

The effect of seasonal variation in abiotic factors on fish community structure in temporary and permanent pools in a tropical wetland

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SUMMARY

1. Fish community structure depends on biotic interactions and abiotic variables. Abiotic variables appear to gain importance in highly variable freshwater systems, such as tropical wetlands where a marked seasonal hydroperiod (dry and wet seasons) modifies water quality and quantity, differentially affecting fish survival and, consequently, modifying species richness and abundance.
2. We evaluated the relationship between abiotic variables and fish community structure in variable (temporary) and stable (permanent) pools that were interconnected in a tropical wetland with marked annual dry and wet seasons.
3. All fish species were able to occupy any of the studied pools, but our results showed distinctive fish community structures in permanent and temporary pools. Community structure was related to temperature, depth, pH and macrophyte coverage. Total fish abundance in the wetland was negatively related to water depth and positively related to macrophyte coverage.
4. Null models of co-occurrence indicated a non-random pattern at the wetland scale and a random pattern within groups of pools with similar characteristics, suggesting that fish communities are structured according to habitat features. We conclude that seasonal abiotic variation and habitat characteristics in this highly variable pristine wetland play major roles in structuring fish communities.

Keywords: abiotic factors, fish community, null models, Sian Ka'an Reserve, Yucatán peninsula

Introduction

A better understanding of patterns and processes that influence community structure is a continuing goal in ecology (Baber *et al.*, 2004). Fish communities are structured by effects working at a regional scale, where abiotic factors limit the breadth of species distributions, and at a local scale, where biotic factors determine species survival within a system (Degani

et al., 1998; Martino & Able, 2003). However, in highly variable aquatic systems, abiotic factors appear to be more important in structuring communities at the local scale (Magoulick, 2000; Baber *et al.*, 2002; Suárez, Petrere & Catella, 2004).

Dynamic environments, such as wetlands, are characterised by periodic drying and flooding events in which the water level changes dramatically (Collinson *et al.*, 1995; Schwartz & Jenkins, 2000). The distinct seasonal rainfall and run-off in wetlands promote changes in water chemistry among dry and wet seasons that directly affect species abundance and richness (Schlosser, 1987; Taylor, 1997). During dry seasons, for example, fish communities experience habitat contractions and extensive mortality

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(of organisms that fail to migrate to refuges), leading to disturbance-dominated population dynamics (Loftus & Kushlan, 1987; Trexler, Loftus & Perry, 2005). During wet seasons, habitats expand and fish survivors disperse from refuges to exploit newly flooded wetlands for food and reproduction (Galacatos, Barriga-Salazar & Stewart, 2004).

The study of fish communities in temporary aquatic systems is relatively new (Schwartz & Jenkins, 2000). Fish are normally absent from temporary habitats (Drenner *et al.*, 2009) and therefore most studies in these systems have focused on invertebrate and amphibian communities (Chase, 2003; Sanderson, Eyre & Rushton, 2005; Da Fonseca *et al.*, 2008; Wissinger, Greig & McIntosh, 2009). Most of the studies on fish communities in temporary waterbodies have been conducted in temperate areas (Capone & Krushlan, 1991) and consequently there is a scarcity of knowledge on the factors affecting fish communities in the tropics (Pazin *et al.*, 2006).

In many wetlands, small temporary waterbodies rarely occur in isolation but are scattered in the landscape among permanent and semi-permanent waterbodies (Sanderson *et al.*, 2005). Fish species composition in temporary habitats often differs from those in permanent habitats (Schneider & Frost, 1996; Williams, 1996; Werner *et al.*, 2007; Wissinger *et al.*, 2009). Hence, these small ecosystems maintain unique species compositions and thus can greatly contribute to landscape diversity (De Meester *et al.*, 2005). To understand community patterns in temporary habitats, studies at a small scale (within systems) are necessary.

Many temporary habitats in the tropics are associated with wetlands. The estimated global value of wetlands for biodiversity, ecosystem services and cultural significance is higher than that of terrestrial ecosystems (Costanza *et al.*, 1997). The rapid loss of wetlands, coupled with the invasion of non-native species, has exacerbated efforts to understand these habitats (Schwartz & Jenkins, 2000; Kobza *et al.*, 2004) and few unaltered wetlands remain from which ecological information can be gathered (Lorenz & Serafy, 2006). One of the few unaltered wetlands is within the Sian Káan Biosphere Reserve (SKBR) in the southeast of the Yucatán peninsula in México.

The hydrological dynamic and topography of SKBR generates a matrix of permanent and temporary pools, in which fish communities seem to be related to

hydrological conditions (Zambrano *et al.*, 2006). All fish species in this wetland are able to occupy temporary or permanent pools in the wet seasons because flooding connects them all (authors' pers. obs.). However, the dry season can change community structure by acting as an environmental filter (Wellborn, Skelly & Werner, 1996) and eliminating species that cannot survive the harsh conditions. Therefore, dry seasons are able to reduce the variability of fish communities among sites (pools) that have similar hydroperiod (Chase, 2007). Here, we test the following hypotheses: (i) fish species occurrence in permanent and temporary pools is determined by a non-random process and (ii) fish community structure is related to abiotic factors linked to the changing hydroperiod and habitat characteristics of this aquatic system.

Methods

Location and site characteristics

The Yucatán peninsula in south-eastern México is a low flat plain of porous limestone that emerged above sea level in recent geological times (Lugo-Hubp, Aceves-Quesada & Espinasa-Pereña, 1992). Most areas near the coast are freshwater wetlands that are seasonally flooded (Zambrano *et al.*, 2006). Although close to a development for Cancún-Tulum tourism, the SKBR has been relatively free of anthropogenic perturbations, and the hydrological regime has remained unmodified (Zambrano *et al.*, 2006).

