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Assessing the Spatiotemporal Relationship between Coastal Habitats and Fish Assemblages at Two Neotropical Estuaries of the Mexican Pacific

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Abstract: Differences in fish assemblages' structure and their relation with environmental variables (due to the variations in sampled seasons, habitats, and zones), were analyzed in two adjacent estuaries on the north Pacific coast of Mexico. Environmental variables and fish catches were registered monthly between August 2018 and October 2020. Multivariate analyses were conducted to define habitats and zones based on their environmental characteristics, and the effect of this variability on fish assemblages' composition, biomass, and diversity (α and β) was evaluated. A total of 12,008 fish individuals of 143 species were collected using different fishing nets. Multivariate analyses indicated that fish assemblages' structure was different between zones due to the presence, height, and coverage of distinct mangrove species. Additionally, factors such as depth and salinity showed effects on fish assemblages' diversity (α and β -nestedness), which presented higher values in the ocean and remained similar in the rest of the analyzed zones and habitats. These results and the differences in species replacement (β -turnover) indicate the singularity of fish assemblages at estuaries (even in areas very close to the ocean), and the necessity to establish local management strategies for these ecosystems.

Keywords: mangrove forests; Marine Protected Areas; α -diversity; β -diversity; multivariate analyses

1. Introduction

Wetland ecosystems play a crucial ecological role due to their high primary productivity and habitat complexity that promotes the presence of multiple species. High habitat complexity at wetlands comprehends heterogeneous structural features, such as mangrove forests, and exclusive physiochemical conditions [1,2], as a result of their location at the interface between freshwater input from rivers and saline water from the sea [3,4], which are mainly determined by waves, tidal regimes, river discharges, coastal currents circulation, and meteorological factors (winds and seasonal precipitation; [5]). Fluctuation of environmental gradients and physical dynamics provide a suitable habitat for different fish species that live within wetlands during part or all of their life cycles [5–10], using them as nurseries, foraging sites, and refuge areas [11–13].

In addition, habitat complexity in wetlands is provided by mangrove forest structures (trees, shrubs, and prop roots), and tidal channels that connect the seaward edge of an estuary or coastal lagoon with the interior landward. These intricate complex

networks protect coastal ecosystems from physical agents (e.g. storms and waves) and facilitate the migration of organisms within the shallow intertidal zone [14,15]. Thus, fish use wetlands during different life stages (juveniles and adults) as residents [16], in nurseries [17,18], or in transient habitats [19,20], which may influence spatial and temporal patterns of ichthyofauna's assemblages.

Numerous studies have shown relationships between fish diversity and water conditions such as salinity [13,21], temperature, clarity [22,23], depth, and tidal ranges [24,25]. In tropical wetlands, spatial and seasonal fluctuations in salinity, temperature, and dissolved oxygen determine changes in fish densities and biomass [6,26]. Additional variables such as coastal geomorphology [27–30], nutrient cycles, and disturbance impacts [31], may also influence the fish distribution, abundance, and biomass.

The relative importance of the different factors influencing fish diversity in wetland ecosystems will vary, which does not necessarily mean that they will be mutually exclusive [11,29,32]. In this sense, the link between physical and biological interactions in wetlands could improve our understanding of ecological processes to propose informed management strategies [33]. However, community-environment studies are scarce for neotropical wetland ecosystems, thus this study aimed to assess the relationship between fish assemblages and coastal habitats, at two adjacent estuarine systems on the north Pacific coast of Mexico.

Both ecosystems have been previously studied in terms of seasonal variations of environmental characteristics and fish community dynamics [34–38], but no attempt to relate fish assemblages to specific habitats within each system has been made. The wetland habitats were defined based on biotic and abiotic factors: mangrove cover and height, the extension of agricultural lands, salinity, water temperature, depth, climatic season, and type of habitat (channel, mangrove creek, lagoon, river, and, ocean). The working hypotheses are A) the *a priori-designed* habitats in both systems differ according to environmental characteristics. B) fish diversity (α and β) and assemblages' structure vary spatiotemporally according to habitat characteristics.

2. Materials and Methods

2.1. Study area

The study was conducted in the estuarine systems of Huizache–Caimanero and Teacapan on the northeastern coast of Mexico (Fig. 1). Huizache–Caimanero is a shallow intermittent estuary with a strong influence of freshwater inputs as it lies between two rivers (Presidio and Baluarte) which are connected to the coastal lagoons by narrow tidal channels surrounded by mangrove forest. This coastal system receives ample fresh water during the rainy season (June to November), which mixes with the seawater from the ocean, creating a typical estuarine circulation pattern. The average area of the coastal system is 175 km², which is reduced to 65 km² during the dry season. This ecosystem was designated as a Ramsar site in 2007 (no. 1689), to protect particular species (e.g., birds, fish, mammals, reptiles, amphibians, and invertebrates), and habitats such as mangrove forests. Teacapan is a tide-dominated estuary with high mangrove density and tall mangrove trees [31]. It has a 1 km long inlet with a depth of 9 m that connects the system with the Pacific Ocean. One river drains into the Teacapan system all year round (Cañas) and presents a main water body called Laguna Agua Grande in the north section. This ecosystem is part of the Biosphere Reserve Marismas Nacionales, a Marine Protected Area established in 2010 to conserve a massive estuarine complex with the largest mangrove forest in the Mexican Pacific.

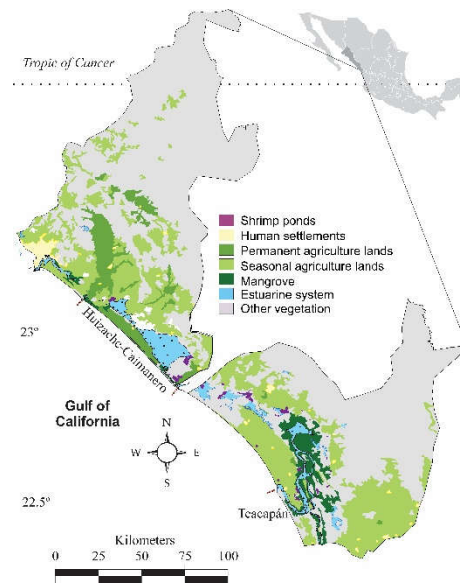


Figure 1. Map of the studied systems indicating the surrounding vegetation and the sampling stations (red dots).

For this study, the two coastal systems were divided into seasons (DCS: dry cold season, DWS: dry warm season, RWS: rainy warm season; [31]), habitat, and zones according to geomorphic and biotic characteristics. Habitats were characterized as (i) Ocean: represents the main inlets of coastal systems with a direct connection with the Pacific Ocean up to depths of 20 m, which present effects of littoral currents, tidal forces, and waves from local wind and previous storms. (ii) Lagoons: describe the principal water bodies of Huizache and Caimanero in the north, and Agua Grande lagoon nearby Teacapan. The Huizache and Caimanero coastal lagoons are part of the same wetland system with a geomorphic separation by a barrier in a narrow zone impeding the free transit of fish and other species through it. Moreover, this wetland does not present a mangrove community within the fringe zone of the main water body. In contrast, the Agua Grande lagoon within the Teacapan estuarine system presents a mangrove forest with large fringe trees of red mangrove *Rhizophora mangle*. (iii) Main tidal channel: corresponds to a wide geomorphic corridor that connects the ocean with the wetland systems. It is strongly influenced by the intense (1.4 m tide range) semi-diurnal tidal cycle of the Pacific Ocean (two high and two low tides every lunar day). (iv) Inner tidal channel: stands for the principal water exchange route between the main tidal channel and the coastal lagoons, where extensive fringe mangrove forests thrive at the interface between water and land. Due to their geomorphic characteristics, the strong tidal currents from the Pacific Ocean are attenuated within these zones. (v) Tidal mangrove creek: correspond to the very narrow water connections within the mangrove fringe community. These habitats are typically shallow and depict depressions at the interface between land and water. Due to the dense mangrove root configuration within these zones, they are usually used as refuges by juvenile fish and crustaceans. (vi) River: describes the streams of fresh water flowing in a meander geomorphic arrangement to the main inlet, thus presenting low salinity and less ocean influence.

