Research Article

The influence of habitat on the spatio-temporal dynamics of fish assemblages in a lagoon-estuarine system of the Mexican Pacific

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ABSTRACT. Fish assemblages change significantly with physical and chemical characteristics of water; however, their response to the variability of geomorphic habitats has been rarely evaluated in lagoon-estuarine in one of these systems of the Mexican Pacific. Spatio-temporal variation of fish assemblage structure was assessed for three habitats: lagoon, estuarine, channel and inlet. The hypothesis was that sheltered areas support comparatively higher richness and abundance of fish species, with more small-sized specimens than the most exposed areas. We found that the ichthyofauna differed significantly among habitats. Several species were smaller in the lagoon compared with the other habitats, suggesting a use of the lagoon as a nursery ground. Moreover, dominant species for the lagoon were rarely found or absent in the inlet, whereas others were found only present or with higher abundance in the inlet. Although seasonal differences in richness and composition were detected, the evidence of fish-habitat associations for many species was noticeable regardless of seasonality, probably due to a high percentage of resident species during the annual cycle. The lagoon supports a greater abundance and species richness, due to a more sheltered and structured habitat, evidencing habitat-driven segregation in fish assemblages, and an aspect that should be incorporated for management of coastal ecosystems.

Keywords: coastal; geoforms; habitat structure; ichthyofauna; nursery; Gulf of Tehuantepec

INTRODUCTION

Lagoon-estuarine systems are formed by a complex matrix of intertidal habitats with distinctive environmental features that play an essential role in support of high fish production (McLusky & Elliott, 2004; Yáñez-Arancibia *et al*., 2004; França *et al*., 2012). In these systems, geomorphological processes originate geoforms (*e.g.*, lagoons, mouths and channels), which are habitats with different physical attributes (*e.g.*, depth, width, substrate) that influence the patterns of composition, richness, abundance, migration and the size-specific spatial use by organisms (Bartholomew *et al*., 2000; Saintilan, 2004; Franco *et al*., 2006; França *et al*., 2009;

Hicks *et al*., 2010). For example, the mouth and its tidal channels are ecotones connecting the marine with the brackish environment (Webster, 2011; Lacerda *et al*., 2014). Furthermore, other geoforms such as lagoons, which are partially enclosed areas with low water circulation and more structural complexity (*e.g.*, muddy bottoms, riverine and submerged vegetation), are reported as critical habitat for juvenile fish feeding and nurseries (Neves *et al*., 2013; Verdiell-Cubedo *et al*., 2013).

Habitat features have been integrated in estuarine fish research as a key factor to understand the structure of ecological assemblages and their relationship with highly variable spatial conditions and allows to define

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connectivity mechanisms between habitats and local migration patterns (Sindilariu *et al*., 2006; Franco *et al*., 2009; Neves *et al*., 2011), as has been shown by several studies carried out in estuaries and coastal lagoons of Europe, South Africa, Australia and South America (Patterson & Whitfield, 2000; Griffiths, 2001; Franco *et al*., 2006; Neves *et al*., 2011; Loureiro *et al*., 2016).

Some studies have been conducted on fish assemblages of Mexican coasts, concerning mainly lagoon-estuarine systems from the Gulf of Mexico and the northwest and central Pacific areas (Warburton, 1978; Mendoza *et al*., 2009; Castillo-Rivera *et al*., 2010; Rodríguez-Romero *et al*., 2011; Ayala-Pérez *et al*., 2014). These studies indicate that physical and chemical changes (*e.g.*, variations in salinity, water temperature, turbidity, dissolved oxygen, etc.) associated with seasonality constitute a significant driver of fish assemblage patterns. However, in the south Pacific of Mexico there are no studies that include the effect of habitat complexity on fish assemblages.

The Gulf of Tehuantepec in the Mexican Southern Pacific is one of the most important fishing areas (Bakun *et al*., 1999; Ortega-García *et al*., 2000; Wilkinson *et al*., 2009). This region has an extensive belt of lagoon-estuarine systems surrounded by mangroves that shelters one of the richest areas for fish fauna in the Tropical Mexican Pacific (Gómez-González *et al*., 2012; González-Acosta *et al*., 2017). The environmental differences between the geomorphic habitats that integrate these systems make them good models to test the spatial effect of its characteristics on biotic assemblages.

The rapid degradation and loss of coastal ecosystems in recent decades has increased interest in fish research and their habitat in estuarine environments (França *et al*., 2012; Sundblad & Bergström, 2014). The knowledge of geomorphic habitats and their effect on fish assemblages constitutes an important baseline for the development of monitoring programs and integrate ecosystem-based management of coastal resources (Pérez-Ruzafa *et al*., 2007; Franco *et al*., 2009; Sheaves *et al*., 2012). Therefore, the specific aims of this study were to i) determine the spatio-temporal variations of fish assemblages in a shallow lagoon-estuarine system and compare its structure in three geomorphic habitats (lagoon, channel, inlet); and to ii) determine their relationships with hydrological parameters (*e.g.*, salinity, dissolved oxygen, depth) and physical attributes (substrate, vegetation, shelter). The tested hypothesis is that fish assemblages are likely to differ among these habitats, with the most complex areas supporting comparatively higher fish abundance, richness and a higher number of small-sized organisms

compared to less complex areas, along spatial and seasonal gradients.

MATERIALS AND METHODS

Study area

La Joya-Buenavista lagoon-estuarine system (LJB) is located at the northeastern corner of Gulf of Tehuantepec, southwest Chiapas, Mexico (15°48'-15°56'N, 93°32'-93°47'W); it is a shallow water body with an area of 47.5 km^2 (Fig.1). The LJB presents a sandy barrier and tides predominantly semidiurnal, with a range of 1.2 m (Lankford, 1977; Contreras, 2010). The water circulation into the system is reduced and depends mainly on the tides and the seasonal freshwater input provided by a few streams. The climate in this area is characterized by a dry season (November-April) and a rainy season (May-October), with a total annual rainfall of 1,441 mm and an average temperature of 28°C. The salinity can vary drastically in some areas, from oligohaline (salinity <5) at the peak of the rains to hyperhaline (salinity >40) in highly protected sites during the dry season (Contreras & Zabalegui, 1991).

