TEMPORAL CHANGES IN SPECIES RICHNESS AND FISH COMPOSITION IN A SUBMERGED VEGETATION HABITAT IN VERACRUZ, MEXICO

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Background. Because estuarine fish communities undergo temporal changes in abundance and species composition, the influence of environmental factors on diel and seasonal variation in the structure of a fish community was evaluated. This information is necessary to extend our knowledge of fish communities in tropical estuaries. The objective of the study was to test the hypothesis that the total number of fish, species richness and fish composition would undergo temporal variations related to the variability of environmental conditions.

Materials and methods. In Pueblo Viejo Lagoon (western Gulf of Mexico), six 24-h sampling cycles every 2 months were carried out. Fish were collected every 2 h during each 24-h cycle using a beach seine net. Data were analysed using repeated measures PERMANOVA and canonical correspondence analysis.

Results. Diel variation in total fish number and species richness tended to peak at dawn and dusk, with significant differences between the periods of day, night and twilight. Total number of fish had significant pulses during the dry season and rainy season, whereas species richness showed a pulse in March–July. Fish community structure was mainly influenced by salinity, temperature, rainfall, and seagrass cover. Seasonally, three fish groups were observed. The fish assemblage during the rainy season was mainly characterized by low-salinity tolerant species. The fish assemblage during the cold-dry period was dominated by species with low-temperature affinities whereas filter-feeding species tended to be dominant during the warm-dry period. Differences in fish assemblages among diel periods were mainly due to some species were typically diurnal, nocturnal or crepuscular.

Conclusion. This study allowed determining that total fish abundance and richness are related at diel level with the transition period between the activities of diurnal and nocturnal species, and with fish strategies of predator avoidance and foraging. At seasonal level, these seem to be coupled to periods of high productivity in the system. Moreover, the fish composition showed a seasonal succession of species, which may be determined by a combination of temporal changes in salinity, rainfall, temperature, and by the different feeding strategies of species.

Keywords: PERMANOVA, constrained ordination, *Ruppia maritima*, seasonal succession, twilight pulses

INTRODUCTION

The variability in composition, abundance, and species richness of estuarine fish communities has been evaluated with consideration of factors such as the time of day, the climatic season, or the relation with environmental heterogeneity. The simple daily periodicity of sunrise and sunset affects the activity of fish, which generates patterns of diel migrations between adjacent habitats usually related to feeding, shelter or reducing the risk of predation, avoidance of inter- and/or intraspecific competition, reproduction, and searching for a physiologically optimum environment (Krumme 2009). Four diel periods can be distinguished that structure the activity patterns of fish: dawn, daytime, dusk, and night. Thus, species may become typically diurnal, nocturnal, or crepuscular (active at dusk and dawn) (Helfman 1993, Moyle and Cech 2004, Ley and Halliday 2007). Many studies have relied on low-frequency temporal sampling, where only a few (two to four) hours of day and night are considered in every cycle of 24 h, to evaluate diel effects (Hoeksema and Potter 2006, Ribeiro et al. 2006, Hagan and Able 2008). However, this reduces the diel analyses only to day/night comparisons. In contrast, few studies have considered a high-frequency temporal design, in which sampling occurs every three or two hours (or less), which allows more precise evaluation of the timing of diel

changes in fish activity throughout a 24-h cycle (Pessanha et al. 2003, Castillo-Rivera et al. 2010, Vasconcellos et al. 2010, 2011, Giarrizzo et al. 2013).

The species composition of estuarine fish communities also presents wide seasonal variations that may be influenced by fluctuations in environmental factors and by factors related to the species' life history. Thus, fish distribution may be affected by factors such as salinity, rainfall regime, and temperature (Jaureguizar et al. 2004, Meynecke et al. 2006, Gillson 2011, Lacerda et al. 2014), as well as biological factors such as spawning and recruitment patterns (Akin et al. 2003, Pessanha et al. 2003, Jaureguizar et al. 2004, Ribeiro et al. 2006, Vasconcellos et al. 2010). In this sense, the presence of submerged vegetation and its corresponding influence on estuarine fish populations is a biological factor that has been well studied worldwide. For many fish species, increased habitat structural complexity due to presence of vegetation can provide for more living space, higher food abundance, and a reduction in predation risk (Akin et al. 2003, Guest et al. 2003, Ribeiro et al. 2006, Nagelkerken 2009).

