wetlands, and scrub-forest swamps (termed savannas) that are shallowly flooded only in the wet season.

The Sian Ka'an Biosphere Reserve (5281.47 km²) is one of the largest Mexican protected areas, with a diversity of habitats ranging from tropical forests, savannas, freshwater marshes, mangroves swamps, lagoons, sandy barrier islands and coral reefs (INE, 1996; Aguilar et al., 2000). Sian Ka'an is a low-elevation karstic region, with little soil development besides calcareous soils under the wetlands and organic soils in the forests and swamps. Exposed limestone bedrock is common in most habitats. The reserve receives most of its water during the wet season (May-June to January-February), although with substantial yearly differences in the time the rain starts and ends, from rainfall that averages 1200 mm per year (Olmsted & Durán, 1990), and from sub-surface flows that move eastward from the centre of the peninsula. The wetlands occur near the coasts where rainfall pools in the lowest elevations and where sub-surface waters emerge through weaknesses in the limestone. The combined picture of the aquatic system of the reserve is a landscape with perennial water bodies (cenotes and lagoons), together with seasonal habitats composed by wetlands and flooded forested swamps.

Aquatic habitats of the reserve encompass a diversity of environmental characteristics and appear to support both widespread and spatially restricted fish species (Schmitter-Soto & Gamboa-Pérez, 1996; Schmitter-Soto, 1998, 1999). Fortunately, the reserve has been free of most anthro-

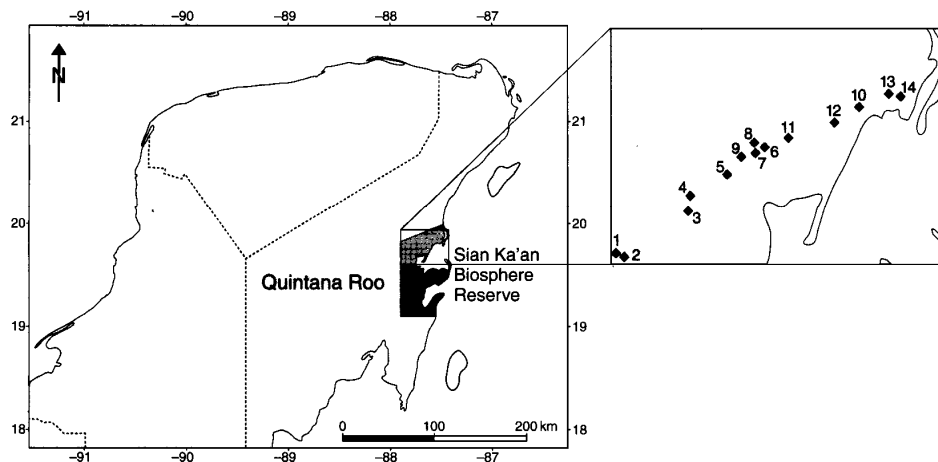


Fig. 1. Sian Ka'an Biosphere Reserve in Quintana Roo, Mexico. Sampling sites are shown, 1, LEN; 2, LES; 3, LIM; 4, Ce3R; 5, CeST; 6, TSAB; 7, TCRA; 8, TPRF; 9, SAB; 10, SLVA; 11, PET; 12, LIR; 13, PREM; 14, MAR.

pogenic perturbations, in marked contrast to the Everglades, which are the focus of a massive ecological restoration effort. Sian Ka'an has remained relatively unmodified by humans mainly because settlement has been limited in both wetlands and uplands, which has recently been enhanced by legal protection afforded by the reserve category. The hydrologic regime of Sian Ka'an has remained unmodified; there have been no introductions of non-native species for sport or aquaculture, with the possible exception of tilapia in one inland cenote (Schmitter-Soto & Caro, 1997), nor has there been marked fishery pressure on native freshwater fishes. The coastline of Quintana Roo is rapidly developing as an international tourist destination with unknown consequences for the reserve. This pristine and extensive tropical wetland system provides an excellent opportunity to explore the basic limnological characteristics of freshwater ecosystems of the Yucatan peninsula, and offers the rare opportunity to collect baseline data before human impacts occur. In this study, our aim was to evaluate the relationship between hydrological conditions, such as temperature, depth, salinity, oxygen, and turbidity, and the fish community structure (specifically species richness, abundance and individual size) in inland aquatic habitats with contrasting morphological and limnetic qualities. Future comparisons with similar data from the Florida Everglades will enable testing

of hypotheses related to ecological factors shaping these communities in karst tropical and subtropical wetlands.