This study analyzed the fish assemblages of three geomorphic habitats in the LJB system: lagoon, channel and inlet (Fig. 1). These habitats were identified mainly based on the qualitative description of physical and morphological characteristics. The depth of the lagoon varies from 0.2 to 1.5 m, with a predominantly muddy substrate, with sparse submerged tree trunks and margins comprised of grass and
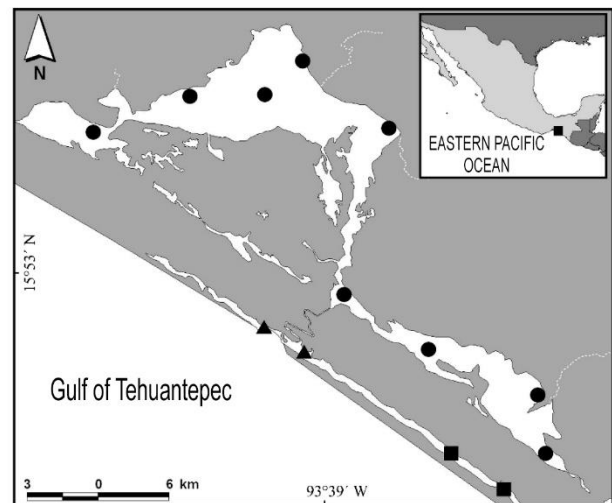

Figure 1. Map of the study area in the La Joya-Buenavista lagoon-estuarine system, Mexico. Symbols represent sampling sites coded by habitat type. Circles: lagoon, squares: channel, triangles: inlet.

fringe/basin mangroves (*Avicennia germinans* L. and *Conocarpus erectus* L.). The channel has a total length of 23 km and varies in width from about 570 m at the mouth to 200 m at the head. Most of the channel zone is surrounded by riverine mangroves (*Rhizophora mangle* L.). Substrate composition changes from muddy, with some sandy patches in the channel, to predominantly sandy in the mouth. The inlet flows into the Gulf of Tehuantepec through an estuary mouth of 157 m of width, the zone most exposed to tidal currents.

Data collection

Sampling was performed bimonthly from 9:00 to 16:00 h, at 13 sites during June 2013-April 2014. Sampling was conducted using monofilament cast nets (4 m diameter with 1.27 cm mesh). This gear could be used in all sites under its temporal variations in depth and habitat conditions, although an *a priori* characterization focused on small and juvenile components was assumed (Sheaves *et al.*, 2007; Stein III *et al.*, 2014). The cast net was operated from the shoreline or a boat by the same individual. Sampling effort was standardized to 10 cast nets. This number of deployments was determined by estimating the values of the asymptotes of plot-based species accumulation curves for each habitat in three pilot sites ($R^2 = 0.99$, 0.94, 0.96). Cast net deployments were done in a radius of up to 50 m, thus avoiding the disturbance effect of three castings at the same point.

The fish specimens were weighed, measured, fixed in 10% formalin, washed in tap water after 48 h, and transferred to 70% ethanol. All fish were identified to species and counted. Scientific names and authorities were corroborated following Fricke *et al.* (2019). Voucher specimens were deposited at the ichthyological collection of the Museum of Zoology of the University of Science and Arts of Chiapas (MZ-P-UNICACH) in Tuxtla Gutiérrez, Mexico. For descriptive purposes, selected dominant species were allocated to four ecological categories according to their salinity tolerance (Myers, 1966; Castro-Aguirre *et al.*, 1999; Day Jr. *et al.*, 2012). These species were also allocated to functional guilds according to their trophic group following the criteria of Elliott *et al.* (2007), with information from Froese & Pauly (2016). Four ecological groups were identified in this study: estuarine (fish that are residents in brackish waters), marine euryhaline (can tolerate a wide range of salinity), marine stenohaline (can tolerate a narrow range of salinity) and secondary freshwater (salt-tolerant inland fish). Likewise, five trophic groups were identified: piscivores, which are species whose diet consists mainly of fish; zooplanktivores, species that feed predominantly on zooplankton; zoobenthivores,

species that feed on bottom invertebrates; detritivores, species that feed on the bottom, selecting fine particles, benthic diatoms, meiofauna and sediments; and omnivores, which feed on algae and a variety of invertebrates.

Hydrological variables were measured on each sampling event before the fish collection. Salinity, water temperature (°C), dissolved oxygen (mg L^{-1}), and pH were determined at the mid-depth of each site using a multiprobe meter (YSI 556). The depth (to the nearest 0.1 m) and water clarity (Secchi´s depth in cm) were also determined.

Habitat structure descriptors (substrate, vegetation and shelter) were examined in the system (in this study, habitat structure was considered as the physical attributes that may provide protection and food for fish species; Green *et al.*, 2012). At each site, a plot of 1 m^2 was randomly positioned to visually evaluate the substrate composition as the percentage covered by muddy, sandy or mixed deposits. The presence of other physical elements as tree trunks and riprap was also recorded. Values for vegetation were assigned based on the dominant marginal coverage (>60% of mangroves or grasses) in a 200 m^2 area adjacent to the sampling site. The shelter was assessed according to the distance of the sites with the inlet or the channel. Following Neves *et al.* (2013), each habitat attribute was assigned a value from 1 to 3 to qualify structure, and these were added to achieve a total score, estimated to obtain the overall degree of physical habitat structure. Each site was categorized with ranges from 3 (lowest habitat structure) to 9 (highest habitat structure). For example, highly exposed sites (such as the mouth) with bare sand substrate and lacking plant (*e.g.*, grasses) or physical structures were qualified with a value of 3, whereas other sites sheltered from the currents (such as the lagoon), with a combination of muddy substrate, submerged trunks and coverage dominated by mangroves would get a score of 9.

Data analysis

The species dominance was determined using the Importance Value Index (IV), estimated as a percentage of the numerical abundance, biomass and frequency of all species (Krebs, 1999). We considered species that, in total, had 75% of the IV as dominant (Peralta-Meixueiro & Vega-Cendejas, 2011).