SKBR (area = 528.47 km²) is located along the east central coast of the Yucatán peninsula. The reserve has a strong seasonal rainfall pattern, receiving most precipitation from May to February (Olmsted & Durán, 1990). During the years of our study, most of the wetland reached its maximum annual water level at the end of the wet season. Water levels generally decline considerably during the short dry season (March–April). The freshwater wetland we studied comprises small permanent pools surrounded by tree islands known as 'petenes' in a flooded marsh matrix of sawgrass (*Cladium jamaicense* Crantz.), gulfcoast spikerush (*Eleocharis cellulosa* Torr. in Urb) and cattail (*Typha dominguensis* Pers.), where numerous temporary pools are also present. Permanent pools are deep (>3 m), oligotrophic, surrounded by palms (*Acoelorrhapha wrightii* Griseb. & H. Wendl.) and swamp hardwoods, common cane (*Phragmites australis* [Cav.] Trin.

Ex Steud) and in some cases, jicaco trees (*Chrysobalanus icaco* L.). Temporary pools are shallow (<1.5 m), surrounded by sawgrass and gulfcoast spikerush. In a previous study, 22 continental freshwater fish species were recorded from the SKBR (Zambrano *et al.*, 2006), with the most representative fish families in this area being Cichlidae, Poeciliidae, Characidae, Rivulidae, Pimelodidae and Symbranchidae.

Sampling took place during the dry and wet seasons in 2007, 2008 and 2009. We selected five permanent and five temporary pools that were similar in surface area and located near each other, such that they were interconnected during the wet season. Not all temporary pools could be sampled every year. In 2007, the wettest year, all five temporary pools were sampled. Only three temporary pools could be sampled in 2008. In 2009, the driest year, no temporary pools held water. Consequently, data from 2009 were not used in part of our analyses.

In all pools, water parameters were measured for 24 h every week during April, August–September and December–January from 2007 to 2009. We deployed a multi-parameter recorder sonde (YSI 6600; YSI Inc., Yellow Springs, OH, U.S.A.) at 0.3 m of depth in each pool to measure water temperature (°C), specific conductivity ($\mu\text{S cm}^{-1}$), total dissolved solids (g L^{-1}), salinity (ppt), saturation oxygen (%), chlorophyll *a* ($\mu\text{g L}^{-1}$) and pH. In this period, a 0.5-L water sample was also taken from each permanent and temporary pool from the surface near the fish sampling area. These were kept on ice for later analyses of nitrate (mg L^{-1}) and ammonium (mg L^{-1}) using a portable colorimeter (LaMotte smart colorimeter; LaMotte Co., Chestertown, U.K.). Water depth (cm) was measured at 30 points selected randomly in each pool, using a weight attached to a graduated nylon rope. Macrophyte coverage (%) was estimated in each pool from digital photographs taken from five points (east, west, north, south and centre), with a 1-m² plastic quadrat as a metric reference for each photograph. Images were processed with SigmaScan Pro 5 (Image Analysis Software; SPSS Inc., Chicago, IL, U.S.A.).

Fish sampling

Gee[®] minnow traps (2-mm mesh and a funnel entrance diameter of 20 mm) were used to estimate catch-per-unit-effort in each permanent and temporary pool. Based on our preliminary data from

different catching methods and according to Kobza *et al.* (2004), these traps are the most effective method for sampling fish in small waterbodies with complex dimensions and irregular edges. We set unbaited minnow traps for 24 h with the top of the trap 7–10 mm above the water surface to prevent fish mortality from low oxygen levels at night. After 24 h, fish were counted and identified *in situ* and then released. In the dry season, fish were sampled for 4 weeks during the 3 years (April 2007–09). In the wet season, fish sampling was conducted for 2 weeks during the warm rainy season (last week of August and first week of September from 2007 to 2009) and 2 weeks during the cool rainy season (last week of December and first week of January 2007–09). The average of fish abundances in each pool was used for comparisons. For fish identification and scientific names, we followed Nelson *et al.* (2004).

Data analysis

To test for differences in abiotic variables within seasons and years, we used one-way analysis of variance (ANOVA) separately for permanent and temporary pools, and pairwise multiple comparisons (Tukey test). We used principal component analysis (PCA) to ordinate abiotic data among permanent and temporary pools across years.

To analyse fish community structure, we normalised all relative abundance data, using the fourth square root transformation. Species exhibiting an abundance lower than 5% of the fish community were considered rare and excluded from analyses because rare species can have a high influence in community simulation tests (McCune & Grace, 2002; Kobza *et al.*, 2004). Non-metric multidimensional scaling (NMDS) was used as an ordination procedure to illustrate differences among fish communities. The NMDS ordination method is based on ranked Bray–Curtis dissimilarity distances and is not susceptible to problems associated with zero truncation. We used fish abundance in each pool to evaluate the percentage contribution of each species to a particular permanent or temporary pool community.

We used a null model of co-occurrence for testing random patterns in presence–absence data (Gotelli, 2000). This type of null model has been used to identify non-random patterns in fish communities, where an external variable (e.g. introduced non-native

species) had an effect on structure (Kobza *et al.*, 2004). We tested species co-occurrence in permanent and temporary pools' communities using the algorithm SIM2 in the EcoSim™ software (<http://garyentsminger.com/ecosim/index.htm>). Simulation with SIM2 using fixed rows–equiprobable columns randomises the occurrence of each species between sites. The co-occurrence index, *C*, provides a standardised effect score to scale the results in units of standard deviations and allows comparisons among tests. Significant differences suggest that deterministic forces (e.g. predation, competition, habitat characteristics) may influence community structure (Gotelli, 2000), while no statistical differences suggest random patterns. We tested for random patterns in fish community structure at two levels: (i) at the habitat level, analysing fish species in permanent and in temporary pools separately and (ii) at the wetland level, analysing fish species in both pool types together.