Methods

Field studies. The Sian Ka'an Biological Reserve includes thousands of hectares of aquatic habitats. For the purpose of the present study, we considered inland waters as those aquatic systems driven by rainfall and ground waters like cenotes and wetlands, excluding mangrove fringes, lagoons or waters on the barrier island. The study area in the central region of the reserve is based on a hydrological gradient running east to west from inland towards the coast, and along a secondary road approximately 40 km long (Fig. 1). The road enables access to the entire array of aquatic habitats present in Sian Ka'an. We characterized hydrological conditions and fish communities at 14 sites in the study area, sampling during the wet season (September 2001 and November 2002) and dry season (March 2002 and April 2003). Sampling stations were located in both permanent and seasonally flooded water bodies, the former sampled in both seasons and the latter only in the wet season. Based on the single published morphological cenote classification, that of Pearse (1936) and Hall (1936; his Fig. 1 illustrates types of cenotes), we grouped the

habitats (hereafter a priori groups) as: 1) Cenotes without vegetation (CNV) (typical cenote; Pearse, 1936); 2) Cenotes with vegetation (CWV) (aguada-like; Hall, 1936; old cenote; Pearse, 1936); 3) Wetlands (WTL) (Mitsch, 1993) and 4) Temporal cenotes (TPC) (cave-like cenote; Hall, 1936). As an intricate tunnel-cave system under the ground, temporal cenotes may have water throughout the year; however, during the dry season water does not reach the surface, rendering it impossible to have access to fish during dry months. We sampled all the cenotes with and without vegetation present in a 5 km reach to the north and south of the road (Fig. 1). We chose wetlands and temporal cenotes sampling sites based on their accessibility by foot from the road. The sampling stations were distributed widely and included a good representation of the aquatic habitats in the study site.

The temporal cenotes were very similar in structure and appearance to solution holes described from the Everglades by Loftus et al. (1992) and Kobza et al. (2004). In Sian Ka'an, those cenotes were mainly located in seasonally flooded scrub forests where leaf fall contributed organic matter to the water. The seasonal freshwater marshes we sampled were densely vegetated with sawgrass (*Cladium jamaicense*), spikerushes (*Eleocharis* spp.) and other graminoids, on which we based the demarcation of the wetlands' boundaries, i.e., their absence was considered as the end of the wetland. In wetlands with longer hydroperiods, floating beds of bladderwort (*Utricularia* spp.), often supporting periphyton mats, covered much of the marsh surface. To describe the physicochemical features of each water body, we collected basic limnetic data on depth, temperature, salinity, pH, dissolved oxygen, and turbidity, during the morning (10:00-12:00 hrs) and with a portable Hydrolab unit. We measured salinity to evaluate marine water influence on those systems close to the coast. Measurements were made at the surface and at 30 cm depth. Area was measured directly on the field with a GPS and with Arcview 3.2; particularly for wetlands, it was considered as the total area covered by the same dominant vegetation.

To have a better list of species, we employed different fishing techniques because no single fish-sampling method was effective in all habitats. In the seasonal wetlands, we used a 1-m² throw trap cleared with dip nets (Jordan et al., 1997) and unbaited minnow traps (Kobza et al., 1997) at-

tached to drift fences (Loftus et al., 2001). We sampled with drift-fences and throw traps in wetlands where sawgrass (*Cladium jamaicense*) and spikerush (*Eleocharis* spp.) were the dominant vegetation, and the maximum water depth was less than 1.5 m. In the cenotes (with and without vegetation) we caught fishes with minnow traps, dip and cast nets, and angling, while temporal cenotes were sampled with minnow traps. In large cenotes, traps were placed in different microhabitats: close to shore with vegetation, close to the shore without vegetation and away from the edge. Each water body was sampled at least three times during the study. Data collected from all fishing techniques during at least one day per water body was used to build the fish list for the study site and the richness analysis. Notwithstanding the different fishing techniques used, all statistical analyses (see below) were conducted only with data from minnow traps, the technique from which we could standardize capture effort. Sampling effort, measured as catch-per-unit-effort (CPUE), was standardized by collecting, during one day, with at least three minnow traps set for 24 hours within each system (i.e. the unit in CPUE is day).

Individual fishes were measured (to the nearest 0.1 cm), weighed (0.1 g), and identified on site using regional taxonomic keys (Greenfield & Thomerson, 1997; Schmitter-Soto, 1998). Nomenclature followed that of Nelson et al. (2004). Only those individuals that could not be readily identified in the field were transported to the laboratory for identification and deposition as vouchers in the National Fish Collection (CNPE) at UNAM. To provide a thorough inventory of fishes in the inland waters studied, we combined data from this study with a snorkelling data collection done in 2001 in Laguna Chunyaxché (by WFL and LZ), and with earlier collections of fishes made by WFL and JCT in the 1980s and 1990s; however, such previous fish data were not included in any of the analyses.