The abundance data were fourth-root transformed to minimize the influence of overly abundant taxa. The data set was divided by the three geomorphic habitats (lagoon, nine sites, inlet and channel, two sites each; Fig. 1) and months were summarized in seasons as pre-wet (June), wet (August-October), pre-dry (December) and dry (February-April). An individual-based rarefac-

tion method was used to estimate the expected number of species in a sample [E (Sn)] and calculate an abundance-corrected dataset to compensate for differences in sampling effort between habitats and seasons. The E (S) was generated for a constant number in a random set of m individuals from the reference sample ($m < n$) (Colwell *et al*., 2012). The variation of the rarefied species richness, as well as that of the environmental parameters between habitat and season, were analyzed using one-way analysis of variance (ANOVA), having verified the assumptions of normality and homogeneity of variances. Non-parametric ANOVA (Kruskal-Wallis test) was used in cases where heteroscedasticity was found even after the logarithmic transformation of data. A Bonferroni test (or Mann-Whitney pairwise to non-parametric test) followed the ANOVA procedures every time that the null hypothesis was rejected at α = 0.05 (Zar, 2010).

Non-parametric multivariate analyses were conducted to assess the spatio-temporal changes in fish assemblage structure (species composition and abundance) and their relationship to environmental parameters, after evaluating the homogeneity of the multivariate dispersion (PERMDISP) (Anderson, 2006). Preliminarily, a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), conducted on a Euclidean similarity matrix of all environmental data, assessed differences, and the interaction between habitats and seasons. Furthermore, principal component analysis (PCA) was performed on the normalized hydrological data (log x+10) to explore gradients in the sampling events. To avoid bias in the PCA related to highly correlated hydrological data, before PCA, a Pearson correlation test was performed, and variables that show high collinearity ($r > 8$) were not considered in this analysis. Later, differences in fish assemblages between habitat and seasons were also assessed by PERMANOVA, including habitat type (fixed factor), seasons (fixed factor), sampling sites (nested in habitat type) and months (nested in seasons), conducted on a Bray-Curtis similarity matrix. A pairwise *post-hoc* comparison was performed, while results off that PERMANOVA were significant.

The similarity percentage analysis (SIMPER) (Clarke, 1993) was used to describe the variance explained per species by habitat. Standard length (SL) data of dominant species selected by SIMPER were compared with a Kruskal-Wallis test and the Mann-Whitney pairwise test to assess possible variations in the size of individuals per habitat.

Finally, distance-based linear modelling (DistLM) (Anderson *et al*., 2008) with a step-wise procedure and an adjusted R^2 selection criterion (Legendre & Anderson, 1999), was performed on the fourth-root abundance matrix and the normalized environmental data (including habitat structure values). The resulting model was represented in a multi-dimensional space with a distance-based redundancy analysis (dbRDA) (McArdle & Anderson, 2001), to assess the relative contributions of environmental variables in structuring fish assemblage and detect a possible spatial gradient. We worked with a 5% significance level ($P \le 0.05$) in all statistical tests. All multivariate analyses were performed with routines in PERMANOVA+ for PRIMER 6 software (Clarke & Gorley, 2006; Anderson *et al*., 2008). All other analyses were carried out with package Vegan in language R, version 3.1.2 (Oksanen *et al*., 2014; R Development Core Team, 2014).

RESULTS

Environmental variation

The PERMANOVA results showed that hydrological variables were significantly different between habitats ($F = 9.25$, $P < 0.01$), seasons ($F = 18.98$, $P < 0.01$) and the interaction (habitat × season, $F = 4.69$, $P < 0.01$). Likewise, differences in some hydrological parameters were consistent ($P < 0.05$) between seasons and habitats, or both. In paired comparisons within temporal factor, major differences between habitats were observed in all seasons ($P < 0.02$), except for the inlet-channel pair; oxygen saturation was low during the dry season in the channel (1 mg L^{-1}; April), while higher concentrations were for the lagoon (5.3-9.5 mg L^{-1}) in the wet and pre-dry seasons. According to an adaptation of the Venice system used to describe salinity zones in estuaries (Whitfield, 1998), the inlet and channel areas are typically polyhaline, ranging from 22.1 to 29.5, whereas the lagoon was significantly different from mesohaline conditions (13). Seasonal variations in salinity were recorded, ranging from oligohaline (wet season; 3.3) to marine conditions (dry; 34.1). Water temperature and pH presented seasonal variations, while the depth and water clarity only showed changes between habitats. The habitat structure score presented its highest mean value for the lagoon (8.6), while the lowest value was obtained for the inlet (3.3) (Table 1).

The PCA of the hydrological variables explained 63.6% of the variance for the first two axes (Fig. 2). This model considered only four explanatory variables after reducing multicollinearity. The PC1 contributed with 36.8% of the explained variance and it was strongly related (based on eigenvectors of correlation matrix) with depth (-0.56) and salinity (-0.45); whereas, the PC2 contributed with 26.8% of the explained variance and better correlated with dissolved oxygen (0.43) and pH (-0.41).

Table 1. Means (and standard deviation) of hydrological parameters in the La Joya-Buenavista lagoon-estuarine system (Mexico), June 2013-April 2014, and results of the ANOVA (*F*) and Kruskal-Wallis test (*H*) analyses for spatial and temporal comparisons for each parameter. Significant *P*-values (<0.05) are in bold. Seasons having the same superscript letter were not significantly different within each temporality. Habitat structure values also are presented. I: inlet; C: channel; L: lagoon.