Despite tropical fish communities in Brazil have been adequately studied for many years (Vilar et al. 2013 and references therein), this type of studies in the northern portion of the western Atlantic region are scarce, and there are also few studies that analyse 24-h cycles (Pessanha and Araújo 2003, Pessanha et al. 2003, Vasconcellos et al. 2010, 2011). Thus, to extend the knowledge of fish communities in tropical estuarine systems in the western Atlantic, fish composition in a submerged-vegetation (*Ruppia maritima*) habitat in Pueblo Viejo Lagoon (western Gulf of Mexico) was studied, using a high-frequency temporal sampling to evaluate diel changes and a bi-monthly regularity to evaluate seasonal changes. Studies on this system are also scarce, despite the identification of the lagoon as a Priority Conservation Area (Arriaga et al. 2002). The presently reported study focused on testing the hypothesis that the total number of fish, species richness and fish composition would undergo diel changes mainly related to light–dark cycles and tidal stage; and seasonal variations principally related to salinity and temperature oscillations.

MATERIALS AND METHODS
Study Area. Pueblo Viejo lagoon (Fig. 1) is a relatively small system (ca. 88.7 km^2) located in the north of the state of Veracruz (22°05′–22°13′N and 97°50′–97°57′W). It opens to the Pánuco River and is located approximately 10 km from the river outflow into the Gulf of Mexico. At its southern end, the lagoon receives an important freshwater discharge from the Tamacuil River. This outflow defines a freshwater-influenced habitat. This habitat is characterized by patches of widgeon grass (*Ruppia maritima*) that occur just below the intertidal zone (Castillo-Rivera and Kobelkowsky 2000). There is maximum *R. maritima* cover in May and minimum cover in July–September. Associated with the widgeon grass patches, there are species of macroalgae such as *Enteromorpha flexuosa*, *Gracilaria verrucosa*, and *Polysiphonia atlantica*. The

substrate is a mixture of mud and silt with fine textured sand, and it is uniform throughout the vegetated habitat. The shoreline of this habitat is covered by mangroves (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*) and secondary vegetation patches (*Mimosa* spp., *Acacia* spp., and *Prosopis* spp.).
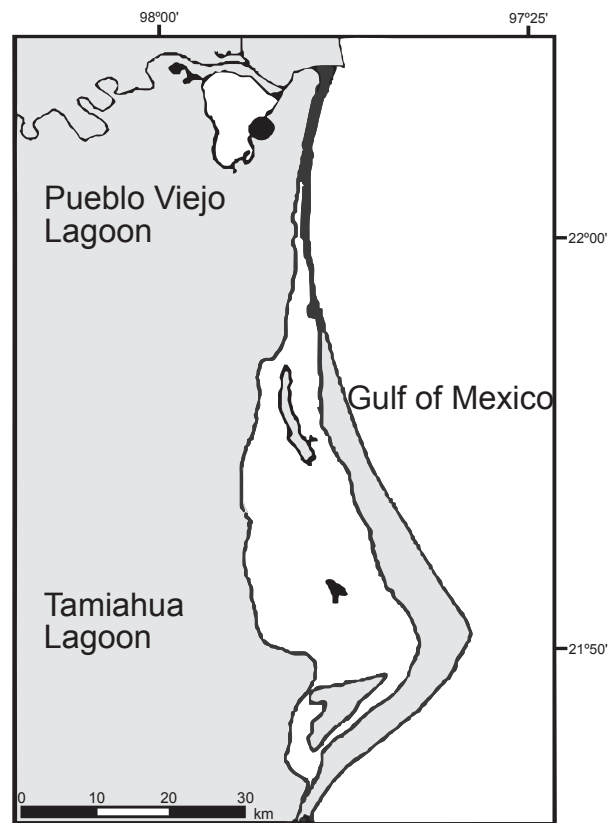
Fig. 1. The geographic location of Pueblo Viejo lagoon, Veracruz; The submerged vegetation habitat is also indicated (●)

The rainfall regime of the area includes a rainy season (from June to October, with the mean value above 120 mm) and a dry season (from December to May, with the mean value below 50 mm), and a total rainfall per year of 989 mm. The coast is predominantly characterized by diurnal tides with a tidal range of about 40 cm. Phytoplankton, chlorophyll, and primary production in the system show two maximum pulses: one during March–April and another in September–October (Contreras 1995).
Data collection. In the submerged-vegetation habitat, six 24-h sampling cycles every 2 months were carried out over a 1-year period. Fish were collected every 2 h during each 24-h cycle. The samples were taken by a beach seine net (30 m long, 1 m deep, and 1 cm mesh size). The net was pulled 50 m parallel to the shore and covered a sampling area of 1500 m^2 in water not deeper than 1 m. Samples were fixed with 10% formalin and preserved with 70% ethanol. The total number of species, the number of individuals per species, and the environmental data were recorded for each sample. The environmental variables

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* Clarke K.R., Gorley R.N. 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

measured during sampling included time of day, seagrass cover, temperature, salinity, and dissolved oxygen. The variations in water level (tidal stage) and the monthly mean rainfall for the system were also recorded.