To understand the relationship between abiotic variables and the fish community, we correlated the pool scores of the three PCA axes to the community scores obtained from NMDS. To identify abiotic variables that affect total fish abundance in the whole wetland, we related total fish abundance to macrophyte coverage, ammonium, chlorophyll *a*, nitrates, pH, water depth, saturation oxygen, salinity, total dissolved solids and temperature, using a multiple regression analysis. Total abundance was logarithmically transformed (\log_{10}), and tolerances lower than 0.1 were used to indicate multicollinearity problems. We evaluated the relative importance of biotic interactions in the fish community, performing correlations among species abundances.

PCA, NMDS and species contribution analyses were performed with the software PRIMER 5.2.9 for Windows (PRIMER-Ltd, Plymouth, U.K.). SPSS 17.0 software was used for correlation and multiple regression analyses (SPSS Inc.).

Results

Pool characteristics

Mean values of abiotic variables in permanent and temporary pools differed in several characteristics across seasons and years. In dry seasons, the number of temporary pools varied because of differential drought effects among years. Water chemistry differed

significantly between seasons in all 3 years (Table 1). Ammonium, salinity and macrophyte coverage showed no significant differences among the 3 years in permanent pools, but the remaining environmental variables differed between years and seasons in both permanent and temporary pools. In the driest year, 2009, a *t*-test showed significant differences between seasons in temperature ($25.6^{\circ}\text{C} \pm 0.35$ SD wet season; $24.35^{\circ}\text{C} \pm 0.25$ dry season; $t = 6.489$, d.f. = 8, $P < 0.001$) and water depth ($72.31\text{ cm} \pm 11.35$ wet season; $24.12\text{ cm} \pm 2.93$ dry season; $t = 9.189$, d.f. = 8, $P < 0.001$) in permanent pools. There were no significant differences between seasons in 2009 for other abiotic variables.

In the 3 years of sampling, PCA explained c. 85% of variation in the first three components (Table 2). PCA clearly separated permanent pools from temporary pools in dry seasons, but pools showed no important differences in wet seasons (Fig. 1). During both seasons of 2007 and 2008, the first component (PC1) revealed strong associations with temperature, water depth, pH and macrophyte coverage. The second component (PC2) showed strong associations with salinity and chlorophyll *a*, and the third component (PC3) showed no associations with abiotic variables.

Fish species abundance and richness

A total of 11 687 fish of 13 species in six families were caught during the 3 years of sampling (mean abundance, percentage occurrence, species scientific names and authorities are shown in Table 3). Poeciliidae had the highest species number (five), while Cichlidae had four species and the other fish families only one species each. Abundances of *Cichlasoma urophthalmus* (1.63%), *Poecilia mexicana* (0.65%) and *Rivulus tenuis* were lower than 5% of the total and were excluded from analyses. *Ophisternon aenigmaticum* abundance was 4.5% of the total but was included in the analysis because of its position as a top predator. The 13 fish species were found in both permanent and temporary pools. *Xiphophorus maculatus*, *C. octofasciatus* and *Heterandria bimaculata* were the most abundant species in permanent pools in both seasons and all years. In temporary pools, *Gambusia sexradiata*, *Thorichthys meeki* and *Parachromis friedrichsthalii* were the most abundant species. *Astyanax aeneus* was more abundant in temporary pools than permanent pools in 2007 in both the dry and wet seasons. In 2008, however, this

Table 1 Mean values for abiotic variables in permanent and temporary pools in wet and dry seasons from 2007 to 2009

	Permanent pools				Temporary pools			
	Wet season		Dry season		Wet season		Dry season	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2007								
Temperature (°C)	27.07*†	0.55	24.43	0.41	28.11*†	0.42	29.78	1.51
Specific conductivity ($\mu\text{S cm}^{-1}$)	1.31*†	0.11	1.47	0.11	1.31†	0.11	1.42	0.07
Total dissolved solids (g L^{-1})	0.85*†	0.08	0.96	0.07	0.84†	0.07	0.93	0.05
Salinity (ppt)	0.73	0.04	0.74	0.06	0.69†	0.11	0.71	0.04
Saturation oxygen (%)	41.02†	25.22	11.16	2.28	32.43†	25.57	9.91	0.60
Water depth (cm)	77.94*	3.49	29.46	3.48	69.61*†	3.55	21.14	3.54
pH	8.99*†	0.05	7.41	0.12	8.99*†	0.33	7.89	0.40
Nitrates (mg L^{-1})	0.01*	0.00	0.01	0.00	0.01*†	0.00	0.01	0.00
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	3.28*	0.50	5.02	0.99	2.38*†	0.57	1.52	0.77
Ammonium (mg L^{-1})	1.70	2.57	0.89	0.28	0.44*†	0.19	0.63	0.14
Macrophyte coverage (%)	71.82	9.69	71.82	9.69	0.00	0.00	0.00	0.00
2008								
Temperature (°C)	23.44	0.35	24.82	0.61	24.57	0.69	27.25	0.35
Specific conductivity ($\mu\text{S cm}^{-1}$)	0.55	0.04	1.40	0.08	0.49	0.01	2.30	0.48
Total dissolved solids (g L^{-1})	0.36	0.03	0.91	0.06	0.32	0.01	1.42	0.30
Salinity (ppt)	0.73	0.04	0.79	0.05	0.69	0.11	0.75	0.05
Saturation oxygen (%)	30.54	8.36	22.49	0.96	36.17	1.60	32.65	5.08
Water depth (cm)	72.31	11.35	65.36	4.29	24.80	8.01	21.22	3.49
pH	7.18	0.09	8.53	0.02	7.76	0.17	8.86	0.13
Nitrates (mg L^{-1})	0.01	0.00	0.03	0.01	0.01	0.00	0.01	0.00
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	7.80	0.52	8.57	5.80	6.67	0.86	71.35	87.90
Ammonium (mg L^{-1})	1.06	1.32	1.13	0.19	0.44	0.19	27.20	13.06
Macrophyte coverage (%)	71.82	9.69	71.82	9.69	0.00	0.00	0.00	0.00
2009								
Temperature (°C)	25.60	0.35	24.35	0.25	–	–	–	–
Specific conductivity ($\mu\text{S cm}^{-1}$)	0.55	0.02	0.54	0.02	–	–	–	–
Total dissolved solids (g L^{-1})	0.35	0.01	0.35	0.01	–	–	–	–
Salinity (ppt)	0.26	0.01	0.26	0.01	–	–	–	–
Saturation oxygen (%)	38.86	34.63	33.99	6.56	–	–	–	–
Water depth (cm)	72.31	11.35	24.12	2.93	–	–	–	–
pH	7.55	0.09	7.55	0.06	–	–	–	–
Nitrates (mg L^{-1})	–	–	0.01	0.00	–	–	–	–
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	–	–	8.65	5.74	–	–	–	–
Ammonium (mg L^{-1})	–	–	0.97	0.23	–	–	–	–
Macrophyte coverage (%)	71.82	9.69	71.82	9.69	–	–	–	–

