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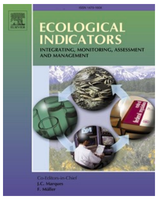

Fish metacommunity structure in estuarine systems of the Honduran coast of the Mesoamerican barrier reef region

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ABSTRACT

Estuarine systems are highly productive ecosystems with diverse fish communities that provide valuable ecosystem services. The structure and ecology of fish communities in the estuarine systems of the Mesoamerican Barrier Reef System region (MBRS) is largely unknown. Here, the fish communities and their relationship with environmental variables were investigated for the first time in sixteen estuarine systems along the Honduran coast of the MBRS. The estuarine systems included estuarine lagoons and estuaries with different mouth dynamics, such as permanently open estuarine systems (POE) and temporary open-closed estuarine systems (TOCE). A total of 154 fish species were identified. Estuarine lagoons exhibited higher abundance and species richness, with Karataska and Chachaguala having the highest species richness (~80 species). Overall, higher diversity was observed in POE systems and during the open mouth phase, likely due to higher dispersion rates. Fish species were classified into different functional groups based on their utilization of estuarine environments. The most abundant category was marine fish (50.6 %), with marine stragglers and marine estuarine-opportunists as the dominant guilds within this category. Freshwater, estuarine, and diadromous fish categories contributed less but similarly. Fish communities in estuarine lagoons and estuaries showed clear differences, although they shared some common species. Estuarine lagoons communities were dominated by the marine category and marine-estuarine-opportunists, while those of estuaries were characterized by the freshwater category and freshwater-estuarine-opportunists. The occupancy varied greatly, with some species present in multiple estuarine systems and others restricted to a single system. Species contribution to β-diversity (SCBD) revealed that species present in a single system made the greatest contribution. Local contribution to total β-diversity (LCBD) ranged between 1.48 and 20.10 %, with the Chachaguala estuarine lagoon being the main contributor. In addition to geomorphological features and estuarine mouth state, distance-based multivariate linear model (DistLM) showed that salinity, pH, bottom vegetation, and dissolved oxygen contributed significantly in explaining the fish metacommunity variation. This study shows the importance of environmental filtering in shaping local fish communities in the MBRS estuarine systems. However, further research is needed to understand the role of dispersion pathways and rates for the integral management of the estuarine fish metacommunity in the region.

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1. Introduction

Estuarine systems are characterized by their high productivity and habitat diversity, making estuarine zones biodiversity hotspots (Day et al., 1989). Fish is one of the most conspicuous and economically important biological groups in these ecosystems (Yáñez-Arancibia, 1985) Estuarine zones support high fish biomass yields that can be partly explained by their high primary production mentioned above and short food webs (Nixon, 1988; Garcia et al., 2007; Capuzzo et al., 2018). Thus, in Central America, for example, artisanal fisheries support more than 1000 local communities (OSPESCA, 2012). In addition, estuarine zones are very important during the life cycle of many fish species, since more than 80 % of coastal fish use estuarine ecosystems in at least one stage of their life (Pauly and Yáñez-Arancibia, 1994, 2012; Cowan et al., 2013). Overall, the high fish abundance and diversity in estuarine zones is linked to the large variability in the ecological conditions in these ecosystems and the abundance and diversity of available resources, such as food, shelter, and spawning grounds (Whitfield, 2017; Teichert et al., 2018). The heterogeneous and dynamic nature of these complex ecosystems allows the coexistence of different taxonomic and functional fish groups (Elliott et al., 2007; Potter et al., 2015). However, the habitat heterogeneity in estuarine ecosystems may prevent assemblage homogenization at the local and regional scale, thus supporting fish metacommunities with high β-diversity even in geographically contiguous areas (Olden et al., 2004; Thrush et al., 2010).

The relationship between different diversity estimates measured at increasing spatial scales (α-, β- and γ-diversity) is affected by several factors. Movement of species among habitats within estuarine ecosystems is spatially and temporally dynamic as it involves interactions between spatial and physical properties (e.g., estuarine mouth open and closed phases), life history, and physiological tolerances (e.g., salinity tolerance), all of which contribute to differences in diversity between systems (Myers, 1927; Yáñez-Arancibia et al., 1994; Matthews, 1998; Habit et al., 2003; Cowan et al., 2013). In addition, the proportion between specialists vs generalists fish species in the metacommunity can affect the occupancy of estuarine systems (Heino, 2013). On the other hand, some species may persist in local assemblages in environments where they do not perform well as competitors, simply due to the continuous influx of individuals from adjacent environments (mass effect) where they are competitively dominant (Mouquet and Loreau, 2003). Thus, potentially high dispersal rates between different lagoons and estuaries contribute to an increase of α-diversity in all of them but tend to decrease β- and γ-diversity (Cruz-Motta et al., 2020).

Fish communities in the Caribbean region and in particular of estuarine systems have been little studied so far, with significant knowledge gaps existing regarding their distribution and ecology. This knowledge is crucial since global scale analysis of fish biodiversity indicates that the Tropical Atlantic region is amongst the richest biogeographic areas (Vasconcelos et al., 2015). So far, available studies in the estuarine zone of the Honduran section of the Mesoamerican Barrier Reef System (MBRS) have focused on taxonomy (e.g., Matamoros et al., 2009, Bussing and Lopez, 2010), reproductive and feeding ecology (Winemiller and Ponwith, 1998), changes in the fish community along the estuarine gradient in some rivers (e.g., Winemiller and Leslie, 1992; Carrasco and Casimiro-Soriguer, 2015), and the effect of climate change on the freshwater species *Chortiheros wesseli* (McMahan et al., 2020). This scarce knowledge limits the capacity of stakeholders, including administration, to properly understand and manage fish populations and communities, which represent an important ecologically-based indicator of environmental quality and an economic resource for local human communities (Yáñez-Arancibia, 1985; Whitfield and Elliott, 2002). In addition, we lack the necessary baseline information on the fish metacommunity of the geomorphologically and ecologically diverse estuarine systems draining into the MBRS coastal waters. This information is essential for future monitoring of the effects of anthropogenic activities and climate change on fish communities in this ecologically important area. To our knowledge, no studies have been published so far on coastal or estuarine fish communities of Central America at large geographic scales or including different types of coastal ecosystems.

To fill this knowledge-gap, we studied the fish communities of sixteen estuarine systems along the Honduran Caribbean coast. More specifically, here, we describe the fish metacommunity of the Honduran MBRS region and relate its structure, characterized by species composition, abundance, and functional groups, with several environmental variables that are likely to affect occupancy and abundance in the different estuarine systems. To accomplish this goal, we investigated how differences in the fish communities between the different estuarine systems were linked to a wide range of local environmental factors, such as their geomorphology (estuarine lagoons and estuaries), dynamics of the estuarine mouth (permanently open and open-closed), seasonality, and biogeochemical properties. Our results contribute to a better understanding of estuarine fish ecology in tropical regions in general, and in the Honduran coast of the MBRS region in particular. This information represents an essential first step to support scientific knowledge–based public policies and integrated conservation plans in the MBRS region, from watershed to coral reefs.