Statistical analyses. Repeated measures PER-MANOVA was used to assess significant differences in total number of fish, species richness, and fish community composition, with diel periods (day, twilight, and night) and months as fixed factors and hour of day as random factor (nested within diel periods). These analyses were performed using PRIMER v7*. PERMANOVA is a routine for testing the simultaneous response of one or more variables to one or more factors, on the basis of any resemblance measure, using multiple random permutations of the analysed data, thus liberating it from the formal assumptions of traditional parametric analogues (Anderson 2001, Anderson et al. 2008).

Thus, according to Anderson et al. (2008), repeated measures analyses for univariate data were applied to the total number of fish and species richness, which were assessed using Euclidean distance (on square-root transformed data), and permutated residuals under a reduced model, Type III (maximum permutations = 9999). This routine also allowed a posteriori pair-wise comparisons among levels of factors (Anderson 2001). Similarly, in order to examine possible differences in fish assemblage structure, repeated measures analysis for multivariate data was applied, which was assessed using Bray–Curtis similarity matrix (on fourth-root transformed data), and permutated residuals under a reduced model, Type III (maximum permutations = 9999). Also, a one-way PERMANOVA for univariate data was employed to check seasonal differences in the densities of the most common species (using unrestricted permutation of raw data).

Moreover, a Durbin–Watson test was applied for each 24-h cycle to determine if the value of the abundance at time t+1 was affected by the value of the abundance at time t as the result of the intense diel sampling (collections every two hours). This test allowed us to determine the independence among samples (Mendenhall and Sincich 2003).

Canonical correspondence analysis (CCA) was applied to the overall fish data matrix (dependent set) and the environmental data matrix (independent set) in order to elucidate relations between biological assemblages of species and environmental variables. This method describes and permits the visualization of the differential habitat preferences (niches) of taxa via an ordination diagram (Ter Braak and Verdonschot 1995). Inter-set correlations of this analysis were used to determine the environmental variables that were most important in determining species abundance (McGarigal et al. 2000). For this analysis, a fourth-root transformation was also applied to abundance data.

RESULTS

During the sampling period, the water temperature varied from 18°C in January to 34°C in July, with a mean value of 24.7°C. The salinity varied between 2‰ in September and 27‰ in May, with a mean value of 14.58‰.

Total fish number and species richness variability. A total of 17 105 fish were collected with a total weight of 49 262.6 g, corresponding to 29 families and 65 species (Table 1). The most-represented families with respect to species number and abundance were: Engraulidae, Clupeidae, Atherinopsidae, and Sciaenidae. Numerically dominant species included *Anchoa mitchilli* (49.28%), *Membras martinica* (7.51%), *Mugil curema* (5.89%) and *Bairdiella chrysoura* (5.05%) (Full authority of all species studied is given in Table 1). In relation to diel variability, the total fish number tended to show pulses at twilight hours, around dusk, and dawn, with low abundance at mid-day. Moreover, according to Durbin–Watson tests, these pulses were independent from the progressive chronological sequence of sampling efforts in each 24 h cycle ($P > 0.05$), except for November, when autocorrelation was detected ($P = 0.03$). Although all sampling cycles started at 14:00 or 16:00 h, capture pulses were commonly detected at dawn and/or dusk. This means that despite intensive diel sampling, in general there was a considerable independence among the collections within each cycle of 24-h. While sampling every two hours on the same site could have an effect on the habitat and the organisms that live there, the high degree of independence among diel samples indicates that this effect may be small.

Thus, the observed pulses showed significant differences among diel periods (Table 2); because the total fish number during twilight was significantly higher (pair-wise comparisons) than during the night (Fig. 2A). Similarly, species richness also tended to show pulses around dawn and dusk, with greater values at night than at mid-day. There were also significant differences among diel periods in species richness (Table 2), but in this case the mean values in the twilight and night were significantly higher than in the day (Fig. 2B).

The monthly mean values of the total fish number varied markedly throughout the annual study cycle (Fig. 3), with significant differences among months (Table 2). Two important pulses were observed: one during January–March (the cold-dry season) and another in September (the rainy season), which were significantly greater than those observed in November and May (pair-wise comparisons). Significant differences in species richness were also recorded across the months of sampling (Table 2), with the highest monthly averages from March to July and the lowest average in September (Fig. 3). Moreover, the significant differences in total number of fish and species richness among months were independent of the diel variation (i.e., there was no significant interaction between factors) (Table 2).

Variability in fish assemblages. Regarding the ordination of CCA (Table 3), the first two canonical axes explained 63.48% of the total constrained variance and showed high correlations between species and environmental variables (>0.93). According to inter-set correlations of this analysis, salinity, temperature, rainfall, and seagrass cover were the most important environmental variables affecting the structuring of the fish community. Moreover, inter-set correlations revealed a relatively low importance of tidal stage and diel effect (day/twilight/night) in community structure.