The zones were assigned upon a visual inspection throughout the edge of the estuarine systems to establish the predominant vegetation at every sampling station, and these were classified as (i) Buttonwood mangrove (*Conocarpus erectus*), (ii) White mangrove (*Laguncularia racemosa*), (iii) Red mangrove (*R. mangle*), (iv) Unvegetated zones, and (v) Ocean.

2.2. Sampling design and procedures

A net of stations was placed at both systems covering all the different habitats, and at each station, the date, salinity (‰), temperature (°C), and depth (m) were recorded with

a Horiba U-50 Series multi-parameter water quality checker. The mangrove height was estimated using a portable Vertex Laser VL400 hypsometer, while the mangrove and agricultural land extension was estimated using vectors over freely available Google Earth images recorded as close as possible to the field campaign date. Given the distance between sampling stations, a constant vector extension of 200 m coastline in front of it was used to quantify the total cover area further inland. These data were used to construct the environmental matrix including biotic and abiotic characterization of each sampling station.

The fish were collected during morning hours and at high tide from August 2018 to October 2020 at monthly intervals. At both estuarine systems, gillnets (mesh size= 2.5, 3, and 3.5 inches) were left adrift in each station (45 minutes) where the depth was over 1.5 m, while cast nets (mesh size= 0.6 inches) were deployed at stations where the depth was below 1.5 m. The fish specimens caught were placed in separate labeled plastic bags and transported in an icebox. Once in the laboratory, the identification of fish specimens was conducted to the lowest taxonomic category possible [39-40]. The total length (mm) and body mass (g) of each fish specimen was measured to the nearest 1 mm and 0.1 g, respectively.

2.3. Data analysis

2.3.1. Environmental data and habitat characteristics

A mean value was obtained for water temperature (°C) and salinity (ppt) for every climatic season, while a mean depth value (m) was determined for every habitat. Mean differences in water temperature and salinity were tested for every season using a one-way ANOVA with the season as the fixed factor. Before the analyses, homogeneity of variances was tested with Cochran's C test. *A posteriori* pairwise comparisons of means were carried out using Tukey's HSD test.

Spatiotemporal variations in environmental parameters (salinity, water temperature, depth, mangrove area, mangrove height, and extension of agricultural lands) were analyzed using multivariate analyses according to different factors (system, season, habitat, and zone), to determine if statistical differences existed among *a priori*-defined zones, and therefore adequately establish patterns of environmental effects on fish assemblages.

A matrix was constructed using each station as columns, and each haul-specific environmental parameter data constituted the rows. Data were normalized (mean of 0, a standard deviation of 1) given that the environmental values had different scales. Pearson's correlation coefficients were used to determine statistically significant correlations between environmental variables. When a significant correlation was found, data were square-root or fourth-root transformed, and the previous analysis was rerun until the correlation was not significant. We used Excel's regression tool to calculate Pearson's correlation coefficients and their respective P-values. Subsequently, a similarity matrix of the standardized and transformed environmental data was constructed using Euclidian distance.

Factors were assigned to each station (estuarine system, climatic season, habitat, and zone), and a PERMANOVA [41] was performed to test the H_0 : sampled stations were not different despite the differences between the analyzed factors. If a P-value was <0.05 the H_0 was rejected, and then pairwise tests were performed to determine which stations were different. Due to the increased risk of inflated type I error (i.e., rejecting the null hypothesis when it is true), we applied a Bonferroni procedure by dividing α (0.05) by the number of comparisons.

Principal coordinates analysis (PCoA), was used to visualize the patterns of environmental data between the sampled stations, and to determine which characteristics best explained the group separation where the PERMANOVA revealed statistical differences. This ordination method produces a two-dimensional scatter plot, and the characteristics of each station are overlaid as vectors. The trajectory of the vector indicates the importance of each environmental characteristic between sampling stations. Both axes have a scale

from $-n$ to n , in which the point $0,0$ is the centroid—the location where all the points would be located if the null hypothesis was true [42].

2.3.2. Fish assemblages

Biomass species composition data was used to determine the degree of similarity in fish assemblages according to the assigned factors (estuarine system, climatic season, habitat, and zone), and their relationship to the environmental factors registered in the study area. Because different sampling methods were used, the species biomass data of each haul were standardized as Catch Per Unit Effort (CPUE), with the effort being defined as area [43], which represents the biomass of individuals in square kilometers for each species (i.e. g/km²). The catch area was calculated based on the gear type, as a circle for the cast net and a rectangle for the gillnet.

Specifically for the gillnet, the swept area was estimated by using a GPS in every fishing operation to determine the beginning and end of the area towed. In addition, using central tendencies and dispersion of the gillnet, the data were bootstrapped approximately 2,000 times until a normal distribution was fitted, and then standardized for $N(\mu, \sigma^2)/\Sigma N(\mu, \sigma^2)$ where N is the Normal distribution, μ is the population mean, and σ^2 is the population variance. Finally, an integration of the error was generated by again bootstrapping the swept area by the gillnet and the total area towed with both fishing gears, so a CPUE was obtained in terms of the area for every haul.

Randomized species accumulation plots were constructed per system to assess the representativeness of the sampling effort. The order in which samples were analyzed was randomized 1,000 times for each new cumulative species sample using Chao's 1 estimator of the absolute number of species in an assemblage. This method is based on the number of rare species found in a sample [44], and the notation is:

$$S_{est} = S_{obs} + \left(\frac{f_1^2}{2f_2} \right)$$

Where S_{est} is the estimated number of species, S_{obs} is the observed number of species in the sample, f_1 is the number of singletons (taxa represented by a single occurrence in the field campaign), and f_2 is the number of doubletons (two occurrences in the field campaign) [45].

To explain the spatiotemporal differences in fish assemblages, a hierarchical analysis was performed using the following levels: estuarine system, climatic season, habitat, and zone. Differences in fish assemblages among these factors were tested using multivariate analyses. A matrix containing i lines (species) and j columns (hauls), was created and from this, a Bray-Curtis similarity matrix was generated using the mentioned levels, where each zone was considered a replicate within each habitat.

To test the H_0 that the fish assemblages did not differ according to these factors, a PERMANOVA was employed with a fixed factor (model type I), and its statistical significance was tested using a type III sum of squares, with 10,000 unrestricted permutations of raw data [41]. The PERMDISP routine on PRIMER v. 6 was conducted with a permutation test to examine the homogeneity of species compositions between factors. Pairwise tests were performed to determine if estuarine systems, climatic seasons, habitats, and zones differed from the others, and a Bonferroni procedure was applied to correct for multiple comparisons.

Additionally, a distance-based linear model permutation test (DistLM) was performed to examine the significance of each environmental variable contributing to the fish assemblages [46,47]. This analysis identified the environmental variables that predict the variation in fish assemblages at the different estuarine systems, climatic seasons, habitats, and zones, and represent it in multivariate space. DistLM did a partitioning of the variation in the data and showed it as a resemblance matrix calculated by multiple regression models [47]. A marginal test first showed the amount of variation explained by each variable when taken alone (ignoring the other variables), and then a sequential test (forward direction) allowed to select of individual variables based on the Akaike information

criterion (AIC) and the Bayesian information criterion (BIC) values. This step allowed us to identify the parsimonious model representing the best combination of environmental variables that explained fish assemblages' composition, and the proportion of explained variation attributed to each variable added to the model as a function of the other variables already present [48]. Based on the parsimonious model selected, a distance-based redundancy analysis (dbRDA) was conducted to visualize the relationship between fish assemblages' composition and environmental variables. The assumption required by DISTLM analysis (the number of samples was higher than the number of variables) was met [48].