2. Material and methods

2.1. Study area

The study was conducted along the 682-km long Caribbean coast of Honduras (Fig. 1), which drains 14 watersheds into the coastal waters of the Mesoamerican Barrier Reef System (MBRS) (Carrasco and Caviedes, 2014). The coast includes nine large river estuarine systems (Coco, Warunta, Patuca, Plátano, Sico, Aguán, Ulúa, Chamelecón, and Motagua), 20 estuarine lagoons and 22 small estuaries. They represent a total water surface area of 1,300 km^2 and $>$ 10,000 km^2 of associated coastal wetlands (Carrasco and Flores, 2008). Here, we studied the fish community in 16 of these estuarine systems, comprising of eight small estuaries and eight estuarine lagoons, scattered along the Honduran Caribbean coast. Relatively small systems were chosen because investigating the fish community in larger river systems was beyond our logistical capacity. Chosen estuaries and estuarine lagoons represent a wide range of geomorphological, hydrodynamic, and ecological conditions (Table 1), with some being permanently open estuaries (POE) and other temporarily open-closed estuarine systems (TOCE). In addition, they are under different levels and types of anthropogenic impact. All of them receive annually a large input of freshwater due to the high precipitation level in the area (2,000 to 3,400 mm yr^{-1}; Paz et al., 2001). Although rainfall occurs throughout the year, it is lower during the dry season (December to April) compared to the rainy season (May to November).

2.2. Fish samplings

The fish community and environmental variables in the different estuarine systems were sampled between April 2010 and January 2018 (Table 1). We attempted to obtain seasonal data (both dry and rainy seasons) as well as replicates from the sampled sites in each system. However, not all of the systems were sampled with the same intensity, primarily due to challenges in field working conditions in the field, especially in relatively remote areas. Nine estuarine systems were sampled only once, five once in the rainy season and four once in the dry season, whereas seven systems were sampled between two to four times in both seasons (Table 1). Despite the limitations in the sampling, the results obtained are of interest to tropical estuarine fish ecology, especially for poorly studied and difficult to access systems in the MBRS and Central America. This information can serve as a basis for future more system-oriented studies with more balanced sampling designs. Nonetheless, the differences in sampling effort were taken into account by normalizing absolute abundances by the number of visits to each

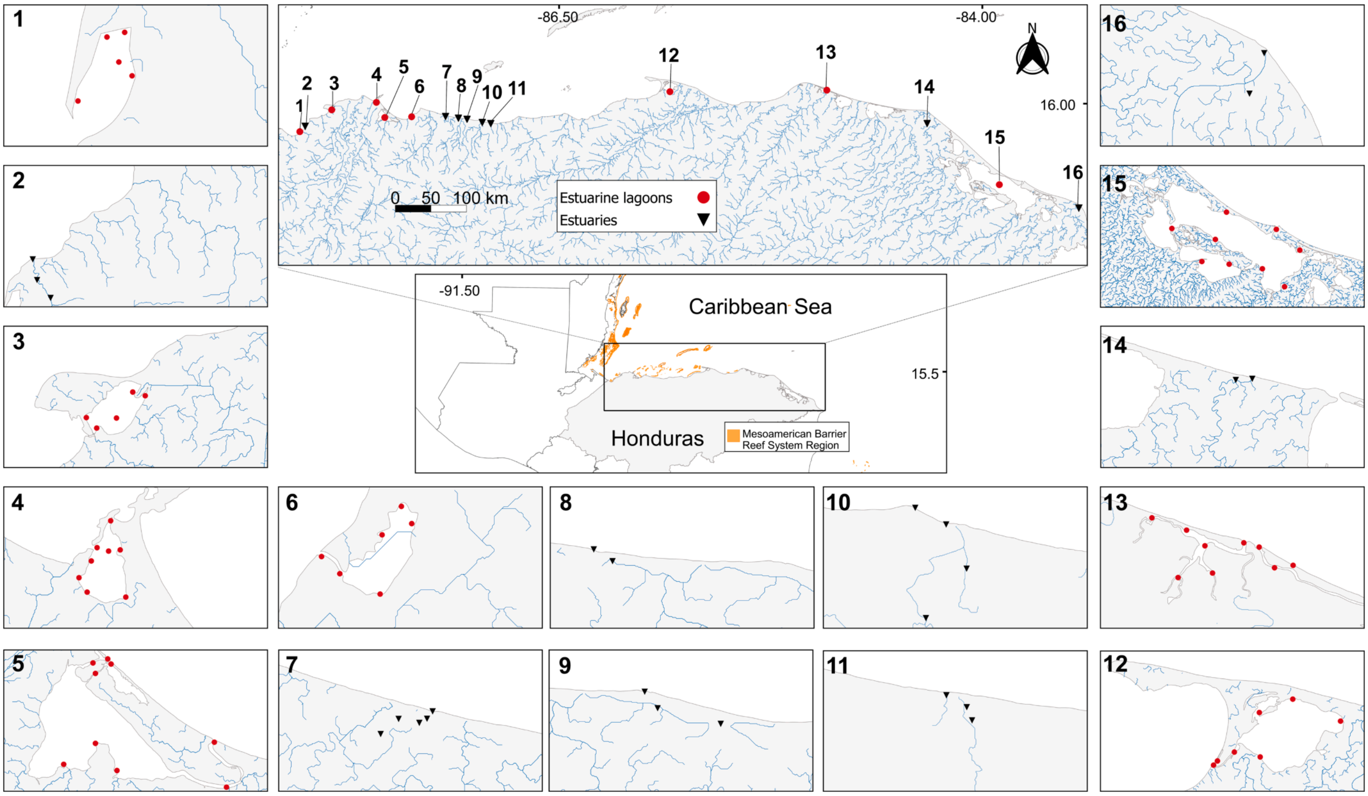

Fig. 1. Location of the estuarine systems sampled in the Honduran Caribbean coast of the MBRS region (Honduras). 1. Chachaguala estuarine lagoon, 2. Chachaguala estuary, 3. Alvarado estuarine lagoon, 4. El Diamante estuarine lagoon, 5. Los Micos estuarine lagoon, 6. Negra estuarine lagoon, 7. Zambuco estuary, 8. Thompson estuary, 9. Cuero estuary, 10. Salado estuary, 11. Zacate estuary, 12. Guaimoreto estuarine lagoon, 13. Bacalar estuarine lagoon, 14. Plátano estuary, 15. Karataska estuarine lagoon, 16. Kruta estuary.

Table 1

General characteristics of the estuarine systems studied along the Honduran Caribbean coast of the MBRS region. The ecosystems were classified in estuaries (E) and estuarine lagoons (EL) according to their geomorphological type, in permanently open (POE) or temporary open-closed (TOCE) estuaries according to their mouth dynamics and in different salinity ranges (Oligo-, Eu-, Polyhaline). Samplings were done in the rainy (R) or dry (D) season, 1 or 2 times each season (R1, D1, R2, D2). The status, open (O) or closed (C), of estuarine mouth during samplings, the number of sampling sites within every estuarine zone and total number of pulls are included as well.