List of species and families recorded during this study

Family	Species
Dasyatidae	*Dasyatis sabina* (Lesueur, 1824)
Elopidae	*Elops saurus* Linnaeus, 1766
Ophichthidae	*Myrophis punctatus* Lütken, 1852
	Ophichthus gomesii (Castelnau, 1855)
Engraulidae	*Anchoa hepsetus* (Linnaeus, 1758)
	Anchoa mitchilli (Valenciennes, 1848)
	Cetengraulis edentulus (Cuvier, 1829)
Clupeidae	*Brevoortia gunteri* Hildebrand, 1948
	Brevoortia patronus Goode, 1878
	Dorosoma cepedianum (Lesueur, 1818)
	Dorosoma petenense (Günther, 1867)
Ariidae	*Ariopsis felis* (Linnaeus, 1766)
	Bagre marinus (Mitchill, 1815)
	Cathorops aguadulce (Meek, 1904)
Batrachoididae	*Opsanus beta* (Goode et Bean, 1880)
	Porichthys porosissimus (Cuvier, 1829)
Eleotridae	*Dormitator maculatus* (Bloch, 1792)
	Eleotris pisonis (Gmelin, 1789)
	Erotelis smaragdus (Valenciennes, 1837)
	Gobiomorus dormitor Lacepède, 1800
Oxudercidae	*Ctenogobius boleosoma* (Jordan et Gilbert, 1882)
	Ctenogobius shufeldti (Jordan et Eigenmann, 1887)
	Evorthodus lyricus (Girard, 1858)
	Gobionellus oceanicus (Pallas, 1770)
Gobiidae	*Bathygobius soporator* (Valenciennes, 1837)
	Gobiosoma bosc (Lacepède, 1800)
Mugilidae	*Mugil cephalus* Linnaeus, 1758
	Mugil curema Valenciennes, 1836
Cichlidae	*Oreochromis aureus* (Steindachner, 1864)
Blenniidae	*Lupinoblennius nicholsi* (Tavolga, 1954)
Atherinopsidae	*Membras martinica* (Valenciennes, 1835)
	Menidia beryllina (Cope, 1867)
Belonidae	*Strongylura marina* (Walbaum, 1792)
	Strongylura notata notata (Poey, 1860)
	Strongylura timucu (Walbaum, 1792)
Fundulidae	*Fundulus grandis* Baird et Girard, 1853
Poeciliidae	*Poecilia mexicana* Steindachner, 1863
Carangidae	*Caranx hippos* (Linnaeus, 1766)
	Oligoplites saurus (Bloch et Schneider, 1801)
	Selene vomer (Linnaeus, 1758)
Paralichthyidae	*Citharichthys spilopterus* Günther, 1862
Achiridae	*Achirus lineatus* (Linnaeus, 1758)
Cynoglossidae	*Symphurus civitatium* Ginsburg, 1951
	Symphurus plagiusa (Linnaeus, 1766)
Syngnathidae	*Syngnathus louisianae* Günther, 1870
	Syngnathus pelagicus Linnaeus, 1758
	Syngnathus scovelli (Evermann et Kendall, 1896)
Trichiuridae	*Trichiurus lepturus* Linnaeus, 1758
Centropomidae	*Centropomus mexicanus* Bocourt, 1868
	Centropomus parallelus Poey, 1860
Gerreidae	*Diapterus auratus* Ranzani, 1842
	Diapterus rhombeus (Cuvier, 1829)
	Eucinostomus melanopterus (Bleeker, 1863)

Table 1 cont.

Family	Species
Haemulidae	*Orthopristis chrysoptera* (Linnaeus, 1766)
	Pomadasys crocro (Cuvier, 1830)
Lutjanidae	*Lutjanus griseus* (Linnaeus, 1758)
Sciaenidae	*Bairdiella chrysoura* (Lacepède, 1802)
	Bairdiella ronchus (Cuvier, 1830)
	Cynoscion arenarius Ginsburg, 1930
	Cynoscion nebulosus (Cuvier, 1830)
	Leiostomus xanthurus Lacepède, 1802
	Micropogonias undulatus (Linnaeus, 1766)
	Pogonias cromis (Linnaeus, 1766)
Sparidae	*Archosargus probatocephalus* (Walbaum, 1792)
	Lagodon rhomboides (Linnaeus, 1766)