SD, standard deviation; –, Insufficient data for analysis or absence of sites.

*Significant differences among years ($P \leq 0.05$).†Significant differences between seasons ($P \leq 0.05$).

species was more abundant in permanent than temporary pools in both seasons.

Fish community structure

There were pronounced differences between fish communities in permanent and temporary pools that were consistent across years (Fig. 2). Correlations of species abundances to NMDS axes showed that *X. maculatus*, *C. octofasciatum*, *H. bimaculata* and *Rham-*

dia guatemalensis were characteristic of fish communities of permanent pools, while *G. sexradiata*, *T. meeki* and *Poecilia orri* were characteristic of temporary pools (Table 4), although minor variations in patterns were present across seasons.

Factors structuring fish communities

Null model tests indicated random patterns of species co-occurrence when permanent (effect size = 1.225,

Table 2 Principal component analysis of abiotic variables in permanent and temporary pools in wet and dry seasons from 2007 to 2008

	Wet season			Dry season		
	PC1	PC1	PC3	PC1	PC2	PC3
<i>2007</i>						
Eigenvalues	3.92	3.14	1.52	5.71	2.41	1.09
%Variation	35.6	28.5	13.8	51.9	21.9	9.9
Cum.%Variation	35.6	64.2	78	51.9	73.8	83.7
Variables						
Temperature (°C)	0.326	-0.399	-0.065	0.386	0.213	-0.005
Specific conductivity ($\mu\text{S cm}^{-1}$)	-0.414	-0.289	0.029	-0.268	0.485	-0.131
Total Dissolved solids (g L^{-1})	-0.437	-0.254	0.017	-0.27	0.484	-0.122
Salinity (ppt)	-0.386	-0.068	-0.185	-0.291	0.453	-0.124
Saturation oxygen (%)	0.251	0.278	-0.39	-0.208	-0.067	0.512
Water depth (cm)	-0.138	0.382	-0.043	-0.346	-0.218	-0.264
pH	0.296	0.249	0.026	0.308	0.254	0.005
Nitrates (mg L^{-1})	0.095	-0.12	-0.743	0.011	-0.162	-0.724
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	-0.243	0.439	0.203	-0.389	-0.166	0.18
Ammonium (mg L^{-1})	-0.286	-0.039	-0.399	-0.314	0.09	0.202
Macrophyte coverage (%)	-0.251	0.441	-0.231	-0.338	-0.32	-0.155
<i>2008</i>						
Eigenvalues	5.55	1.83	1.66	7.33	1.62	0.93
%Variation	50.5	16.6	15.1	66.6	14.7	8.5
Cum.%Variation	50.5	67.1	82.2	66.6	81.3	89.8
Variables						
Temperature (°C)	0.374	-0.032	0.28	-0.339	0.129	0.266
Specific conductivity ($\mu\text{S cm}^{-1}$)	-0.382	0.236	0.132	-0.336	0.029	-0.218
Total Dissolved solids (g L^{-1})	-0.382	0.238	0.128	-0.328	0.025	-0.246
Salinity (ppt)	-0.155	-0.477	-0.023	0.054	-0.713	0.137
Saturation oxygen (%)	0.246	0.39	-0.036	-0.281	0.372	0.217
Water depth (cm)	-0.247	0.273	0.525	0.315	0.246	-0.148
pH	0.384	0.01	0.209	-0.354	-0.058	-0.235
Nitrates (mg L^{-1})	-0.134	-0.219	0.644	0.25	0.296	-0.63
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	-0.324	0.127	-0.39	-0.24	-0.408	-0.494
Ammonium (mg L^{-1})	-0.154	-0.606	0.009	-0.331	0.084	-0.132
Macrophyte coverage (%)	-0.359	-0.015	-0.029	0.359	-0.105	-0.142

PC1, Principal component 1; PC2, Principal component 2; PC3, Principal component 3.

$P = 0.126$) and temporary pools (effect size = 0.463, $P = 0.296$) were analysed separately. This suggests a randomly structured fish community within each type of system. However, the null model indicated a non-random pattern when permanent and temporary pools were analysed together (effect size = 3.786, $P = 0.002$).