Estuarine systems	Geomorphology	Mouth dynamics	Salinity class	Sampling season	Mouth status	Sampling sites	Total samplings	Totals hauls
Chachaguala	EL	POE	Eu	R1/D2	O3	5	15	90
Chachaguala	E	TOCE	Oligo	D1	C1	3	3	18
Alvarado	EL	POE	Poly	R1	O1	5	5	30
El Diamante	EL	POE	Poly	D1	O1	8	8	48
Los Micos	EL	TOCE	Oligo	R1	O1	9	9	54
Negra	EL	TOCE	Poly	D1	C1	6	6	36
Zambuco	E	TOCE	Oligo	D1	C1	5	5	30
Thompson	E	TOCE	Oligo	R1/D2	O3	2	6	36
Cuero	E	TOCE	Oligo	R1/D2	O2/C1	3	9	54
Salado	E	TOCE	Oligo	R1/D2	O3	4	12	72
Zacate	E	TOCE	Oligo	R1/D2	O1/C2	3	9	54
Guaimoreto	EL	POE	Eu	R1	O1	7	7	42
Bacalar	EL	TOCE	Oligo	R1	O1	9	9	54
Plátano	E	POE	Oligo	R1	O1	2	2	12
Karataska	EL	POE	Oligo	R2/D1	O3	9	27	162
Kruta	E	POE	Oligo	R2/D1	O3	2	6	36

estuarine system.

Fish sampling consisted in six hauls of a beach seine net (31.5 m long, 2 m high, with 5 mm mesh) at every sampling site within a given estuarine system. At every sampling site, two people walked at each end of the seine extending and pulling it to form a semicircle and then closing it to form a complete circle. The distance between different pulls in a given sampling site was approximately 15 m. Every haul represents an area (complete circle) of approx. 79 m^2, therefore, a surface of about 474 m^2 was sampled at one sampling site on each visit. The fish caught in the six hauls were aggregated and considered as the total catch at each sampling site on each visit. Sampling sites were chosen to have the maximum representativeness of environmental gradients, e.g., salinity and range of habitats present in each estuarine system. The number of sampling sites and number of visits to the same estuary varied (Table 1). To account for differences in the sampling effort on the estuarine systems, fish abundances are reported as Catch Per Unit Effort (CPUE, Schrandt et al., 2018; https://www.fao.org). CPUE for each species was calculated as the total abundance in all sampling sites within a given system and visits to the estuarine system divided by the total number of samplings in that specific system (sampling sites × visits = Total samplings in each ecosystem, Table 1).

Collected fish were identified to the lowest possible taxonomic level, counted, preserved in 10 % formalin and deposited at the Universidad Nacional Autónoma de Honduras collection. In addition, fish were classified into functional groups according to Potter et al. (2015). These functional groups are determined by the ways in which fish species use estuarine systems and are categorized into four types: marine, estuarine, diadromous, and freshwater fish. Every category contains two or more guilds, e.g., the Marine category has the following guilds: Marine estuarine-dependent, Marine estuarine-opportunist, Marine straggler. The conservation status of the fish species were categorized according to IUCN red list (https://www.iucnredlist.org/).

2.3. Fish diversity

Alpha diversity (within system diversity) was measured as the number of species (S) and the Shannon-Weaver index ($\acute{H}$) based on CPUE units per system. Species evenness (E) was calculated as $\acute{H}/\acute{H}_{max}$, where $\acute{H}_{max}$ = Ln S (Pielou,1966). Gamma diversity (regional diversity) was calculated similarly to α-diversity but pooling all estuarine ecosystems together. Gamma diversity is therefore the total diversity of the fish metacommunity in the studied estuarine zone of the MBRS region. Beta diversity is the variation in composition of the fish community between the 16 estuarine systems. There are many different approaches and indices to estimate β-diversity (Whittaker, 1960; Vellend, 2001; Koleff et al., 2003; Anderson et al., 2011). Here, we used the approach of Legendre and De Caceres (2013), according to which total β-diversity (BD_T) is calculated as the variance of the community data matrix (Y), with species abundances expressed in CPUE as described before. This approach allows estimating both the relative contribution of each estuarine system and of individual species to the overall β-diversity as described below.

The matrix $Y = y_{ij}$ is the data table containing species abundance expressed in CPUE, formed by i = 1 to n estuarine systems (row vectors) and j = 1 to S species (column vectors). These abundance data were transformed using the Hellinger transformation (eq. (1) as recommended (Legendre and De Caceres, 2013), where y_{i+} is the sum of row i according to the following equation:

$$y'_{ij} = \sqrt{(y_{ij}/y_{i+})} \tag{1}$$

To calculate BD_T as the variance of the transformed community data matrix ($\acute{Y} = y'_{ij}$), first we calculate a new matrix in which the elements s_{ij} are the square deviations of the transformed abundances in a given estuarine system i to the average of abundance of a given species j in the n estuaries (column means), according to following equations:

$$s_{ij} = (y'_{ij} - y_j)^2 \tag{2}$$

The total sum of squares (SS_T) is the sum of all s_{ij} (3)

$$SS_T = \sum\nolimits_{i=1}^{n} \sum\nolimits_{j=1}^{S} s_{ij} \tag{3}$$

Total β-diversity (BD_T) was calculated from SS_{Total} according to equation (4).

$$BD_T = SS_T/(n-1) \tag{4}$$

SS_T and BD_T have been proposed as measures of β-diversity (Legendre et al., 2005; Legendre and De Caceres, 2013).

SS_T can be partitioned into the contributions of individual estuarine systems and of individual species to the overall β-diversity. The local contribution of the estuarine system i to the overall β-diversity ($LCBD_i$) and the individual species contribution j to the overall β-diversity ($SCBD_j$) were calculated by equations (5)–(6) and 7–8, respectively.

$$SS_i = \sum\nolimits_{i=1}^{n} s_{ij} \tag{5}$$

$$LCBD_i = SS_i/SS_T \tag{6}$$

$$SS_j = \sum\nolimits_{j=1}^{S} s_{ij} \tag{7}$$

$$SCBD_j = SS_j/SS_T \tag{8}$$

In order to test the efficiency of our sampling effort, concerning the number of species reported in the study area, we represented the number of species against sampling effort (species sampling relationship, SSR) in each estuarine system. Different equations have been used to analyze SSR data (Dengler, 2009). Here, we chose to use a function that allows estimating a theoretical maximum number of species (S_{max}) for each estuarine system (Tjørve, 2003; Dengler, 2009), instead of using the well-known power function for the species area relationship, where the number of species do not have an asymptotic upper limit. Therefore, SSR data were fitted to a regular hyperbole equation, mathematically identical to the Michaelis-Menten function (equation (9),

$$S = \frac{S_{max}A}{K_A + A} \tag{9}$$

where, S is the number of species, S_{max} is the estimated maximum number of species, K_A is a semi-saturation constant, and A is the sampling effort.

2.4. Environmental conditions

During fish sampling, a number of environmental variables were measured in the same sampling sites. Salinity (PSU), temperature (°C), dissolved oxygen (%), and pH were measured with a YSI 556 multiparameter probe (YSI Inc., Yellow Springs Ohio, USA). Water column turbidity was measured using a Secchi disk (30 cm diameter). Sediments were classified in two categories, sand and mud-silt, by macroscopic observation. Bottom vegetation was expressed as the percentage of sampling sites where it was present within each estuarine system. The depth of the sampling site was determined using a graded string and a plumb bob. In addition, every estuarine system was classified according to its geomorphology (estuary or estuarine lagoon), type of estuarine mouth dynamics (temporary open-closed or permanently open estuaries), mouth status during sampling (open or closed), salinity characteristics (oligohaline, polyhaline, mesohaline, or euryhaline), and sampling season (dry or rainy) (Table 1, Table S1). The geographic location of each sampling site was determined using a GPS (Garmin GPSMAP 64 s).