The sequence of families follows Nelson et al. (2016) and the species are sorted alphabetically within each family. All fish names according to Froese and Pauly (2016).
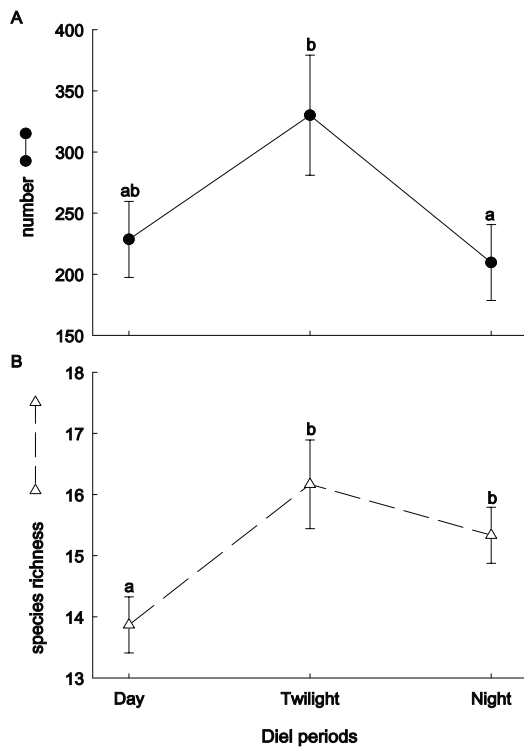
Fig. 2. Mean and standard error values by diel period of (**A**) total fish number and (**B**) species richness (untransformed data); According to pair-wise comparisons, different letters indicate means with significant differences
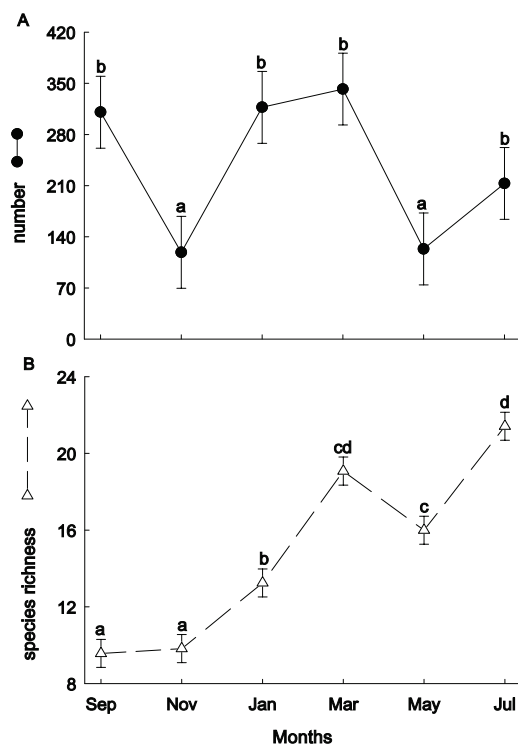
Fig. 3. Mean values and standard errors for monthly values of (**A**) total number of fish and (**B**) species richness (untransformed data), in a submerged vegetation habitat of Pueblo Viejo lagoon; Pulses related to periods of high productivity in the system were observed; According to pair-wise comparisons, different letters indicate means with significant differences

The CCA also revealed relations between species abundance and environmental variables (salinity, rainfall, temperature, and seagrass cover). The fish assemblage structure showed three different time-related patterns (Fig. 4). The first was represented by the months of September and July, and some samples from November (rainy season, with low salinity and low seagrass density). The second pattern included samples from January and March (cold-dry period). The third pattern was considered to represent a transitional period and included all samples of May (high salinity, temperature, and seagrass density). The fish assemblage during the period of low salinity and low seagrass cover included *A. mitchilli*, *M. martinica*, *B. chrysoura*, and *Cathorops aguadulce*. During the cold-dry period, the species assemblage included *M. curema*, *Lagodon rhomboides*, *Anchoa hepsetus*, *Orthopristis*

chrysoptera, and *Leiostomus xanthurus*. The third group related to the period of high salinity and greater seagrass cover (warm-dry period), included *Menidia beryllina*, *Brevoortia patronus*, *Brevoortia gunteri*, and *Cetengraulis edentulus*. Multivariate repeated measures revealed significant differences in fish assemblages among months (Table 4). Regarding to individual abundance of dominant species, all species mentioned above showed significant differences among months (Table 5).

Although the CCA showed a negligible influence of the diel effect, multivariate repeated measures also revealed significant differences in fish composition among diel periods (Table 4). Thus, the two most numerically abundant species, *A. mitchilli* and *M. martinica*, showed twilight pattern and had regular pulses at dawn and dusk. *Menidia beryllina*, *A. hepsetus*, and *B. patronus* presented a typical diurnal pattern, whereas *C. aguadulce*, *Opsanus beta*, and *Citharichthys spilopterus* were mainly captured at night. However, additional species were more abundant in the

Table 2

Results from univariate repeated-measure PERMANOVA to test effects of diel (day/twilight/night) and month on the total fish abundance and species richness

|	Source of variance	df	MS	*F*	*P*
Total fish number	Diel	2	1.377	4.285	0.039
	Months	5	1.995	7.891	0.001
	Hour (diel)	9	0.321	1.271	0.270
	Diel × months	10	0.488	1.931	0.079
	Error	45	0.253		
Species richness	Diel	2	0.042	5.837	0.024
	Months	5	0.299	33.746	0.0001
	Hour (diel)	9	0.007	0.807	0.606
	Diel × months	10	0.011	1.183	0.330
	Error	45	0.009		

df = degrees of freedom, MS = mean square, *F* = Pseudo-*F*, *P* = *P*-value by permutation.).