Statistical analyses. We used discriminant analysis (DA) to validate the classification of the different water bodies (a priori groups) described above. DA is a test used to find a variable or component (a linear combination of response variables) that will discriminate best between a priori defined groups of samples (Huberty, 1994). This analysis was done based on our measurements of physical parameters and the season of

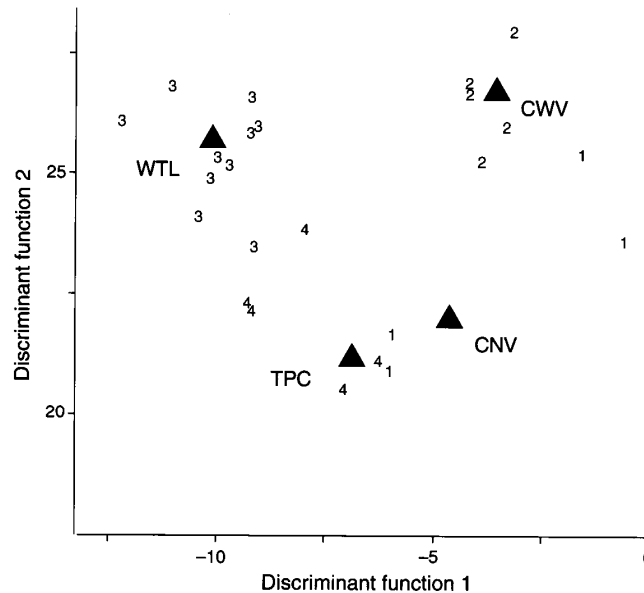


Fig. 2. Results of the discriminant analysis (DA) for the different water bodies: CNV (1), cenotes without vegetation; CWV (2), cenotes with vegetation; WTL (3), wetlands; TPC (4), temporal cenotes.

sampling, with the program Brodgar 2.5.1 (Highland Statistics). Prior to DA, we standardized data to a mean of zero and standard deviation of one; for depth values we also reduced outliers and normalized the data with a square-root transformation.

As mentioned above, species richness, relative abundance (CPUE) and relative biomass (CPUE) were estimated only from minnow traps samples for which we could standardize capture effort. An accumulation curve (Mao Tau-Sobs; Colwell, 2005) was used to compare number of species between systems. This method gives 95% confidence limits, which can be used to statistically compare differences between systems (Colwell et al., 2004). We pooled the fish data from all sites in each habitat group identified by DA (sample sets) and used a sample-based rarefaction test to build a cumulative sampling-effort curve. Following Colwell et al. (2004), the expected number of species for a given replicated set of samples can be estimated under the assumption of random sample order (Gotelli & Colwell, 2001) using the program EstimateS (Colwell, 2005). This procedure allows for the estimation of both expected richness and its confidence limits, together with

a direct statistical comparison of richness between sample sets (Colwell et al., 2004).

We also evaluated variation in average fish size among groups and seasons for the most abundant fish families, using Kruskal-Wallis and Dunn's post-hoc tests to examine differences in average fish size among groups, and Mann-Whitney (M-W) rank tests for comparisons between seasons (Siegel & Castelan, 1988).

Results

Physical environment of Sian Ka'an wetlands.

The dimensions of the four habitats differed in depth and area: cenotes without vegetation were highly variable in size, ranging from 2-3 m in diameter to more than 30 m and in depth from one meter to more than 20 m. Cenotes with vegetation were nearly 40 m in diameter and depth of 13 m. Temporal cenotes were normally small (<0.1 ha) and shallow (<1.5 m). All wetlands were over 10 ha in size and shallow (<1 m depth) (Table 1). DA analysis confirmed the a priori grouping of water systems; the system group with highest differences were cenotes with vegetation

and wetlands (Fig. 2), which showed a 66.6 % difference based on the Mahalanobis distance index (Huberty, 1994), whereas temporal cenotes and cenotes without vegetation were the most

similar (93 %) ones. DA results also showed that turbidity, temperature, depth and oxygen were the variables with more weight in separating groups, being turbidity the highest influence on