A similarity of percentage analysis (SIMPER, Bray-Curtis similarity index, and cut-off at 90%), was used to determine the contribution of species to the average dissimilarity among the analyzed factors (estuarine system, climatic season, habitat, and zone; [49]. Upon identification of the factors that contribute to the observed differences, α -diversity indices were computed based on haul-specific species biomass data standardized by the CPUE. Specifically, we used Hill numbers (i.e. effective numbers of species, qD) which have been recognized as the most appropriate method for evaluating diversity [50–52]. The indices used were 0D (species richness; gives disproportionate weight to rare species because is not sensitive to species biomass; [50]), 1D (exponential of Shannon's entropy; the number of common species in the community as it weights each species according to its biomass in the sample; [52]), and 2D (inverse Simpson concentration; the number of dominant species in the community as it favors species that present high biomass; [52]). Formulas of the Hill numbers have already been extensively detailed [50,52]. Finally, the biomass per species matrix was transformed to presence/absence to calculate the local contribution of each sample to both components of β -diversity (turnover and nestedness), using the Sorensen dissimilarity coefficient.

Biomass, Hill numbers (0D , 1D , and 2D), and β -diversity components (turnover and nestedness) calculated per sampling station were used as response variables in Additive Generalized Models (GAMs), while explanatory variables were the environmental factors that presented an effect on fish assemblages according to the previous multivariate analyses. GAMs replace the linear form $\Sigma\beta_iX_i$ with a sum of smooth functions $\Sigma S_j(X_j)$, where the $S_j()$'s are unspecified functions that are estimated using a scatterplot smoother, in an iterative procedure called local scoring algorithm which proves to be useful in uncovering nonlinear covariate effects [53].

Species accumulation curves, Hill numbers, and multivariate analyses were completed using the PRIMER 7 statistical package with the PERMANOVA+ 1 add-on (PRIMER-E, serial no. 7875), while GAMs were performed using the "mgcv" package [54], and β -diversity components (turnover and nestedness) were calculated using the function "beta.div.comp" of the package "adespatial" [55], in R [56].

3. Results

3.1. Environmental data and habitat characteristics

There were marked seasonal differences in temperature and salinity in both systems, which were following the established seasons (DCS, DWS, RWS). The mean water temperature fluctuated from $19.50\text{C} \pm 1.96$ (DCS) to $37.10\text{C} \pm 1.37$ (RWS), and it changed significantly according to the latter (RWS: $F_{(1, 10887)} = 262.59$, $p < 0.05$), which coincides with the summer and early autumn. The salinity showed high variations depending on the zone and season, as it was significantly lower during the rainy season (RWS: $F_{(1, 10887)} = 20.534$, $p < 0.05$) at the Huizache lagoon (1.0 ± 0.9 ppt), compared to the dry season at the same estuarine system (35.3 ± 0.6 ppt). In both seasons the mean salinity was similar in the mouth of the lagoon and the coastal areas. The depth also showed high variations depending on the habitat, where the lagoons and the tidal mangrove creeks were the shallowest habitats (mean depth: 1.07 ± 0.25 m), followed by the river (1.3 ± 0.66 m), the inner tidal channel (3.01 ± 1.7 m), the main tidal channel (5.66 ± 2.6 m), and the oceanic habitats (9.76 ± 4.1 m) that were the deepest habitats of the study area.

A statistically significant correlation was not found among environmental variables, after normalization (Pearson's correlation coefficient = 3.94, $p > 0.05$). PERMANOVA revealed statistically significant differences between the estuarine systems of Huizache-Caimanero and Teacapan (pseudo- $F_{1,56} = 6.45$, $p=0.001$), the climatic seasons (pseudo- $F_{2,56} = 5.09$, $p=0.001$); habitat (pseudo- $F_{7,56} = 10.24$, $p=0.001$), and the zone (pseudo- $F_{4,56} = 12.6$, $p=0.001$). In terms of climatic seasons, differences were found between the warm seasons (DWS and RWS) and the cold ones (DCS), but no differences were found between both warm seasons (supplementary material Table 1).

For the habitat, the analysis showed well-differentiated groups: oceanic habitat; Huizache and Caimanero lagoons; Agua Grande lagoon together with the inner tidal channel and the mangrove creek; and the main tidal channel (supplementary material Table 2). In terms of zones, all were different from each other except for unvegetated zones and those inhabited by buttonwood mangroves (supplementary material Table 3). The differences between estuarine systems and habitats seemed to be determined by the zones since Teacapan only has red mangroves and ocean zones, whilst Huizache-Caimanero has white and buttonwood mangroves, unvegetated zones, and the ocean. The observed differences were related to environmental variables shown as vectors in the PCoA graph (Fig. 2), where clear-cut groups were formed according to zones and systems. The horizontal axis explains most of the variation (38.2%) which is related to mangrove height and cover, which was higher in the red mangrove forest of Teacapan compared to the Huizache-Caimanero system. The vertical axis explains 23.2% of the variation, which is related to depth, temperature, and salinity, which was higher in the ocean of both systems, and in Teacapan's main tidal channel (where the inlet connects the system with the sea). The extension of the agricultural land was related to both axes, and also relevant in Teacapan, where the extension of this zone was higher than in the Huizache-Caimanero system.

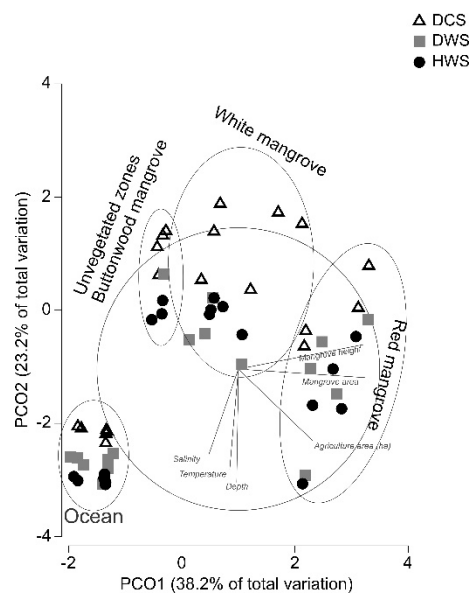


Figure 2. PCoA graph showing relationships among environmental variables with systems, habitats, zones and seasons.

3.2. Fish assemblages

The sample-based rarefactions using Chao 1 model showed that the sampling effort was representative for both estuarine systems (Fig. 3), with 88.23% of the potential species richness recorded in Huizache-Caimanero, and 87.68% in Teacapan.

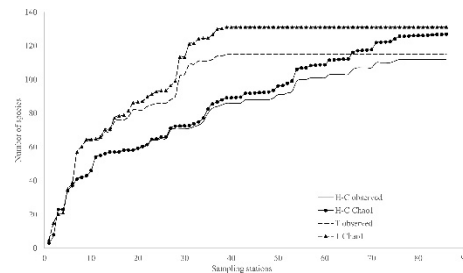


Figure 3. Fish species accumulation model for the different estuarine systems studied. The model used was Chao1.