2.5. Statistical analysis

Environmental variables with skewed distributions (i.e., salinity and bottom vegetation) were log (x + 1) transformed and all variables were then normalized to eliminate differences in scales. Resemblance between systems based on the environmental variables was measured calculating the Euclidean distance. Then, non-metric multidimensional scaling analysis (nMDS) was used to visualize the ordination of the estuarine systems of Honduran coast of MBRS region based on the environmental variables. Similarly, fish abundance (expressed in CPUE) at either the taxonomic or functional group (categories or guilds) levels were square-root transformed to down-weigh the effect of overly abundant “species”. Resemblance between systems was estimated using the Bray-Curtis similarity index (Bray and Curtis, 1957).

Statistical differences for different factors (estuaries vs estuarine lagoons, open vs closed phase, etc.) either at the univariate (species richness, diversity, or individual environmental variables) or the multivariate level (environmental variables, taxonomy, guilds, or categories) were tested using a one-way PERMANOVA followed by posthoc tests when a clear difference was found (Anderson et al., 2009). In order to determine which species were primarily responsible for the observed differences between estuaries and estuarine lagoons, the Similarity Percentage (SIMPER) analysis was carried (Clarke and Warwick, 2001).

The relationships between the fish assemblages and functional groups resemblance matrices with the environmental variables were analyzed by distance-based multivariate linear model analysis (DistLM). We used eight environmental variables (temperature, salinity, dissolved oxygen, pH, turbidity, sediment type, depth, and bottom vegetation) and an AICc (second-order Akaike Information Criterion) model selection criterion to select the model that minimizes the loss of information. Environmental variables were first checked for covariance. No variables had a correlation of > 0.8 so all were included in the analysis.

PERMANOVA tests were performed in PAST 4.03 (Harper et al., 2020). All remaining statistical procedures were performed in the PRIMER 6 + PERMANOVA statistical package (PRIMER Ltd).

3. Results

3.1. Environmental variability

The sixteen estuarine systems investigated in the Honduran coast of MBRS region represent a wide range of environmental conditions to which fish must adapt (Table 1, Table S1). Salinity ranged between freshwater in the area sampled in the Zacate estuary and almost marine conditions (33.6 PSU) in the Chachaguala estuarine lagoon during the dry season. Temperature (23–32.7 °C), DO (6.1–7.9 mg O_2 L^{-1}), pH (6.1–8.1) and turbidity estimated by Secchi disk depth varied between systems and within the same system between seasons. In general, turbidity was high in all environments, likely limiting the presence of benthic vegetation to only a few estuarine lagoons, like Karataska, El Diamante, Alvarado, and Chachaguala (Table S1). Estuarine lagoons presented generally mud-silty sediments, while in estuaries the dominant type of sediment was sand (Table S1).

nMDS analysis of the environmental variability, based on the eight environmental variables studied, separated clearly estuaries from estuarine lagoons, mainly along the first axis (One-way PERMANOVA, F = 7.3816; P = 0.001) (Fig. 2a). Axis 1 of the nMDS ordination plot correlated strongly with salinity, pH, DO, and bottom vegetation, whereas axis 2 correlated with turbidity, depth, and sediment type.

Estuaries and estuarine lagoons differed clearly in a number of variables averaged over the sampling period (temperature, salinity, DO and pH), but not in turbidity (Table 2), with values being generally higher in estuarine lagoons. Within each type of system, seasonal differences were observed in temperature, salinity, DO, pH, and turbidity in both type of systems, with higher values recorded in the dry season for most variables.

Table 2

Mean water column characteristics of the sixteen estuarine systems (eight estuaries and eight estuarine lagoons) sampled along the Honduran Caribbean coast of the MBRS region. The average ± standard deviation for estuaries and estuarine lagoons are presented in the two first columns. The averages ± standard deviation for estuaries and estuarine lagoons distinguishing dry and rainy seasons are presented in the remaining four columns. Different superscript letters (a-b, estuaries vs estuarine lagoons; and a-d, season between estuaries and estuarine lagoons) indicate statistically clear differences between means ($p < 0.05$, pairwise comparison).

Environmental variables	Average Estuaries	Estuarine lagoons	Seasonal average Estuaries		Estuarine lagoons	
			Dry	Rainy	Dry	Rainy
Temperature (°C)	27.7 ± 3.1^{a}	29.2 ± 2.9^{b}	29.2 ± 2.4^{a}	25.6 ± 2.9^{b}	31.85 ± 1.3^{c}	27.5 ± 2.4^{d}
Salinity (UPS)	1.5 ± 3.6^{a}	14.6 ± 13.6^{b}	1.9 ± 4.5^{a}	0.8 ± 1.5^{a}	21.3 ± 12.7^{b}	10.5 ± 12.5^{c,d}
Diss. oxygen (mgL^{-1})	6.7 ± 0.7^{a}	7.3 ± 0.5^{b}	6.6 ± 0.6^{a}	6.9 ± 0.8^{a}	7.6 ± 0.5^{b}	7.2 ± 0.5^{c,d}
pH	6.8 ± 0.7^{a}	7.7 ± 0.4^{b}	6.9 ± 0.5^{a}	6.5 ± 0.8^{b}	7.8 ± 0.4^{c}	7.7 ± 0.5^{c,d}
Secchi disk (cm)	50.6 ± 54.0^{a}	58.9 ± 41.7^{a}	67.8 ± 59.5^{a}	25.3 ± 31.3^{b}	76.8 ± 55.3^{a,c}	47.8 ± 25.0^{d}