Table 1. Continental aquatic systems studied and basic limnetic variables measured in Sian Ka'an, Quintana Roo, Mexico, during dry and wet seasons (dry-wet). Locality refers to the name given in the field to each water body, and group system to each of the four groups of water bodies obtained with the DA analysis (see Fig. 2). \bar{x} , average; sd, standard deviation

locality	season	depth (m)	temperature (°C)	turbidity (NTU)	pH	salinity	oxygen (mg·l ⁻¹)
Group system: Cenote without vegetation (CNV)							
Ce3R	dry	20.00	26.0	1.30	7.50	0.46	2.00
Ce3R	wet	20.00	23.0	1.20	8.00	0.50	1.50
Ce5T	dry	1.20	25.3	5.00	8.00	3.20	3.00
Ce5T	wet	1.20	24.9	5.00	7.20	0.26	7.20
\bar{x}		10.60	24.8	3.13	7.68	1.11	3.43
sd		10.85	1.3	2.17	0.39	1.40	2.59
Group system: Cenote with vegetation (CWV)							
LEN	dry	13.00	26.9	3.00	8.90	0.28	7.30
LES	dry	10.00	26.0	0.75	7.80	0.50	7.60
LIM	dry	10.00	29.3	2.10	7.60	0.11	7.00
LIM	wet	10.00	28.0	1.80	7.00	0.12	5.20
LIM	wet	10.00	30.0	2.30	8.00	0.10	6.80
\bar{x}		10.60	28.0	1.99	7.86	0.22	6.78
sd		1.34	1.6	0.82	0.69	0.17	0.93
Group system: Wetland (WTL)							
LIR	dry	0.60	27.0	333.00	8.30	0.00	3.60
LIR	wet	0.60	30.0	563.45	7.16	0.32	2.60
LIR	wet	0.20	27.0	345.00	7.20	0.26	3.20
LIR	wet	0.15	27.0	563.45	7.16	0.32	2.60
MAR	dry	0.40	30.0	220.00	8.40	5.01	2.10
MAR	wet	0.50	27.8	250.00	8.00	5.40	4.50
PET	dry	0.50	26.2	256.00	8.00	0.20	3.20
PET	wet	0.45	32.0	297.00	7.48	0.24	5.31
PET	wet	1.50	28.3	300.00	7.00	0.20	6.30
PET	wet	1.50	28.3	297.00	7.48	0.24	5.31
PREM	wet	0.26	30.5	500.00	8.00	2.23	3.20
PREM	wet	0.26	30.0	500.00	8.00	2.23	3.20
PREM	wet	0.32	28.5	500.00	8.00	2.23	3.20
PREM	wet	0.50	26.3	500.00	8.00	2.23	3.20
PREM	wet	0.50	26.2	429.40	7.53	2.12	3.16
\bar{x}		0.55	28.3	390.29	7.71	1.55	3.64
sd		0.41	1.8	121.67	0.45	1.76	1.17
Group system: Temporal cenote (TPC)							
SAB	wet	0.20	34.0	4.00	7.00	0.00	3.20
SLVA	wet	0.40	26.0	3.00	8.00	0.00	4.00
TCRA	wet	1.00	31.2	42.00	6.80	0.30	6.30
TPRF	wet	1.20	26.2	2.00	7.00	0.20	5.30
TSAB	wet	0.30	33.0	38.00	7.00	0.20	2.30
\bar{x}		0.62	30.1	17.80	7.16	0.14	4.22
sd		0.45	3.8	20.33	0.48	0.13	1.60

the separation (64.6 %) (Fig. 2; Table 1). For example, wetlands had the highest mean values of turbidity (> 550 NTU). Also, mean temperatures varied with the depth of the habitats; deeper systems had lower temperature than shallower

ones, while dissolved-oxygen concentrations showed a contrasting pattern with respect to depth, in which cenotes with vegetation (deep) and temporal cenotes (shallow) had higher oxygen concentrations than wetlands or cenotes

Table 2. Fish species recorded in continental aquatic systems studied in Sian Ka'an (SK), Quintana Roo (QR), Mexico. Reference: 1, collected in present study; 2, observed in present study; 3, Schmitter-Soto (1998); 4, Ramo & Busto (1992). Asterisks indicate species collected in study area but not within the water bodies analyzed.

