



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

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# **POSGRADO EN CIENCIAS BIOLÓGICAS**

INSTITUTO DE BIOLOGÍA

**“DINÁMICA ESTACIONAL EN LA COMUNIDAD DE  
PECES EN PETENES DE LA RESERVA DE LA  
BIÓSFERA DE SIAN KA´AN, QUINTANA ROO”**

## **T E S I S**

QUE PARA OBTENER EL GRADO ACADÉMICO DE

### **DOCTOR EN CIENCIAS**

P R E S E N T A

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Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 28 de febrero de 2011, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **ESCALERA VÁZQUEZ LUIS HUMBERTO** con número de cuenta **505016892** con la tesis titulada: **"Dinámica estacional en la comunidad de peces en petenes de la Reserva de la Biósfera de Sian Ka'an, Quintana Roo"**, realizada bajo la dirección del **DR. LUIS ZAMBRANO GONZÁLEZ**:

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Atentamente  
"POR MI RAZA HABLARÁ EL ESPÍRITU"  
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Dra. María del Coro Arizmendi Arriaga  
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y aún así el mar te matará, pero si  
eres buen marino sabrás en donde  
te encuentras al momento de morir.

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## RESUMEN

Los humedales de Sian Ka'an, Quintana Roo, presentan una marcada estacionalidad relacionada al régimen hídrico, lo que provoca variación en el nivel de agua. Esto produce una dinámica de parches representados por pozas permanentes (Petenes) y pozas temporales. La dinámica hidrológica promueve diferencias en el tiempo de conexión entre estas pozas, produciendo variaciones en las tasas de migración de peces presentes en la comunidad. Por lo tanto, este humedal representa un excelente sistema para el estudio de los procesos que determinan la diversidad y estructura de las comunidades animales. En este trabajo se analizó si la diversidad de la comunidad íctica se explica por procesos aleatorios (Cap I). Para esto determinamos las tasas de migración de las especies de acuerdo a: 1) modelos desarrollados por teóricos neutrales y por 2) métodos que evalúan tasas de migración con datos empíricos. Utilizando modelos neutrales, la distribución de abundancia de las especies se ajusta a una comunidad neutral. Sin embargo al utilizar métodos no neutrales para estimar tasas de migración, la distribución de abundancia de las especies no se ajusta a una comunidad neutral. Al tomar en cuenta los atributos biológicos de las especies, es difícil cumplir el supuesto que todas las especies en una comunidad son funcionalmente equivalentes. Aunado a esto, la variación estacional representa un filtro ambiental que afecta diferencialmente a las especies, al generar cambios en los factores abióticos. Por lo tanto se estudió el efecto de los factores abióticos y características del hábitat en la estructura de la comunidad de peces en pozas temporales (hábitats variables) y pozas permanentes (hábitats estables), las cuales se encuentran interconectadas dentro de un humedal con una marcada estacionalidad (lluvias y secas) (Cap. II). Los resultados mostraron que los factores más importantes relacionados con la estructura de la comunidad fueron: temperatura, profundidad, pH y cobertura vegetal, y que la estructura de la comunidad es diferente entre pozas permanentes y pozas temporales, lo cual sugiere que la estructura de las comunidades está relacionada con las características del hábitat. Estos resultados nos indican que la variación estacional juega un papel importante en la estructuración de la comunidad en este humedal. La variación ambiental se considera parte de los patrones hídricos del sitio, sin embargo, la duración de la época seca y la frecuencia de los eventos de inundación en la época de lluvias afecta diferencialmente a las especies. Considerando estas variaciones, evaluamos el impacto de la variación del régimen hídrico

sobre los patrones en la abundancia de las poblaciones de las especies del humedal (Cap. III). Los resultados muestran que los años 2008 y 2009 tuvieron un mayor número de días secos respecto al 2007. Las abundancias de cada especie presentaron diferencias respecto al tipo de hábitat, estacionalidad y año. Ninguna especie estuvo relacionada con el número de días secos a lo largo de los tres años de muestreo. Las especies que presentaron relaciones con los patrones de inundación fueron *A. aenus*, *R. guatemalensis* y *G. sexradiata*. La abundancia de *A. aenus* y *G. sexradiata* presentaron una relación positiva respecto al número de días inundados, mientras que *R. guatemalensis* mostró un efecto negativo respecto a los días de inundación. Las relaciones en los cambios de la abundancia de cada especie está relacionada con los patrones en el régimen hídrico del humedal de Sian Ka'an, así como con la clasificación de historias de vida de las especies (equilibrio, estacional u oportunista). El presente estudio muestra que la riqueza y abundancia de las especies de peces responde a la dinámica hidrológica del humedal, dando como resultado una comunidad de peces estructurada estacionalmente. Dicha estructura no se explica por modelos neutrales y se comprueba que los factores ambientales y la variación estacional juegan un papel más importante en estructurar la comunidad. Así también, se muestran los cambios que presentan las especies respecto a la abundancia relacionados al régimen hídrico del humedal. Este estudio es una de las primeras aproximaciones para conocer como se genera y mantiene la diversidad de peces en un humedal estacional.

## ABSTRACT

The Sian Ka'an wetlands present a pronounced seasonality related to the hydrologic regime, promoting variation in the water level. This produces a patchy dynamics represented by permanent (Petenes) and temporary pools. The hydrological dynamics promotes differences in time among pools connections, producing variations in fish migration rates. Thus, this wetland represents an excellent system for the study of processes that determine diversity and structure in animal communities. In the present study, random processes were evaluated as drivers of diversity in the fish community (Chap. I). To accomplish this, we determined fish species migration rates according to: 1) models developed by neutral theorists and; by 2) methods that evaluate migration rates with empirical data. Using neutral models, the species distribution abundance (SAD) fits to a neutral community. However, using non-neutral methods, the SADs do not fit to neutrality. Considering biological attributes, is difficult to accomplish the assumption that all species in a community are ecologically equivalent. In addition, the seasonal variation represents an environmental filter, affecting species differentially in relation to changes in abiotic factors. Therefore, the effect of the abiotic factors and habitat characteristics on the fish community in permanent (stable habitat) and temporary (variable habitat) pools, interconnected into a matrix of a seasonal wetland (Chap. II). Results showed that fish community in permanent pools is different compared to those of temporary pools. Temperature, depth, pH and vegetative cover, were the abiotic factors strongly related to fish community. This suggests that the habitat characteristics are factors related to fish community. The seasonal variation produce patterns in hydrological regime playing an important role in structuring seasonal fish communities. However, duration and frequency of dry and flood events affects species differentially. Considering these variations, we evaluated the relation of the wetland hydrological regime to species population patterns (Chap. III). Results showed that years 2008 and 2009 presented more dry days compared to 2007. Each species presented differences in abundances according to type of habitat, season and year. Number of dry days was not related to abundances to any species along the three years of sampling. The flood event was positively related to species such as *A. aenus*, and *G. sexradiata*; while *R. guatemalensis* was negatively related. We conclude

that, in the Sian Ka'an wetland the hydrological pattern is related to the species abundance. In the present study we showed that the species richness and abundance in fish species is a response to the wetland hydrological regime, and that seasonal fish communities are result of the abiotic interactions and habitat characteristics. These communities are not explained by neutral models, proving that environmental factors, habitat characteristics and species life history and biological attributes play a major role in structuring seasonal communities. The present study is one of the first approximations to know how fish diversity is generated and maintained in seasonal tropical wetlands.

## INTRODUCCIÓN GENERAL

El entendimiento de los factores, mecanismos y procesos que influyen sobre la estructura de la comunidad, es uno de los objetivos de mayor interés en la teoría ecológica (Hubbell, 2001; Chave, 2004; Tilman, 2004; Chase, 2007). A pesar de muchas décadas de desarrollo teórico y experimental, aún existe un debate sobre si las especies en las comunidades representan un grupo selecto de organismos ecológicamente compatibles (teorías deterministas), o simplemente son un subgrupo aleatorio del conjunto o “pool” regional de especies (teorías estocásticas). Muchos estudios han mostrado que la competencia y las condiciones ambientales pueden seleccionar a las especies que coexisten en un sitio en particular, e influir la abundancia local (Tilman, 1982; Wellborn et al., 1996). Estos estudios sustentan la teoría de ensamblaje de comunidades por diferenciación de nicho, la cual propone que las comunidades representan subgrupos no aleatorios de especies compatibles. Recientemente el debate sobre la estructura de la comunidad, se ha vigorizado por el desarrollo de la teoría neutral de diversidad y biogeografía (Bell 2000; Hubbell, 2001; Chave et al., 2002). Los modelos neutrales proponen que la estructura de las comunidades resulta de procesos estocásticos como colonización y extinción, y que no está influenciada por los caracteres de las especies, generando así comunidades ensambladas principalmente por dispersión. La diferencia entre las teorías deterministas y las teorías que proponen que las comunidades son resultado de procesos estocásticos, han generado una gran controversia en los últimos años (Simberloff y Conner, 1981; Gotelli y Graves, 1996; Hubbell, 2001, 2006).

La teoría neutral originalmente propuesta por Hubbell (2001) propone que la distribución de las especies en las comunidades está gobernada por un reemplazo aleatorio de individuos de una especie por individuos de otra, y supone una equivalencia funcional entre las especies. Este supuesto de equivalencia funcional implica que todos los individuos dentro y entre las especies tienen la misma probabilidad de reproducción y mortalidad. Por lo tanto, es clave para las predicciones de patrones neutrales en la distribución de la abundancia de especies (Chave 2004; Hubell, 2001, 2006). Hoy en día existen diferentes modelos neutrales: el modelo neutral de Bell (2000), el modelo

extendido de Hubbell (2001), y el modelo espacialmente estructurado de Chave et al. (2002).

La evidencia empírica a favor de las teorías estocásticas se ha obtenido principalmente en comunidades altamente diversas de bosques tropicales lluviosos a mayores escalas espacio-temporales (Latimer et al., 2005; Volkov et al., 2007), mientras que la mayoría de la evidencia empírica a favor de las teorías deterministas contempla estudios a escalas locales. En un esfuerzo por demostrar la validez de las teorías deterministas a mayores escalas, Kneitel y Chase (2004) proponen que las diferencias de nicho entre las especies, son resultado de compromisos (“trade-offs”), proveen una explicación convincente para los patrones de diversidad de especies en múltiples escalas espaciales, que permiten el desarrollo de una visión más general de la diversidad. De manera que incluir la teoría de nicho en este contexto espacial, provee una alternativa a los modelos neutrales (estocásticos) para explicar los niveles de diversidad a diferentes escalas espaciales.

Tanto las teorías que se basan en diferenciación de nicho (deterministas) como las teorías neutrales (estocásticas), han provisto ideas valiosas, pero ambas presentan explicaciones parciales sobre los patrones de diversidad. Este debate se ha tratado de forma dicotómica, intentando explicar la estructura de la comunidad mediada exclusivamente por procesos deterministas o exclusivamente por procesos estocásticos. Sin embargo, estas teorías no están necesariamente en conflicto. Por el contrario, pueden ser complementarias. El nuevo marco conceptual propuesto (i.e. Chave, 2004; Gaston y Chow, 2005; Holt, 2006; Chase, 2007; Mouillot, 2007; Vergnon et al., 2009; Palma, 2010) resalta la necesidad de desarrollar modelos mixtos que incorporen tanto procesos estocásticos como deterministas (modelos presumiblemente más cercanos a como realmente la naturaleza trabaja), y que exploren los factores que determinan la importancia relativa de cada uno.

En este sentido, un gran número de estudios se han enfocado en determinar cuáles son los factores que estructuran la comunidad en sistemas dulceacuícolas. La mayor parte de estos estudios, sugieren que las condiciones ambientales presentes afectan de manera

diferencial a los organismos que se encuentran en ellos. Estas condiciones son más constantes a lo largo del año en cuerpos de agua más grandes con regímenes de disturbio menores, mientras que en cuerpos de agua pequeños, las condiciones locales pueden ser severas en la temporada seca (Capone y Krushlan, 1991), ya que se generan cambios drásticos en las condiciones fisicoquímicas del agua (Mendonça et al., 2005). De manera que a nivel local, la estructura de la comunidad de peces está influenciada por las características fisicoquímicas del agua (Mendonça et al., 2005).

Los principales factores abióticos relacionados con la estructura de la comunidad son la temperatura del agua, contenido de oxígeno, tipo y disponibilidad de hábitat, profundidad, transparencia (Súarez, 2001, 2004; Zambrano et al., 2006), pH, tipo de sustrato y conductividad. También se ha reconocido que los factores bióticos como: la disponibilidad de alimento, producción primaria (Degani et al., 1998), depredación y competencia, mantienen la estructura y diversidad en las comunidades (Zaret y Rand, 1971).

Las variaciones en la cantidad y calidad de agua en ambientes acuáticos, están altamente relacionadas con los patrones hidrológicos (e.g. Kushlan, 1976; Collinson et al., 1995; Magoulick 2000; Baber et al., 2002; Magoulick y Kobza, 2003; Matthews y Marsh-Matthews, 2003; Baber et al., 2004; Brock et al., 2003; Pazin et al., 2006), y en algunas ocasiones se consideran como condiciones constantes de perturbación (ver Magoulick y Kobza, 2003). Por lo tanto, las comunidades de peces en ambientes altamente variables pueden estar influenciadas por estos eventos de disturbio, cambiando en mayor parte, la estructura, composición y procesos funcionales en comunidades locales (Magoulick, 2000), sobreviviendo únicamente aquellas especies que pueden resistir condiciones adversas y grandes hacinamientos por tiempos prolongados.