Correlations between PCA scores and NMDS axes revealed significant negative correlations in wet seasons (PCA axis 2/NMDS axis 1: $r = -0.695$, $P = 0.025$; PCA axis 1/ NMDS axis 1: $r = -0.73$, $P = 0.015$; for 2007 and 2008, respectively) and significant positive correlations in dry seasons (PCA axis 1/NMDS axis 1: $r = 0.91$, $P < 0.001$; PCA axis 1/NMDS axis 1: $r = 0.95$; $P < 0.001$; for 2007 and 2008, respectively). Correlat-

tions between abiotic variables and NMDS axis 1 indicated that temperature, water depth, macrophyte coverage and pH were highly correlated in wet and dry seasons, in 2007 and 2008 (Table 5). Other abiotic variables such as chlorophyll *a*, conductivity, ammonium and nitrates were correlated with NMDS axis 1, but these were not constant across years and seasons (Table 5).

Multiple regression analysis showed that 60.1% of the variance in total fish abundance was related to abiotic variables (abundance [\log_{10}] = $1.951 + 0.412$ Macrophyte Coverage - 0.033 Ammonium + 0.018 Chlorophyll *a* - 25.643 Nitrate - 0.092 pH - 0.019 Water Depth + 0.474 SO - 0.431 Saturation Oxygen + 0.597 Dissolved Solids + 0.013 Temperature;

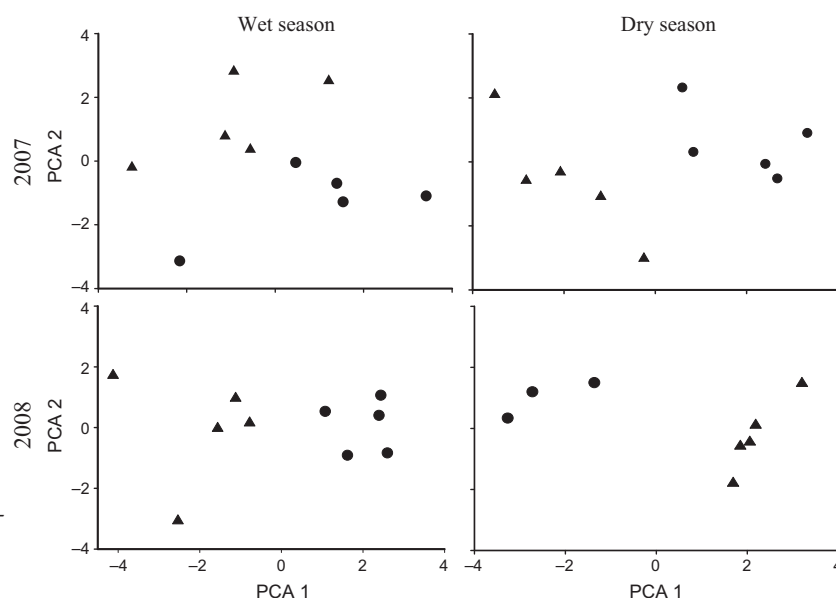


Fig. 1 Principal components analysis of abiotic variables for permanent (triangles) and temporary (circles) pools in wet and dry seasons in 2007 and 2008.

$R^2 = 0.601$, $F_{10,38} = 1.27$, $P = 0.002$). Abundance was predicted by water depth ($P < 0.001$, Tolerance = 0.36; Fig. 3a) and macrophyte coverage ($P = 0.035$, Tolerance = 0.34; Fig. 3b) but not by temperature ($P = 0.664$, Tolerance = 0.23), salinity ($P = 0.829$, Tolerance = 0.67), dissolved solids ($P = 0.438$, Tolerance < 0.001), ammonium ($P = 0.12$, Tolerance = 0.058), chlorophyll *a* ($P = 0.16$, Tolerance = 0.13), nitrates ($P = 0.116$, Tolerance = 0.4), pH ($P = 0.572$, Tolerance = 0.23) and saturation oxygen ($P = 0.536$, Tolerance = 0.43).

Fish abundance correlations revealed that *G. sexradiata* and *A. aeneus* was the only pair highly correlated ($r = 0.822$). Abundance relations among the other species were all $\leq r = 0.5$. No significant negative correlation was found.

Discussion

Rainfall-driven hydrology is a key factor in the seasonality of tropical aquatic environments (Sander-son *et al.*, 2005), and the wetland in this study has significant seasonal hydrological variation and spatial flooding heterogeneity. Dry seasons are characterised by extreme values of most limnetic variables, suggesting that environmental conditions can be harsh for fish, especially in temporary pools. During the dry season, pools were clustered into two groups. Permanent pools were deeper, more vegetated and colder than shallower and warmer temporary pools. How-

ever, in the wet season, floods connected all pools and created a system that was relatively homogeneous in water quality.

The fish species found in permanent and temporary pools are widely distributed in wetlands and cenotes (sinkholes) and represent 59% of all continental fish diversity in the SKBR (Zambrano *et al.*, 2006). At the habitat scale (permanent or temporary pools), we found a random pattern in fish species occurrence, which is likely to be related to homogeneity among the pools. At the whole wetland scale, fish species occurrence showed a non-random pattern and seems to be structured by deterministic factors in each type of habitat (e.g. pool morphology, abiotic factors or biotic interactions).