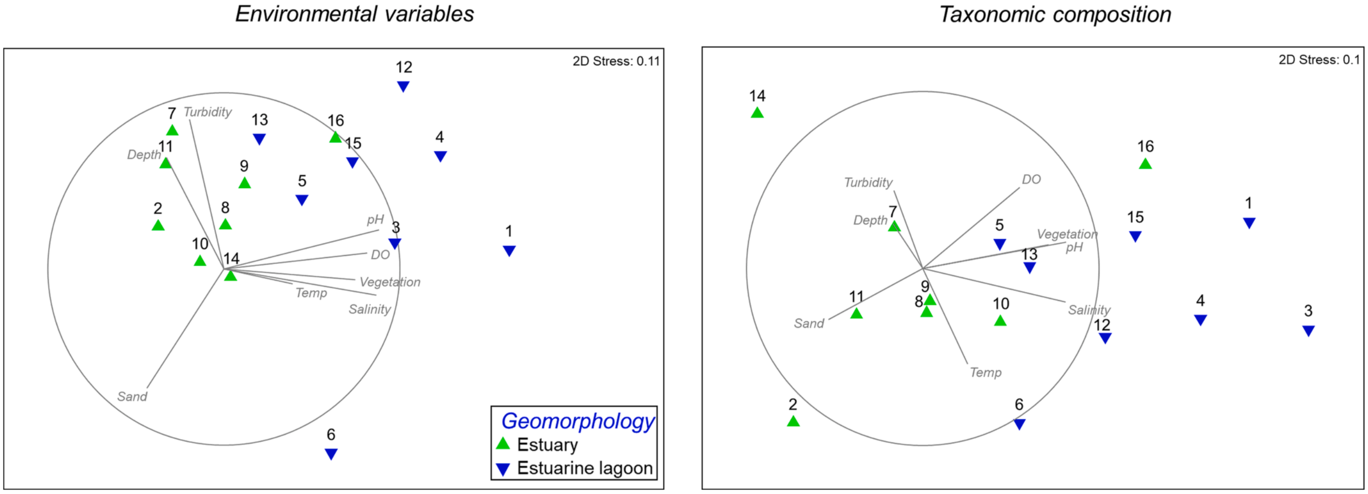

Fig. 2. nMDS ordination plots of the estuarine systems sampled along the Honduran Caribbean coast of MBRS region based on the similarity calculated from (a) the environmental variables using the Euclidean distance and (b) taxonomic community composition of fish using the Bray Curtis similarity index on square root transformed abundance data. Vectors indicate the Pearson correlations of the enviromental variables analysed with the ordination plot. Numbers in the plots correspond to the systems sampled: 1. Chachaguala estuarine lagoon, 2. Chachaguala estuary, 3. Alvarado estuarine lagoon, 4. El Diamante estuarine lagoon, 5. Los Micos estuarine lagoon, 6. Negra estuarine lagoon, 7. Zambuco estuary, 8. Thompson estuary, 9. Cuero estuary, 10. Salado estuary, 11. Zacate estuary, 12. Guaimoreto estuarine lagoon, 13. Bacalar estuarine lagoon, 14. Plátano estuary, 15. Karataska estuarine lagoon, 16. Kruta estuary.

3.2. Fish relative abundance and species richness

Collected fish (43,653 specimens) were classified in 19 orders, 45 families, 95 genera, and 154 species (Table S2). Based on the IUCN red list of threatened species, twelve species were classified as data deficient, 135 as least concerned, 2 as near threatened (*Lutjanus analis* and *Lutjanus synagris*), 2 as vulnerable (*Megalops atlanticus* and *Epinephelus itajara*) and 1 as an endangered species (*Anguilla rostrata*). We found only one exotic species, *Oreochromis niloticus*, which was widely distributed in 6 estuaries and 4 estuarine lagoons so far (>62 % of the estuarine systems).

The species sampling effort relationship (SSR) showed an asymptotic increase in S that differed between estuarine systems, both in the initial S value and the slope (Fig. S1a). SSR data fitted well to a regular hyperbole function (Pearson coefficients between 0.884 and 0.999, $p < 0.05$), allowing the estimation of the maximum number of species (S_{max}) for each estuary (Fig. S1b). The comparison between the observed number of species and S_{max} showed that we collected between 43 and 114 % of S_{max} (Table 3). Only in the Salado estuary, did we collect a higher number of species than predicted. Overall, we collected 76 ± 22 % of S_{max}, which is a good representation of the fish fauna in the estuarine zone of the MBRS region.

Local fish communities showed important differences in fish diversity and abundance between systems (Fig. 3, Table 3). The Shannon index (H́) ranged between 1.49 and 3.55, whereas evenness (E) ranged between 0.5 and 0.91 (Table 3). Species richness ranged between 17 and 83 species, recorded in the Platano estuary and Karataska estuarine lagoon, respectively. The regional species diversity (γ-diversity), estimated either by total number of species (S) or Shannon index (H́), was much higher than the local diversity (α-diversity) in any of the estuarine systems, with differences being more clear in S than in H’ (Table 3). Total fish abundance varied greatly between the studied estuarine systems as well (97.7——808.1 CPUE), with the highest values recorded in the Chachaguala estuarine lagoon (Fig. 3). Fish abundance in estuarine lagoons was significantly higher than in estuaries (One-way PERMANOVA, F = 2.694, P = 0.004) and in POE than TOCE estuarine systems (One-way PERMANOVA, F = 16.43, P = 0.0001). Overall, fish abundance covaried positively with salinity, dissolved oxygen, pH, and bottom vegetation (results not shown). The estuarine mouth dynamics in TOCE seemed to affect local abundance and diversity of fish, being higher during the estuarine mouth open phase (i.e., rainy season) in both estuarine lagoons and estuaries (One-way PERMANOVA, F = 3.448, P = 0.0001). However, no clear differences in fish abundance and diversity were observed between POE estuarine lagoons and estuaries.

Table 3
Fish metacommunity diversity analysis of the estuarine systems sampled along the Honduran Caribbean coast of the MBRS region. Number of species observed (S), number of exclusive species in every system ($S_{excl.}$), estimated maximum number of species (S_{max}), Shannon index (H’), Evenness (E) and Local contribution of a given system to SS_T (LCBD) in %. The ecosystems were classified in estuaries (E) and estuarine lagoons (EL) according to their geomorphological type.

Systems	S	$S_{excl.}$	S_{max}	H’	E	LCBD
Chachaguala EL	79	15	85	2.63	0.60	20.10
Chachaguala E	24	4	54	2.27	0.71	6.42
Alvarado EL	44	4	55	1.91	0.50	9.35
El Diamante EL	55	3	108	2.63	0.66	6.62
Los Micos EL	48	0	50	2.97	0.77	4.18
Negra EL	32	0	48	2.44	0.70	1.48
Zambuco E	34	0	39	2.82	0.80	2.63
Thompson E	43	1	47	2.97	0.79	3.34
Cuero E	43	0	47	3.08	0.82	1.70
Salado E	62	3	54	3.11	0.75	4.63
Zacate E	40	3	63	2.66	0.72	5.04
Guaimoreto EL	54	2	125	2.80	0.70	5.17
Bacalar EL	50	0	51	3.55	0.91	3.62
Plátano E	17	2	40	1.49	0.53	4.36
Karataska EL	83	8	94	2.79	0.63	11.02
Kruta E	61	4	88	3.05	0.74	10.33
TOTAL	154	49		3.79	0.75	100

The fish species differed in their degree of occupancy, evaluated here as the number of estuarine systems in which a given species was found. Only one species, *Caranx latus* was present in all but one of the estuarine systems studied, with no species present in all the systems. On the other end, 49 species (32 % of total) were found in just one system in the region (Table 3, Fig. S2). The number of these exclusive species (S_{excl}) varied considerably between the estuarine systems, with S_{excl} being highest in Chachaguala and Karataska estuarine lagoons, with 15 and 8 exclusive species, respectively (Table 3).

The overall β-diversity, estimated according to Legendre and De Caceres (2013), was 7.92. The contribution of each species to the overall β-diversity (SCBD) ranged between 0.19 and 0.79 % (0.65 ± 0.16 %), being inversely related to occupancy in the estuarine systems of the MBRS region (r = 0.953, n = 154, $p < 0.05$). The fish species contributing less to the overall β-diversity was *C. latus*, being present in most estuarine systems, while the major contributors were the 49 species present in only one estuary (Fig. S3). The local contribution of the different estuarine systems to β-diversity (LCBD) ranged from 1.48 to 20.1 % (Table 3, Fig. 4a). The summed LCBD of just four systems, the Chachaguala, Karataska, and Alvarado estuarine lagoons, and Kruta Estuary, was higher than 50 % (Fig. 4b). In general, higher levels of α-diversity, estimated as S and H́, and LCBD were observed in the estuarine systems located in the east and west extremes of the studied region (Table 3, Fig. 4).