Los factores abióticos con los que se encuentra relacionada la estructura de la comunidad dependen en gran medida del tipo de ecosistema acuático. Por ejemplo, en ríos, existe una mayor relación con la longitud y tamaño del río y velocidad de la corriente (Zaret y Rand, 1971), mientras que en algunos lagos tropicales (e.g. en Ecuador y Costa



Rica), los gradientes altitudinales muestran una alta relación con los patrones en la estructura de la comunidad (Bussing y López, 1977; Galacatos et al., 2004). En humedales, la estructura de la comunidad se ha relacionado con los diferentes periodos hídricos (hidroperiodo), los cuales pueden durar desde pocos días o semanas (humedales efímeros), hasta años (humedales permanentes o semipermanentes (Magoulick y Kobza 2003; Kobza et al., 2004). Los factores abióticos parecen tener mayor importancia en estructurar comunidades de hábitats altamente variables, tales como: marismas (Kushland, 1976), riachuelos (Harrell, 1978, Matthews y Styron, 1981) y pequeños lagos (Tonn and Magnuson, 1982). No obstante, la gran mayoría de estos trabajos carece de un análisis de los patrones de distribución de la abundancia de las especies a una escala espacio-temporal mayor, y no contemplan la posible participación de procesos estocásticos en la estructuración de la comunidad.

Estudios recientes que tratan de explicar los patrones de diversidad y estructura de las comunidades de peces a una escala espacio-temporal mayor demuestran que tanto procesos estocásticos como deterministas juegan un papel importante en estructurar la comunidad. Por ejemplo, Magurran y Henderson (2003) estudiaron una comunidad íctica durante un período 21 años, y muestran que la composición de especies se repartió en especies persistentes con una distribución de abundancia no estocástica, y especies ocasionales con una distribución que se ajusta a modelos estocásticos. Chase (2007) en un estudio experimental con pozas permanentes con régimen hídrico estable y pozas temporales sometidas a eventos de sequía, muestra que la estructura de la comunidad en las pozas permanentes está gobernada por procesos estocásticos, mientras que la estructura de la comunidad de las pozas temporales que sufrieron eventos de sequía está relacionada con procesos deterministas que probablemente resultan de la selección de nicho. Estos estudios demuestran que los procesos estocásticos pueden jugar un papel importante en el ensamble de la comunidad en sistemas acuáticos relativamente estables. Sin embargo, los caracteres de las especies, así como la severidad del ambiente y la variación estacional en los factores abióticos, le otorgan una mayor importancia relativa a los procesos deterministas en la estructuración de las comunidades en sistemas acuáticos dinámicos.

Finalmente, como un modelo nulo para el estudio de la dinámica de la comunidad, las teorías neutrales proveen predicciones que pueden ayudar a determinar la importancia relativa de factores estocásticos o deterministas para la estructura de la comunidad. Sin embargo, se requiere de datos que capturen el comportamiento dinámico de sistemas ecológicos, y así, distinguir los efectos de los diferentes mecanismos y/o factores responsables en estructurar la comunidad. Estudios recientes sugieren que ambientes dinámicos en los que se presentan condiciones extremas, pueden ayudar a comprender la importancia relativa de los procesos que ensamblan la comunidad, así como identificar los factores que influyen dichos procesos (Chase, 2007). Las comunidades ícticas en pozas pequeñas de agua dulce, representan un sitio ideal para explorar los efectos de la severidad ambiental sobre los patrones de ensamble de comunidades, debido a que éstos albergan altos niveles de diversidad y funciones ecosistémicas importantes (Fukami, 2004). La composición de la comunidad de estas pozas en algunas ocasiones puede ser altamente variable, sugiriendo un posible papel en el ensamblaje estocástico de la comunidad (Chase y Leibold, 2002; Chase, 2003). Así mismo, la sequía estacional puede alterar la estructura de la comunidad al actuar como un fuerte filtro ambiental (Wellborn, 1996).

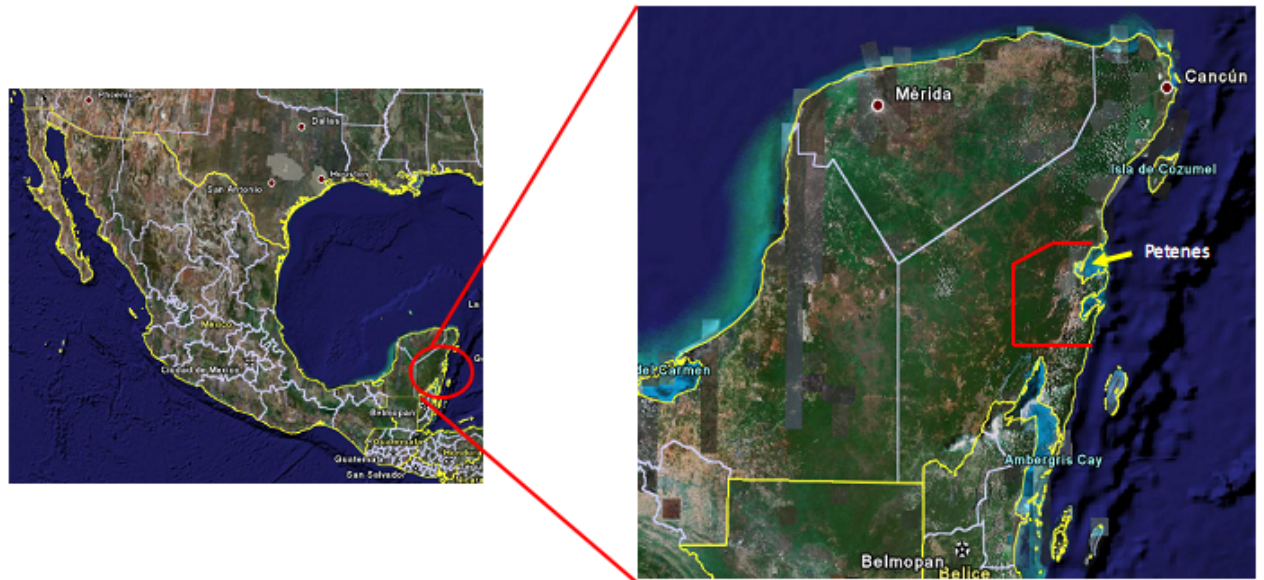
Los humedales de Sian Ka'an presentan una dinámica hídrica estacional, en donde se encuentran inmersos hábitats acuáticos permanentes y temporales, en los cuales, la conectividad o aislamiento está relacionada con el régimen hídrico estacional. (Zambrano et al., 2006). Esta característica hace de los humedales de Sian Ka'an un excelente modelo para estudiar patrones de ensamblaje de las comunidades ícticas dulceacuícolas, conocer los factores que están relacionados con la estructura de la comunidad, así como determinar cambios poblacionales de las diferentes especies en condiciones altamente variables que podrían explicar los cambios en la estructura de la comunidad.

## **SISTEMA DE ESTUDIO**

La Reserva de la Biosfera de Sian Ka'an (area = 528.47 km<sup>2</sup>), se encuentra en el estado de Quintana Roo, Municipio de Carrillo Puerto (Figura 1). La reserva cuenta con cenotes, humedales y cuerpos de agua temporales que presentan una marcada estacionalidad en su ciclo hídrico (Zambrano et al., 2006), dado que el agua acumulada tiende a evaporarse en la época de secas, mientras que en la época de lluvias gran parte del terreno está inundado (García-Bedoya, 2004).

Dentro de los humedales se encuentran pequeños cuerpos de agua permanentes conocidos como petenes, los cuales no han sido estudiados a pesar de que aparentemente desempeñan un papel importante en el funcionamiento del humedal, como sitios de refugio para el mantenimiento de la diversidad íctica. Las condiciones físicas y químicas del agua (oxígeno disuelto, pH, conductividad, temperatura) de los petenes y el humedal, presentan un amplio rango de variación a lo largo del año, particularmente en la época de secas (Baber et al., 2002). Por ejemplo, la temperatura del agua puede llegar hasta 35 °C y la concentración de amonio hasta 5 partes por millón (Zambrano et al., 2006). Durante la época de lluvias con el aumento del nivel de agua, los petenes se conectan a pozas temporales a través de zonas inundables, mientras que en la época de secas estos petenes se aíslan al disminuir el nivel de agua. Estudios previos reportan 22 especies de peces para la Reserva de la Biosfera de Sian Ka'an (Zambrano et al., 2006), de las cuales 13 (59%) (Tabla 1; Figura 2) se encuentran en el área representada por petenes.

Por los antecedentes expuestos, los petenes de la Reserva de la Biosfera de Sian Ka'an y el humedal al que estos pertenecen, representan un excelente modelo para el estudio de los patrones, procesos y mecanismos y factores que estructuran la comunidad. Además, la severidad ambiental en la época de secas permite estudiar el efecto de filtros ambientales sobre los mecanismos y factores que estructuran la comunidad.



**Figura 1.-** Ubicación geográfica de zona de Petenes dentro de la Reserva de la Biosfera de Sian Ka'an, Quintana Roo, México (Modificado de Google Earth 2011).

**Tabla 1.-** Especies encontradas en la zona de petenes en la Reserva de la Biosfera de Sian Ka'an.

Familia	Especie
Symbranchidae	<i>Ophisternon aenigmaticum</i> (Rosen & Greenwood 1976)
Characidae	<i>Astyanax fasciatus</i> (Cuvier 1819)
Poeciliidae	<i>Poecilia orri</i> (Fowler 1943) <i>P. mexicana</i> (Steindachner 1863) <i>Heterandria bimaculata</i> (Heckel 1848) <i>Gambusia sexradiata</i> (Hubbs 1936) <i>Xiphophorus maculatus</i> (Günther 1866)
Cichlidae	<i>Cichlasoma urophthalmus</i> (Günther 1862) <i>C. octofasciatus</i> (Regan 1903) <i>C. meeki</i> (Brind 1918) <i>C. friedrichsthalii</i> (Heckel 1840)
Rivulidae	<i>Rivulus tenuis</i> (Meek 1904)
Pimelodidae	<i>Rhamdia guatemalensis</i> (Quoy & Gaimard 1984)



*Astianax aeneus*



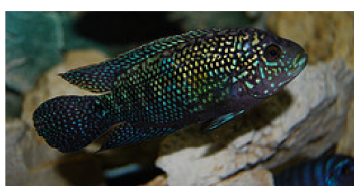
*Cichlasoma urophthalmus*



*C. meeki*



*Gambusia sexradiata*



*C. octofasciatus*



*C. friedrichsthalii*



*Poecilia orri*



*Xiphophorus maculatus*



*Heterandria bimaculata*



*P. mexicana*



*Rivulus tenuis*



*Ophisternon aenigmaticum*



*Rhamdia guatemalensis*

**Figura 2.-** Especies de peces encontradas en la zona de petenes la Reserva de la Biosfera de Sian Ka'an.

## **HIPÓTESIS GENERAL**

Debido a que la variación estacional produce un filtro ambiental que afecta a las especies, la estructura y diversidad de la comunidad íctica del humedal de Sian Ka'an estará determinada principalmente por factores y procesos no estocásticos, donde los factores abióticos y los atributos de las especies tendrán mayor importancia.

## **HIPÓTESIS PARTICULARES**

- La estacionalidad promueve cambios en la conexión de los sitios y dispersión de las especies dentro del humedal, por lo tanto la capacidad de dispersión y migración asociada a los atributos de cada especie explicará la diversidad de la comunidad del humedal.
- Los factores abióticos y características del hábitat fluctúan estacionalmente en el humedal, por lo que la estructura de la comunidad de peces estará relacionada con los cambios estacionales de factores abióticos y con las características de hábitat.
- La variación estacional e interanual del régimen hídrico (sequía e inundaciones) del humedal, promueve fluctuaciones ambientales que afectan de manera diferencial a los procesos biológicos que influyen sobre las poblaciones de las especies.

## **OBJETIVO GENERAL**

Estudiar la dinámica de la comunidad íctica en un humedal compuesto por petenes y pozas temporales en la Reserva de la Biósfera de Sian Ka'an y determinar los mecanismos y factores asociados a la estructura y diversidad de la comunidad.

## **OBJETIVOS PARTICULARES**

- Determinar si la migración de las especies explica los patrones de diversidad de la comunidad íctica.
- Analizar el efecto de la variación estacional de los factores abióticos sobre la estructura de la comunidad de peces.
- Analizar la respuesta de las poblaciones de peces a la variación estacional e interanual del régimen hídrico del humedal.



## **ESTRUCTURA DE LA TESIS**

En el presente trabajo se analizó la dinámica estacional de la comunidad íctica en un humedal. Para ello primero se determinó si los patrones de diversidad de la comunidad están determinados por procesos estocásticos o por procesos deterministas asociados a la capacidad de dispersión y migración de las especies. Estos resultados se presentan en el capítulo I.

Posteriormente en el capítulo II se analizó el efecto de la variación estacional de los factores abióticos y las características del hábitat sobre la estructura de la comunidad de peces.

Finalmente, en el capítulo III se analizaron las respuestas de las poblaciones de cada especie de la comunidad a la variación estacional e interanual del régimen hídrico del humedal.

# CAPÍTULO I

## ASSESSING THE IMPORTANCE OF MIGRATION AND BIOLOGICAL ATTRIBUTES IN THE ORGANIZATION OF A FISH COMMUNITY IN A SEASONAL WETLAND BY NEUTRAL MODELING\*

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\*Artículo para someter en la revista *OIKOS*

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## **Abstract**

Migration rate is an important parameter to describe biodiversity patterns in neutral models. However, migration rates are difficult to measure in large natural communities. Sian Ka'an wetlands present water level seasonal variation related to the hydrological dynamics, producing a patchy community represented by temporary and permanent pools. Hydrological dynamics determines differences in time connections among these pools, allowing the estimation of the migration rates of fish in the community. We obtained migration rate using the neutral theory framework and by using empirical migration rates methods. Both migration results (neutral and natural) were tested according with the Hubbell's (2001) neutral model. The studied fish community fits to neutral community predictions using migration rates obtained by neutral methods, whereas using empirical migration data from no-neutral methods, the biodiversity community patterns are not explained by neutral theory. When we use empirical migration data and consider on species identity is difficult to assume that all species in a community are functionally equivalent. In the present study, migration rate jointly to life history traits and species attributes are important in determining fish community.