A total of 12,008 fish individuals were collected pertaining to 143 species (Huizache-Caimanero: 112 species, Teacapan: 115 species recorded), being the most important species in terms of biomass the striped herring *Lile stolifera* (25.7%), followed by the Congo sea catfish *Cathorops fuerthii* (7.1%) and the mullet *Mugil curema* (6.4%). Huizache-Caimanero system was characterized by high biomass of small pelagics (*L. stolifera* 39.6%, *Anchoa walkeri* 5.5%), mullets (*Mugil curema* 7.4%, *M. cephalus* 5.2%), and the Congo sea catfish (10.1%). In contrast, the Teacapan system did not show any species with such dominance, and two Myliobatiformes accounted for 16% (*Rhinoptera steindachneri* 10.7%, *Aetobatus narinari* 5.3%), followed by the tete sea catfish *Ariopsis seemanni* (10.7%), and the milkfish *Chanos chanos* (6.15%). The rest of the species represented less than 6% of the total biomass. In terms of abundance, the striped herring and the mullets were also very important (21.7% and 11.7% respectively), but in terms of numbers, the Pacific crevalle jack was the second in importance (6.42%). In Huizache-Caimanero was also characterized by a high number of small pelagics (*L. stolifera* 34.6%, *Anchoa walkeri* 6.2%) and mullets (*Mugil curema* 5.8%, *M. cephalus* 4.4%), but in terms of abundance, the invasive species Tilapia (*Oreochromis* sp.) was the third in importance (5.8%). In Teacapan, the two most important species in terms of the number of individuals were the Pacific crevalle jack (13.3%) and the mojarra (*Diapterus peruvianus*, 11.1%) (Table 1).

Table 1. Total and relative abundance and biomass of the fish species analyzed in this study. a=abundance, b=biomass, HC=Huizache-Caimanero, T=Teacapan, Tot.=total of the two systems combined.

Species	a HC	a T	a Tot.	a% HC	a% T	a% Tot.	b HC	b T	b tot.	b% HC	b% T	b% Tot.
<i>Lile stolifera</i>	2591	10	2601	34.6	0.2	21.7	1852.8	0.0	1852.9	39.6	0.0	25.7
<i>Cathorops fuerthii</i>	158	84	242	2.1	1.9	2.0	476.0	39.5	515.5	10.2	1.6	7.1
<i>Mugil curema</i>	432	261	693	5.8	5.8	5.8	348.3	110.6	458.9	7.4	4.4	6.4
<i>Mugil cephalus</i>	331	266	597	4.4	5.9	5.0	242.8	127.9	370.7	5.2	5.0	5.1
<i>Ariopsis seemanni</i>	34	232	266	0.5	5.1	2.2	41.1	271.3	312.3	0.9	10.7	4.3
<i>Chanos chanos</i>	194	81	275	2.6	1.8	2.3	141.1	155.8	296.9	3.0	6.1	4.1
<i>Rhinoptera steindachneri</i>	2	7	9	0.0	0.2	0.1	0.3	272.5	272.8	0.0	10.7	3.8
<i>Anchoa walkeri</i>	464	5	469	6.2	0.1	3.9	255.6	0.1	255.7	5.5	0.0	3.5
<i>Elops affinis</i>	168	145	313	2.2	3.2	2.6	163.5	75.7	239.2	3.5	3.0	3.3
<i>Oreochromis</i> sp.	437	44	481	5.8	1.0	4.0	162.8	22.7	185.5	3.5	0.9	2.6
<i>Occidentarius platypogon</i>	46	28	74	0.6	0.6	0.6	84.6	95.8	180.4	1.8	3.8	2.5
<i>Cynoscion xanthulus</i>	192	8	200	2.6	0.2	1.7	138.8	5.1	144.0	3.0	0.2	2.0
<i>Rhencus macracanthus</i>	74	95	169	1.0	2.1	1.4	32.9	101.4	134.3	0.7	4.0	1.9
<i>Aetobatus narinari</i>	0	2	2	0.0	0.0	0.0	0.0	134.1	134.1	0.0	5.3	1.9

<i>Bagre panamen-</i> <i>sis</i>	56	42	98	0.7	0.9	0.8	51.2	79.8	131.0	1.1	3.1	1.8
<i>Diapterus peru-</i> <i>vianus</i>	151	503	654	2.0	11.1	5.4	26.9	87.9	114.8	0.6	3.5	1.6
<i>Opisthonema lib-</i> <i>ertate</i>	15	214	229	0.2	4.7	1.9	7.1	96.5	103.6	0.2	3.8	1.4
<i>Caranx caninus</i>	169	602	771	2.3	13.3	6.4	66.5	31.7	98.2	1.4	1.3	1.4
<i>Nematistius pec-</i> <i>toralis</i>	1	48	49	0.0	1.1	0.4	0.3	96.4	96.7	0.0	3.8	1.3
<i>Albula vulpes</i>	1	70	71	0.0	1.5	0.6	1.3	94.9	96.2	0.0	3.7	1.3
<i>Oligoplites altus</i>	23	67	90	0.3	1.5	0.7	8.2	69.9	78.1	0.2	2.8	1.1
<i>Ariopsis guate-</i> <i>malensis</i>	34	25	59	0.5	0.6	0.5	24.2	53.3	77.4	0.5	2.1	1.1
<i>Centropomus</i> <i>robalito</i>	143	67	210	1.9	1.5	1.7	62.7	6.2	68.9	1.3	0.2	1.0
<i>Chloroscombrus</i> <i>orqueta</i>	177	103	280	2.4	2.3	2.3	39.4	27.3	66.7	0.8	1.1	0.9
<i>Eucinostomus</i> <i>currani</i>	23	97	120	0.3	2.1	1.0	3.7	51.2	54.8	0.1	2.0	0.8
<i>Polydactylus ap-</i> <i>proximans</i>	18	11	29	0.2	0.2	0.2	43.2	11.5	54.7	0.9	0.5	0.8
<i>Katsuwonus</i> <i>pelamis</i>	0	3	3	0.0	0.1	0.0	0.0	52.7	52.7	0.0	2.1	0.7
<i>Sphyrna lewini</i>	8	7	15	0.1	0.2	0.1	23.2	25.9	49.1	0.5	1.0	0.7
<i>Caranx caballus</i>	25	45	70	0.3	1.0	0.6	14.9	31.6	46.5	0.3	1.2	0.6
<i>Rhencus pana-</i> <i>mensis</i>	28	42	70	0.4	0.9	0.6	12.3	32.6	44.9	0.3	1.3	0.6
<i>Trachinotus</i> <i>paitensis</i>	2	36	38	0.0	0.8	0.3	2.1	39.6	41.7	0.0	1.6	0.6
<i>Strongylura ex-</i> <i>ilis</i>	3	0	3	0.0	0.0	0.0	39.9	0.0	39.9	0.9	0.0	0.6
<i>Cetengraulis</i> <i>mysticetus</i>	21	184	205	0.3	4.1	1.7	0.2	36.5	36.8	0.0	1.4	0.5
<i>Dormitator</i> <i>latifrons</i>	112	120	232	1.5	2.7	1.9	34.2	1.7	35.9	0.7	0.1	0.5
<i>Mobula japanica</i>	1	0	1	0.0	0.0	0.0	26.9	0.0	26.9	0.6	0.0	0.4
<i>Peprilus snyderi</i>	10	24	34	0.1	0.5	0.3	3.5	22.3	25.8	0.1	0.9	0.4
<i>Scomberomorus</i> <i>sierra</i>	18	1	19	0.2	0.0	0.2	19.3	5.5	24.8	0.4	0.2	0.3
<i>Eucinostomus</i> <i>entomelas</i>	53	24	77	0.7	0.5	0.6	17.5	3.5	21.0	0.4	0.1	0.3
<i>Gerres cinereus</i>	22	53	75	0.3	1.2	0.6	6.3	12.6	18.9	0.1	0.5	0.3
<i>Haemulopsis ax-</i> <i>illaris</i>	31	0	31	0.4	0.0	0.3	17.4	0.0	17.4	0.4	0.0	0.2
<i>Menticirrhus na-</i> <i>sus</i>	4	5	9	0.1	0.1	0.1	2.0	15.1	17.0	0.0	0.6	0.2
<i>Eugerres axillaris</i>	40	42	82	0.5	0.9	0.7	9.7	7.2	16.9	0.2	0.3	0.2
<i>Lutjanus argen-</i> <i>tiventris</i>	20	17	37	0.3	0.4	0.3	1.9	13.9	15.8	0.0	0.5	0.2
<i>Haemulopsis ni-</i> <i>tidus</i>	12	49	61	0.2	1.1	0.5	5.2	7.4	12.6	0.1	0.3	0.2
<i>Larimus efful-</i> <i>gens</i>	132	13	145	1.8	0.3	1.2	9.3	3.3	12.6	0.2	0.1	0.2
<i>Pliosteostoma</i> <i>lutipinnis</i>	133	24	157	1.8	0.5	1.3	11.9	0.3	12.2	0.3	0.0	0.2
<i>Synodus scituli-</i> <i>ceps</i>	0	13	13	0.0	0.3	0.1	0.0	11.8	11.8	0.0	0.5	0.2
<i>Peprilus medius</i>	20	10	30	0.3	0.2	0.2	7.2	4.6	11.8	0.2	0.2	0.2