family	species	reference	new record
Megalopidae	<i>Megalops atlanticus</i>	2, 3	
Elopidae	<i>Elops saurus</i>	4	
Characidae	<i>Astyanax altior</i>	1	
	<i>Hyphessobrycon compressus</i>	1*	SK
Pimelodidae	<i>Rhamdia guatemalensis</i>	1	
Batrachoididae	<i>Opsanus beta</i>	4	
Belonidae	<i>Strongylura notata</i>	1*, 3, 4	
Apocheilidae	<i>Rivulus tenuis</i>	1	
Cyprinodontidae	<i>Cyprinodon artifrons</i>	1	
	<i>Floridichthys polyommus</i>	1*	
	<i>Jordanella pulchra</i>	1	
Poeciliidae	<i>Belonesox belizanus</i>	1	
	<i>Gambusia sexradiata</i>	1	SK
	<i>Gambusia yucatanana</i>	1	
	<i>Heterandria bimaculata</i>	1	SK
	<i>Poecilia mexicana</i>	1	
	<i>Poecilia orri</i>	1	
	<i>Poecilia velifera</i>	1	
	<i>Xiphophorus maculatus</i>	1	SK
Atherinidae	<i>Atherinomorus stipes</i>	4	
Synbranchidae	<i>Ophisternon aenigmaticum</i>	1	SK
Centropomidae	<i>Centropomus undecimalis</i>	2	
Lutjanidae	<i>Lutjanus apodus</i>	2	
	<i>Lutjanus griseus</i>	2, 3	
Gerreidae	<i>Eucinostomus argenteus</i>	4	
	<i>Eucinostomus gula</i>	3	
	<i>Eucinostomus harengulus</i>	3	
	<i>Eugerres plumieri</i>	2, 3	
Cichlidae	<i>Cichlasoma affinis</i>	1	
	<i>Cichlasoma friedrichsthalii</i>	1	
	<i>Cichlasoma meeki</i>	1	
	<i>Cichlasoma octofasciatum</i>	1	
	<i>Cichlasoma robertsoni</i>	1	
	<i>Cichlasoma spilurus</i>	1	
	<i>Cichlasoma urophthalmus</i>	1	
	<i>Cichlasoma salvini</i>	1	
	<i>Cichlasoma synspilum</i>	2	
	<i>Petenia splendida</i>	1	
Mugilidae	<i>Agonostomus monticola</i>	2	QR
	<i>Mugil curema</i>	3, 4	
Eleotridae	<i>Gobiomorus dormitor</i>	2, 3	
Gobiidae	<i>Evorthodus lyricus</i>	4	

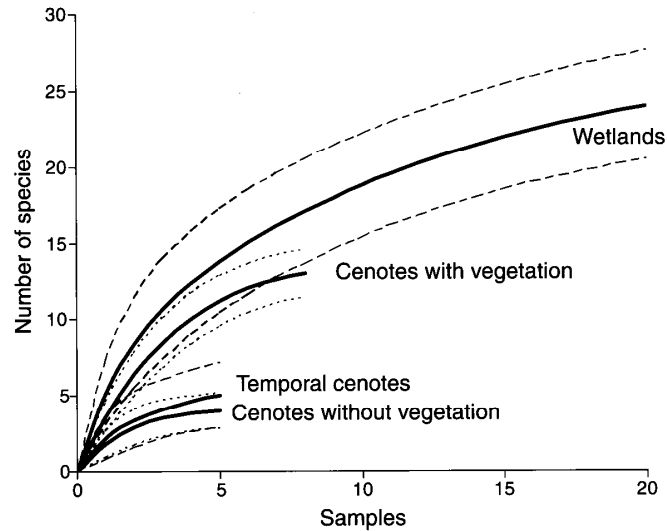


Fig. 3. Accumulation curve analyses of fish species recollection for each type of water body. Names correspond to each of the four groups of water bodies obtained with the DA analysis (see Fig. 2).

without vegetation (Table 1). Although some systems were closer to the coast, salinity had no influence in the separation of the groups; similarly, pH had no influence on group membership (2.47 % and 9.67 % of differences, respectively – Mahalanobis distance index). Only one of the cenotes without vegetation (CeST) and the wetlands closest to the coast (MAR and PREM; Fig. 1) had high salinity values during the dry season, while pH was mostly slightly basic (Table 1), because of the limestone bedrock and soils.

Fish assemblages of Sian Ka'an inland waters. Of the 42 fish species within 18 families listed in Table 2 for central eastern Quintana Roo, we sampled or observed 34 species belonging to 14 families. Fifteen species of the Quintana Roo ichthyofauna are tolerant of high salinities, including elopids, megalopids, gerreids, eleotrids and one cichlid species (*Cichlasoma synspilum*), known from lakes and streams draining into coastal lagoons at the northern end of the reserve. Because the present study focused only on inland freshwater systems, we sampled none of the marine species, however, our sampling did take 100 % of the salt-intolerant species. The families Pimelodidae, Synbranchidae and Aplocheilidae were represented by one species each, while Characidae

had two species. Cichlidae and Poeciliidae were the most speciose families in the inland waters. *Cyprinodon artifrons* and *Floridichthys polyommus* are endemic to the Yucatan peninsula (Schmitter-Soto, 1998). We found five new records for the Sian Ka'an Reserve (Table 2): *Gambusia sexradiata* (Poeciliidae), *Heterandria bimaculata* (Poeciliidae), *Hyphessobrycon compressus* (Characidae), *Ophisternon aenigmaticum* (Synbranchidae), and *Xiphophorus maculatus* (Poeciliidae); *Agonostomus monticola* (Mugilidae) is a new record for the state of Quintana Roo (Table 2).