**Keywords:** Migration, biological attributes, fish community, seasonality, wetland, neutrality.

## Introduction

The understanding of maintenance and origin of biodiversity has been the main goal in ecology. The theoretical development, experimentation, and field data on the study of ecological communities, have not a general idea about whether species abundances in communities represent a selected group of ecologically compatible organisms, or are a random subset of the regional species pool (Fuller et al. 2005). Niche-assembly theory of community structure suggests that communities represent non-random subsets of compatible species (Kneitel and Chase 2004; Tilman 2004), selected by competition and environmental conditions at a particular location (Bohannan and Lenski 2000; Brown et al. 2001). This theory is challenged by neutral hypotheses that propose that communities are random assemblages of species (Connor and Simberloff 1984).

Neutral community models are based on dynamic biological processes. Their dynamic nature means that neutral models can make testable predictions about patterns in space and time simultaneously (Bell 2005; Hubbell 2001, 2006, 2010). Hubbell proposed the “Unified Neutral Theory of Biogeography and Biodiversity” (UNTB), describing complex natural communities in a concise way. This theory offers a simple explanation of biodiversity patterns such as species-abundance distributions and species-area curves, assuming that all species are equivalent in their competitive ability (Holyoak et al. 2006). In the UNTB, the neutral patterns result from stochastic processes of birth, death, speciation and immigration (Etienne 2005), in which only the potential species richness of the community ( $\theta$ , fundamental biodiversity number) and the immigration parameter ( $m$ , its degree of isolation) are the relevant parameters in the model (Alonso and McKane 2004; Etienne 2005). In this model, when individuals die in a local community, they are replaced by offspring of other individuals from the same local community, or by immigrants from the regional species pool, maintaining the total number of individuals constant. This allows a saturated-equilibrium dynamics (Hubbell 2001; Wootton 2005).

The neutral model has been tested empirically in a few experimental and natural systems. In some of them, neutrality models predict community diversity by random

processes (i.e. Hubbell 2001; Muneeppeerakul et al. 2008), but others fail to explain diversity by neutral models (i.e. Adler 2004; Chase 2007; Fuller et al. 2005; Wootton 2005). Results from these studies suggest that the processes of community assembly can be different when examining patterns of biodiversity at different spatial and temporal scales. Problems in testing neutral models are related to parameters estimation. The applicability of sampling formulas generated to obtain  $\theta$  and  $m$  simultaneously has been questioned (Munoz et al, 2007).

In UNTB, the immigration parameter  $m$  (the probability that a death in the local community is replaced by the offspring of an individual from outside the local community) is obtained from the species abundance distribution (SAD), in a spatially implicit community, considering the assumption that a semi-isolated local community receives immigrants from a larger community that operates on a slower timescale (Chisholm and Lichstein 2009). In terms of interpretation,  $m$  obtained from UNTB has no clear biological relations to SADs, because it does not consider many processes that are known to operate in real ecosystems (Chisholm and Lichstein 2009).

Wootton (2005) suggests  $m$  is one of the several key parameters underlying the model dynamics, but it is difficult or nearly impossible to measure directly. General relationships describing the dependence of  $m$  on patterns of species dispersal and sampling design are not yet available (Chisholm and Lichstein 2009). Previous studies have estimated  $m$  by fitting theoretical neutral models to SADs in different ecosystems including: tropical forests, coral reefs and South African Fynbos (Ettiene 2005; Latimer et al. 2005; Volkov et al. 2007). However, the estimation of  $m$  in these studies is based on neutral assumptions which are not compared to no-neutral methods (Clark and Rosenzweig 1994; Haila and Hanski 1993; Harrison et al. 1988). Therefore, approaches for obtaining fundamental parameters with no-neutral methods are needed to compare the results obtained by neutral models (Munoz et al 2008; He and Hu 2005).

The goal of the present study was to estimate the migration parameter  $m$  from a neutral sampling formula and from a no-neutral method, and generate SADs under neutral

Hubbell's assumptions using the different  $m$  obtained. We used the Sian Ka'an Biosphere Reserve wetlands as study model. Sian Ka'an wetlands are located near to the coasts where most of the areas are freshwater wetlands that are seasonally flooded (Zambrano *et al.*, 2006). The hydrologic dynamics and topography of the reserve generate a matrix of wetlands comprising small permanent and temporary pools. Although close to a development for Cancún-Tulum tourism, the reserve has been relatively free of anthropogenic perturbations, and the hydrologic regime has remained unmodified (Zambrano *et al.*, 2006). Therefore, pristine and dynamical attributes of the system, and the responses of fish species compositions to hydrological variation offers the opportunity to understand community processes related to migration patterns. Comparisons on migration rates from empirical data and those obtained from neutral models can consolidate studies on neutrality, using methods according to systems dynamics and stability.

## Methods

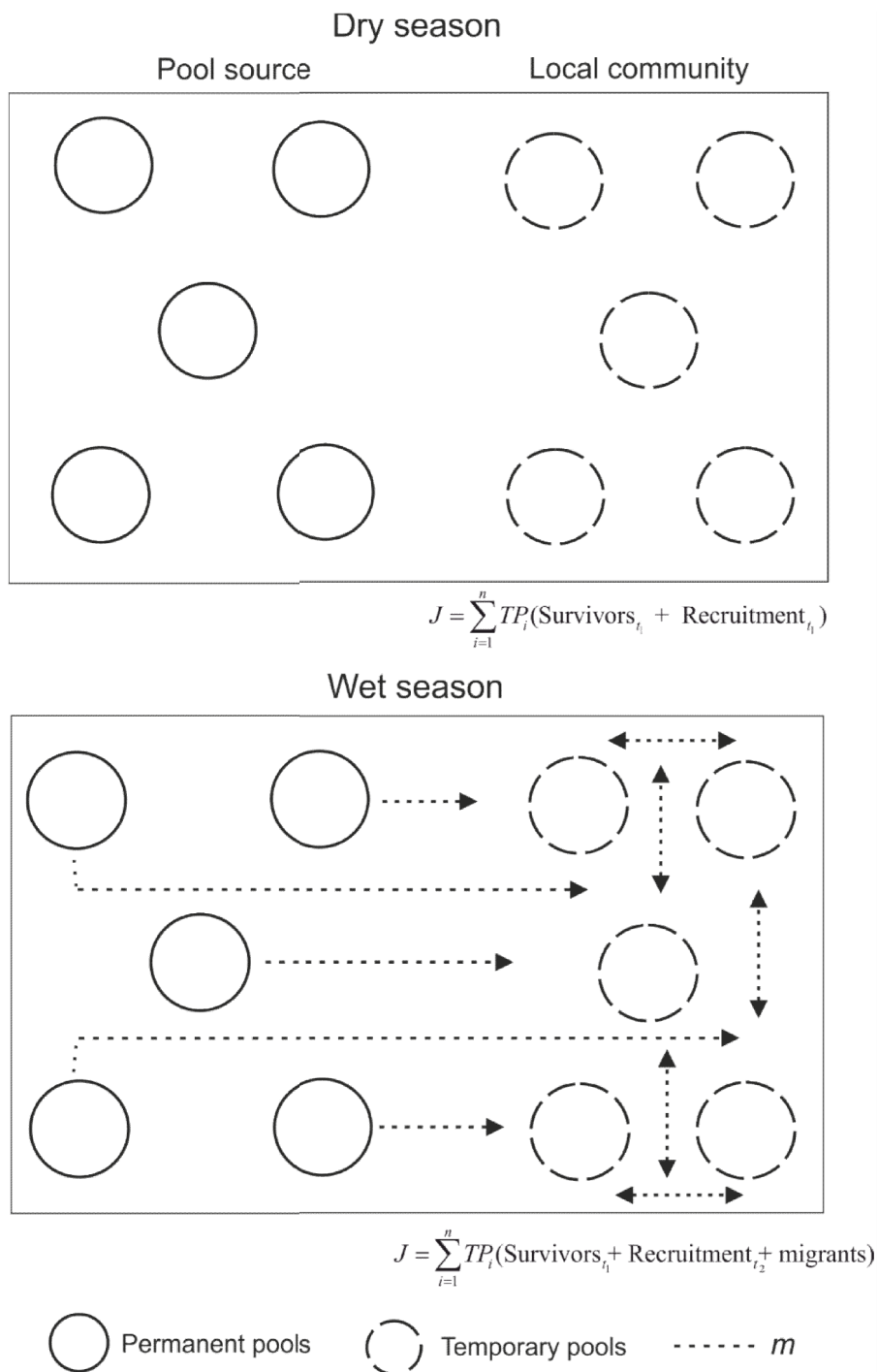
### *Study system*

The Sian Ka'an Reserve (area = 528.47 km<sup>2</sup>) is located in the east central coast of the Yucatan peninsula. The Reserve has a strong seasonal rainfall pattern, receiving most precipitation from May to February (Olmsted and Durán 1990). During the years of our data recording, 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 (Escalera-Vázquez and Zambrano 2010). This freshwater wetland comprises small permanent and temporary pools. In the Sian Ka'an Reserve wetland, 22 continental freshwater fish species were recorded (Zambrano *et al.*, 2006), with the most representative fish families in this area being Cichlidae, Poeciliidae, Characidae, Rivulidae, Pimelodidae and Symbranchidae.

Sian Ka'an wetland is an excellent system to study processes maintaining diversity of fish community for several reasons: 1) the system presents seasonal variation in water level, which allows to collect data on population and community dynamics considering dry

and wet seasons; 2) the size scale used can be considered as a mesocosm that allows the estimation of different parameters; and 3) the wetland can be considered as a local community linked to a source of individual via permanent pools. In dry season most fish remain in permanent pools, we assumed that fish migration in this system is from permanent pools (source pool) to temporary pools in wet seasons when water level reaches its maximum (Fig. 1). Therefore, the number of individuals ( $J$ ) in the local community in dry seasons is the result of the sum of the survivors in dry season ( $t_1$ ) and the recruits that were born in the same time ( $t_1$ ). Meanwhile, in wet seasons  $J$  is the result of the sum of the survivors in the previous time (dry season;  $t_1$ ), the new recruits that were born in wet season ( $t_2$ ) and the migrants from the pool source (Fig. 1). We considered seasonality in this wetland as a disturbance process. Disturbance generates deaths or emigration of local individuals, and eventually, the replacement of individual for births or immigration from the local or external community, disturbance is an assumption considered in Hubbell's model.

Sampling took place during dry and wet seasons from 2007 to 2010. 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 wet seasons.



**Figure 1.** Schematic representation of seasonal dynamics in the Sian Ka'an wetland, considering permanent and temporary pools in dry and wet season.  $J$ = local community size;  $TP$  = temporary pools;  $m$  = migration rate.



*Obtaining J,  $\theta$  and m parameters*

Based on our sampling method, we were able to use a spatial implicit model for metacommunities, considering that each temporary pool is a sample of the local community (wetland). We calculated the average size of the observed metacommunity size, and used this as an approximation of  $J_M$ . Based on species abundance data, we estimated  $\theta$  and  $m$  based on maximum-likelihood method from the Etienne (2005) metacommunity implicit algorithm (Equation 1). Estimations with Etienne's sampling formula (2005) use all information in the data considering that abundances are correlated to the zero-sum assumption.

Equation 1

$$P[D, \theta, m, J] = \frac{J!}{\prod_{i=1}^S n_i \prod_{j=1}^J \Phi_j!} \frac{\theta^S}{(\theta)_J} x \sum_{A=S}^J K(D, A) \frac{(\theta)_J I^A}{(\theta)_A (I)_J}$$

Once we got  $J_M$ ,  $\theta$  and  $m$ , we simulated 1000 species abundance curves according to Hubbell's neutral model. The 1000 simulations were compared with the observed species abundance curve using an analysis of covariance (ANCOVA) to find statistical differences among the observed and the neutral curves. To determine which migration rate fits neutrality, we used four arbitrary values of  $m$  with different magnitude degrees (1.0, 0.1, 0.01 and 0.001) generating species abundance distributions under the UNTB.

*Estimating m from empirical data*

Pools in Sian Ka'an represent a patchy location, where fish migration depends on movement of individuals among sites. To make an approach of migration rate, we estimated seasonal migration rate for each year from our data according to Gotelli and Taylor (1999). The migration rate is calculated as follows:

$$P_i = \frac{\text{Number of times a site was unoccupied at time } (t) \text{ but was occupied at time } (t + 1)}{\text{number of time the site was occupied at time } (t)}$$

We estimated  $m$  for each species because the fish species in this wetland show different biological attributes (Table 1), that can influence their migration ability (Wellborn et al. 1996). Rates obtained were averaged across species for each site in each year to give a migration rate/year. We estimated  $\theta$  including the obtained  $m$  for each year and simulated 1000 species abundance curves according to Hubbell's neutral model but including  $\theta$  and  $m$  obtained from the empirical data. We compared the observed SAD curves using an analysis of covariance (ANCOVA) to find statistical differences among the observed and the obtained curves. We will refer to the  $m$  obtained from Ettiene (2005) as "neutral  $m$ " and the  $m$  obtained from Gotelli and Taylor (1999) as "natural  $m$ ".