<i>Cynoscion stolzmanni</i>	24	3	27	0.3	0.1	0.2	8.3	3.1	11.4	0.2	0.1	0.2
<i>Selene peruviana</i>	21	54	75	0.3	1.2	0.6	0.9	9.7	10.6	0.0	0.4	0.1
<i>Micropogonias altipinnis</i>	27	0	27	0.4	0.0	0.2	10.4	0.0	10.4	0.2	0.0	0.1
<i>Cynoscion reticulatus</i>	30	11	41	0.4	0.2	0.3	8.7	1.6	10.3	0.2	0.1	0.1
<i>Eucinostomus argenteus</i>	14	7	21	0.2	0.2	0.2	9.9	0.0	9.9	0.2	0.0	0.1
<i>Haemulopsis leuciscus</i>	7	5	12	0.1	0.1	0.1	4.8	4.2	9.0	0.1	0.2	0.1
<i>Chaetodipterus zonatus</i>	4	23	27	0.1	0.5	0.2	2.0	6.0	8.0	0.0	0.2	0.1
<i>Micropogonias ectenes</i>	9	5	14	0.1	0.1	0.1	5.7	2.1	7.8	0.1	0.1	0.1
<i>Trachinotus rhodopus</i>	0	5	5	0.0	0.1	0.0	0.0	7.8	7.8	0.0	0.3	0.1
<i>Hemicaranx leucurus</i>	4	15	19	0.1	0.3	0.2	2.0	5.5	7.5	0.0	0.2	0.1
<i>Cynoscion squamipinnis</i>	11	0	11	0.1	0.0	0.1	6.9	0.0	6.9	0.1	0.0	0.1
<i>Scomber japonicus</i>	4	3	7	0.1	0.1	0.1	4.7	2.1	6.9	0.1	0.1	0.1
<i>Achirus mazatlanus</i>	70	134	204	0.9	3.0	1.7	6.0	0.3	6.4	0.1	0.0	0.1
<i>Umbrina xanti</i>	3	1	4	0.0	0.0	0.0	2.1	3.5	5.7	0.0	0.1	0.1
<i>Conodon serrifer</i>	16	0	16	0.2	0.0	0.1	5.6	0.0	5.6	0.1	0.0	0.1
<i>Cyclopsetta querna</i>	8	5	13	0.1	0.1	0.1	1.5	3.8	5.2	0.0	0.1	0.1
<i>Bagre pinnimaculatus</i>	5	3	8	0.1	0.1	0.1	3.4	1.8	5.2	0.1	0.1	0.1
<i>Tylosurus crocodilus</i>	0	1	1	0.0	0.0	0.0	0.0	5.2	5.2	0.0	0.2	0.1
<i>Gobiomorus maculatus</i>	33	12	45	0.4	0.3	0.4	4.2	0.9	5.1	0.1	0.0	0.1
<i>Anchovia macrolepidota</i>	41	19	60	0.5	0.4	0.5	3.3	1.3	4.6	0.1	0.1	0.1
<i>Oligoplites saurus</i>	5	2	7	0.1	0.0	0.1	4.1	0.5	4.5	0.1	0.0	0.1
<i>Centropomus viridis</i>	4	17	21	0.1	0.4	0.2	3.8	0.4	4.2	0.1	0.0	0.1
<i>Dorosoma smithi</i>	0	16	16	0.0	0.4	0.1	0.0	4.0	4.0	0.0	0.2	0.1
<i>Sphyraena ensis</i>	1	0	1	0.0	0.0	0.0	3.7	0.0	3.7	0.1	0.0	0.1
<i>Hemicaranx zelotes</i>	0	6	6	0.0	0.1	0.0	0.0	3.4	3.4	0.0	0.1	0.0
<i>Paralichthys woolmani</i>	1	0	1	0.0	0.0	0.0	3.4	0.0	3.4	0.1	0.0	0.0
<i>Menticirrhus elongatus</i>	5	1	6	0.1	0.0	0.0	3.3	0.0	3.3	0.1	0.0	0.0
<i>Pseudobatos leucorhynchus</i>	1	0	1	0.0	0.0	0.0	3.1	0.0	3.1	0.1	0.0	0.0
<i>Selar crumenophthalmus</i>	7	1	8	0.1	0.0	0.1	2.2	0.6	2.8	0.0	0.0	0.0
<i>Cyclopsetta panamensis</i>	5	7	12	0.1	0.2	0.1	0.0	2.8	2.8	0.0	0.1	0.0
<i>Caranx vinctus</i>	1	3	4	0.0	0.1	0.0	0.6	2.1	2.7	0.0	0.1	0.0
<i>Oligoplites refulgens</i>	5	3	8	0.1	0.1	0.1	1.2	1.5	2.7	0.0	0.1	0.0