Number of species sampled with minnow traps was highest in wetlands, with 18 species, while cenotes with vegetation had 14, temporal pools 4, and cenotes without vegetation showed the lowest richness with only 3 species. The accumulation curve appeared to be reaching an asymptote for temporal cenotes, while the results for cenotes with vegetation and wetlands suggested a relatively thorough sampling of fish species in those habitats (Fig. 3).

Based on the species richness results, the water systems are separated in two: those with the highest richness (CWV and WTL) are significantly different from those with lower richness (TPC and CNV) (sample-based rarefaction; Fig. 3; Colwell et al., 2004). The dominant families col-

lected were Poeciliidae (relative abundance 46 %), Cichlidae (40 %) and Characidae (9 %) (Table 3). Poeciliids were present in all habitats, and that was the only family represented in some temporal cenotes. The dominant poeciliid species was *Gambusia yucatana*, present at 57 % of all sites. Two other widespread species, *Astyanax altior* and *Cichlasoma urophthalmus*, occurred at 43 % and 21 % of sites, respectively. Five of the seven families present were collected in seasonal cenotes and wetlands, while permanent cenotes with and without vegetation held only two and three families, respectively.

Average fish size varied from 2-6 cm in most families, except for much larger synbranchids and pimelodids; *R. tenuis* was the smallest species at adult size (Table 3). The largest fishes were cichlids sampled in cenotes with vegetation (K-W, d.f. = 3, $P < 0.001$; cenotes with vegetation different to wetlands), while poeciliids and characids size did not vary among systems (K-W, d.f. = 3, $P = 0.07$; K-W, d.f. = 3, $P = 0.187$, respectively) (Fig. 4). The most abundant families, Cichlidae, Poeciliidae and Characidae, all showed significant differences in average size among habitats (Fig. 4).

When all families were considered, fish size was larger during the dry season (4.27 cm) than in the wet season (3.74 cm) (M-W, $n = 1632$, $P < 0.001$). Cichlids were mainly responsible for this pattern (dry: 4.8 cm and wet: 4.4 cm) (M-W, $n = 750$, $P < 0.001$); the opposite pattern was seen for characids, which averaged larger in the wet season (4.68 vs 3.6 cm) (M-W, $n = 161$, $P < 0.001$). Poeciliids were also larger during the wet season (3.0 vs 2.65 cm), but the difference was not statistically significant ($P = 0.07$).

Discussion

The water bodies we sampled in Sian Ka'an could be grouped by morphology and physical characteristics that were linked to variation in the limnetic variables measured. In general, wetlands and temporal cenotes were shallower, tended to be more turbid, had higher temperatures and slightly lower dissolved-oxygen levels. Deeper systems had lower temperature than shallower ones, while cenotes with vegetation (deep) and temporal cenotes (shallow) had higher oxygen

Table 3. Fish species collected in continental aquatic systems studied in Sian Ka'an, Quintana Roo, Mexico. N, number of individuals collected in minnow traps; AS, relative abundance per species (%); AF, relative abundance per family (%); BF, average biomass per family (g); LF, average length by family (cm).

family	species	N	AS	AF	BF	LF
Characidae	<i>Astyanax aeneus</i>	170	9.33	9.33	1.72	4.39
Pimelodidae	<i>Rhamdia guatemalensis</i>	16	0.88	0.88	22.57	12.83
Rivulidae	<i>Rivulus tenuis</i>	5	0.27	0.27	0.05	1.18
Cyprinodontidae	<i>Cyprinodon artifrons</i>	41	2.25	3.07	0.28	1.66
	<i>Jordanella pulchra</i>	15	0.82			
Poeciliidae	<i>Belonesox belizanus</i>	19	1.04	45.83	1.20	3.25
	<i>Gambusia sexradiata</i>	129	7.08			
	<i>Gambusia yucatana</i>	406	22.28			
	<i>Heterandria bimaculata</i>	89	4.88			
	<i>Poecilia mexicana</i>	43	2.36			
	<i>Poecilia orri</i>	113	6.20			
	<i>Xiphophorus maculatus</i>	35	1.92			
Synbranchidae	<i>Ophisternon aenigmaticum</i>	2	0.11	0.11	82.94	46.80
Cichlidae	<i>Cichlasoma affinis</i>	81	4.45	40.50	4.07	5.71
	<i>Cichlasoma friedrichsthalii</i>	53	2.91			
	<i>Cichlasoma meeki</i>	51	2.80			
	<i>Cichlasoma octofasciatum</i>	139	7.63			
	<i>Cichlasoma robertsoni</i>	4	0.22			
	<i>Cichlasoma salvini</i>	64	3.51			
	<i>Cichlasoma spilurus</i>	6	0.33			
	<i>Cichlasoma urophthalmus</i>	339	18.61			
	<i>Petenia splendida</i>	1	0.05			