*Ecological drift dynamics under UNTB*

For SADs that fit to neutral model (by year), we simulated random birth, death and migration with Hubbell's neutral dynamics algorithm. We determined the proportions of species in the observed community, starting with a single individual of a single species ( $J = 1, S = 1$ ). New individuals were incorporated to the community until the maximum size,  $J$ , was reached. With probability  $\theta / (\theta + j - 1)$ , an individual is assigned to be a new (previously unrecorded) species, where  $J$ , is the current number of individuals in the community. With probability  $1 - [\theta / (\theta + j - 1)]$ , the individual is randomly assigned to a pre-existing species. In the latter case, the probability of being assigned to a particular species  $i$ , is equal to the

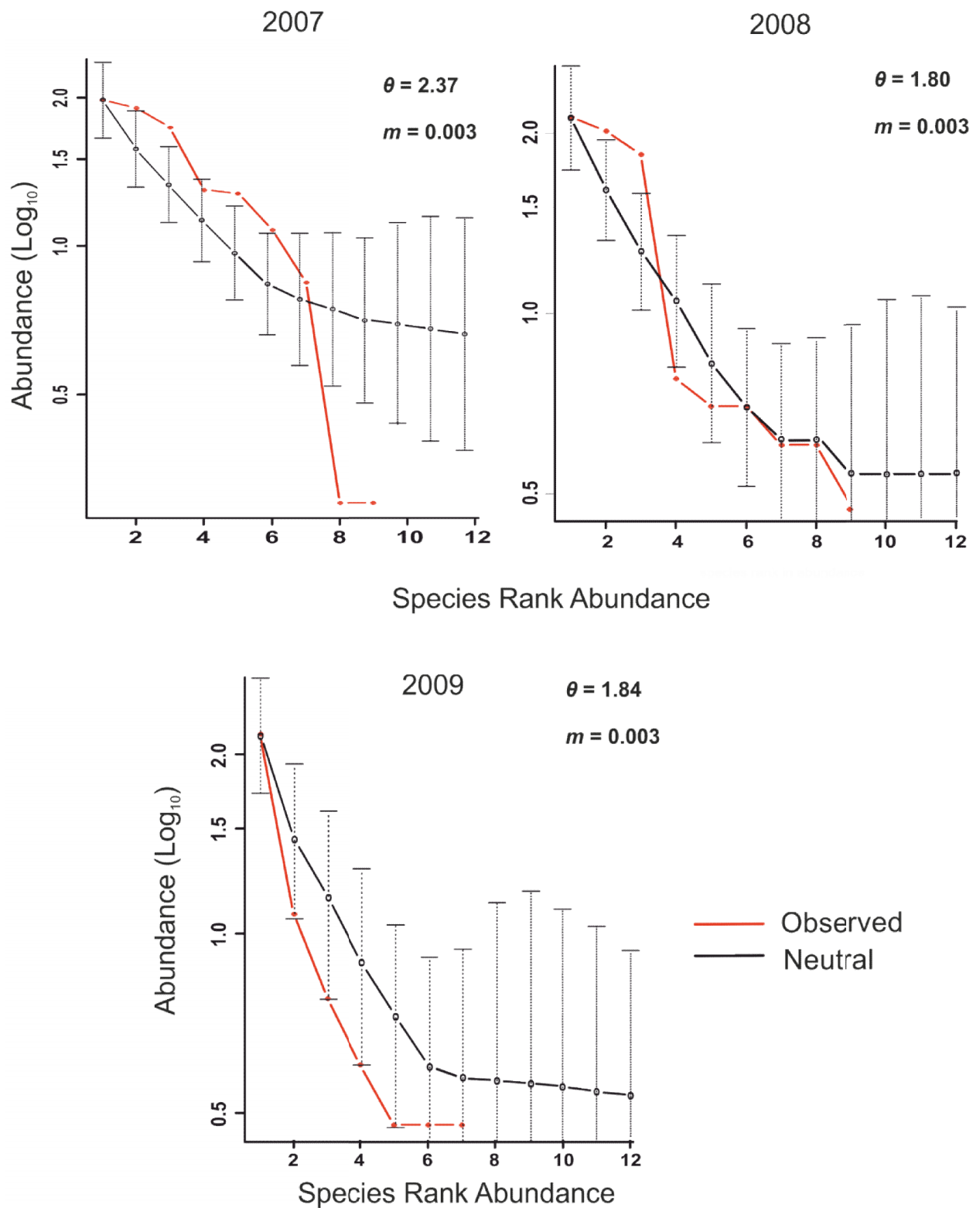
current proportion of that species in the community. This process is continued until all  $J$  individuals have been added and assigned to a species  $i$ .

To model ecological drift under UNTB, we used four parameters: 1) the natural community size,  $J$ ; 2) the per capita probability of migration,  $m$ ; 3) the disturbance level,  $D$ , which is the proportion of the community that is replaced each generation; and 4) simulation of the community dynamics for 1000 generations.  $D$  was estimated from empirical data recorded in wet and dry seasons from Sian Ka'an wetland, assuming the decrease in mean total abundance in dry season was the result of individual deaths and migrations. The mean abundance decrease obtained from three year of sampling was used as an estimation of  $D$ . Analyses were performed with the package "untb" developed by Hankin (2007) for the software R 2.11.1 for windows. We classified biological attributes of each species based on literature available for family, genus or species.

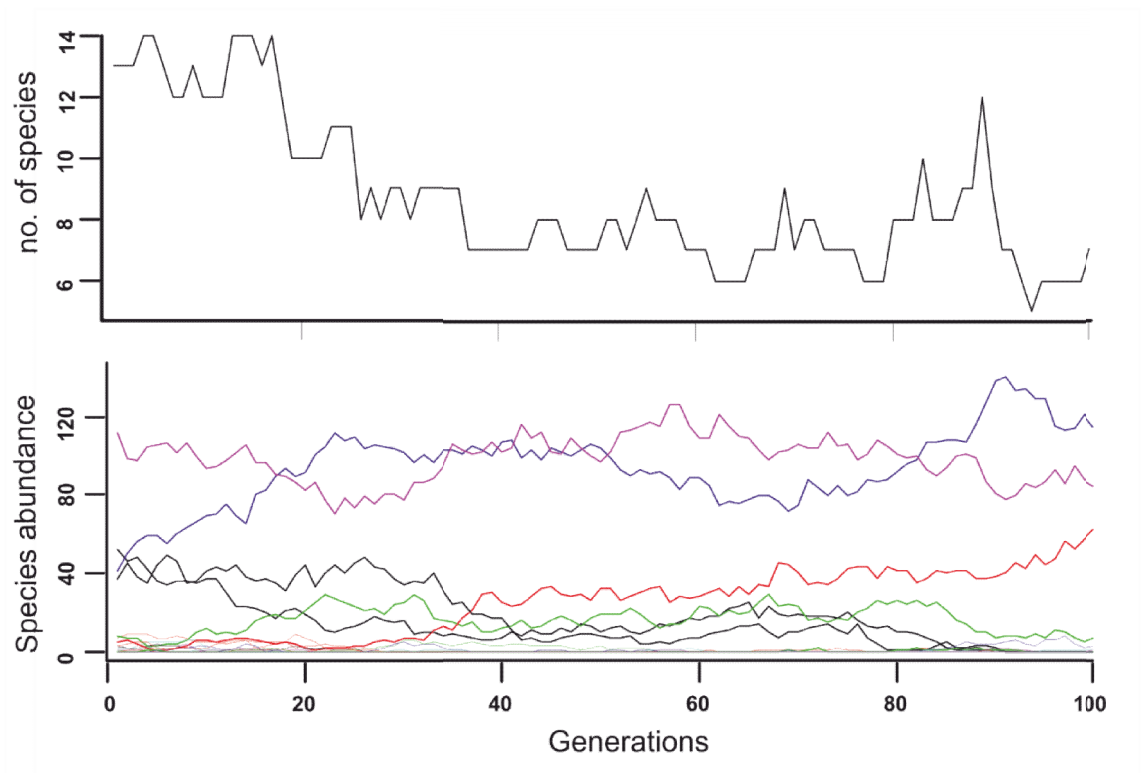
## Results

SADs obtained from parameters  $\theta$  and  $m$  from maximum likelihood method from Ettiene's formula (2005) in each year, are shown in figure 2.  $\theta$  values were around 2 and the neutral  $m$  remained constant (0.003) for the three years. The 100% of the SADs curves obtained from simulations of neutral communities were not statistically different ( $P > 0.001$ ) compared to the observed SADs curves in the three years of sampling, indicating that the neutral  $m$  produced SADs fit to the neutral model. This suggests that in this dynamical system, SADs might respond to neutrality considering the neutral model assumptions. Neutral curves present a horn dispersion shape, indicating that the most abundant species are less variable, and these species are more susceptible to neutrality than mid and rare species. This was also observed for SADs obtained from low neutral  $m$  (0.01 and 0.001).

Simulations of ecological drift under UNTB were performed just for the SADs obtained from the neutral  $m$  (Fig. 3). Ecological drift showed that the maximum number of species is 14 until the 20<sup>th</sup> generation, considering up and down fluctuations of the number of species is among 6 and 8. Abundances of each species fluctuate along the 100 generations. We found that the pattern of dominant, mid and rare species remains along generations. Two dominant species represent the community and replaced each other over several generations. Meanwhile, abundance fluctuations change the dominance of mid and rare species more frequently than dominant species. This suggests that the SAD is dynamical along generations, but the pattern of dominant-mid-rare species is found at any generation.



**Figure 2.** Observed SADs curve (red line), and SADs curve obtained from neutral  $m$  (black line) for each year. Neutral SADs values are represented by the mean and standard deviation of 1000 simulations (error bars).



**Figure 3.** Simulation under UNTB using neutral  $m$  along 100 generations. Each colored line represents one species in the community.

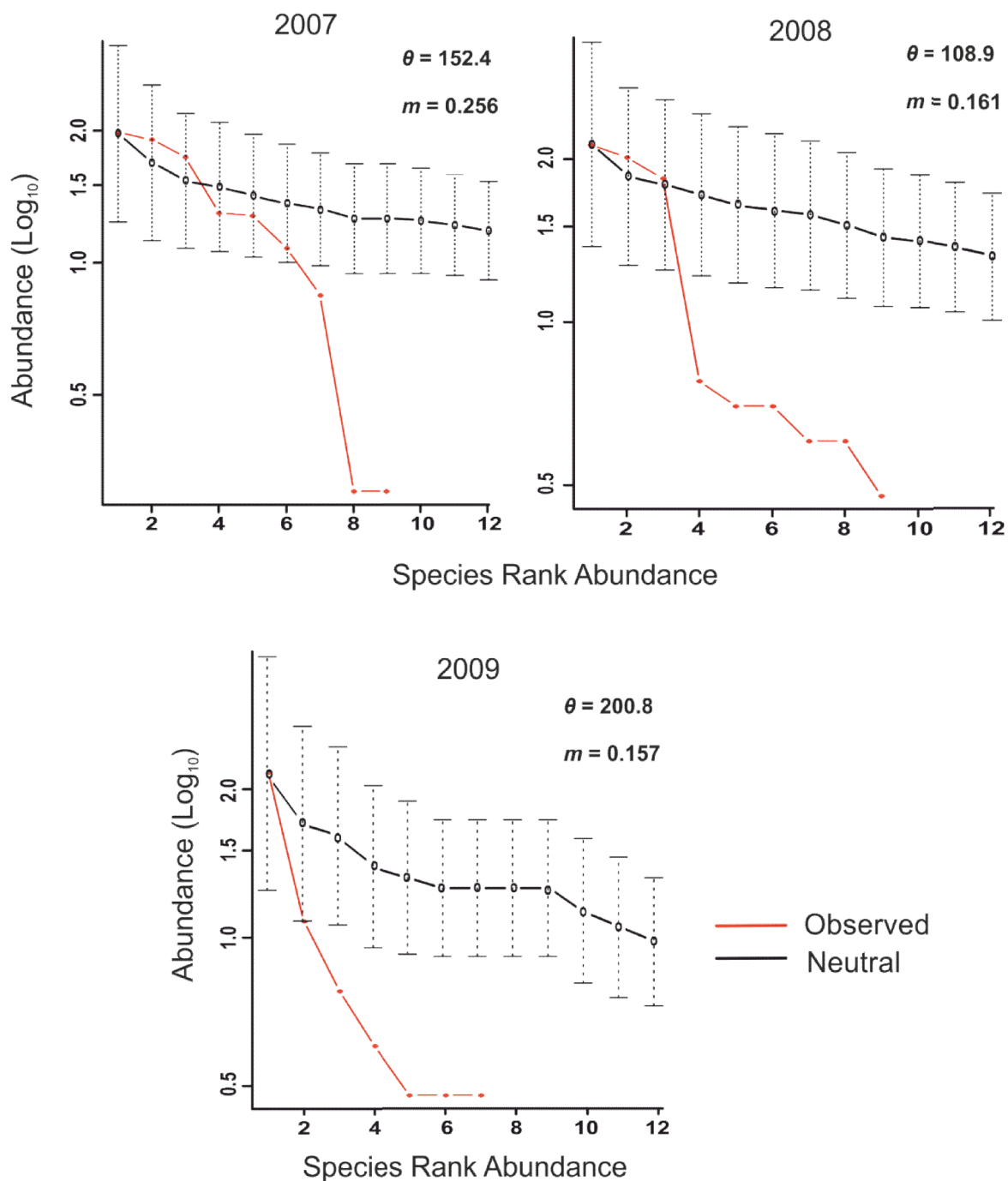
On the other hand, SADs obtained by simulating the arbitrary values of 0.1 and 1.0 for  $m$ , did not fit to neutrality predictions (Table 1), suggesting that communities in which individuals present high migration rates can not be explained by neutral models. Furthermore, natural  $m$  is much higher than the obtained from neutral  $m$ , thus  $\theta$  is higher as well (Table 2). The lowest natural  $m$  values in the three years is 0.157, which means that migration rate in Sian Ka'an pools is higher than expected for neutral models and we did not simulate ecological drift under UNTB. The SADs obtained from the natural  $m$  in the three years are shown in figure 4. Classification of the main biological attributes obtained from available literature is shown in table 3.

**Table 1.** Percentage (%) of simulations that were statistically different ( $P < 0.001$ ) from the neutral model, using four values (arbitrary) of  $m$ .