The nMDS ordination of the systems studied based on their fish community taxonomic composition showed considerable dispersion, suggesting large variations in the fish community in each estuarine system (Fig. 2b). Despite the high dispersion, estuaries and estuarine lagoons were clearly separated along the first axis of the NMDS ordination plot (One-way PERMANOVA, F = 2.694; P = 0.0038), consistent with the ordination based on the environmental variables (Fig. 2a). The first axis correlated most with salinity (r = 0.83), pH (r = 0.82) and vegetation (r = 0.72) with higher values of these variables in estuarine lagoons (Fig. 2b, Table 2).

Fish assemblages in estuaries and estuarine lagoons were different. Species richness (S) was higher in estuarine lagoons (135 species) than in estuaries (106 species) when the whole region is considered (One-way PERMANOVA, F = 3.291; P = 0.040). Some species were recorded in both estuaries and estuarine lagoons (87 species, 56.5 %), while others were found only in estuaries (19 species, 12.2 %) or in estuarine lagoons (48 species, 31.2 %) (Table S3). In general, estuarine lagoons presented higher S_{excl}, S_{obs} and S_{max} than estuaries and contributed more to overall β-diversity (Table 3).

3.3. Fish functional groups

Fish species in the estuarine systems of the Caribbean Honduran coast of the MBRS region were classified into 4 functional categories and 11 guilds according to Potter et al. (2015) (Fig. 5). Marine fish was the most abundant category with 78 species representing 50.6 % of the total. Freshwater, estuarine, and diadromous categories had similar contributions with 29, 24, and 23 species, respectively (Fig. 5). Within the marine category, the guilds marine straggler and marine estuarine-opportunist were dominant with 35 and 34 species, respectively, representing 45 % of the total species (Fig. 5, Table S2 and S4).

Estuaries and estuarine lagoons were arranged in two clearly distinct groups in the nMDS plots based on both fish categories and fish guilds (categories One-way PERMANOVA, F = 5.7945; P = 0.006 and guilds One-way PERMANOVA, F = 5.7945; P = 0.007) (Fig. 6). The nMDS ordination plot showed that the categories of marine and estuarine fish were strongly (r_p = 0.91 and r_p = 0.89) associated with the first axis separating the two estuarine system types with highest values in estuarine lagoons. In contrast, diadromous and freshwater fish were strongly

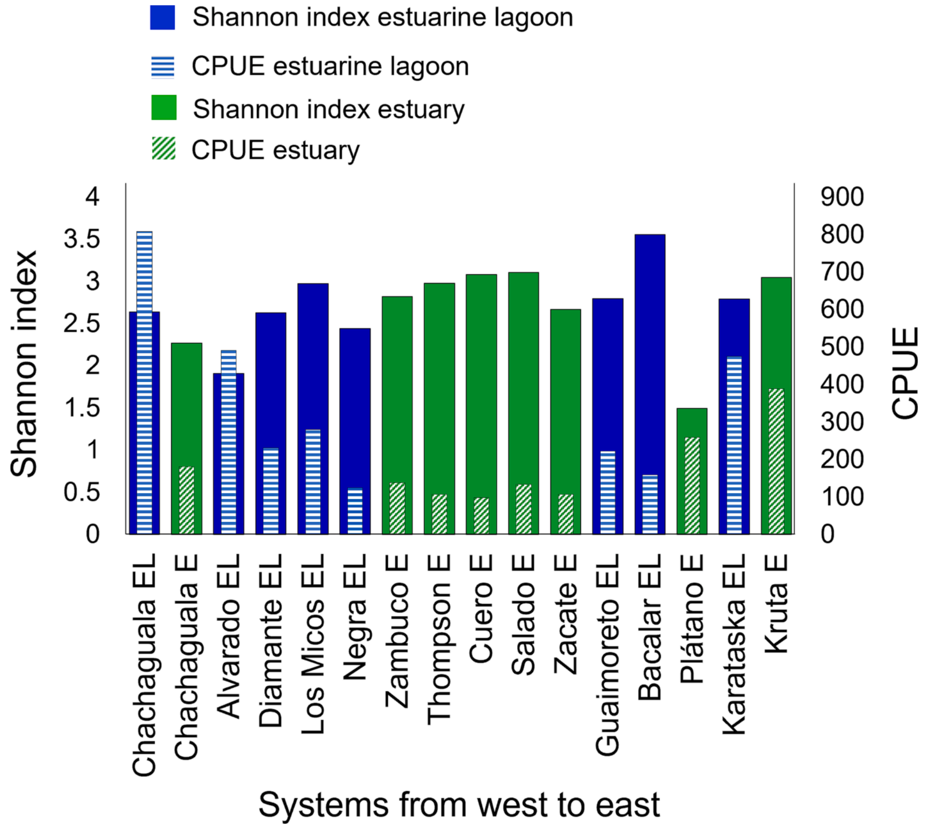

Fig. 3. Fish community Shannon index (H́) and abundance (CPUE) in 16 estuarine systems sampled along of the Honduran coast of the MBRS region ordered from west to east. EL: Estuarine lagoon E: estuary.

associated ($r_p = 0.76$ and $r_p = 0.83$) with the second axis (Fig. 6a). However, no other measured variable correlated strongly with this axis ($r > 0.4$) that could explain the variation observed (data not shown). The guilds semi-catadromous, amphidromous (diadromous category), freshwater straggler, (freshwater category) were associated with estuaries. In contrast, the guilds marine estuarine-opportunist, marine estuarine-dependent, marine straggler (marine category), estuarine freshwater, solely estuarine, and estuarine-marine (estuarine category) were associated with estuarine lagoons (Fig. 6b).

3.4. Similarity and differences between estuaries and estuarine lagoons fish communities

We used the SIMPER analysis to investigate further which species contributed more to the similarity and dissimilarity among the fish metacommunities in both environments. The similarity of the fish communities within estuaries was 38.61 %. Nine of the 31 species identified in total contributed 51.70 % to the similarity within estuaries, whereas the rest of the species contributed each less than 0.92 %. Species such as *Poecilia gillii* (7.79 %) *Cryptoheros cutteri* (7.47 %), *Dajaus monticola* (6.86 %), *Gobio dormitor* (6.26 %)*, Vieja maculicauda* (5.74 %), *Caranx latus* (5.31 %), *Poecilia orri* (4.83 %), *Amphilophus robertsoni* (3.90 %), and *Dormitator maculatus* (3.81 %) were major contributors to the similarity within estuarine fish communities. More than half of these species belong to the freshwater category and in particular the freshwater-estuarine-opportunist guild (Table 2, Suppl. mat.). In the case of estuarine lagoons, similarity within systems was 39.96 %. Twelve of the 40 species identified in total contributed 50.70 % to their similarity, with the rest of the species contributing each less than 0.70 %. Major contributors to the similarity between fish communities within estuarine lagoons were *Atherinella milleri* (11.16 %), *Sphoeroides testudineus* (5.26 %), *Diapterus rhombeus* (4.56 %), *Mayaheros urophthalmus* (3.86 %), *Anchoa* cf. *belizensis* (3.66 %), *Citharichthys spilopterus* (3.61 %), *Eucinostomus melanopterus* (3.38 %), *Gambusia nicaraguensis* (3.29 %), *C. latus* (3.19 %), *Trinectes maculatus* (3.14 %), *Eugerres plumieri* (2.83 %) and *Mugil curema* (2.73 %). Half of these species belong to the marine category and more specifically the marine-estuarine-opportunist guild (Table 2, Suppl. mat).