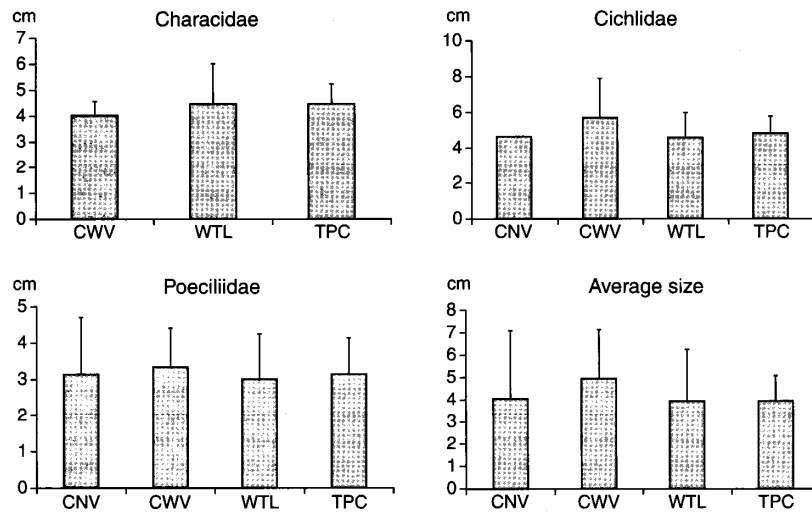


Fig. 4. Average fish size (cm) for the Cichlidae, Poeciliidae and Characidae fish families and average fish size (cm) considering all organisms within each water system group (DA analysis, see Fig. 2). CNV, cenotes without vegetation; CWV, cenotes with vegetation; WTL, wetlands; TPC, temporal cenotes. Standard deviation is shown.

concentrations than wetlands or cenotes without vegetation. As expected, wetlands closest to the coast experienced the greatest salinity changes between dry and wet seasons. The four groups of aquatic habitats depicted in this study reflected not only their morphology and form of origin (Hall, 1936; Pearse, 1936), but also ecological characteristics known to influence their suitability for aquatic life, particularly fishes. Similar gradients of karstic wetlands have been noted in the Everglades (Craighead, 1971; Kushlan, 1990 [Fig. 10.10 illustrates wet prairies]; Snyder et al., 1990 [Fig 8.3 illustrates a solution hole]).

Rainfall-driven hydrology is a key factor in seasonality of tropical and subtropical aquatic environments. The relative impact of seasonal versus inter-annual variation (also reflecting temporal variation in rainfall) depended on the depths of habitats in Sian Ka'an. All wetlands we sampled exhibited significant seasonal water-level fluctuation, but were inundated in both rainy seasons we studied. In contrast, most of the temporal cenotes we examined showed strong inter-annual variation because they failed to re-fill in the relatively dry wet season of 2002. These temporal cenotes, located at slightly higher elevations

than the other habitats, seemed dependent on high precipitation levels (even by Yucatan wet-season standards) to raise the water table to flood them. Thus, seasonality imposes a dichotomy of aquatic systems based on depth at Sian Ka'an: the shallow habitats that are dynamic in water level (drying in many or most years), salinity and temperature, and the deeper systems that are relatively stable throughout the year. In addition, spatial heterogeneity is markedly higher in the shallow-water bodies, because they have more structure provided by aquatic plants, woody debris and detritus. Deeper habitats, such as large cenotes, are often simpler in structure, have little area for the establishment of aquatic vegetation, and may have thermoclines that divide the cenotes into two relatively isolated systems.

The environmental differences between the shallow and deep habitats can be linked to variation in fish-species richness and life cycles. Other things being equal, aquatic systems that provide greater habitat complexity support higher species richness than less complex ones (Matthews, 1998), while the more stable the system, the better support it provides for fishes with non-seasonal life cycles. Vegetation in the habitat complexity in Sian Ka'an seems to be a key factor

for fish richness, hosting significantly more species in wetlands and cenotes with vegetation. The frequency and degree of drying at our study sites, with the exception of permanent cenotes, may be enough to over-ride local effects of habitat structure. Nevertheless, a more important feature of this ecosystem could be its relative lack of topography; flooding unites much of the region into a continuous pool of aquatic habitat in most wet seasons, facilitating dispersal and colonization of fishes into formerly dry habitats. Thus, these aquatic systems may function as patchy population sites for many fish species (Hanksi & Gilpin, 1997).