Table 3

Results of canonical correspondence analysis (CCA) of the overall fish data matrix and the environmental data matrix

	Axis 1	Axis 2
Cumulative Constrained percentage	37.28	63.48
Species-environmental variables correlations	0.936	0.938
Inter-set correlations between environmental variables and species scores		
Rainfall	0.784	−0.326
Salinity	−0.600	0.682
Temperature	0.555	0.619
Dissolved oxygen	−0.432	−0.195
Tidal stage	−0.295	0.135
Seagrass cover	−0.236	0.572
Day/twilight/night effect	0.025	0.094

Diel periods were considered to be in a light-dark gradient in an ordinal scale with values of 2 (day), 1 (twilight), and 0 (night).
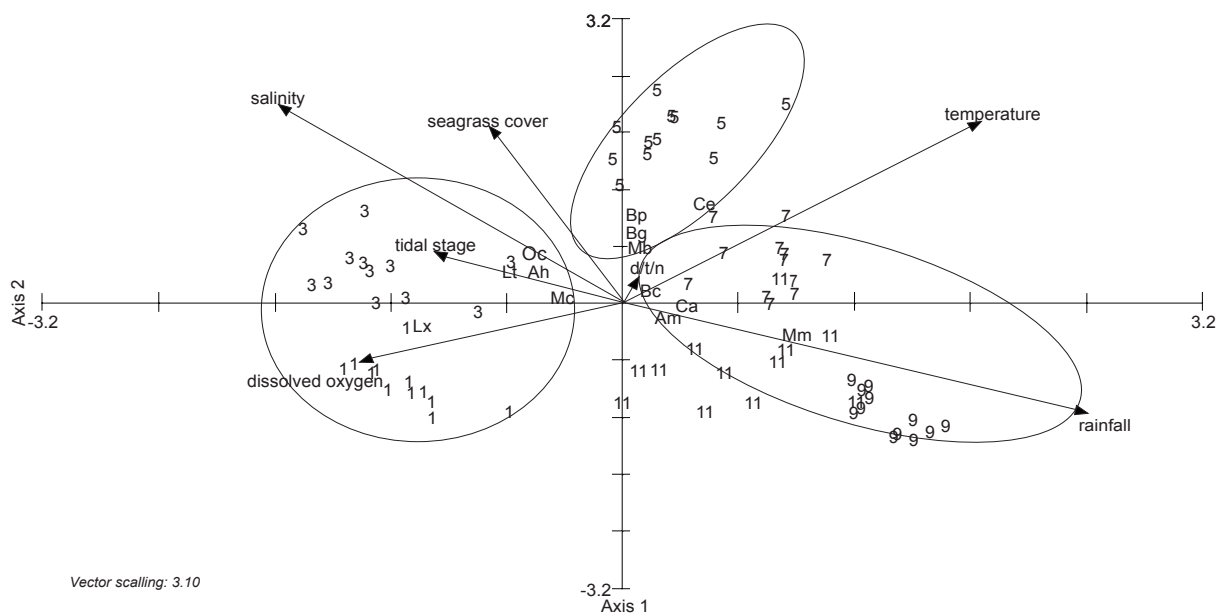
Fig. 4. Canonical correspondence analysis tri-plot of the overall species, months of sampling (represented by numbers) and environmental variables (vectors); The habitat preferences of the most abundant species (89.30% of total fish abundance) including *A. mitchilli* (Am); *M. martinica* (Mm); *B. chrysoura* (Bc); *C. aguadulce* (Ca); *M. curema* (Mc); *L. rhomboides* (Lr); *A. hepsetus* (Ah); *O. chrysoptera* (Oc); *L. xanthurus* (Lx); *M. beryllina* (Mb); *C. edentulus* (Ce); *B. gunteri* (Bg); and *B. patronus* (Bp)

day or in the night throughout the year. For example, in January *M. curema* and *L. xanthurus* were more abundant during daylight hours, but in March they were more abundant at night. For this reason, interaction between diel and seasonal factors was significant (Table 4).

Table 4

Results from multivariate repeated-measure PERMANOVA to test effects of diel (day/twilight/night) and month on the abundances of all species

Source of variance	df	MS	*F*	*P*
Diel	2	2730.6	3.641	0.0004
Months	5	11224.0	18.153	0.0001
Hour (diel)	9	749.91	1.213	0.1189
Diel × months	10	988.48	1.599	0.0007
Error	45	618.32		

df = degrees of freedom, MS = mean square, *F* = Pseudo-*F*, *P* = *P*-value by permutation.