Fish community structure was consistently different between temporary and permanent pools across years. This is not surprising because species composition of standing-water communities often differs between permanent and temporary habitats (Schneider & Frost, 1996; Williams, 1996; Werner *et al.*, 2007; Wissinger *et al.*, 2009). The three fish life history strategies that have been identified (equilibrium, seasonal and opportunistic) and their relationships to certain habitat characteristics (according to habitat templet theory: Southwood, 1977; Townsend & Hildrew, 1994) may explain the differential distribution of species in these systems. Fish species with an 'equilibrium strategy' have parental care and prolonged breeding seasons and live in deeper and more stable habitats such as

Table 3 Mean fish abundances (MA) and occurrence (%) of each species caught in permanent and temporary pools in wet and dry seasons from 2007 to 2009

Season	Year	Permanent pools				Temporary pools			
		Wet		Dry		Wet		Dry	
Species		MA	(%)	MA	(%)	MA	(%)	MA	(%)
<i>Characidae</i>									
<i>Astyanax aeneus</i>	2007	23	0.10	67	0.12	123	0.27	179	0.11
Günter, 1860	2008	934	0.30	100	0.04	135	0.18	16	0.03
	2009	6	0.02	87	0.09	*	*	*	*
<i>Rivulidae</i>									
<i>Rivulus tenuis</i>	2007	0	0.00	0	0.00	0	0.00	16	0.01
Meek, 1904	2008	14	0.00	11	0.00	0	0.00	0	0.00
	2009	0	0.00	0	0.00	*	*	*	*
<i>Cichlidae</i>									
<i>Cichlasoma octofasciatus</i>	2007	17	0.08	214	0.39	20	0.04	2	0.00
Regan, 1903	2008	97	0.03	111	0.05	267	0.36	12	0.02
	2009	55	0.21	263	0.27	*	*	*	*
<i>C. urophthalmus</i>	2007	2	0.01	25	0.05	1	0.00	2	0.00
Günter, 1862	2008	0	0.00	4	0.00	0	0.00	0	0.00
	2009	0	0.00	0	0.00	*	*	*	*
<i>Parachromis friedrichsthalii</i>	2007	11	0.05	10	0.02	28	0.06	56	0.03
Heckel, 1840	2008	1	0.00	9	0.00	1	0.00	32	0.06
	2009	0	0.00	0	0.00	*	*	*	*
<i>Thorichthys meeki</i>	2007	8	0.04	18	0.03	39	0.09	108	0.06
Brind, 1918	2008	0	0.00	5	0.00	7	0.01	46	0.09
	2009	0	0.00	4	0.00	*	*	*	*
<i>Poeciliidae</i>									
<i>Xiphophorus maculatus</i>	2007	124	0.56	73	0.13	165	0.36	224	0.13
Günter, 1866	2008	1542	0.50	1440	0.60	5	0.01	24	0.05
	2009	136	0.52	315	0.32	*	*	*	*
<i>Heterandria bimaculata</i>	2007	33	0.15	57	0.10	2	0.00	4	0.00
Heckel, 1848	2008	339	0.11	625	0.26	14	0.02	3	0.01
	2009	59	0.23	290	0.29	*	*	*	*
<i>Gambusia sexradiata</i>	2007	1	0.00	0	0.00	65	0.14	1032	0.62
Hubbs, 1936	2008	129	0.04	83	0.03	287	0.39	305	0.60
	2009	1	0.00	6	0.01	*	*	*	*
<i>Poecilia orri</i>	2007	0	0.00	4	0.01	8	0.02	40	0.02
Fowler, 1943	2008	10	0.00	9	0.00	9	0.01	71	0.14
	2009	0	0.00	0	0.00	*	*	*	*
<i>P. mexicana</i>	2007	0	0.00	0	0.00	1	0.00	8	0.00
Steindachner, 1863	2008	0	0.00	0	0.00	0	0.00	0	0.00
	2009	0	0.00	0	0.00	*	*	*	*
<i>Symbranchidae</i>									
<i>Ophisternon aenigmaticum</i>	2007	4	0.02	4	0.01	2	0.00	5	0.00
Rosen and Greenwood, 1976	2008	0	0.00	3	0.00	4	0.01	1	0.00
	2009	3	0.01	6	0.01	*	*	*	*
<i>Pimelodidae</i>									
<i>Rhamdia guatemalensis</i>	2007	0	0.00	75	0.14	2	0.00	2	0.00
Günter, 1864	2008	37	0.01	7	0.00	6	0.01	0	0.00
	2009	0	0.00	13	0.01	*	*	*	*

*Temporary pools were absent.

slow-flowing ponds, river channels and most lakes (Winemiller, 1989; Lamouroux, Poff & Angermeier, 2002; Vila-Gispert, Moreno-Amich & García-Berthou,

2002). This seems to be the strategy of *C. octofasciatus*, *H. bimaculata*, *R. guatemalensis* and *O. aenigmaticum*, which are abundant in permanent pools of the SKBR.