	Season	Inlet	Channel	Lagoon	Spatial	Temporal
	Water temperature (°C)					
	Pre-wet[a]	31.4 (0.1)	32.0 (0.4)	33.1 (1.6)	$H = 2.99$	$F = 36.84$
	Wet[a]	30.5 (0.1)	30.1 (1.3)	31.5 (2.5)	$P = 0.224$	$P = \mathbf{0.000}$
	Pre-dry[b]	28.6 (0.0)	27.5 (0.1)	25.8 (1.7)		
	Dry[a]	30.7 (1.1)	32.6 (1.3)	32.3 (1.4)		
	Depth (cm)					
	Pre-wet	89.4 (0.4)	50.3 (4.2)	55.3 (16.1)	$H = 7.3$	$H = 3.21$
	Wet	66.3 (8.5)	82.7 (64.9)	80.5 (52.5)	$P = \mathbf{0.026}$	$P = 0.361$
	Pre-dry	147.5 (0.0)	181.4 (49.5)	73.2 (28.1)	I, C > L	
	Dry	80.2 (77.5)	96.1 (35.7)	44.1(24.4)		
	Water clarity (cm)					
	Pre-wet	87.4 (0.2)	47.5 (4.2)	52.4 (16.1)	$H = 7.31$	$H = 3.21$
	Wet	66.3 (8.5)	40.0 (11.9)	55.4 (20.0)	$P = \mathbf{0.026}$	$P = 0.361$
	Pre-dry	145.0 (1.8)	125.6 (49.5)	40.0 (18.1)	I, C > L	
	Dry	69.5 (77.1)	86.3 (35.7)	44.5 (24.0)		
	Dissolved oxygen (mg L^{-1})					
	Pre-wet[ab]	4.6 (0.1)	2.4 (1.0)	4.8 (1.2)	$F = 25.08$	$F = 4.45$
	Wet[b]	4.4 (0.0)	4.4 (0.5)	5.4 (1.4)	$P = \mathbf{0.000}$	$P = \mathbf{0.006}$
	Pre-dry[ab]	3.4 (0.3)	2.5 (0.3)	6.5 (1.9)	L > I, C	
	Dry[ac]	1.9 (0.9)	2.4 (1.8)	4.6 (1.2)		
	Salinity					
	Pre-wet[a]	31.9 (0.1)	20.3 (1.5)	14.1 (5.8)	$F = 8.37$	$F = 43.32$
	Wet[b]	23.6 (8.9)	16.7 (5.9)	3.3 (2.4)	$P = \mathbf{0.006}$	$P = \mathbf{0.000}$
	Pre-dry[ab]	29.1 (0.6)	17.5 (2.1)	7.1 (2.3)	I, C > L	
	Dry[c]	34.0 (0.5)	34.1 (0.4)	27.7 (5.6)		
	pH					
	Pre-wet[a]	8.4 (0.1)	8.2 (1.0)	8.9 (1.0)	$F = 2.78$	$F = 10.37$
	Wet[b]	7.5 (0.5)	7.6 (0.3)	7.1 (0.7)	$P = 0.068$	$P = \mathbf{0.000}$
	Pre-dry[bc]	7.4 (0.1)	7.6 (1.0)	7.7 (0.7)		
	Dry[ac]	7.1 (1.2)	6.7 (0.3)	8.8 (0.8)		
		Inlet	Channel	Lagoon		
	Substrate	1.1 (0.1)	2.2 (0.2)	2.9 (0.2)		
	Vegetation	1.2 (0.3)	3.0 (0.0)	2.8 (0.5)		
	Shelter	1.1 (0.1)	2.1 (0.1)	2.9 (0.1)		
	Mean value	3.3 (0.4)	7.3 (0.4)	8.6 (0.5)		

(Row label rotated at left: Hydrological parameters)

Fish assemblage structure

Two thousand sixty-four fish individuals were collected by cast net (from 76 sampling events during the study period) and were identified in 48 species and 21 families. The fish assemblage in the LJB was dominated by *Lile gracilis* (13.91%), followed by *Astatheros macracanthus* (10.08%) and *Eucinostomus currani* (9.98%); only three species, *Mugil curema*, *Dormitator latifrons* and *Gerres simillimus* contributed with an amount as large as 36.78% of the total biomass.

According to the IV, 15 species together contribute 75% of relative value (Table 2).

Although the LJB system showed a significant environmental variation between seasons, the fish fauna exhibited their main variations across habitat types. The observed number of species per habitat was 35 in the lagoon, 20 in the inlet and 17 in the channel. Significant differences were found between habitat with the standardized richness [E (S$_{1251}$)], ranging from 13 taxa (channel) to 26 taxa (lagoon) ($H = 6.98$, $P <$
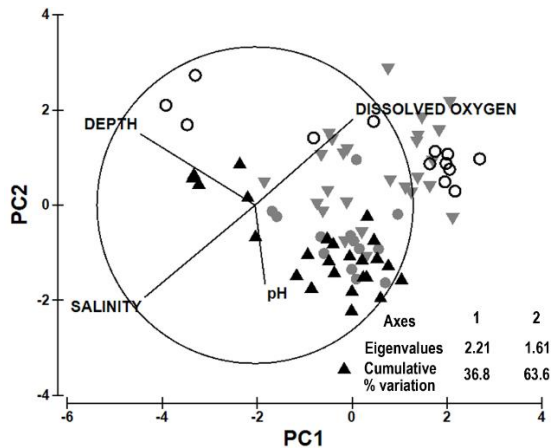
Figure 2. Principal component analysis environmental biplot, La Joya-Buenavista lagoon-estuarine system, Mexico. The length and direction of the vectors represent the strength of the relationship concerning a unit circle. Symbols represent an individual sampling event coded by season. Gray circles: pre-wet, gray inverted triangles: wet, white circles: pre-dry, black triangles: dry.

0.05) (Fig. 3a). Differences were found between seasons with the E (S_{710}), ranging from 20 taxa (pre-wet) to 33 taxa (pre-dry), although these were not significant ($F = 1.7$, $P > 0.05$) (Fig. 3b).

Spatial and temporal variation of fish assemblages

The PERMANOVA results conducted showed that fish assemblages differed significantly at the spatial level (habitat, sampling site; $P < 0.01$). At the temporal level, differences between seasons were also detected, but not by month or their interactions (Table 3).

According to the SIMPER analysis, the average dissimilarity among habitats ranged from 88.3 to 97.3%. Most of the dissimilarity between lagoon-inlet and inlet-channel was due to the species *E. currani* (14.7 and 16%, respectively), while *Centropomus robalito* presented a high contribution (12.8%) in the dissimilarity between the lagoon and channel (Table 4). Regarding the functional guilds in the mouth and lagoon, euryhaline species ($\bar{X} = 61.8\% \pm 29.3$) and omnivores ($\bar{X} = 58.8\% \pm 30.9$) were dominant in abundance, while estuarine residents (53.8%) and zooplanktivores (44.1%) were more abundant in the channel.