Dissimilarity between fish communities from estuaries and estuarine lagoons was on average 68.80 %. The greatest contribution was made by 13 species out of 71 in total, contributing 33.86 % to the dissimilarity. The rest of the species contributed each less than 0.94 %. Major contributors to dissimilarity were *A. lyolepis* (4.0 %), *A. milleri* (3.83 %), *S. testudineus* (3.10 %) *D. rhombeus* (3.0 %), *D. monticola* (2.77 %), *E. melanopterus* (2.67 %), *A. belizensis* (2.50 %), *M. urophthalmus* (2.06 %), *P. gillii* (2.05 %), *Gerres cinereus* (2.03 %), *V. maculicauda* (1.99 %), *Astyanax aeneus* (1.97 %) and *C. cutteri* (1.89 %). These species belonged mostly to the marine (n = 5) and freshwater (n = 5) categories and to the marine-estuarine-opportunist and freshwater-estuarine-opportunist guilds, followed by estuarine (n = 2) and diadromous species (n = 1) (Table 2, Suppl. mat.).

3.5. Selectedenvironmental drivers of fish metacommunity

The DistLM analysis allowed investigating which of the environmental variables measured could contribute in explaining the variability of the fish metacommunity, both when it was characterized in terms of taxonomic composition and of functional groups. Marginal test results of individual variables showed that pH (28.3 %), salinity (27.7 %), bottom vegetation (20.9 %) and dissolved oxygen (17.3 %) explained each a significant fraction of the fish metacommunity variability based on its taxonomic composition and abundance (Table S4). The inclusion of more explanatory variables showed that the most parsimonious models were a combination of salinity, pH, and bottom vegetation, explaining

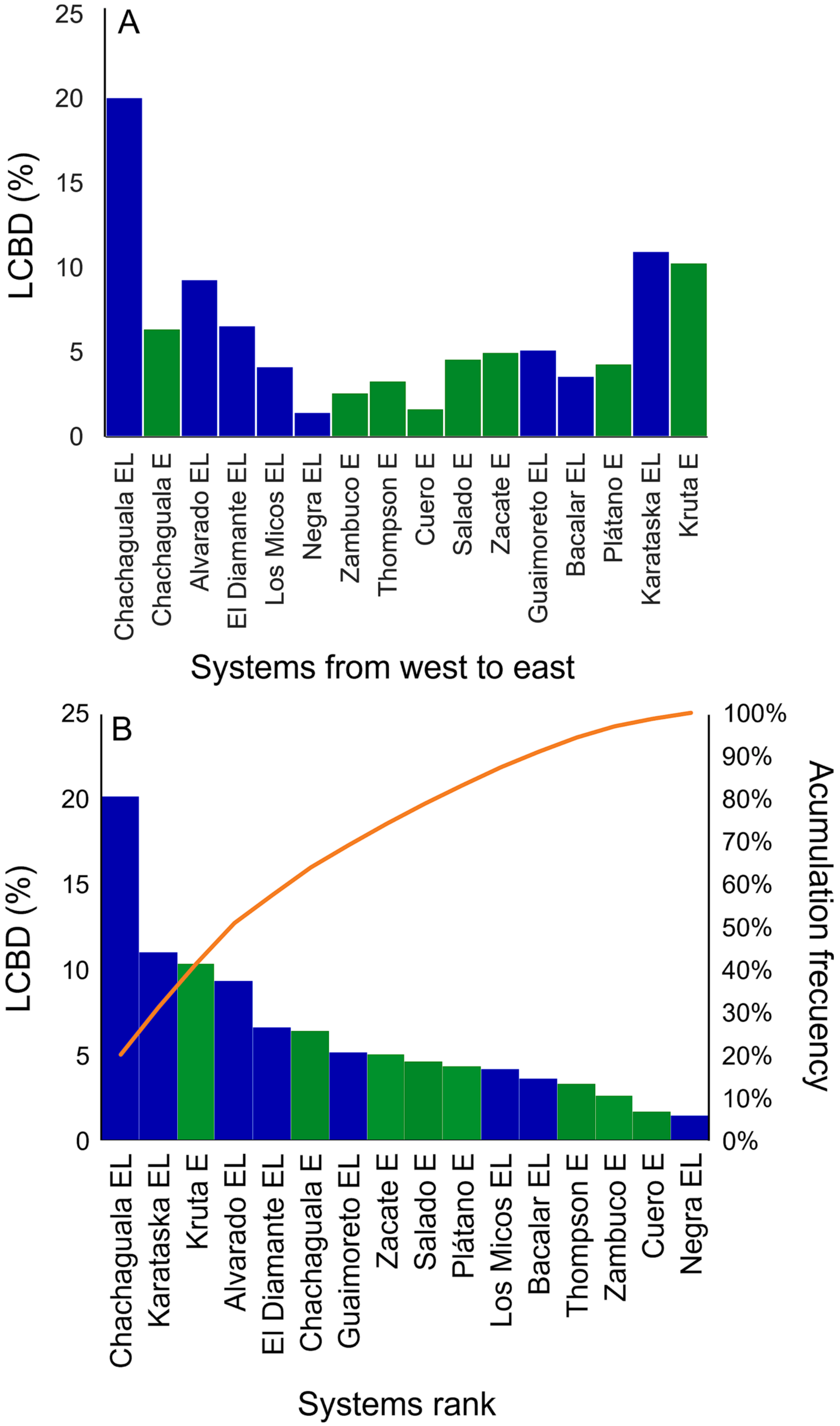

Fig. 4. (A) Local contribution of estuarine systems to overall β-diversity (LCBD) for the 16 estuarine systems sampled along the coastal Honduran MBRS region and (B) LCBD of each system ranked according to its contribution from highest to lowest and accumulated LCBD (orange line). Estuarine lagoons and estuaries are colored in blue and green respectively. EL: Estuarine lagoons, E: Estuaries.

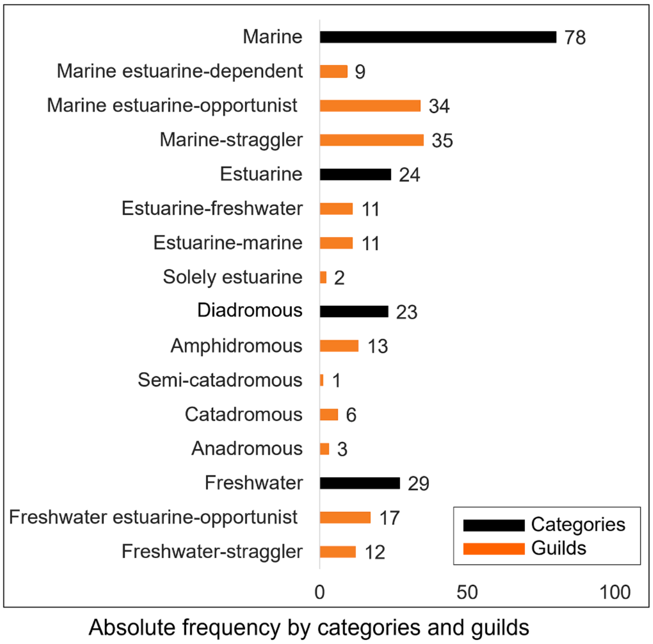

Fig. 5. Number of fish species belonging to the different functional groups from the sixteen estuarine systems sampled along the Honduran Caribbean coast of the MBRS region. Fish were classified in four categories and every category in eleven guilds according to Potter et al. (2015).