Year	$m$ (arbitrary)	% ( $P < 0.001$ )
2007	1	100
	0.1	91
	0.01	0
	0.001	0
2008	1	98
	0.1	97
	0.01	0
	0.001	0
2009	1	100
	0.1	4
	0.01	0
	0.001	0

**Table 2.** Migration rates for each fish species present in the Sian Ka'an wetland.

Species	$m$
<i>A. aeneus</i>	0.44
<i>C. octofasciatus</i>	0.34
<i>H. bimaculata</i>	0.16
<i>C. friedrichsthalii</i>	0.16
<i>C. meeki</i>	0.17
<i>X. maculatus</i>	0.20
<i>O. aenigmaticum</i>	0.16
<i>R. guatemalensis</i>	0.19
<i>C. urophthalmus</i>	0.06
<i>P. orri</i>	0.21
<i>G. sexradiata</i>	0.30
<i>P. mexicana</i>	0.01
<i>R. tenuis</i>	0.10



**Figure 4.** Observed SADs curve (red line), and SADs curve obtained from natural  $m$  (black line) for each year. Neutral SADs values are represented by the mean and standard deviation of 1000 simulations (error bars).



**Table 3.** Main Biological attributes of the fish species present in the Sian Ka'an wetland.

Species	Biological attributes						
	Dispersion	Maturation rate	Breeding type	Breeding time	Range T°C tolerance	Adaptive strategy	Parental care
<i>A. fasciatus</i>	high	high	eggs	seasonal	low	opportunistic	No
<i>P. orri</i>	high	high	livebearing	constant	high	opportunistic	No
<i>P. mexicana</i>	high	high	livebearing	constant	high	opportunistic	No
<i>G. sexradiat</i>	high	high	livebearing	constant	high	opportunistic	No
<i>X. maculatus</i>	high	high	livebearing	constant	high	opportunistic	No
<i>Heterandria bimaculata</i>	high	high	livebearing	constant	high	opportunistic	No
<i>O. aenigmaticum</i>	low	low	eggs	seasonal	high	Intermediate	No
<i>R. guatemalensis</i>	low	low	eggs	seasonal	low	Intermediate	No
<i>Cichlasoma urophthalmus</i>	low	low	eggs	seasonal	low	Periodic	Yes
<i>C. octofasciatus</i>	low	low	eggs	seasonal	low	Periodic	Yes
<i>C. meeki</i>	low	low	eggs	seasonal	low	Periodic	Yes
<i>C. friedrichstali</i>	low	low	eggs	seasonal	low	Periodic	Yes
<i>R. tenuis</i>	low	low	eggs	seasonal	high	Periodic	No

## Discussion

We sampled a typical Sian Ka'an wetland to determine if random processes explain the pattern of diversity by using equations developed by neutral theorists to obtain parameters required for neutral Hubbell's model. Even when the spatial and time scale used in this study is lower than other studies (e.g. Muneeppeerakul et al. 2008), the sites isolation for short periods (months) related to hydrological dynamics allows to make quantifiable changes on key parameters to understand the diversity of fish communities (Taylor and Warren 2001). This wetland has strong seasonal hydrological variation and spatial flooding heterogeneity, in which the rainy season promotes a habitat expansion, while the dry season reduces the habitat extension (Escalera-Vázquez and Zambrano 2010). This hydrological dynamic is related to connections among habitats, leading to isolation in dry seasons or promoting dispersal events in wet seasons (Taylor and Warren 2001). Considering that the sampling interval is important to determine migration dynamics, we conducted sampling according to the system's dynamics to record variability in species composition. For example, given that fish survivors migrate from permanent pools to exploit newly flooded areas, it is possible to estimate the  $m$  of fish species, thereby allowing a direct comparison between the "natural" estimated  $m$  and those estimated from neutral models.

Based on the UNTB model and parameters obtained from an equation developed by neutral theory which assume ecological equivalence and a community in equilibrium (zero-sum assumption), the observed SADs fit a 100% to the predicted neutral SADs. But, when we performed the analyses with higher values of  $m$ , the observed SADs do not fit to neutral SADs at any year. This suggests that fish migration in this wetland should be lower to predict neutrality. Hubbell (2001) described the community diversity curves for fish in Río Negro, where the predicted pattern fits to neutrality, and found that the estimation of  $\theta$  and  $m$  is lower compared to other animal communities; he argues that this result is because in the upstream the migration rate is lower than in the downstream. Following Ettiene's (2005) sampling formula, we obtained similar  $m$  results than Hubbell's, but in wetlands there is no upstream and downstream dynamics. Thus, if migration in this wetland is

regulated by the hydrology and topography in each area, why did we obtain similar  $m$  results considering neutral assumptions? A possible explanation is that the parameter  $m$  in Ettiene's equations is obtained from the same SADs, considering that the more abundant species have higher  $m$  (Leigh 2007), not considering natural mechanisms (e.g. hydrology) related to species migration. In this wetland, it is difficult to consider only random process structuring the fish community and that all individuals have constant and equal migration rates. Seasonal variation is responsible for the annual variation in species richness and SADs in the natural community. We found that 2009 was the driest year compared to 2007 and 2008; this influenced the number of connection among pools. Years of low rainfall can generate low values of  $m$ . In addition, we obtained different migration rates for each species, being higher for Poecilids ( $m \approx 2.5$ ) and lower for rivulids ( $m = 0.1$ ). Despite of the annual variation in this wetland, other methods used to estimate migration (e.g. microsatellites, tags) showed that migration for cichlids (e.g. Terai et al 2006), poecilids (e.g. Baer 1997; Vázquez-Domínguez et al. 2009) and *Astyanax* sp. (e.g. Prioli 2002; Pazza 2007) are higher than those needed to fit neutrality. Fish migration ability is related to flood and dry events in wetlands and to fish biological attributes and life history traits (Wellborn et al. 1996).

Periodic hydrological variation in rivers and wetlands plays a significant role in generating responses for various biological attributes such as gonad maturation, migration, recruitment, growth and feeding (Winemiller 1989; Beissinger 1995; DeAngelis et al. 1997, 2010; Gomes and Agostinho 1997; Poff et al. 1997; Taylor et al. 2003; Agostinho 2004; Lytle and Poff 2004). Periodic drying imposes severe constraints on species behaviour, development and life history traits, and only those species able to survive in the stressful conditions of a drying aquatic system might be successful in these habitats (Kobza et al. 2004). Fish species found in the studied pools present different life history traits (Table 3), for example Poeciliidae is a livebearing fish family with early maturation (Miller 2005) able to reestablished population from just a few mature females (Meffe and Snelson 1989). *Rivulus* spp. are able to produced dormant eggs (Miller 2005) and adults can survive 25-60 h out of water allowing colonization by flipping in dry seasons (Pazin et al. 2006). Cichlids present seasonal variation and parental care in established nests (Miller 2005 ),

which can be related to a poor migration rate. McGill (2006) suggested that if adaptation to heterogeneous environmental condition is important, the species abundance will be determined by the tolerance or fitness to environmental conditions and not by drift; the latter can explain why the obtained SADs in this study did not fit to neutrality. An alternative explanation to no-neutral SADs is related to the strength of biological interactions (Wootton 2005), because these interactions cause that species abundances are not independent of each other (McGill et al. 2006). However, theoretical work suggests that biological interactions such as competition and predation are more important in stable and persistent systems (Kokkoris et al. 1999).

The use of neutrality as a null hypothesis is useful to explain the biodiversity patterns, if random processes are not capable to explain SADs, thus the importance of deterministic processes is revealed. In this system, neutral models did not explain the patterns of biodiversity, when it is considered a differential capability of migration from fish based on their biology, suggesting that deterministic processes might be more important in structuring the fish community. Abiotic factors and habitat characteristics have been proposed as the main factors structuring fish communities in highly variable aquatic systems (Magoulick 2000, Baber et al. 2002, Suárez et al. 2004). Therefore future studies are needed to test this hypothesis in this seasonal wetland.

### **Acknowledgements**

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## CAPÍTULO II

### **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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# 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 km<sup>2</sup>) 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 dominguis* Pers.), where numerous temporary pools are also present. Permanent pools are deep (>3 m), oligotrophic, surrounded by palms (*Acoelorrhaphes wrightii* Griseb. & H. Wendl.) and swamp hardwoods, common cane (*Phragmites australis* [Cav.] Trin.

Ex Steud) and in some cases, jicaco trees (*Chysobalanus 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 ( $\text{g L}^{-1}$ ), 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 ( $\text{mg L}^{-1}$ ) and ammonium ( $\text{mg L}^{-1}$ ) 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-m<sup>2</sup> 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<sup>®</sup> 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 ( $\text{Log}_{10}$ ), 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 ( $25.6\text{ }^{\circ}\text{C} \pm 0.35\text{ SD}$  wet season;  $24.35\text{ }^{\circ}\text{C} \pm 0.25$  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
<i>2007</i>								
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 ( $\text{g L}^{-1}$ )	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 ( $\text{mg L}^{-1}$ )	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 ( $\text{mg L}^{-1}$ )	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
<i>2008</i>								
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 ( $\text{g L}^{-1}$ )	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 ( $\text{mg L}^{-1}$ )	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 ( $\text{mg L}^{-1}$ )	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
<i>2009</i>								
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 ( $\text{g L}^{-1}$ )	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 ( $\text{mg L}^{-1}$ )	–	–	0.01	0.00	–	–	–	–
Chlorophyll <i>a</i> ( $\mu\text{g L}^{-1}$ )	–	–	8.65	5.74	–	–	–	–
Ammonium ( $\text{mg L}^{-1}$ )	–	–	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 ( $\text{g L}^{-1}$ )	-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 ( $\text{mg L}^{-1}$ )	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 ( $\text{mg L}^{-1}$ )	-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 ( $\text{g L}^{-1}$ )	-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 ( $\text{mg L}^{-1}$ )	-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 ( $\text{mg L}^{-1}$ )	-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). Correla-

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;

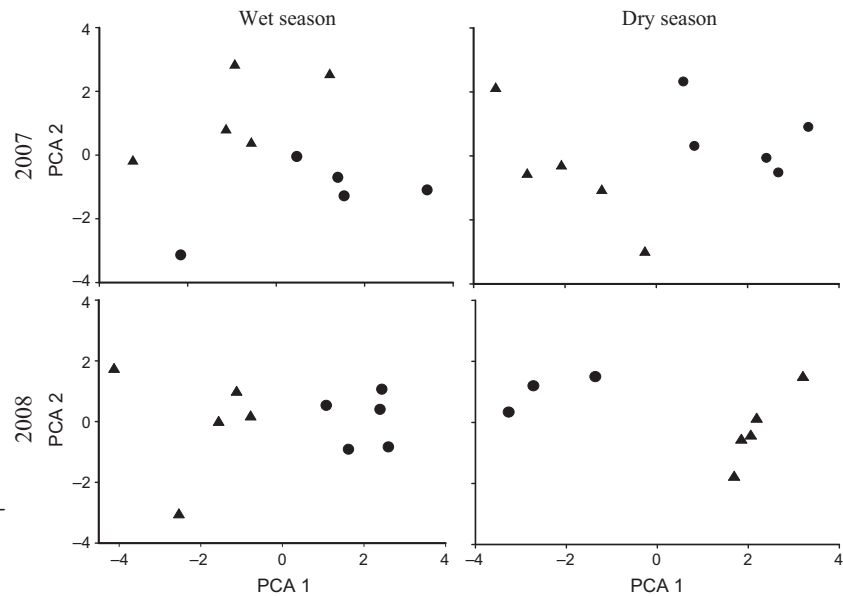


Fig. 1 Principal components analysis of abiotic variables for permanent (triangles) and temporary (circles) pools in wet and dry seasons in 2007 and 2008.

$R^2 = 0.601$ ,  $F_{10,38} = 1.27$ ,  $P = 0.002$ ). 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

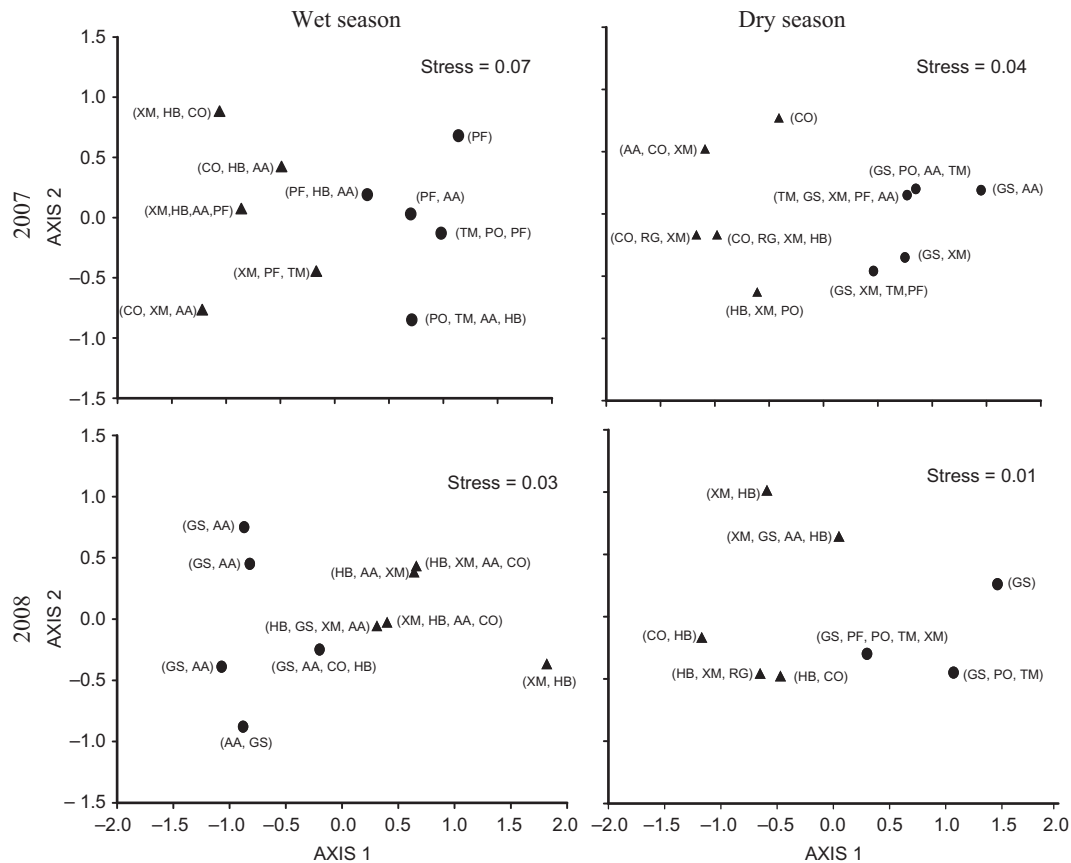
Season	Year	Permanent pools				Temporary pools			
		Wet		Dry		Wet		Dry	
Species		MA	(%)	MA	(%)	MA	(%)	MA	(%)
<i>Characidae</i>									
<i>Astyanax aeneus</i>	2007	23	0.10	67	0.12	123	0.27	179	0.11
Günter, 1860	2008	934	0.30	100	0.04	135	0.18	16	0.03
	2009	6	0.02	87	0.09	*	*	*	*
<i>Rivulidae</i>									
<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 poeciliids 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).