The mean fish size differed among the three habitats ($H = 62.26$, $P < 0.01$). Standard length data showed that some of the dominant taxa (*A. macracanthus*, *M. curema*, *E. currani*, *D. latifrons*) were smaller in the lagoon compared with other habitats according to the Mann-Whitney test. In the case of *Lutjanus argentiventris*, which was not captured in the lagoon, the smaller specimens corresponded to the inlet. On the
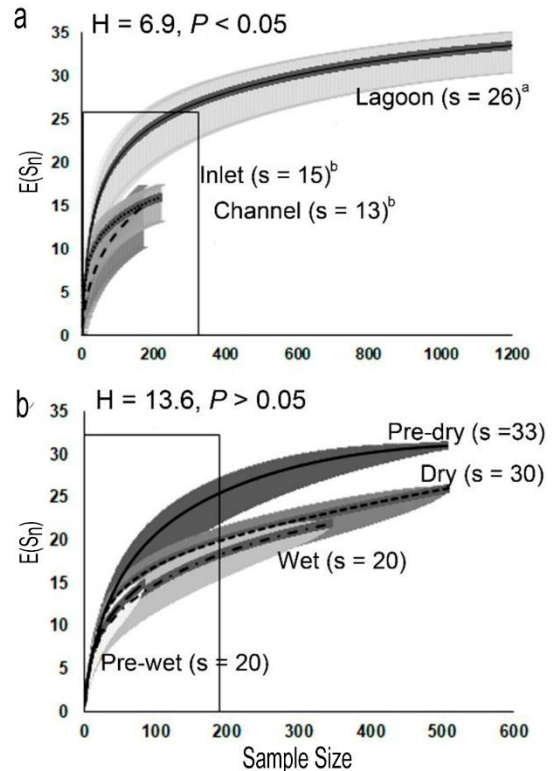

Figure 3. Rarefaction curves of the expected number of species as a function of sample size calculated by a) habitat and b) season; La Joya-Buenavista lagoon-estuarine system, Mexico. The bars indicate the subsample limits for the number of species and specimens. For the standardized richness values sharing the same letter were not statistically different at $P < 0.05$ with the non-parametric ANOVA and the Mann-Whitney *post-hoc* test.

other hand, *L. gracilis* and *Atherinella guatemalensis* were species whose size does not differ between habitats (Fig. 4).

Relationship between fish assemblages and environmental parameters

The DistLM analysis identified four environmental variables strongly correlated with the fish assemblages when tested in isolation (marginal tests; Table 5). However, in the best solution of the full model (sequential tests, adjusted $R^2 = 0.48$), only habitat structure, salinity and depth together were enough to explain significantly 43% of the total variance. Selected variables by the step-wise procedure were displayed as vectors in the dbRDA ordination plot (Fig. 5). Fish assemblages modeled by four predictor variables revealed two gradients. The first gradient was related to habitat structure and salinity, which kept inlet sites separated from lagoon and channel sites. The second gradient was mainly driven by dissolved oxygen and

Table 2. Relative importance value of the fish species for the La Joya-Buenavista lagoon-estuarine system (Mexico). Relative values based on the total number of specimens (2,064), total biomass (17,027.83 g) and the number of sampled sites (13). n: numerical abundance; SL: size ranges in standard length; %n: relative abundance; %B: relative biomass; %F: relative frequency; %IV: relative importance value.

Family	Specie	n	SL (cm)	%n	%B	%F	%IV
Clupeidae	*Lile gracilis* Castro-Aguirre & Vivero, 1990	287	3.3-8.2	13.91	5.52	6.42	8.61
Cichlidae	*Astatheros macracanthus* (Günther, 1864)	208	2.1-13.4	10.08	9.44	5.88	8.47
Mugilidae	*Mugil curema* Valenciennes, 1863	129	4.3-21.7	6.25	12.41	4.28	7.65
Gerreidae	*Eucinostomus currani* Zahuranec, 1980	206	1.5-9.5	9.98	8.13	4.81	7.64
Eleotridae	*Dormitator latifrons* (Richardson, 1844)	115	1.7-15.7	5.57	14.34	2.67	7.53
Gerreidae	*Gerres simillimus* Regan, 1907	82	1.9-18.3	3.97	10.03	5.35	6.45
Gerreidae	*Diapterus brevirostris* (Sauvage, 1879)	113	2.3-8.8	5.47	5.90	6.42	5.93
Poeciliidae	*Poecilia nelsoni* (Meek, 1904)	200	1.7-5.1	9.69	2.30	3.21	5.07
Centropomidae	*Centropomus robalito* Jordan & Gilbert, 1882	121	3.1-16.7	5.86	3.48	4.28	4.54
Cichlidae	*Amphilophus trimaculatus* (Günther, 1867)	81	2.3-12.7	3.92	1.54	3.21	2.89
Atherinopsidae	*Atherinella guatemalensis* (Günther, 1864)	63	1.6-6.5	3.05	0.15	4.28	2.49
Carangidae	*Oligoplites altus* (Günther, 1868)	16	6.5-18.7	0.78	2.95	2.67	2.13
Poeciliidae	*Poecilia sphenops* Valenciennes, 1846	75	2.0-5.1	3.63	1.14	1.07	1.95
Engraulidae	*Anchoa mundeola* (Gilbert & Pierson, 1898)	26	4.0-8.4	1.26	0.60	3.74	1.87
Gobiidae	*Gobionellus microdon* (Gilbert, 1892)	23	5.3-15.0	1.11	1.19	3.21	1.84
Eleotridae	*Gobiomorus maculatus* (Günther, 1859)	29	7.5-14.1	1.41	2.58	1.07	1.68
Clupeidae	*Opisthonema libertate* (Günther, 1867)	47	5.2-7.9	2.28	1.18	1.07	1.51
Gerreidae	*Eugerres axillaris* (Günther,1864)	9	7.3-14.1	0.44	1.53	2.14	1.37
Centropomidae	*Centropomus armatus* Gill, 1863	20	6.3-14.4	0.97	1.49	1.60	1.36
Atherinopsidae	*Membras gilberti* (Jordan & Bollman, 1890)	27	8.3-11.1	1.31	1.49	1.07	1.29
Gerreidae	*Eugerres lineatus* (Humboldt, 1821)	9	6.3-7.5	0.44	0.64	2.67	1.25
Carangidae	*Caranx caninus* Günther, 1867	10	4.0-13.4	0.48	1.01	2.14	1.21
Centropomidae	*Centropomus nigrescens* Günther, 1864	15	4.7-9.6	0.73	0.64	2.14	1.17
Lutjanidae	*Lutjanus argentiventris* (Peters, 1869)	14	5.1-10.3	0.68	1.09	1.60	1.12
Engraulidae	*Anchoa lucida* (Jordan & Gilbert, 1882)	15	5.3-8.7	0.73	0.39	2.14	1.08
Lutjanidae	*Lutjanus novemfasciatus* Gill, 1862	10	4.2-9.4	0.48	0.51	2.14	1.04
Mugilidae	*Mugil cephalus* Linnaeus, 1758	2	13.0-23.4	0.10	1.45	1.07	0.87
Ariidae	*Ariopsis guatemalensis* (Günther, 1864)	15	3.4-8.1	0.73	0.21	1.60	0.85
Hemiramphidae	*Hyporhamphus naos* Banford & Collette, 2001	5	17.4-22.5	0.24	1.19	1.07	0.83
Poeciliidae	*Poeciliopsis fasciata* (Meek, 1904)	14	1.6-2.2	0.68	0.02	1.60	0.77
Engraulidae	*Anchovia macrolepidota* (Kner, 1863)	15	6.5-14.3	0.73	1.01	0.53	0.76
Paralichthyidae	*Citharichthys gilberti* Jenkins & Evermann, 1889	7	5.8-14.1	0.34	0.72	1.07	0.71
Clupleidae	*Lile nigrofasciata* Castro-Aguirre, Ruiz-Campos & Balart, 2002	12	6.2-7.4	0.58	0.32	1.07	0.66
Carangidae	*Oligoplites saurus* (Bloch & Schneider, 1801)	4	10.3-14.5	0.19	0.62	1.07	0.63
Ariidae	*Cathorops liropus* (Bristol, 1897)	3	12.2-13.7	0.15	0.63	1.07	0.61
Lutjanidae	*Lutjanus colorado* Jordan & Gilbert, 1882	2	8.9-15.8	0.10	0.60	1.07	0.59
Centropomidae	*Centropomus viridis* Lockington, 1877	5	5.6-11.0	0.24	0.31	1.07	0.54
Tetraodontidae	*Sphoeroides annulatus* (Jenyns, 1842)	3	4.5-5.2	0.15	0.14	1.07	0.45
Ariidae	*Cathorops steindachneri* (Gilbert & Starks, 1904)	4	4.7-5.5	0.19	0.06	1.07	0.44
Achiridae	*Achirus mazatlanus* (Steindachner, 1869)	3	3.1-3.8	0.15	0.02	1.07	0.41
Poeciliidae	*Poeciliopsis pleurospilus* (Günther, 1866)	9	1.8-3.2	0.44	0.05	0.53	0.34
Anablepidae	*Anableps dowei* Gill, 1861	3	6.6-11.5	0.15	0.26	0.53	0.31
Mugilidae	*Mugil hospes* Jordan & Culver, 1865	2	8.3-10.2	0.10	0.23	0.53	0.29
Haemulidae	*Haemulopsis axillaris* (Steindachner, 1869)	1	10.8	0.05	0.21	0.53	0.26
Haemulidae	*Orthopristis chalceus* (Günther, 1864)	1	10.1	0.05	0.19	0.53	0.26
Labridae	*Halichoeres dispilus* (Günther, 1864)	1	8.4	0.05	0.07	0.53	0.22
Gobiidae	*Aboma etheostoma* Jordan & Starks, 1895	2	1.7-1.8	0.10	0.00	0.53	0.21
Characidae	*Astyanax aeneus* (Günther, 1860)	1	4.6	0.05	0.02	0.53	0.20