The new records of fishes within the reserve and for the state have increased understanding of regional fish diversity and species distributions, but also demonstrate how much remains to be learned about the ichthyofauna of the region. *Agonostomus monticola*, new to Quintana Roo, is a species native to the western area of the peninsula, while most species new to the reserve were known from elsewhere on the peninsula or were marine derived. Species richness was lower than might be expected for a neotropical continental ichthyofauna, but may be explained by the relative lack of aquatic habitat diversity in the state, by seasonality of most aquatic habitats, and by zoogeographic history (Miller, 1966; Arita & Vázquez-Domínguez, 2003). Inland habitats are predominantly lentic, and the wetlands are subject to wide seasonal and inter-annual fluctuations in water depth and area; both temporal and permanent cenotes may become stratified, resulting in depleted dissolved-oxygen levels near the bottom. These situations present significant challenges to fish survival. The dominance by small-bodied, short-lived fishes in those habitats is a product of such conditions: fishes, like livebearers and killifishes (Lewis, 1971), with morphological adaptations to enable them to use aquatic surface respiration, were common in our samples of wetlands and temporal cenotes. The accessory respiratory organs of catfishes and synbranchid eels, which we collected in wetlands and cenotes, allow their successful colonization of oxygen-deficient waters. In general terms, the ichthyofauna of Sian Ka'an is more similar to that of the Everglades (Loftus & Kushlan, 1987), if we consider cichlids as ecological analogues for centrarchid sunfishes, than to wetlands of South America in which numerous species of siluriform and characiform fishes predominate (Machado-Alli-

son, 1993). Livebearers and killifish species dominate both Sian Ka'an and the Everglades fish communities, probably reflecting a shared ecological filter of potential fish colonists. Anthropogenic introductions of cichlids from Central America, such as the Mayan cichlid (*C. urophthalmus*) and impending invasion by Old World synbranchids, such as the swamp eel (*Monopterus albus*), have made the Everglades fish fauna even more similar to Sian Ka'an in modern times (Trexler et al., 2001; Collins et al., 2002).

Diversity differences were observed regarding species richness and fish families. Cenotes with vegetation and wetlands had a higher number of species and families; shallower systems were more diverse compared to deeper ones. Not surprisingly, wetlands had higher fish diversity than temporal cenotes, particularly given their size differences. However the contrasting differences between similar size systems such as cenotes with and without vegetation suggest that other factors, such as spatial complexity, might play an important role in the establishment of species. Vegetation not only provides refuge and spawning areas but also generates a food supply within this oligotrophic system. Vegetation both contributes to, and consumes, dissolved oxygen. Furthermore, average fish size varied among aquatic systems: the largest fishes were found in cenotes without vegetation when all families were considered together; when analyzed separately, the largest cichlids and poeciliids were found in cenotes with vegetation and the largest characids in the wetlands. These findings may be the result of food availability or predation differences among habitats; for instance, periphyton, a potentially important food-web component, is more abundant in wetlands than cenotes. Characids and cichlids are predators, but the former may also obtain periphyton-based food resources, while the latter are efficient insectivores and piscivores, prey that are abundant in the cenotes (Greenwood, 1994). Additionally, because cenotes are deeper and more stable water bodies, they often have simpler food webs (Schmitter-Soto et al., 2002) and more and larger predators compared to shallower systems, which may limit the numbers of smaller individuals of cohabiting species. A major factor related to size differences is system stability; limnetic characteristics were less variable in cenotes compared to wetlands, which change dramatically between dry and wet seasons. By releasing large-bodied fish species with multi-year

life spans from the threat of dry-season mortality, stable habitats allow those species to survive and grow. On the contrary, poeciliids and characids, with shorter life cycles, may be capable of responding to extreme changes during the year (Meffe & Snelson, 1989). It is likely that the rapid life cycle of poeciliids and characids begins during the wet season when fish reach sexual maturity.

The information gathered in the present study is the first step in investigating the ecology of this tropical wetland. Of particular interest is the comparison of food-web structure and responses of component species to physical factors, especially the seasonal hydrology. The potential to compare data with similar wetlands of the Caribbean region will allow testing of ecological hypotheses such as energy flow in oligotrophic wetlands, species richness patterns in tropical versus sub-tropical wetlands, and differences in species composition and size-structure among habitats.

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