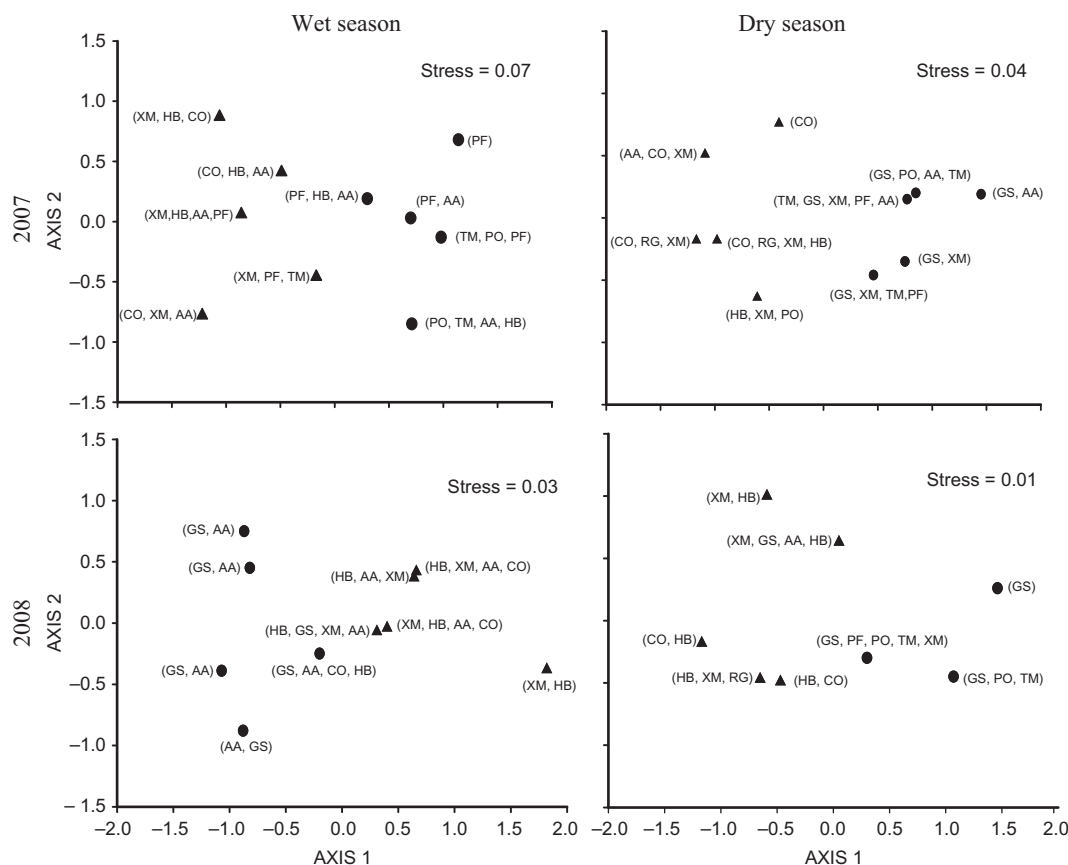


Fig. 2 Non-metric multidimensional scaling ordinations of fourth square root fish community data in permanent (triangles) and temporary (circles) pools in wet and dry seasons in 2007 and 2008. Species that contributed 90% or more to the fish community are represented in parentheses: GS = *G. sexradiata*, AA = *A. aeneus*, TM = *T. meeki*, XM = *X. maculatus*, HB = *H. bimaculata*, PO = *P. orri*, PF = *P. friedreshthalii*, CO = *C. octofasciatum*, RG = *R. guatemalensis*.

These species are typically associated with deeper-shaded waters (Miller, 2005).

Fish associated with temporary pools in the SKBR are categorised either in the 'seasonal strategy' or in the 'opportunistic strategy'. Fish in temporary pools must cope with periodic drying periods that impose severe constraints on development and life history (Gelwick *et al.*, 2001; DeAngelis, Trexler & Loftus, 2005). Fish with the 'seasonal strategy' have synchronised reproduction, with high fecundity, during the early wet season and inhabit seasonal ecosystems (Winemiller, 1989; Lamouroux *et al.*, 2002; Vila-Gispert *et al.*, 2002). Fish with this strategy in the SKBR, including *A. aeneus*, *R. tenuis* and *T. meeki*, are widespread and tolerate a wide variety of habitats such as seasonal ponds, rivers and coastal lagoons (Miller, 2005). Most poecilids in the SKBR wetlands are categorised as 'opportunistic strategy', living in fluc-

tuating and shallow habitats such as small streams, river channels, temporary pools and wetlands (Gelwick *et al.*, 2001; Vila-Gispert *et al.*, 2002; DeAngelis *et al.*, 2005). These species, including *G. sexradiata* and *P. mexicana*, are usually small with early maturation and an ability to rapidly colonise (Miller, 2005).

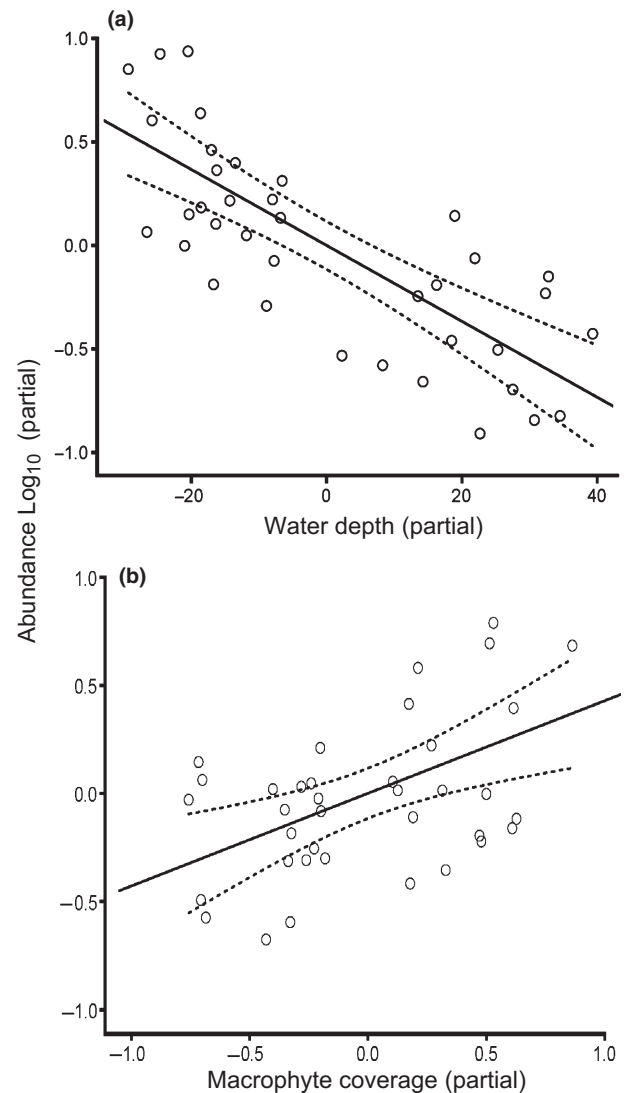
In seasonal habitats such as river floodplains or wetlands, fish community structure is related to abiotic variables that change in response to hydroperiod, including water depth, temperature, dissolved oxygen and macrophyte coverage (Capone & Krushlan, 1991; Magoulick, 2000; Gelwick *et al.*, 2001; Pazin *et al.*, 2006; Louca *et al.*, 2009), rather than pH, area, water velocity or water discharge, which are important in rivers and lakes (Lamouroux *et al.*, 2002; Öhman *et al.*, 2006). Contrasting seasonal hydroperiods seem to affect fish community structure and total abundance in the whole of the studied wetland.