DISCUSSION

Total fish number and species richness variability. Total number of fish showed significant differences among diel periods with regular pulses at dusk and dawn (Fig. 2, Table 2). These results may be due to the diel abundance patterns of species, which have pulses at dawn and dusk. This was found to be the case with the numerically dominant species *A. mitchilli* and *M. martinica*. Twilight pulses of the total number of fish may also be caused by migrations during the transition period created by the beginning and end of the activities of fish species with diurnal and nocturnal habits (Hobson et al. 1981, Helfman 1993, Rickel and Genin 2005). Diel migrations at sunset and sunrise may correspond to the immigration which takes the fish to their foraging grounds, and the emigration which takes them back to their resting sites (Krumme 2009). Thus, these movements of the fish generate pulses in abundance during twilight, when the submerged vegetation could play an important role. In this sense, these patterns in abundance and habitat use by species in 24-h cycles may result from periodicity in foraging activity, avoidance of predators or the interaction of both (Helfman 1993, Pessanha et al. 2003, Hoeksema and Potter 2006, Hagan and Able 2008).

In the same way, species richness showed significant differences among diel periods, but with a twilight–night pattern (Fig. 2, Table 2). Similarly, various authors have recorded important activity pulses for fish species at dusk or dark hours, both in tropical estuaries (Pessanha and Araújo 2003, Pessanha et al. 2003, Ley and Halliday 2007, Castillo-Rivera et al. 2010, Lacerda et al. 2014) and temperate estuaries (Layman 2000, Griffiths 2001, Guest et al. 2003). In contrast, species richness was consistently greater during the night in a bare substrate environment in Pueblo Viejo lagoon (Castillo-Rivera et al. 2010). This may be partly due to the presence of vegetation that acts as a protection area and allows greater twilight activity for species with nocturnal habits. Indeed, when only habitats within estuaries are considered, vegetated habitats mostly provide more protection from predation than unvegetated habitats (Nagelkerken 2009).

The seasonal pattern of total fish abundance (Fig. 3) showed significant differences among months (Table 2). The pulses during September and January–March might be related to production processes within the system, as Pueblo Viejo lagoon has important primary production pulses during March–May and July–September (Contreras 1995). Moreover, during rainy season there are significant inputs of exogenous nutrients and allochthonous organic matter via the rivers and watershed of the lagoon, which also stimulate increased primary production (Milton 2009).

Table 5

Monthly mean number of abundant species and one-way univariate PERMANOVA results (for all cases degrees of freedom = 5/66)

Species	Mean number						PERMANOVA	
	Jan	Mar	May	Jul	Sep	Nov	*F*	*P*
Anchoa mitchilli	148.0	145.5	16.17	73.50	233.0	86.25	10.10	0.0001
Membras martinica	2.83	0.92	2.42	30.83	59.17	10.92	15.80	0.0001
Bairdiella chrysoura	10.00	10.42	4.75	40.58	5.33	0.83	12.29	0.0001
Cathorops aguadulce	0.92	1.17	0.0	17.25	1.92	0.0	15.98	0.0001
Menidia beryllina	1.42	3.0	36.30	12.00	1.58	3.50	12.86	0.0001
Cetengraulis edentulus	0.0	0.0	9.75	0.67	0.17	0.0	13.55	0.0001
Brevoortia gunteri	2.42	1.17	5.08	3.75	0.17	0.0	9.77	0.0001
Brevoortia patronus	0.0	0.0	10.00	0.0	0.0	0.0	10.10	0.0001
Mugil curema	58.25	9.75	5.92	1.17	1.08	7.75	8.56	0.0001
Lagodon rhomboides	35.25	27.42	4.92	1.17	0.08	0.0	31.61	0.0001
Anchoa hepsetus	0.0	38	0.25	0.25	0.17	0.0	24.74	0.0001
Orthopristis chrysoptera	0.0	36.3	0.67	1.42	0.0	0.0	78.19	0.0001
Leiostomus xanthurus	5.83	8.33	0.0	0.0	0.0	0.0	15.12	0.0001

F = Pseudo-*F*, *P* = *P*-value by permutation.

Production processes and rainfall (Yáñez-Arancibia et al. 1993, Meynecke et al. 2006, Gillson 2011, Castillo-Rivera 2013) commonly influence fish abundance in various estuarine communities.

Species richness also showed significant differences ($P < 0.001$) among months (Fig. 3), with high mean values during March (dry season) and July (rainy season). Similar pulses in species richness during the summer have also been observed in fish communities of the western Atlantic (Layman 2000, Akin et al. 2003, Murphy and Secor 2006). The seasonal pattern of species richness in habitats with submerged vegetation also seems to be associated with an increase in the primary production within the system. The lower species richness in September (rainy season) may be the result of the low salinity during this month. Low salinity restricts the immigration of stenohaline species.