<i>Centropomus nigrescens</i>	3	1	4	0.0	0.0	0.0	2.6	0.0	2.6	0.1	0.0	0.0
<i>Selene brevoortii</i>	1	9	10	0.0	0.2	0.1	0.1	2.4	2.5	0.0	0.1	0.0
<i>Albula nemoptera</i>	1	7	8	0.0	0.2	0.1	0.5	2.0	2.5	0.0	0.1	0.0
<i>Lutjanus novemfasciatus</i>	5	3	8	0.1	0.1	0.1	2.4	0.1	2.5	0.1	0.0	0.0
<i>Centropomus armatus</i>	1	10	11	0.0	0.2	0.1	0.4	1.9	2.3	0.0	0.1	0.0
<i>Hyporhamphus unifasciatus</i>	2	0	2	0.0	0.0	0.0	2.3	0.0	2.3	0.0	0.0	0.0
<i>Centropomus medius</i>	3	10	13	0.0	0.2	0.1	1.9	0.1	2.0	0.0	0.0	0.0
<i>Stellifer fuerthii</i>	146	79	225	1.9	1.7	1.9	1.2	0.8	2.0	0.0	0.0	0.0
<i>Trachinotus kennedyi</i>	1	3	4	0.0	0.1	0.0	0.5	1.4	2.0	0.0	0.1	0.0
<i>Isopisthus remifer</i>	7	70	77	0.1	1.5	0.6	1.7	0.2	1.9	0.0	0.0	0.0
<i>Eleotris picta</i>	1	0	1	0.0	0.0	0.0	1.6	0.0	1.6	0.0	0.0	0.0
<i>Paralonchurus goodei</i>	40	12	52	0.5	0.3	0.4	1.5	0.0	1.6	0.0	0.0	0.0
<i>Stellifer illecebrosus</i>	86	0	86	1.1	0.0	0.7	1.5	0.0	1.5	0.0	0.0	0.0
<i>Bodianus diploaenia</i>	2	0	2	0.0	0.0	0.0	1.3	0.0	1.3	0.0	0.0	0.0
<i>Hoplopagrus guentherii</i>	0	1	1	0.0	0.0	0.0	0.0	1.2	1.2	0.0	0.0	0.0
<i>Deckertichthys aureolus</i>	3	1	4	0.0	0.0	0.0	0.9	0.2	1.1	0.0	0.0	0.0
<i>Orthopristis chalcus</i>	1	1	2	0.0	0.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0
<i>Gobionellus microdon</i>	16	3	19	0.2	0.1	0.2	0.9	0.1	1.0	0.0	0.0	0.0
<i>Oreochromis mossambicus</i>	1	0	1	0.0	0.0	0.0	0.9	0.0	0.9	0.0	0.0	0.0
<i>Cynoscion othonopterus</i>	1	0	1	0.0	0.0	0.0	0.9	0.0	0.9	0.0	0.0	0.0
<i>Pomadasys branickii</i>	2	0	2	0.0	0.0	0.0	0.8	0.0	0.8	0.0	0.0	0.0
<i>Bairdiella icistia</i>	2	0	2	0.0	0.0	0.0	0.8	0.0	0.8	0.0	0.0	0.0
<i>Opisthonema medirastre</i>	0	2	2	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.0	0.0
<i>Alectis ciliaris</i>	0	1	1	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.0	0.0
<i>Carangoides otrynter</i>	0	2	2	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.0	0.0
<i>Prionotus ruscaius</i>	0	4	4	0.0	0.1	0.0	0.0	0.6	0.6	0.0	0.0	0.0
<i>Epinephelus labriformis</i>	2	0	2	0.0	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0
<i>Chaetodon humeralis</i>	0	1	1	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.0	0.0
<i>Ophichthus zophochir</i>	1	0	1	0.0	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0
<i>Selene orstedii</i>	0	1	1	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0
<i>Polydactylus opercularis</i>	1	0	1	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0
<i>Myrichthys aspetocheiros</i>	0	1	1	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0
<i>Etropus crossotus</i>	6	0	6	0.1	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0

<i>Anchoa nasus</i>	1	0	1	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0
<i>Symphurus elongatus</i>	93	4	97	1.2	0.1	0.8	0.1	0.0	0.1	0.0	0.0	0.0
<i>Anchoa lucida</i>	2	1	3	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0
<i>Citharichthys gilberti</i>	2	0	2	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0
<i>Urotrygon munda</i>	19	0	19	0.3	0.0	0.2	0.1	0.0	0.1	0.0	0.0	0.0
<i>Balistes polylepis</i>	1	3	4	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0
<i>Eucinostomus gracilis</i>	0	13	13	0.0	0.3	0.1	0.0	0.1	0.1	0.0	0.0	0.0
<i>Sphoeroides annulatus</i>	0	2	2	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
<i>Gymnura marmorata</i>	0	2	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Urotrygon chilensis</i>	2	27	29	0.0	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus guttatus</i>	0	11	11	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Narcine vermiculata</i>	0	5	5	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stellifer sp</i>	0	3	3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Fundulus xenicus</i>	27	0	27	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Trinectes fonsecensis</i>	4	3	7	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Micropogonias megalops</i>	0	6	6	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Microgobius sp</i>	1	1	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Syacium ovale</i>	1	6	7	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Pseudupeneus grandisquamis</i>	0	5	5	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sphoeroides lobatus</i>	0	4	4	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Brachygenys californiensis</i>	0	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ariosoma gilberti</i>	0	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Urotrygon nana</i>	0	4	4	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Anchoa mundeola</i>	0	2	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Larimus acclivis</i>	2	0	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Trichiurus lepturus</i>	2	0	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Abudefduf troschelii</i>	0	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Pseudobatos glaucostigma</i>	0	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Urobatis halleri</i>	0	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Opisthopterus dovii</i>	1	0	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Species richness between zones presented differences, with the highest values in the ocean zone of Teacapan (90 species) and Huizache-Caimanero (72 species), followed by the red mangrove forest (70 species), the white mangrove forest (57 species), the buttonwood mangrove forest (51 species), and the unvegetated zone with 28 fish species. The PERMANOVA results showed significant differences among estuarine systems (Pseudo- $F_{1,56} = 2.483$, $p = 0.003$), habitats (Pseudo- $F_{7,56} = 2.283$, $p = 0.001$), and zones (Pseudo- $F_{4,56} = 2.8$,

$p=0.001$), but no differences were found among climatic seasons (Pseudo- $F_{2,56}=1.206$, $p=0.177$). The pairwise comparisons showed that most of the habitats presented different fish assemblages, except for contiguous habitats at each estuarine system as Caimanero and Huizache lagoons ($t=1.12$, $p=0.026$), and these with the tidal mangrove creek, the inner tidal channels and the river at the Huizache-Caimanero system. Also, the inner tidal channel and the tidal mangrove creek with the Agua Grande lagoon in the system of Teacapan did not present significant differences (supplementary material table 4). In terms of zones, the pairwise comparisons between them showed that only the unvegetated zone and buttonwood mangrove forest were not statistically different ($t=0.894$, $p=0.603$; Supplementary material table 5).

The DistLM marginal test (Table 2) indicated that environmental variables of salinity, mangrove height, mangrove area, and depth were significant predictors of fish biomass. This information was used to create a dbRDA plot (Fig. 4), in which the first two axes explained 68.24 % of the variability in the fitted model. A gradient was revealed in the horizontal axis across the zones, with high to low salinity and depth from left to right, and high (white mangrove) to low (red mangrove) mangrove height from right to left. Higher salinities and depths were found in the oceanic habitat of both estuarine systems and the main tidal channel of Teacapan, while the inner parts of the estuarine systems were shallower and presented low salinity due to the influence of freshwater inputs.

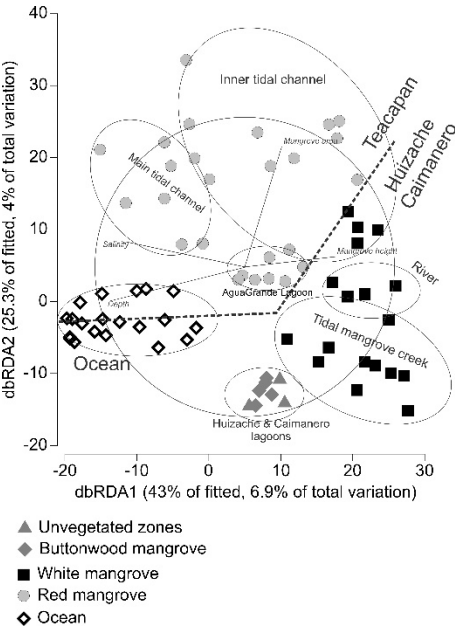


Figure 4. Distance-based redundancy analysis plot of the DISTLM describing the patterns of the fish assemblages using the environmental variables analyzed.

Table 2. Marginal test of the distance based linear model (DISTLM) showing the relationships of the different environmental factors with the fish assemblages. * indicates a statistically significant result.