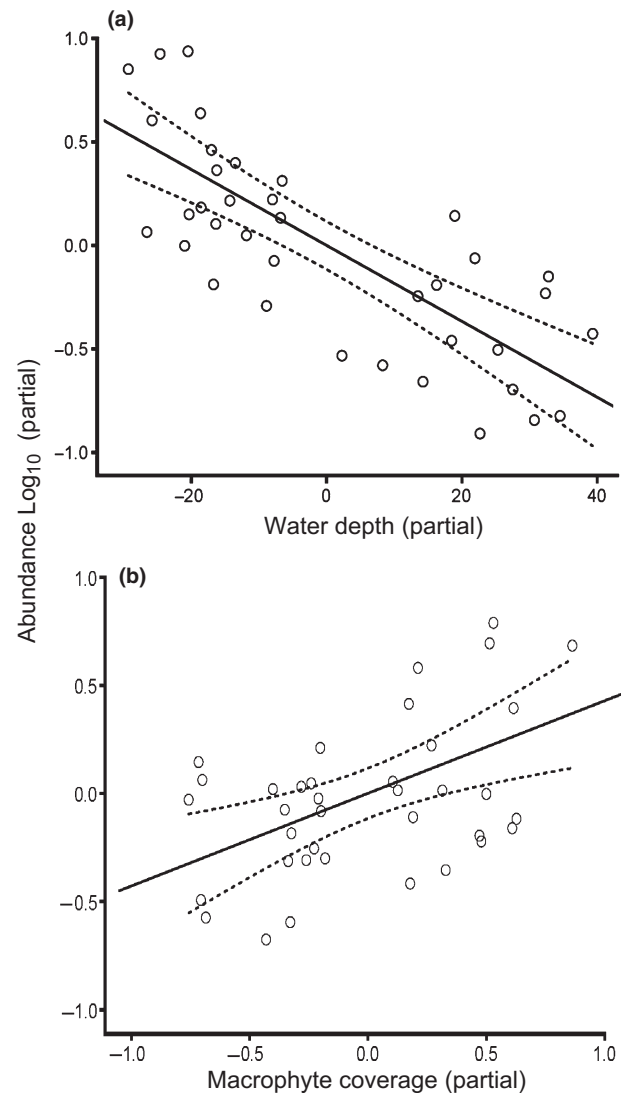
In seasonal habitats such as river floodplains or wetlands, fish community structure is related to abiotic variables that change in response to hydroperiod, including water depth, temperature, dissolved oxygen and macrophyte coverage (Capone & Krushlan, 1991; Magoulick, 2000; Gelwick *et al.*, 2001; 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	
	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 $r$
<b>2007</b>	
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 $\alpha$ ( $\mu\text{g L}^{-1}$ )	-0.858
Macrophyte coverage (%)	-0.929
Ammonium ( $\text{mg L}^{-1}$ )	-0.440
<b>2008</b>	
Wet season	
Temperature (°C)	-0.642
pH	-0.854
Chlorophyll $\alpha$ ( $\mu\text{g L}^{-1}$ )	0.697
Macrophyte coverage (%)	0.823
Nitrates ( $\text{mg L}^{-1}$ )	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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## CAPÍTULO III

### FISH POPULATION RESPONSES TO HYDROLOGICAL VARIATION IN A SEASONAL WETLAND\*

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## Abstract

The hydrological regime promotes environmental fluctuations at different time scales (days, seasons, years) that affect populations and communities of fish species in wetlands. Periodic hydrological variation in wetlands cues various biological attributes such as gonad maturation, migration, recruitment, growth and feeding. Water level variations in wetlands can cause high fish mortality in dry periods, but in wet seasons floods promote pulses of nutrients and reproductive events, influencing death and birth rates of the species, causing variation of natural populations over time. Hydrological variation affects differently fish species with different life history traits. We examined the response of local populations of 10 fish species to seasonal and interannual hydrological variation in a wetland of the Sian Ka'an Biosphere Reserve, identifying temporal patterns in fish populations, and assessing the role of hydrological variation on these patterns. Patterns of fish species abundances presented differences in habitat, seasons and year. We found that flood has a positive effect on populations of the species *A. aenus* and *G. sexradiata*. Populations of *R. guatemalensis* were negatively affected by flood. These fish species have a different life history strategy (equilibrium, seasonal and opportunistic, respectively). The seasonal dynamic of the studied wetland is related to the patterns of fish species abundances, and these in turn respond to this system variation according to the exhibiting strategy. Despite the observation that the studied species were resistant and resilient in some extent to the occurrence of relatively long dry periods, there was indication that stronger and more enduring effects would probably have occurred if the dry period had lasted for a few more years, as it might be expected under a scenario of increasing dryness.

**Keywords:** Hydrological regime variation, fish population, flood, dry periods, tropical wetland

## **Introduction**

The hydrological regime is of central importance in sustaining the ecological processes in flowing and flooding water systems, because it promotes environmental fluctuations that affect the populations of species and communities (Richter et al. 1996, Poff et al. 1997, Coops et al. 2003). Periodic hydrological variation in rivers and wetlands plays a significant role in generating responses for various biological attributes such as gonad maturation, migration, recruitment, growth and feeding (Winemiller 1989; Beissinger 1995; DeAngelis et al. 1997, 2010; Gomes and Agostinho 1997; Poff et al. 1997; Taylor et al. 2003; Agostinho et al. 2004; Lytle and Poff 2004; Adite et al. 2006). The hydrological regime can fluctuate on different time scales (from days to decades) depending on regional climatic conditions (Poff et al. 1997, Coops et al. 2003). In general, wetlands are characterized by a seasonal variation in hydrological conditions, showing periodic drying and flooding events (Mitsch and Gosselink 2009).

Water level variations in wetlands can cause high fish mortality in dry periods (DeAngelis et al. 1997; Kobza et al. 2004), but in wet seasons floods promote pulses of nutrients and reproductive events (Poff et al. 1997; Agostinho et al. 2004). Thus, in these ecosystems, water level fluctuations influence death and birth rates of the species, causing variation of natural populations over time (DeAngelis et al. 1997, 2005; Ruetz et al. 2005). Previous studies demonstrated that hydrological variation affects differently to fish species with different life history traits (Winemiller 1989; DeAngelis et al. 1997, 2005; King et al. 2003; Agostinho et al. 2004). These studies emphasized that to understand the effect of hydrological variation in a particular ecosystem, to study the population responses of overall species is needed.

Fish population responses to hydrological regime has been extensively studied in rivers (e.g. Gomes and Agostinho 1997; Marchetti and Moyle 2001; Agostinho et al. 2004; Keaton et al. 2005; Gubiani et al. 2007; Magalhaes et al. 2007; Franssen et al. 2006). However, wetlands have been less studied (DeAngelis et al. 1997, 2010; Ruetz et al. 2005; Adite et al. 2006). Understanding the role of hydrological variation in ecosystem functioning has become even more crucial especially with current concerns about global



climate change that predict an increased of interannual variability (Coops et al. 2003; Wantzen et al. 2008). Thus, reference data on tropical wetlands exhibiting natural hydrological variation are necessary for future evaluations of the impact of climate change on these ecosystems.

The Sian Ka'an Reserve present a matrix of seasonal freshwater wetlands, located near to the coast in Quintana Roo, México. The topography generates small permanent pools, which are potential refuges for fish in dry periods. Although close to a development for Cancún-Tulum tourism, the reserve presents a large area free of anthropogenic perturbations and no-native species, and the hydrologic regime has remained unmodified (Zambrano et al. 2006). Therefore, this pristine and dynamical characteristics of the system, and the responses of fish species to hydrological variation offers the opportunity to understand population dynamics and species responses to extreme changes to flood and dry periods.

In this study, we examined the response of local populations of ten fish species to seasonal and interannual hydrological variation in a wetland of the Sian Ka'an Biosphere Reserve. We studied several species exhibiting different life history traits to evaluate if their responses differ among fish strategies. Our objectives were to: (1) identify temporal patterns in fish populations and (2) assess the role of hydrological variation on these patterns. We hypothesized that hydrological fluctuations affect species with distinct life strategies differently.

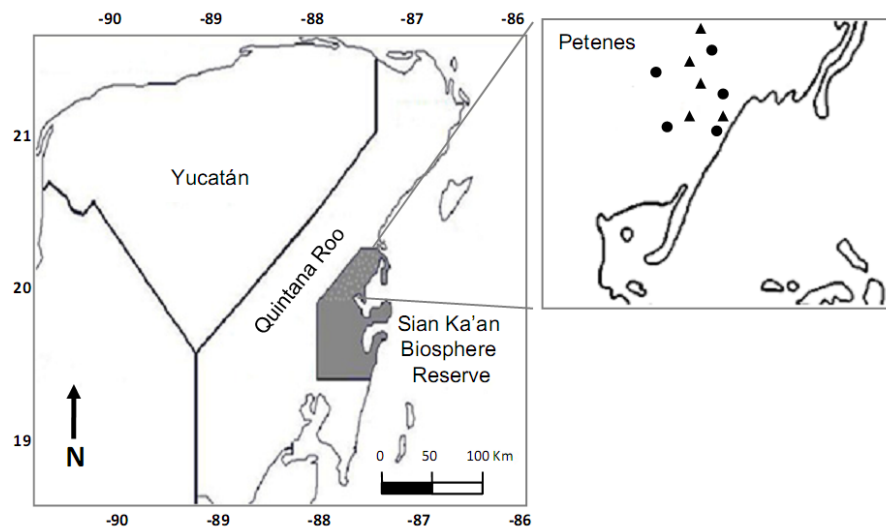
## **Methods**

### *Study area*

Sian Ka'an Biosphere Reserve (528.47 km<sup>2</sup>) is located along the east central coast of the Yucatan peninsula in southeastern Mexico (Fig. 1). The hydrologic dynamics and topography of Sian Ka'an Reserve generate a matrix of wetlands. During the dry season,

most of the water bodies are reduced and isolated. Therefore, this system offers the opportunity to understand changes in fish populations according to the hydrologic regime.

The wetlands at the Sian Ka'an reached their maximum annual water level at the end of the wet season (February-March). Water levels decline substantially during the short dry season (March-April). This wetland comprises small permanent pools surrounded by tree islands known as petenes in a flooded marsh matrix of sawgrass (*Cladium jamaicensis*), gulfcoast spikerush (*Eleocharis cellulosa*) and cattail (*Typha dominguensis*), where numerous temporary pools are also present. Permanent pools are oligotrophic, surrounded by palms (*Acoelorrhaphes wrightii*) and swamp hardwoods, common cane (*Phragmites australis*), and in some cases jicaco trees (*Chrysobalanus icaco*). Temporary pools are surrounded by sawgrass and gulfcoast spikerush. In a previous study, 13 continental freshwater fish species were recorded from this wetland (Escalera-Vázquez and Zambrano 2010), with the most representative fish families in this area being Cichlidae, Poeciliidae, Characidae, Rivulidae, Pimelodidae and Symbranchidae.



**Figure 1.** Map of the study site in the Sian Ka'an wetland. Triangles show the localization of temporary pools; Circles represent permanent pools.

Samplings were carried out in dry season (April) warm rainy season (August) and cold rainy season (January) during a three consecutive years (from April 2007 to January 2010). We selected five permanent and five temporary pools located near each other, such that they were interconnected during a wet season. Pools were characterized measuring mean depth and area. We monitored daily water level and temperature deploying a data logger (HOBO; Onset Computer Corporation, Bourne, MA, U.S.A.) in all pools. pH was measured for 24 hrs every week during the sampling period, using a multi-parameter logger (YSI 6600; YSI Inc., Yellow Springs, OH, U.S.A.).

#### *Fish sampling and environmental data*

Gee<sup>®</sup> minnow traps (2 mm mesh and a funnel entrance diameter of 20 mm) were used to catch fish. According to Kobza et al. (2004), these traps are the best method for sampling fish in small water bodies with complex dimensions and irregular edges. We set minnow traps for 24 hrs with the top of the trap 7-10 mm above the water surface to prevent fish mortality from low oxygen levels at night. The average of fish density per m<sup>2</sup> for each pool was used for comparisons. We used common and scientific names of identified fishes following Nelson et al. (2004).

#### *Data analysis*

We performed the analyses with species exhibiting abundances higher than 5% of the community according to Escalera-Vázquez and Zambrano (2010), to avoid a preponderance of samples with zero specimens. The studied species were: *Astyanax aeneus* Günther (Characidae), *Heterandria bimaculata* Heckel (Poeciliidae), *Gambusia sexradiata* Hubbs (Poeciliidae), *Xiphophorus maculatus* Günther (Poeciliidae), *Poecilia orri* Fowler (Poeciliidae), *Cichlasoma meeki* Brind (Cichlidae), *C. octofasciatus* Regan (Cichlidae), *C.*

*friedrichsthalii* Heckel (Cichlidae), *Ophisternon aenigmaticum* Rosen and Geenwoog (Symbranchidae) and *Rhamdia guatemalensis* Günter (Pimelodidae).