Variability in fish assemblages. In the CCA, axes 1 and 2 together explained a high percentage of the variance of the ordination. From this analysis, the salinity, rainfall, temperature and seagrass cover gradients were revealed to be the most important driving forces in the structure of fish composition in the studied habitat (Table 3). Thus, seasonal variability in fish assemblages reflected these environmental gradients, with the formation of different groups related to the months of the year (Fig. 4). The repeated measures analysis of multivariate data (Table 4) and the one-way univariate analysis (Table 5) supported the results from the CCA, showing significant differences in fish composition among months.

The fish assemblage of the low salinity period (rainy season) was characterized by the presence of *A. mitchilli*, *M. martinica*, *B. chrysoura*, and *C. aguadulce*. Although *A. mitchilli* was dominant during all months, the changes in its abundance throughout the annual cycle are related directly to the rainfall regime (Castillo-Rivera 2013). The seasonal behaviour of *M. martinica* and *C. aguadulce*, which both have detritus as an important food resource in their diet and are tolerant to low-salinity conditions, has also been observed to be associated with the rainfall regime (Castillo-Rivera 2012). On the other hand, species that feed on zooplankton such as *M. beryllina* and those that feed on phytoplankton such as *C. edentulus*, *B. gunteri*, and *B. patronus* are predominant during the warm-dry season (Castillo-Rivera et al. 1996, Castillo-Rivera and Kobelkowsky 2000) when the system has a higher seagrass cover and an important pulse of plankton. The fish assemblage of the cold-dry period (January–March) was dominated by *M. curema*, *L. rhomboides*, *A. hepsetus*, *O. chrysoptera*, and *L. xanthurus*, which have mainly subtropical and warm-temperate preferences (Froese and Pauly 2016) with occurrences restricted to the colder months.

The pulses of maximum abundance during different months represent a seasonal succession of species, which has been observed in many coastal systems (Yáñez-Arancibia et al. 1993, Akin et al. 2003, Pessanha et al. 2003, Jaureguizar et al. 2004, Ribeiro et al. 2006, Vasconcellos et al. 2011). This progression of the abundance mediated by pulses is markedly influenced by the life history strategies of the species. These strategies might have an adaptive value with respect to the optimum use of the available resources, allowing an adequate seasonal partitioning of food and space resources and thus decreasing possible intra-specific competition. Thus, the seasonal changes in fish abundance in the studied habitat may be determined by a combination of temporal changes in salinity, rainfall, temperature, and the different feeding strategies of the species.

Many studies have found little diel variation in fish assemblages, despite a greater number of species and individuals captured at dusk and/or at night (Layman 2000, Griffiths 2001, Pessanha et al. 2003). However, in the presently reported study, repeated measures results indicated that there were multivariate significant differences in fish assemblages among diel periods. These differences are mainly due to the fact that some species were typically diurnal (e.g., *M. beryllina*, *A. hepsetus*, and *B. patronus*), nocturnal (e.g., *O. beta*, *C. aguadulce*, and *C. spilopterus*) or crepuscular (e.g., *A. mitchilli* and *M. martinica*). Moreover, the submerged vegetation may also alter the diel behaviour of species. For example, in this study, *A. hepsetus* showed a mainly diurnal behaviour that contrasts with the nocturnal behaviour recorded in environments without submerged vegetation (Castillo-Rivera et al. 2010). This change in behaviour is related to the protection that this type of vegetation offers (Nagelkerken 2009), which enables species to have a greater diurnal activity.

Although the influence of the tide on fish populations has been recognized in many studies, in the Gulf of Mexico the tidal influence is virtually absent (Krumme 2009, Nagelkerken 2009). Thus, in Pueblo Viejo lagoon, the negligible influence of the tidal stage over fish community structure and composition was probably caused by the restricted lagoon-ocean exchange (Fig. 1), which reduces the tidal range from approximately 40 cm off the coast to < 15 cm inside the lagoon. Pessanha and Araújo (2003) observed little tidal influence on the fish community in Sepetiba Bay, Brazil (maximum tidal height < 1.0 m). In contrast, in estuaries with a higher tidal range (>1.0 m), tides have a major influence on fish community structure (Layman 2000, Ribeiro et al. 2006, Lacerda et al. 2014). Therefore, on coasts with low tidal range, the activity patterns of fishes could be primarily synchronized with the day–night cycle (Krumme 2009).

The majority of studies on diel variation have sampled only a few hours for each 24-h period, often focusing on the high and/or low tides during day and night periods (Guest et al. 2003, Ribeiro et al. 2006, Hagan and Able 2008). Our study utilized a single-site approach with high-frequency temporal sampling (every 2 h) to evaluate diel effects. Although, our sampling strategy allowed us to detect patterns at a finer temporal scale throughout a 24-h period, including dawn and dusk faunal patterns, it did not allow us to evaluate spatial variability in these patterns. Another potential limitation of the sampling method was the use of a seine net, which can be highly selective to small species that are close to the shore (e.g., *A. mitchilli* and *M. martinica*).

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