Variable	SS(trace)	Pseudo-F	<i>p</i>	Prop.
Temperature	3815.5	1.07	0.34	0.02
Salinity*	10101.0	2.92	0.00	0.05
Mangrove height*	10311.0	2.98	0.00	0.05
Mangrove area*	7993.2	2.28	0.00	0.04
Agriculture area	5557.6	1.57	0.04	0.03
Depth*	12166.0	5.03	0.00	0.16

In the vertical axis, a gradient of high to low mangrove coerture was observed, with higher values in Teacapan (due to large extensions of red mangrove forests), in

comparison with Huizache-Caimanero which presented small to medium patches of white mangrove. According to the dbRDA which includes the information on fish assemblages' composition (Fig. 4), the sampled stations of Teacapan were grouped in the top left while the ones of Huizache-Caimanero were grouped in the bottom right. Also, in this analysis four habitat types were identified, which are similar to the results from the PERMANOVA: oceanic zone, buttonwood mangrove forests/unvegetated zones, white mangrove forests, and red mangrove forests. Evident groups according to habitats were not observed, although the fish assemblages from the same habitat grouped close to each other.

The fish species contributing prominently to the Huizache-Caimanero system assemblage were mainly the mullets (*M. curema* and *M. cephalus*), the machete (*Elops affinis*), the tilapia (*Oreochromis spp.*), and the Pacific fat sleeper (*Dormitator latifrons*), whilst in Teacapan the main contributing species were the Pacific cownose ray (*Rhinoptera steindachneri*), grunts (*Rhencus macracanthu* and *Haemulopsis leuciscus*), and catfishes (*Ariopsis seemanni* and *Cathorops fuerthii*).

For habitats, the fish species contributing prominently to the oceanic assemblage were the common hammerhead shark (*Sphyrna lewini*), the Pacific cownose ray, the jack (*Caranx caninus*), scombrids (*Scomber japonicus* and *Katsuwonus pelamis*), and demersal species such as catfishes (*Bagre panamensis* and *Occidentarius platypogon*), and croakers (*Micropogonias altipinnis*, *Cynoscion squamipinnis*, *C. stolzmanni*, and *Umbrina xanti*). For the red mangrove zone, a suite of species from different environments was found, including marine organisms present in the main tidal channel such as golden cownose ray (*Rhinoptera steindachneri*), marine and estuarine species such as grunts (*Rhencus macracanthus*, *Oligoplites spp.*, *Pomadasys spp.*, *Haemulopsis spp.*), catfishes, and the roosterfish (*Nematistius pectoralis*). Also, typical estuarine species such as the milkfish (*Chanos chanos*) and snooks (*Centropomus spp.*) were present at this zone. For the white mangrove zone, which included all the channels in the Huizache-Caimanero system, the most representative species were two small pelagics (striped herring *Lile stolifera* and persistent anchovy *Anchoa walkeri*), the machete (*E. affinis*), and mullets (*M. curema* and *M. cephalus*), which were also the most abundant species in this estuarine system. For the buttonwood mangrove forests/unvegetated zone, the tilapia (*Oreochromis spp.*) and the Pacific fat sleeper (*D. latifrons*) which are usually freshwater species, were the ones characterizing this zone.

Although the three measures of alpha diversity (0D , 1D , and 2D) tended to decrease from the oceanic zone towards the inner parts of the estuaries (Fig. 5), the only zone that showed statistical differences was the oceanic with higher values than the other zones according to the GAMs ($t^0_D=2.07$, $p<0.05$; $t^1_D=2.768$, $p<0.05$; $t^2_D=2.881$, $p<0.05$). For all the other cases, GAMs showed values of $t<1.9$, $p>0.05$.

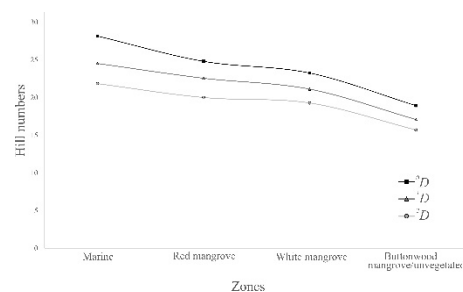


Figure 5. Average value of the three Hill numbers used in the different zones .

For beta diversity, the nestedness component (species richness differences) did not show significant differences between zones ($t_{\beta_{sne}}<1.6$, $p>0.2$), while the spatial turnover (species replacement) was different, due to the higher values in the ocean ($t_{\beta_{stu}}>28.94$, $p<0.01$) compared to the rest of the zones that did not show significant differences among them at the pairwise analyses ($t<0.98$, $p>0.32$).

4. Discussion

On a global scale, comparisons of wetland equivalence across regions have begun to appear in the literature [57,58], but caution is advised especially when they do not account for biases caused by the sampling of different regional and habitat settings, or the use of different sampling methodologies and effort. This study is the first comparison of the fish assemblages in tropical wetland ecosystems from the same geographical region that accounts for different habitats and standardizes the sampling methodologies.

4.1. Environmental data and habitat characteristics

The seasonal variation in temperature and salinity reported in this study is similar to findings for other tropical regions [7], and the variability previously registered for these systems [31]. In addition, differences were also observed between Teacapan and Huizache-Caimanero, with Teacapan being classified as a tide-dominated estuary while Huizache-Caimanero can be considered as an intermittent estuary. The measure of physical, biological, and other environmental variables also allowed identifying zones within the studied systems. The first zone corresponds to the estuarine habitats in Teacapan inhabited by red mangrove forests in good conditions as reflected by their high height and cover, despite the presence of agricultural lands in contiguous areas. In contrast, the Huizache-Caimanero system showed two zones corresponding to white mangrove and the buttonwood mangrove/unvegetated zones, but with a deteriorated condition, and therefore less height and covered area. This condition has previously been reported [31], and was attributable to large human settlements nearby. Finally, another zone was identified in the oceanic area for both estuarine systems.

Regarding physicochemical and environmental parameters, the salinity, temperature, and depth were higher in the oceanic zone, with an observed gradient from the main tidal channel connected to the sea, towards the inner channels of Teacapan and Agua Grande lagoons where the depth decreases considerably and the effect of the river drainage increase, reducing the salinity and temperature. For Huizache-Caimanero, an abrupt difference was observed due to the limited connection to the sea associated with shallow depths and high sedimentation. Therefore, the inner parts were more influenced by the drainage of both rivers which decreased the salinity and temperature. In all the zones, a change associated with the season was also observed with DCS showing lower temperatures and higher salinities, DWS presenting higher temperature and salinity, and the HWS with lower salinities but higher temperatures. Nonetheless, this factor was not as important as other variables to define zones and habitats within the systems.

4.2. Fish assemblages

The most comprehensive study of the ichthyofauna in the southern Sinaloa shelf, which included both systems studied in the present work, registered 600 fish species from the coastal area up to the isobath of 110 m with an approximate study area of 6,400 km² with a perimeter of ~700 km, using a large suite of fishing gears (trawl nets, gill nets, seine nets, hook and line, spearguns, and rotenone) and boats (from skiffs to research vessels) [59]. In contrast, the present study registered fewer species (143 species), which could be associated with a less covered area of ~200 km² (150 km² at Huizache-Caimanero and 50 km² at Teacapan), shallower sampling depths (~20 m in the oceanic area adjacent to the systems), and fewer fishing techniques employed (gill nets, seine nets, and cast nets fitted in skiffs).

The total species richness registered in the present work represents 23.8% of the total reported in the area, where the richness of Teacapan represents 19.2%, and the one in Huizache-Caimanero represents 18.7 %; therefore, in terms of richness per km², the value in Teacapan is higher. The number of species found in this work is higher than those previously reported in the same systems [31], which reported 61 species for Huizache-Caimanero and 51 species for Teacapan. Other studies conducted in the Teacapan estuarine

system reported 76 species [34,38]. For Huizache- Caimanero, between 60 and 44 species have been previously registered [35, 61].

Also, the richness reported in this paper is higher compared to other estuarine ecosystems in the Tropical Mexican Pacific, such as a coastal lagoon of Oaxaca [61], or two estuarine lagoon systems in southern Chiapas [62]. These results are consistent with the range of species richness values for the 12 coastal lagoons along the Mexican Pacific coast, which is between 3 and 73 species with an average of 30 species [63].