To examine the response of fish populations to hydrological variation, duration of flood and dry periods preceding each sampling event were estimated. Duration of flood was defined as the number of days in which water level was  $> 50$  cm for the temporary pools in the floodplain, and 50 cm above the maximum depth of each permanent pool. An increased of 50 cm in the water level in this system ensures that all pools are connected. Duration of dry periods was defined as the number of days in which water level was  $< 10$  cm for temporary pools, because at this water level fish are trapped in organic material (i.e. periphyton). In the case of permanent pools, duration of dry periods was estimated as the number of days that the water level remained with  $<$  half of their maximum depth.

Time series analyses were performed using a mixed linear model (based on maximum likelihood) to test for differences in hydrological variation (duration of flood and dry periods) and fish density among habitats, seasons, years, seasons nested in years and the interaction between habitat and year (Littell et al. 1996). Covariance structure was modeled as first-order autoregressive process (Littell et al. 1996), because this covariance structure showed the best fit. Site was used as the random subject factor. Fish density was transformed using  $\log_{10}(x + 1)$  to stabilize the variance.

To evaluate the effect of hydrological variation on the fish populations, we modelled fish species populations that exhibited a significant temporal variation through time series analyses using mixed linear models with fish density as response variable; duration of flood periods, duration of dry periods, mean of depth, temperature, and pH as the potential predictor variables; and a first-order autoregressive covariance structure. Analyses were performed for each habitat for those species that showed significant differences between habitats. We applied a stepwise procedure with both backward and forward selection to identify candidate models. Akaike Information Criterion (AIC) was used to select a set of models with the best overall fit to the data. Only models in which all

terms were significant ( $P < 0.05$ ) were reported. All analyses were conducted in SAS software version 9.2 (SAS Institute, Cary, NC, U.S.A.).

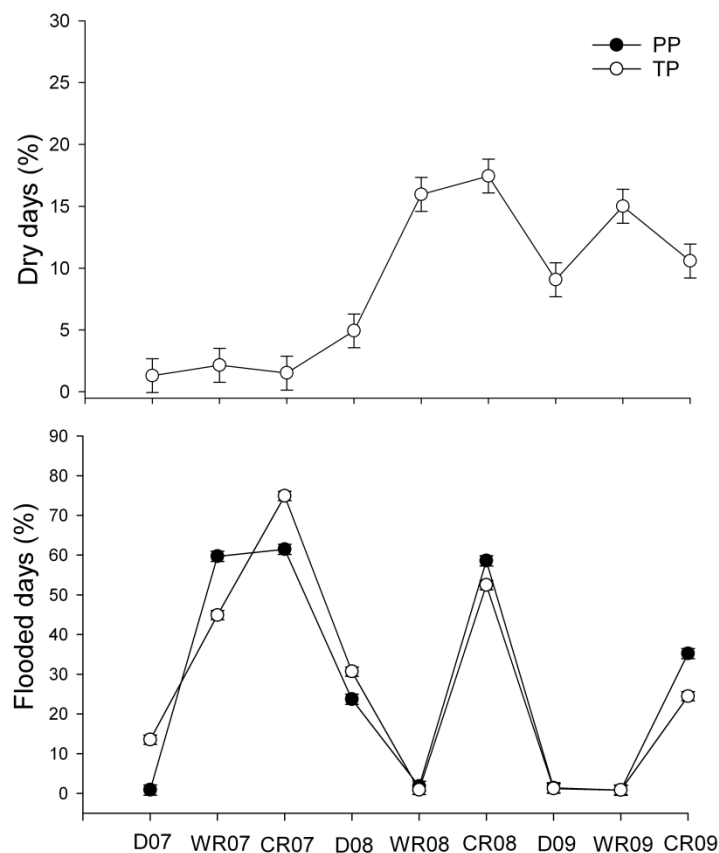
## Results

### *Hydrological regime*

The duration of flood in the studied wetland (Fig. 2) showed significant differences across years, seasons and seasons nested with year, but no in habitat (Table 1). However there was a significant difference in the interaction between year and habitat (Table 1). Permanent pools did not show dry periods (Fig. 2), while temporary pools showed significant variation in dry periods across years, seasons and seasons nested with year (Table 1). According to our data 2008 and 2009 were drier and exhibited a lower number of days of floods.

### *Fish population patterns*

The density of fish species: *A. aeneus*, *G. sexradiata*, *H. bimaculata* showed a significant variation across years and seasons (Table 2). These species also showed a significant difference between habitats (Table 2). *A. aeneus* and *H. bimaculata* were more abundant in permanent pools (Fig. 3), and *G. sexradiata* was more abundant in temporary pools (Fig. 3). *C. friedrichsthalii* density only showed a significant variation across years but not a seasonal and habitat variation (Table 2). *X. maculatus*, *R. guatemalensis* and *O. aenigmaticum* only showed a significant seasonal variation, but only *X. maculatus* and *R. guatemalensis* showed a significant difference between habitats (Table 2). Both were more abundant in permanent pools (Fig. 3). *C. meeki* and *P. orri* densities did not showed significant variation over time and between habitats (Table 2; Fig. 3).

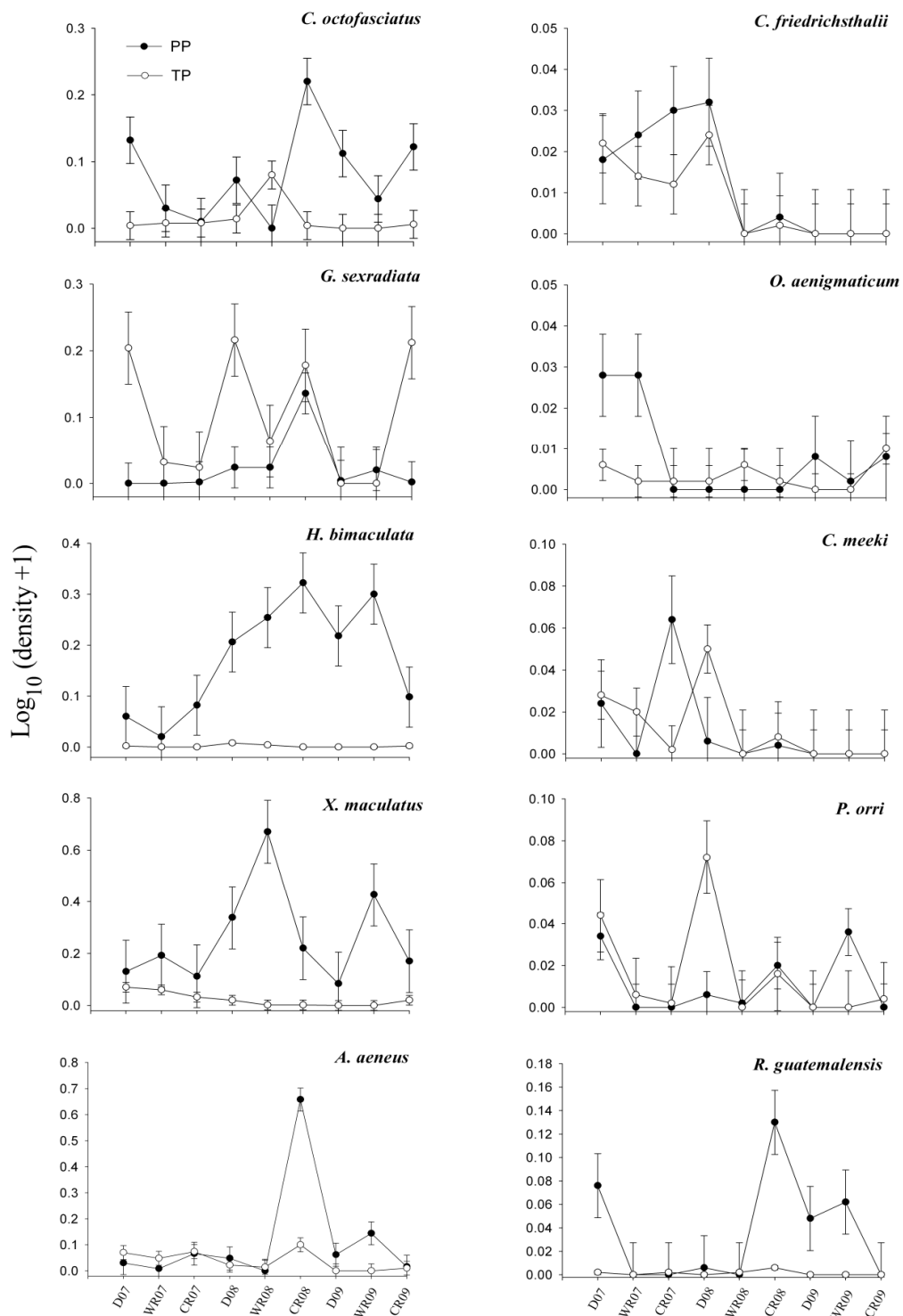


**Figure 2.** Hydrological regime (percentage in days) in temporary and permanent pools in the Sian Ka'an wetland. Error bars represent  $\pm 1$  SE. Least-squares means and standard errors were estimated based on the mixed linear model. PP = Permanent pools, TP = Temporary pools. Permanent pools did not present dry days, and are not showed in the upper plot. X axis represents sampling seasons (D = Dry, WR = Warm rainy, and CR = Cold rain) and years (07 = 2007, 08= 2008, and 09 = 2009).

**Table 1.** Variation of hydrological parameters. A Mixed Linear Model was used to test for interannual and seasonal differences in flood and dry regimen. Flood represents the number of days when water level: i) was > 50 cm in temporary pools; and ii) was 50 cm above from depth of each permanent pool. Dry represents the number of days when water level: i) was < 10 cm in temporary pools; and ii) diminished half of the depth of each permanent pool.

	Flood			Dry		
	df	F	P	df	F	P
Habitat	1, 64	0.88	0.352	-	-	-
Year	2, 64	197.64	< <b>0.001</b>	2, 32	146.51	< <b>0.001</b>
Season	2, 64	364.84	< <b>0.001</b>	2, 32	11.04	< <b>0.001</b>
Season (Year)	4, 64	208.48	< <b>0.001</b>	4, 32	5.76	<b>0.001</b>
Year x Habitat	2, 64	19.96	< <b>0.001</b>	-	-	-





**Figure 2.** Fish population patterns in permanent and temporary pools over time. The three sampling periods within years describe general seasonal patterns. Error bars represent  $\pm 1$  SE. Least-squares means and standard errors were estimated based on the mixed linear model. PP = Permanent pools, TP = Temporary pools. X axis represents sampling seasons (D = Dry, WR = Warm rainy, and CR = Cold rain) and years (07 = 2007, 08= 2008, and 09 = 2009).

**Table 2.** A Mixed Linear Model was used to test for interannual, seasonal and habitat differences in fish density ( $\text{Log}_{10}(\text{density} + 1)$ ).

	df	<i>A. aeneus</i>		<i>G. sexradiata</i>		<i>H. bimaculata</i>		<i>P. orri</i>		<i>X. maculatus</i>	
		F	P	F	P	F	P	F	P	F	P
Habitat	1, 8	27.62	<b>0.001</b>	8.19	<b>0.021</b>	20.58	<b>0.002</b>	0.55	0.48	13.44	<b>0.006</b>
Year	2, 16	16.67	<b>&lt;0.001</b>	4.19	<b>0.022</b>	11.16	<b>0.001</b>	1.22	0.351	2.74	0.095
Season	2, 18	18.77	<b>&lt;0.001</b>	4.42	<b>0.027</b>	0.4	0.679	3.21	0.064	7.61	<b>0.004</b>
Season (Year)	4, 30	23.09	<b>&lt;0.001</b>	3.11	<b>0.029</b>	3.45	<b>0.02</b>	2.55	0.060	1.27	0.304
Year x Habitat	2, 16	15.03	<b>&lt;0.001</b>	0.21	0.813	10.46	<b>0.001</b>	1.63	0.228	4.27	<b>0.027</b>

	df	<i>C. friedrichsthalii</i>		<i>C. meeki</i>		<i>C. octofasciatus</i>		<i>R. guatemalensis</i>		<i>O. aenigmaticum</i>	
		F	P	F	P	F	P	F	P	F	P
Habitat	1, 8	0.53	0.486	0.02	0.892	19.68	<b>0.002</b>	14.71	<b>0.005</b>	0.57	0.473
Year	2, 16	5.54	<b>0.015</b>	2.79	0.091	1.93	0.177	0.46	0.637	1.84	0.191
Season	2, 18	2.39	0.120	1.18	0.330	2.75	0.091	0.73	0.495	0.88	0.431
Season (Year)	4, 30	2	0.120	0.67	0.619	2.68	0.051	5.49	<b>0.002</b>	2.9	<b>0.039</b>
Year x Habitat	2, 16	0.22	0.802	1.09	0.360	0.67	0.523	0.37	0.696	1.84	0.191

### *Effect of hydrological regime on fish populations*

*C. meeki*, *C. octofasciatus* and *P. orri* were excluded from these analyses because they did not show a significant variation over time (Table 2). Flood duration was a significant predictor for the density of *A. aeneus*, *G. sexradiata* and *R. guatemalensis* ( $P < 0.05$ ; Table 3). Flood had a positive effect on the density of *A. aeneus* and *G. sexradiata* and a negative effect on the density of *R. guatemalensis* (Table 3). Dry duration was a significant predictor only for *X. maculatus* and it had a negative effect on fish density (Table 3). The density of these fish species, as well as the density of *H. bimaculata* and *C. friedrichsthalii* was also significantly influenced by other environmental variables such as temperature, pH and depth (Table 3).

**Table 3.** Model obtained for each species from a mixed linear model. All variables showed are statistically significant ( $P < 0.05$ ).