Table 4 Pearson correlations coefficients (r values) of species abundances and non-metric multidimensional scaling axes in wet and dry seasons in 2007 and 2008. Only significant correlations are shown ($P < 0.05$)

Year	2007		2008	
Season	Wet r	Dry r	Wet r	Dry r
<i>Axis 1</i>				
<i>C. octofasciatus</i>		-0.875		
<i>T. meeki</i>	0.748			
<i>H. bimaculata</i>	-0.745			
<i>G. sexradiata</i>		0.745		-0.816
<i>P. orri</i>	0.703			-0.71
<i>R. guatemalensis</i>		-0.761	0.786	
<i>Axis 2</i>				
<i>X. maculatus</i>				0.808
<i>H. bimaculata</i>				0.723
<i>Axis 3</i>				
<i>A. aeneus</i>				0.723
<i>C. octofasciatus</i>	-0.671			
<i>X. maculatus</i>	0.668			

Table 5 Pearson correlations coefficients (r values) of abiotic variables and non-metric multidimensional scaling axes in wet and dry seasons in 2007 and 2008. Only significant correlations are shown ($P < 0.05$). MDS axes 2 and 3 did not present significant correlations to any abiotic variable

Abiotic variable	MDS Axis 1 r
2007	
Wet season	
Temperature (°C)	-0.888
Specific conductivity ($\mu\text{S cm}^{-1}$)	-0.687
Saturation oxygen (%)	-0.929
pH	-0.747
Macrophyte coverage (%)	0.902
Dry season	
Temperature (°C)	0.956
Water depth (cm)	-0.918
pH	0.726
Chlorophyll a ($\mu\text{g L}^{-1}$)	-0.858
Macrophyte coverage (%)	-0.929
Ammonium (mg L^{-1})	-0.440
2008	
Wet season	
Temperature (°C)	-0.642
pH	-0.854
Chlorophyll a ($\mu\text{g L}^{-1}$)	0.697
Macrophyte coverage (%)	0.823
Nitrates (mg L^{-1})	0.252
Dry season	
Temperature (°C)	0.716
Water depth (cm)	-0.728
Macrophyte coverage (%)	-0.894

**Fig. 3** Partial regressions, testing the effects of (a) water depth and (b) macrophyte coverage on total fish abundance. Only significant relationships are shown ($P < 0.05$). Dotted lines indicate 95% confidence intervals.

Specifically, community structure was related to water depth, macrophyte coverage, pH and temperature, while abundance was affected only by water depth and macrophyte coverage.

Macrophyte coverage is positively related to food availability for fish, such as insects and other invertebrates (Díaz-Valenzuela, unpubl. data). Macrophytes also provide spawning sites and shelter from potential predators (Gelwick *et al.*, 2001; Ye *et al.*, 2006). Water depth is normally positively related to fish abundance (e.g. Therriault & Kolasa, 1999; Brooks

et al., 2005) because a greater volume provides more space to support more individuals. Nevertheless, we found a negative relationship between total fish abundance and water depth in pools of the SKBR, a pattern that may be related to fish migration to shallow waters in the wet season for breeding and feeding. But fish may move to permanent pools in the dry season to obtain refuge (Lowe-McConnell, 1975; Loftus & Kushlan, 1987).

The structure of fish communities depends on the strengths of various biotic and abiotic factors. Most of the literature suggests that fish communities in variable aquatic systems are influenced mainly by local abiotic factors (e.g. Rahel, 1984; Loftus & Eklund, 1994; Suárez *et al.*, 2004), with little or no influence of biotic factors (e.g. Snodgrass *et al.*, 1995). Nevertheless, biotic interactions such as competition and predation have been shown to be important factors structuring some fish communities (Peckarsky & Dodson, 1980; Matthews, Harvey & Power, 1994; Magoulick, 2000). In our study, the lack of negative relationships between pairs of species in pools suggests low competition among the species. However, predation may be influential given our finding that 38.5% of species are predators (two top predators, *R. guatemalensis* and *O. aenigmaticum*, and three opportunistic predators, *A. aeneus*, *C. octofasciatus* and *P. friedrichsthalii*; Neil, 1984). Perhaps the strength of the environmental filter obscures any competitive and predator–prey interactions that exist and further research is called for.

Small temporary waterbodies usually occur scattered in the landscape among permanent and semi-permanent waterbodies (Sanderson *et al.*, 2005). This is the case of our study system of permanent pools in a flooded marsh matrix, where numerous temporary pools are also present. At the landscape scale, habitat patches provide corridors when they are connected and refuges when they are isolated and perform an important role in the maintenance of biodiversity and ecological processes such as metacommunity and metapopulation processes (DeAngelis *et al.*, 1997; Magoulick & Kobza, 2003; Kobza *et al.*, 2004; De Meester *et al.*, 2005).

We found that abiotic variables and habitat characteristics are the major factors structuring fish communities in the pristine SKBR wetland. We suggest that the presence of permanent and temporary pools in the SKBR may play an important role in maintaining fish

diversity at the landscape scale since they showed dissimilar fish communities and can function as refuges in extreme dry seasons.

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