According to the rarefaction models, the species found in the present study are close to the estimated number of species per estuarine system. Therefore, the differences with previous studies seem to be related to the sampling effort, the area covered, and the variety of fishing gears utilized, besides other intrinsic characteristics of the estuarine systems that might affect the richness, such as the presence and cover of mangrove forests, and human activities (e.g. fishing, agricultural lands; [64–66].

In terms of species composition, Huizache-Caimanero is inhabited mostly by small pelagics, as these species had already been reported as the main component of fish larvae in this system [67], and represented the higher biomass in the present study. Considering that this system has low salinity throughout the year due to its characteristic as an intermittent estuary with a strong influence of two rivers, it was expected that species with a strong association to brackish and freshwater were dominant. In the case of Teacapan, the influence of a large inlet and a permanent connection to the sea influences the species composition, as two batoids were the most important species in terms of biomass, but also the typical estuarine conditions of this system seem to favor the presence of estuarine species such as catfish.

According to the PERMANOVA and the DistLM analyses, fish assemblages seemed to be characterized by the a priori-defined zones, and then by the habitats. The variables that affected the structure and composition of the fish assemblages were salinity, depth, and mangrove height, which explained 43% of the fitted variation. Salinity and water depth were important predictors in the oceanic zone and were gradually decreasing towards the inner parts of the Teacapan system, in which fish assemblages were also influenced by the red mangrove height. In contrast, for Huizache-Caimanero an abrupt change in species composition from the ocean to the inner zones was observed, probably due to the seasonal ephemeral inlet that limits the seas' influence on this system during the dry season. However, a gradual change in fish species composition was observed in the inner zones from the white mangrove forests towards unvegetated zones and buttonwood mangrove forests, which were predicted by the mangrove height.

The vertical axis from the dbRDA plot explained 25.3% of the fitted variation, indicating that another important predictor was the extension of the mangrove forests, which was more prominent in the red mangroves of Teacapan, and some limited areas of the white mangroves of Huizache-Caimanero. The height of the mangrove trees and the overall extent of the forest can be considered as a proxy for determining the ecological status of the ecosystem in semiarid regions [37]. The areas where the mangrove forest has tall trees with large basal areas and low density of stems are indicative of sites with pristine conditions by estuarine circulation (as the red mangrove forests of Teacapan), or with a strong and persistent influence of freshwater inputs (as the white mangrove forests of Huizache-Caimanero). In the case of the buttonwood mangrove forests and unvegetated zones, these zones result from the combination of intermittent freshwater inputs and shallow areas with a high rate of sedimentation.

According to the SIMPER, the oceanic zone in both systems was predominantly inhabited by marine species such as pelagic elasmobranchs, scombrids, jacks, and also by demersal species that enter the estuarine systems as croakers (Sciaenidae) and catfish, among other species. The red mangrove zone, which included all the inner habitats at Teacapan, was characterized by marine species such as pelagic batoids, estuarine species like milkfish and snooks (*Centropomus* spp.), as well as species that use these zones to complete parts of their life cycle as roosterfish, drum, and catfish. Specifically, the catfish was already characterized as a key species for this system[31], because it requires the

typical estuarine variation in salinity to adequately complete its life cycle [68]. Thus, the presence of this species in the area might be indicative of the importance of seasonal fluctuations to the growth and colonization of fish in red mangroves habitats. Similarly, in the white mangrove forests the dominance of tilapia, herrings, and anchovies that usually inhabit freshwater and estuarine ecosystems [69], might be an indication of the effect of the salinity and the hydrological regime on the composition of fish assemblages.

The buttonwood mangrove/unvegetated zone, which included the lagoons of Huizache-Caimanero, was a shallow area (~1 m dep) that presented mud and standing water with low salinity. In this area, the characteristic species were tilapias and sleepers, which inhabit brackish and freshwater areas with muddy and sandy sediments [69]. Altogether, these results indicate that fish assemblages respond to the surrounding environment, which also influences the zone, as defined by the vegetation. Typical estuarine systems with hydrological regimes that favor the presence of red mangroves as Teacapan are inhabited by a large suite of fish including marine and estuarine species that require typical estuarine systems to complete their life cycles. In contrast, zones with predominantly freshwater and brackish conditions as the channels in the Huizache-Caimanero system, favor the presence of white mangroves that will be inhabited by estuarine species that can tolerate these conditions. Finally, shallow muddy, standing waters with low salinity as Huizache-Caimanero lagoons, are not adequate for mangrove forests to thrive, thus are inhabited by other species that prefer those conditions generated by the lack of connection with the Pacific Ocean that restricts the influence of saltwater, especially during the dry season when the ephemeral inlet of the Presidio River mouth remains closed by a sand barrier. At the beginning of the rainy season, the freshwater flow throughout the Presidio River increases considerably, but its mouth remains closed by the sand barrier that starts breaking only if the amount of fresh water is sufficient, thus opening the lagoon to the ocean.

While there are no published works regarding this physical process at the Presidio River, [70] studied a similar ephemeral river (Quelite) located 50 km north of the study area. The Quelite River presents similar fluvial geomorphological characteristics to the Presidio River, and the same mangrove species thrive along its riverbank. In this sense, the overall process of opening the sand barrier at Quelite River generally takes a few days, and the result consists of a massive plume of freshwater input into the ocean [71]. Thus, the opening of the sand barrier at the Huizache-Caimanero lagoon results in an increase in the amount of freshwater from the Presidio River to the oceanic zone, causing an overall decrease in salt concentration and temperature within the coastal system, and changes in the associated fish assemblages.

The complexity of the mangrove habitat, red in Teacapan and white in the Huizache-Caimanero estuarine systems, attracts many species of fishes that utilize the mangrove as breeding and nursery areas for juveniles. For example, the red mangrove develops a complex network of aerial roots towards the main water body, that protect juvenile fish and other organisms from large predators [11,72]. In the case of the white mangrove, it does not have aerial roots, so its function as protection zones for juvenile fish could be reduced in comparison with the red mangrove. However, the white mangrove tends to thrive in coastal systems with low salinity, which limits the access of oceanic predators.

Related to nutrient availability, mangrove-dominated habitats are different from other coastal ecosystems and therefore favor the presence of fishery resources at the nursery and breeding stages [23,32]. Previous studies have found that species composition, biomass, and diversity of estuarine fish have strong relationships with the different environmental factors, especially temperature and salinity [3]. Our results revealed the importance of salinity to define fish assemblages' composition, as this factor could act as a physiological barrier due to osmoregulatory stress or reduced foraging efficiency, which is often reflected by low fish species richness, biomass, and mixed fish composition of marine, estuarine and freshwater species [14,18,27,73,74].

Factors contributing to these patterns seemed to be a combination of changes in habitat structure (especially the presence or absence of mangrove trees), water conditions,

and substratum characteristics. One of the reasons for the increased diversity of fish in the oceanic zone could be associated with high habitat complexity that allows the presence of a wide variety of species with distinct requirements for reproduction, refuge, and food [11,12]. In addition, red mangrove areas of Teacapan also presented high species richness, which might be associated to the supply of nutrients from the nearby mangrove areas that are consumed directly (e.g. detritus) or indirectly (through the structure features attracting preys) by different fish species [75].

Studies have shown that losses of mangrove habitats had negative effects on the fish biomass and diversity [18,76]. However, during the last decade deforestation of mangrove forests has been extensive throughout the world [77–79]. Describing differences in fish assemblages' composition at each habitat and the relation with environmental variables is essential to understand fish fauna dynamics at these "critical habitats" and to propose local management strategies for each estuarine system [80], based on the life histories of its species and the different hydrological factors reported at the Teacapan and Huizache-Caimanero lagoons in the present study.

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