Table 3. Results of PERMANOVA based on Bray-Curtis dissimilarities on fish abundance data in response to season, habitat, months, sampling sites, and their interactions in the La Joya-Buenavista lagoon-estuarine (LJB) system (Mexico). d.f.: degrees of freedom, MS: mean square; *F*: *pseudo-F* statistic value, *P*: *P*-values by permutation. Permutated residuals under a reduced model (Type III). The maximum number of permutations = 9,999. Significant *P*-values (<0.05) are in bold.

Source of variation	d.f.	MS	*F*	*P*
Habitat (Ha)	2	25960	11.24	**0.0001**
Season (Se)	3	5438.5	2.35	**0.002**
Sampling site (Si, nested in Ha)	10	3748.1	1.62	**0.008**
Month (Mo, nested in Se)	2	2397	1.04	0.426
Ha × Se	6	5098.3	2.21	**0.0004**
Ha × Mo	4	2314.3	1.00	0.474
Se × Si	30	2459.6	1.06	0.348
Residuals	20	2310		

Table 4. Discrimination of 10 fish species based on its relative contribution among habitats by SIMPER analysis; La Joya-Buenavista lagoon-estuarine (LJB) system (Mexico). Ecological category: E: estuarine resident, EU: marine euryhaline, ST: marine stenohaline, SF: secondary freshwater. Functional group: DV: detritivore, OV: omnivore, PV: piscivore, ZB: zoobenthivore, ZP: zooplanktivore, I: inlet, C: channel, L: lagoon.

Species	Ecological category	Functional group	Spatial distribution			Contribution (%)		
			I	C	L	L *vs* I	L *vs* C	I *vs* C
Eucinostomus currani	EU	OV	■		■	14.66	3.52	16.01
Centropomus robalito	EU	PV		■	■	2.35	12.79	10.02
Diapterus brevirostris	EU	OV	■	■	■	7.09	6.72	5.68
Lile gracilis	E	ZP	■	■	■	5.72	8.62	2.49
Astatheros macracanthus	SF	OV		■	■	4.88	7.62	4.43
Dormitator latifrons	E	DV		■	■	-	8.86	6.47
Atherinella guatemalensis	E	ZB	■		■	7.55	-	6.90
Lutjanus argentiventris	ST	PV	■		■	5.17	-	4.78
Gerres simillimus	EU	OV	■	■		4.65	5.86	-
Mugil curema	EU	DV	■		■	4.58	2.93	2.99

depth, discriminating against the lagoon sites from the channel sites.

DISCUSSION

The specific richness in the LJB system (48 species) was higher than that described in other ecological studies carried out in the Gulf of Tehuantepec. In the southern Gulf, richness varied between 31 species in the Chantuto-Panzacola system (Díaz-Ruiz *et al*., 2004) and 40 in Carretas-Pereyra (Velázquez-Velázquez *et al*., 2008). However, in the first case, comparisons between the fish assemblages should be taken with caution, due to the difference in the sampling effort and method. In the second case, the sampling was more comparable with this study, and differences in richness and composition may be due to less marine influence due to mouth dynamics (Gómez-González *et al*., 2012). Although it has been pointed out that the use of a single fishing gear results in a biased sample of the assemblage (Clement *et al*., 2014), in estuarine

wetlands the use of cast nets is highly effective for achieving a broad taxonomic representation in several shallow habitats, and with accurate estimate of abundances (Sheaves *et al*., 2007; Sheaves & Johnston, 2009). However, highly complex habitats should be explored to avoid underrepresenting the cryptic fish fauna.