Species	PP	PT
<i>A. aeneus</i>	$y = 1.0932 + 0.2278$ (Flood) $+ 0.0656$ (T°C)	$y = -0.03461 + 0.001566$ (Depth)
<i>G. sexradiata</i>	$y = 0.3634 + 0.0373$ (Flood) $- 0.048$ (pH)	$y = 0.09715 - 0.0029$ (Depth) $+ 0.1493$ (Flood) $- 0.1063$ (pH)
<i>H. bimaculata</i>	$y = 0.6907 - 0.0686$ (pH)	-
<i>R. guatemalensis</i>	$y = 0.4383 - 0.04951$ (Flood) $- 0.05125$ (T°C)	-
<i>X. maculatus</i>	-	$y = 0.0516 - 0.02633$ (Dry)
<i>C. friedrichsthalii</i> *	$y = - 0.06822 + 0.009868$ (pH)	

## Discussion

The species in the studied Sian Ka'an wetland are classified into three general life history strategies: equilibrium, seasonal and opportunistic (Winemiller 1989). Fish exhibiting the equilibrium strategy present long time generations, large investment in individual offspring and delayed maturation. Seasonal fish have synchronized reproduction and high fecundity during the early wet season; and the opportunistic fish have early maturation and frequent reproduction (Winemiller 1989; Rose and Cowan 2000). According to this classification, *C. friedrichsthalii*, *C. octofasciatus*, *C. meeki*, *H. bimaculata*, *R. guatemalensis* and *O. aenigmaticum* exhibit an equilibrium strategy (Winemiller 1989; Lamouroux et al. 2002; García Berthou and Moreno-Amich 2002; Escalera-Vázquez and Zambrano 2010, Chap. II in this thesis), whereas *A. aeneus*, *X. maculatus* and *P. orri* show a seasonal strategy (Vila-Gispert et al. 2002; Escalera-Vázquez and Zambrano 2010, Chap. II in this thesis). *G. sexradiata* belongs to the opportunistic strategy (Gelwick et al. 2001; DeAngelis et al. 2005).

According to our hypothesis we found different population responses among fish. In general, the density of fish with the equilibrium strategy did not show a seasonal and inter-annual variation. The density of seasonal species showed a seasonal variation (but for *P. orri* the variation was marginal,  $P = 0.064$ ), and the opportunistic species *G. sexradiata*

showed significant fluctuations in density over time. These results are consistent with the population responses reported for fish belonging to each life history strategy since populations of opportunistic fish can recover rapidly from dry periods that kill large numbers of organisms, and maintain large populations in the face of high mortality in the adult stage; seasonal fish have seasonally fluctuating populations; and populations of fish with equilibrium strategies are generally stable populations (Winemiller 1989, Rose and Cowan 2000, De Angelis et al. 2005).

Given that floods occupy large areas of the terrestrial environment (floodplain) to water bodies and promote pulses of nutrients from decomposition of inundated floodplain vegetation, providing important resources and nursery grounds for fish (Richter et al. 1996, Poff et al. 1997; Agostinho et al. 2004), we expected that most fish populations increased with an increase of the duration of floods. However, responses to floods differed among species (Gomes and Agostinho 1997; Grossman et al. 1998; Matthews and Marsh-Matthews 2003; Magalhaes et al. 2007; Gubiani et al. 2007). We found that flood has a positive effect only on populations of two species, *A. aenus* and *G. sexradiata*. On the other hand, populations of *R. guatemalensis* showed the opposite pattern, it was negatively affected by flood. These results may be explained by differences in life history traits, habitat preferences, abiotic tolerances, migration ability, and feeding habits (Magalhaes et al. 2007, DeAngelis et al. 1997).

Interestingly, these species represent the three life history strategies found in this wetland, and they showed significant differences in their density between habitats: *G. sexradiata* was more abundant in temporary pools, *R. guatemalensis* in permanent pools and *A. aenus* did not show a clear pattern, but it appears to be associated to both temporary and permanent pools. *G. sexradiata* and *A. aenus* are rapid colonizers that tolerate a wide variety of habitats (Miller 2005; Ruetz et al. 2005; Escalera-Vázquez et al. unpub. work: Chap. I of this thesis) and feed on areas near vegetated shorelines where their food (benthic invertebrates and insects) is abundant (Greenfield and Thomerson 1995), explaining the positive effect that flood had on their populations. On the other hand *R. guatemalensis* is a predator fish (Miller 2005), therefore the negative effect of flood on the population of this

species can be explained by dispersion of prey from permanent pools to the floodplain associated to a rise in water level, diminishing the availability of food in permanent pools for this species.

The effects of dry periods did not showed a significant effect on fish populations, with the exception of *X. maculatus* in temporary pools. However, pH that might be indirectly related to water level in pools had a significant positive effect on the density of *C. friedrichsthalii*, and a negative effect on that of *H. bimaculata*. Significant effects of environmental variables such as dissolved oxygen, temperature and pH on fish populations imply that population changes can be related to drought-induced variations in water quality (Attrill and Power 2000). Besides the biological tolerances on the species, one of the factors helping to mitigate the severity of the effects of dry periods are permanents an quasi-permanent water bodies which serve as refuges for fish during these dry periods (DeAngelis et al. 1997, 2010; Magoulick and Kobza 2003; Kobza et al. 2004; Magalhaes et al. 2007).

Despite the differences of habitat preference among species in the studied wetland, all species can be present in one time or other in permanent pools (Fig. 3), suggesting that permanent pools can function as refuges for some fish in dry periods. Because of isolation and crowding, population control may be more complex at these pools during dry periods (Snodgrass et al. 1996; Chick et al. 2004). For example, fish must tolerate oxygen and nutrient depletion, high susceptibility to predation and diseases, and intra and inter-specific competition (De Angelis et al. 1997; Turner et al. 1999; Trexler et al. 2002; Loftus and Eklund 1994; Taylor et al. 2001; Gawlick 2002; Kobza et al. 2004; Ruetz et al. 2005). For this reason, the abundance of species habiting in widely varying environments depends on the duration of dry periods and the ability of species to persist harsh conditions, which suggests that species inhabiting the Sian Ka'an wetland are adapted to persist highly fluctuating hydrological conditions.

Species composition and rank abundances that stayed essentially the same over time in face of major environmental variation has already been reported in mediterranean-

type streams (Moyle and Vondracek 1985, Magalhaes et al. 2007) and other systems with harsh environmental conditions (Matthews 1986; Eby et al. 2003; Matthews and Marsh-Matthews 2003). This is consistent with habitat template theory that states the sequential seasonal and highly variable floods and drying events are primary landscape filters that reduce the species pool to those evolutionarily adapted to cope with the prevailing harsh environmental patterns (Southwood 1977; Poff et al. 1997).

Despite the observation that the studied species were resistant and resilient in some extent to the occurrence of relatively long dry periods, there was some indication that stronger and more enduring effects would probably have occurred if the dry period had lasted for a few more years, as it might be expected under a scenario of increasing dryness. Continued monitoring will allow us to identify the most susceptible species to hydrological variation.

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## DISCUSIÓN GENERAL

La mayor parte de los hábitats acuáticos temporales en los trópicos están asociados a humedales. El valor estimado de los humedales en cuanto a diversidad, servicios ecosistémicos y significado cultural es más alto que para ecosistemas terrestres (Costanza et al. 1997). La pérdida acelerada de los humedales asociada a cambios antropogénicos y la introducción de especies no-nativas, han generado esfuerzos en conjunto para entender el funcionamiento de estos ecosistemas (Schwartz y Jankins, 2000; Kobza et al, 2004). Desafortunadamente, solo pocos humedales presentan alteraciones mínimas, de los cuales podamos reunir información confiable sobre procesos y patrones ecológicos (Lorenz y Serafy, 2006).

Los humedales de Sian Ka'an están situados en un área con un impacto antropogénico mínimo, presentan cambios estacionales perceptibles a lo largo del tiempo generando una dinámica de parches de hábitats permanentes y temporales, y albergan una gran diversidad de especies de peces. Estas características permiten estudiar y determinar patrones en la estructura de comunidades ícticas, así como los procesos involucrados en la generación de dichos patrones. De forma particular, el régimen hídrico que presenta este humedal permite evaluar la relación entre la variación ambiental (tanto estacional como interanual) y la estructura de la comunidad, así como la respuesta de las poblaciones de las especies a lo largo del tiempo.

La mayoría de los trabajos sobre la diversidad y estructura de las comunidades naturales indican que las especies forman un conjunto de organismos ecológicamente compatibles, y que la riqueza y abundancia en un ecosistema es el resultado de las características de hábitat, además de las diferentes interacciones (e.g. depredación, competencia, mutualismos) que se presentan en un tiempo y espacio (Chave 2004; Tilman 2004; Morin 2005; Chase 2007). Sin embargo, en la última década se ha tratado de explicar los patrones de diversidad mediante modelos neutrales, que proponen que los individuos son funcionalmente equivalentes y la estructura de la comunidad resulta de procesos estocásticos como colonización y extinción, generando así comunidades

ensambladas principalmente por dispersión (Chave, 2004; Hubell, 2005, 2006). Por lo anterior, para determinar qué tipo de procesos explican los patrones de diversidad de la comunidad íctica de los humedales de Sian Ka'an, inicialmente se utilizó un modelo neutral como una hipótesis nula (Cap. I). Someter a prueba hipótesis nulas es útil para explorar explicaciones más sencillas de los patrones de diversidad, ya que si los procesos aleatorios no explican la diversidad y estructura de las comunidades, esto da la pauta a explorar y revelar la importancia de procesos deterministas.

Los resultados obtenidos mostraron la diversidad de peces Sian Ka'an no se explica por modelos neutrales (procesos estocásticos) debido a que la tasa de migración de los peces es mayor a la que se esperaría en una comunidad estructurada aleatoriamente o por deriva ecológica (Cap. I). Esto sugiere la existencia de factores deterministas relacionados a procesos de ensamblaje de nicho, ya que se ha reportado que en ambientes dinámicos, los factores abióticos y las características de hábitat están altamente relacionados con la estructura de la comunidad (Magoulick 2000, Baber et al. 2002, Suárez et al. 2004). Por lo tanto en el capítulo siguiente, exploramos las relaciones que existen entre la variación en los factores abióticos con la estructura de la comunidad, considerando la estacionalidad del sitio y la diferencia entre hábitats estables (Petenes) y hábitats altamente variables (pozas temporales) (Cap. II).

Los resultados obtenidos mostraron que la estructura de la comunidad estuvo determinada por factores deterministas (de ensamblaje de nicho). Las características de los hábitats estuvieron altamente relacionadas con la estructura de la comunidad, generando diferencia entre comunidades de sitios permanentes y sitios temporales. Esta diferencia en la estructura de la comunidad de ambos tipos de hábitats se mantuvo sin importar la variación estacional (lluvias y secas), confirmando que en ambientes estacionales la estructura de la comunidad en peces esta altamente relacionada con el cambio en las variables abióticas, en respuesta al régimen hídrico (Capone & Kushlan, 1991; Snodgrass et al., 1995; Magoulick, 2000; Gelwick et al., 2001; Pazin et al., 2006; Louca et al., 2009). No obstante, a nivel poblacional el patrón en las abundancias de cada especie estuvo relacionado de manera diferencial a la estacionalidad y a las diferencias en el régimen

hídrico registradas a lo del muestreo (Cap. III). Por ejemplo, la duración de los períodos de inundación tuvo un efecto positivo para algunas especies (*A. aenus*, *G. sexradiata*, *C. friedrichsthalii*) y negativo para otras (*R. guatemalensis*, *H. bimaculata*). Contrario a nuestras expectativas la duración del período de sequía no mostró un efecto significativo sobre la abundancia de las especies, lo cual puede ser explicado por adaptaciones particulares de las especies para tolerar un amplio rango de condiciones ambientales y estrés hídrico, así como por la presencia de pozas permanentes que funcionan como sitios de refugio (Matthews 1981; Eby et al 2003; Matthews and Marsh-Matthews 2003; DeAngelis et al. 1997; Gawlick 2002; Kobza et al. 2004, Ruetz et al. 2005; Trexler et al. 2002, Loftus y Eklund 1994).

De manera general, los resultados muestran que la estructura de las comunidades son resultado de la asociación de los cambios ambientales con las respuestas que generan las especies de acuerdo a las estrategias de vida, preferencias de hábitat, tolerancia a factores abióticos, capacidad de migración y hábitos alimenticios particulares (Magalhaes et al 2007, DeAngelis et al 2005). Las diferentes historias de vida (equilibrio, oportunista y estacional) (Winemiller 1989) se ven representadas por una o varias especies presentes en el humedal de Sian Ka'an. Esto demuestra que en el humedal de estudio hay especies que están adaptadas a condiciones hidrológicamente cambiantes, pero también hay especies que requieren de refugios ambientales en la época de secas. Esto es consistente con la teoría del mosaico de hábitat (*Habitat template theory*), la cual propone que las altas variaciones que presenta un ecosistema respecto a los eventos de inundación y sequía funcionan como un primer filtro ambiental en el paisaje, reduciendo el *pool* de especies a solo aquellas que están evolutivamente adaptadas a ambientes con patrones estacionales altamente cambiantes (Southwood 1977; Poff et al 1997).

A nivel de paisaje, un hábitat compuesto por “parches” provee corredores cuando están conectados en época de lluvias, así como de refugios cuando hay aislamiento en la temporada seca, permitiendo procesos relacionados al funcionamiento de metacomunidades y metapoblaciones (DeAngelis *et al.*, 1997; Magoulick & Kobza, 2003; Kobza *et al.*, 2004; De Meester *et al.*, 2005). Nuestros resultados (cap. II y III) indicaron

de manera consistente que existen especies asociadas preferentemente a un tipo de hábitat en el humedal. Por ello, la presencia de pozas permanentes y pozas temporales dentro de los humedales de Sian Ka'an es de vital importancia para mantener la diversidad y procesos ecológicos a nivel de paisaje. Este estudio es una de las primeras aproximaciones para conocer como se genera y mantiene la diversidad de peces en un humedal tropical.

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