According to our hypothesis, we found that the fish fauna varied significantly within each geomorphic habitat. When abundances of 48 species at 72 sampling events are ordered on the two primary axes of dbRDA (Fig. 5), a spatial pattern response in fish assemblages on the lagoon, inlet and the channel is identified (Table 4; Fig. 3, 5). The lagoon exhibits a greater richness (35 spp.) with smaller sizes, compared to the inlet (20 spp.) and the channel (17 spp.), suggesting differentiated use of the habitat or the existence of assemblages with their ecological attributes. The above could also be reflected in the percentages of the functional guilds in each habitat (*e.g.*, a greater number of omnivores in the lagoon; Table 4).
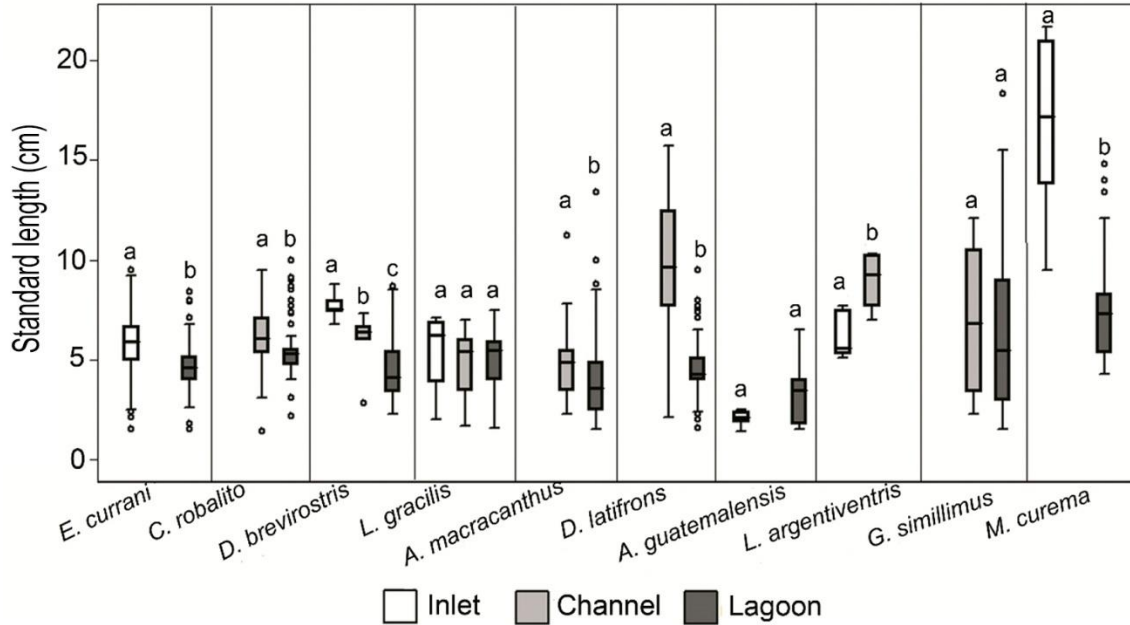
Figure 4. Standard length distribution of 10 species identified by SIMPER. Within species, the distributions sharing the same letter were not significantly different on *P* < 0.05 with the non-parametric ANOVA and the Mann-Whitney pairwise test.
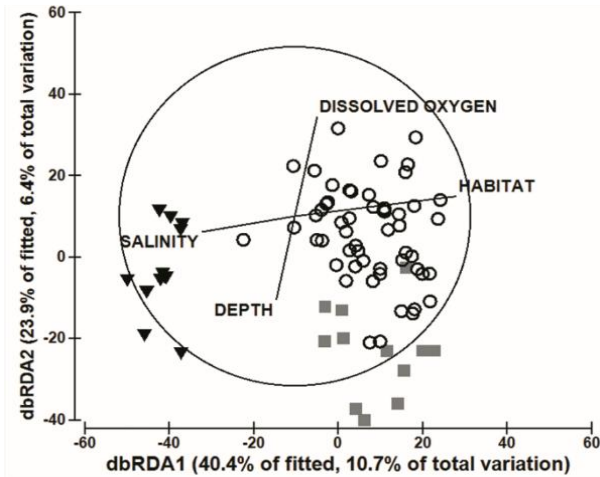

Figure 5. Distance-based redundancy analysis biplot based on linear modelling for fish abundance data, La Joya-Buenavista lagoon-estuarine system, Mexico. Vectors indicate correlations between the four environmental parameters of most significance in the model and the axes. The length and direction of the vectors represent the strength of the relationship concerning a unit circle. Symbols represent an individual sampling event coded by habitat. Black triangles: inlet, gray squares: channel, white circles: lagoon.

In the LJB system, the connectivity among the three geomorphic habitats may be a key attribute that defines the small-scale variation of fish assemblages. Similar

Table 5. Marginal and sequential tests result for the distance-based linear models based on fish abundance data in the La Joya-Buenavista lagoon-estuarine (LJB) system (Mexico). SS: sum of squares; *F*: *pseudo-F* statistic value; *P*: *P*-value of permutation test for the relationship between the fish assemblages and environmental parameters. Significant *P*-values (<0.05) are in bold.

Variable	SS trace	*F*	*P*
Marginal test			
Habitat structure	11536	4.25	**0.001**
Depth	6417	2.17	**0.036**
Dissolved oxygen	6163	2.02	**0.042**
Salinity	6088	1.99	**0.046**
Water clarity	4375	1.38	0.209
pH	3694	1.15	0.300
Water temperature	1799	0.54	0.847
Sequential test			
Habitat structure	11536	4.25	**0.001**
Depth	6713	2.74	**0.009**
Salinity	4091	1.76	**0.050**

spatial patterns were described by França *et al*. (2009) and Neves *et al*. (2013) in temperate and tropical coastal lagoons. If the habitats offer differentiated resources in food and shelter, the sequential use of these will favor an efficient use of the lagoon-estuarine system as a whole (Abrantes *et al*., 2015; Loureiro *et al*., 2016). Also, the results obtained here are consistent

with the theory that the seascape/landscape structure plays a determinant role in the structure of fish assemblages (Kimirei *et al.*, 2013).

Although differences were found at the temporal level, the spatial variations among geomorphic habitats were more significant (Table 3), probably due to a higher number of dominant species residing into the system during the entire annual cycle, and whose movements depend on the availability of resources (Lukey *et al.*, 2006; Herzka *et al.*, 2009). Another explanatory factor could be the relative environmental stability of the system. The significant spatio-temporal interactions detected, habitat × season and between sampling sites, can be indicative of seasonal pulses that define variations in physical and chemical properties within the same ecological or spatial unit (Yáñez-Arancibia *et al.*, 1983; Roselli *et al.*, 2013). However, the lowest relationship found at a temporal scale could be because only one annual cycle was evaluated. Therefore, a study in time series would be required to corroborate these results.

The presence of large areas of complex habitats, like mangroves, is a key factor why fish use lagoon estuarine systems as nurseries. Mangroves support more diverse and abundant small-sized fish assemblages, as they favor greater protection from predators and increase food availability (Nagelkerken *et al.*, 2002; Hindell & Jenkins, 2004; Piko & Szedlmayer, 2007; Green *et al.*, 2012; Neves *et al.*, 2013). The sheltered lagoon and the riverine mangroves that border the channel are suitable habitats for the fish fauna in the LJB system. However, during the dry season, the mangrove root system is not available for fishes; thus, the lack of physical structure may result in a reduction of shelter. Therefore, the highest abundance and richness of species in the lagoon, compared with the other habitats, suggests that this area has a significant ecological value. In this order, Franco *et al.* (2006) and Verdiell-Cubedo *et al.* (2013) have reported high abundance values in shallow habitats with small patches of macrophytes or perimetral lagoon marshlands, suggesting that juvenile fish use open-lagoon areas for feeding (Arceo-Carranza & Chiappa-Carrara, 2013; Kathoon *et al.*, 2014). The high abundance of species with detritivore, zoobenthivore and zooplanktivore feeding habits (*e.g.*, *Mugil curema*, *Lile gracilis*, *Atherinella guatemalensis*) were recorded in the lagoon area (Table 4), suggesting that both the physical and biotic attributes of this habitat influenced the population traits of these species.

The proximity of mangroves and mixed substrates also contributes to increasing the complexity of the channel; however, this habitat presented less abundance and richness concerning the inlet, considered of low complexity (Lacerda *et al.*, 2014). However, it has been reported that in tropical estuaries, there are lower values of abundance and richness associated with the mouth area (Neves *et al.*, 2013). Even though, in our study, the inlet is the richest species area of all estuarine channel, which may be due to the occurrence of rare species, mainly of stenohaline affinity (Peralta-Meixueiro & Vega-Cendejas, 2011), during the pre-dry and dry seasons. During the rainy season, freshwater inputs modify the hydrology (salinity, dissolved oxygen, temperature), with a higher number of estuarine species attracted to the beach by a high density of such prey (*e.g.*, *Litopenaeus* spp.). On the other hand, during the dry season, the beach environment becomes similar to the marine zone, with a lower abundance of fish but a higher richness and dominance of some families (*e.g.*, Carangidae and Sciaenidae).

A meaningful relationship has been founded for several environments between the habitat complexity and the structure of animal assemblages. The ecological paradigm holds that the most complex and physically heterogeneous habitats will support more diverse communities (Stewart *et al.*, 2000). An increase in available refuges due to microtopographic variations of the substrate or physical structures also has been shown to reduce inter and intra-specific competition for space, which potentially increases the richness and abundance of fish (Almany, 2004; Consoli *et al.*, 2018).

Some of the dominant species found in the lagoon and the channel are secondary freshwater and estuarine residents (*e.g.*, *Dormitator latifrons* and *Astatheros macracanthus*). The distribution and population structure of this group are determined by a temporal pattern affecting hydrological conditions (Díaz-Ruiz *et al.*, 2004; Velázquez-Velázquez *et al.*, 2008). During the rains, larger organisms were found in the channel, while juveniles of these species occurred in the lagoon during the pre-dry and dry seasons, suggesting a local migration from the streams to mesohaline environments.

In the LJB system, families such as Gerreidae and Mugilidae present greater abundances of larger organisms in the inlet than in the lagoon, suggesting that the sandy bars play an important and specific role for providing habitat. For example, in northern Australia, Blaber *et al.* (1995) found that the tidal environment, located between the mouth of an open estuary and the adjacent lower marine zone, sustains a relatively complex fish assemblage, composed by dependent juveniles as well as groups of opportunistic species that are move through three habitats (estuary, inshore and offshore waters). The structure of a similar assemblage occurs in the inlet of the LJB system, where juveniles of some species (*e.g.*, *Lutjanus argentiventris*)

were found exclusively in this area, and others of distribution extended by all habitats without variations in their size (*e.g.*, *L. gracilis*).

Water depth could be a parameter strongly correlated to abundance and size structure in the biotic assemblages of an estuarine system. A general pattern observed shows that larger fishes will be more abundant in deeper habitats, whereas smaller ones will be more abundant in shallow environments (Hutchinson *et al.*, 2014; Mustamäki *et al.*, 2015; Becker *et al.*, 2017). In the LJB system, the greatest depths were recorded in the channel, which may explain the occurrence of larger specimens from families as Lutjanidae, Centropomidae and Cichlidae (Fig. 4); this habitat could be used as a transit or feeding zone in mangroves and marginal lowlands. Hypoxia and low-depth are significant barriers to the presence of larger predatory fish in the lagoon. They affect their ability to move and evade predation, due to physiological stress (Patterson & Whitfield, 2000; Shoji *et al.*, 2005), so greater impact towards recruits will be inflicted by small and juvenile piscivores (Baker & Sheaves, 2009); further evidence for a specific trophic structure for each habitat in the environment (Tecchio *et al.*, 2015).

Although there were seasonal differences, the evidence of fish-habitat associations for many species was broad regardless of seasonality, probably because a high percentage of resident species in the system was found during the annual cycle. However, sampling needs to be expanded to compare contiguous systems and between-year variations in order to corroborate these conclusions. Several anthropogenic pressures are affecting the lagoon estuaries of the Gulf of Tehuantepec, whose vulnerability has increased in recent years as a result of the lack of planning in the coastal basin. Due to their ability to respond to environmental changes, fish assemblages are a potential tool for monitoring the ecological integrity of coastal systems, so their study should be continued. Likewise, coastal management should be developed to conserve the mosaic of habitats that integrate all the system, rather than distinct habitats.

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