35.5——38.4 % of the variation observed (Table S5). When the fish metacommunity was analysed in terms of functional groups, as either categories (results not shown) or guilds, we obtained similar results. Individual variables like salinity (43.3 %), pH (40.8 %) and bottom vegetation (22.7 %) explained an important fraction of functional groups variability (Table S6). The most parsimonious model solutions, incorporating more explanatory variables, included salinity and pH in most of them explaining about 60 % of the variation (Table S7).

4. Discussion

This study represents the first characterization of the fish metacommunity of different types (POE, TOCE) of estuarine lagoons and estuaries in the southern coast of the MBRS region. The fish metacommunity was sampled across a wide range of environmental conditions (Table 1, 2) and, therefore, represents a comprehensive evaluation of the fish fauna in the region, encompassing from freshwater to marine species. The fish metacommunity was very rich and diverse with species belonging to different functional groups inhabiting selectively different systems.

4.1. *Taxonomic and functional characteristics of the fish metacommunity*

The sixteen estuarine systems in the Honduran MBRS region support a diverse fish fauna of 154 species. The high species richness found in this so far little-studied region, agrees with global and regional patterns showing that the biogeographic Tropical Atlantic region is among the richest for fish (Vasconcelos et al., 2015). According to the IUCN red list, the conservation status of most of these species (95 %) is little known, but we detected two threatened, two vulnerable, and one endangered species (Table S2). Regarding the way in fish species use the estuarine systems, they were classified into 4 functional categories and 11 guilds (Potter et al., 2015). The most abundant category was that of marine fish, with marine straggler and marine estuarine-opportunist being the dominant guilds within this category. The freshwater, estuarine, and diadromous categories presented lower but similar contributions (Fig. 5). The diverse fish metacommunity in the estuaries of the MBRS region face considerable anthropogenic impacts such as habitat loss, pollution, overfishing, including the presence of invasive species like *Oreochromis niloticus* (Mohamed et al., 2020; Wing et al., 2021), a cichlid of African origin, which is widespread in the rivers of the region (Matamoros et al., 2009; Carrasco and Casimiro-Soriguer et al., 2015), and in the estuaries and estuarine lagoons of the MBRS region, as well. While the focus of the present study was not the analysis of individual species, we have provided a current base line to address the potential effect of future anthropogenic pressures, including climate change, on the fish fauna in the southern coast of the MBRS region, since changes in fish communities can be used as sentinels of environmental quality (Whitfield and Elliott, 2002).

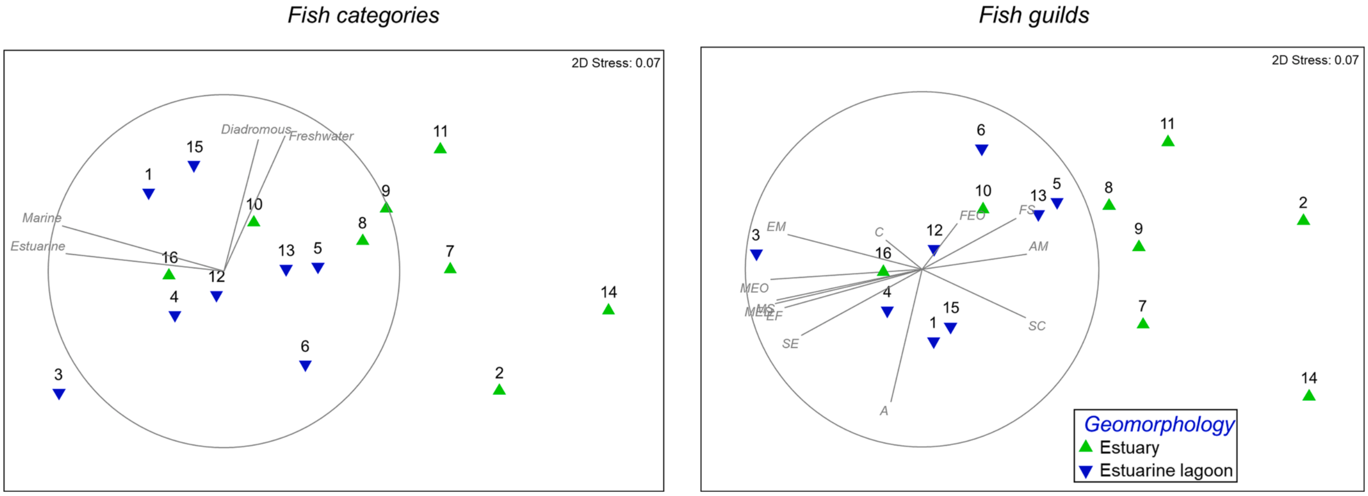

Fig. 6. Nmds ordination plots of the estuarine systems sampled along the honduran caribbean coast of the mbrs region based on the similarity calculated from the square root transformed fish functional groups abundance. fish species were classified by (a) categories and (b) guilds. Vectors indicate the Pearson corelations of the enviromental variables analysed with the ordination plot. A = anadromous, SE = solely estuarine, AM = amphidromous, MEO = marine estuarine-opportunist, EF = estuarine freshwater, SC = semi-catadromous, EM = estuarine-marine, and MED = marine estuarine-dependent. Numbers in the plots from west to east: 1. Chachaguala estuarine lagoon, 2. Chachaguala estuary, 3. Alvarado estuarine lagoon, 4. El Diamante estuarine lagoon, 5. Los Micos estuarine lagoon, 6. Negra estuarine lagoon, 7. Zambuco estuary, 8. Thompson estuary, 9. Cuero estuary, 10. Salado estuary, 11. Zacate estuary, 12. Guaimoreto estuarine lagoon, 13. Bacalar estuarine lagoon, 14. Plátano estuary, 15. Karataska estuarine lagoon, 16. Kruta estuary.

Diversity of local fish communities (α-diversity) in the estuarine systems studied differed considerably (Table 3, Fig. 3). The values recorded in the MBRS region are in the upper range worldwide (Vasconcelos et al., 2015), making this region a biodiversity hotspot for estuarine fish even when maximum species richness was likely underestimated by 24 % approximately according to SSR (Table 3). SSR differed between estuarine systems likely due to differences in habitat heterogeneity. The initial slope and S_{max} increase with environmental heterogeneity, because heterogeneous environments can provide more diverse habitats and niches and thus can support more diverse fish assemblages (He and Legendre, 2002; Shen et al., 2009; Powell et al., 2013). In addition, the slope and the general shape of SSR have been shown to be affected as well by fishing and other anthropogenic disturbances (Tittensor et al., 2007; Novaglio et al., 2016) which vary both in their degree and types in the systems studied.

Total fish abundance was very different among the different systems, with the abundances recorded here being higher in general than those observed in temperate estuaries (Wyda et al., 2002; Teichert et al., 2018). Abundance reacher up to about 800 CPUE (about 170 fish 100 m^{-2}) in the permanently open estuarine lagoon Chachaguala (Fig. 3, Table S3). Fish abundance was significantly higher in the estuarine lagoons than in the estuaries and in POE compared to TOCE systems in the Honduran coast of the MBRS region. Similar differences between fish assemblages depending on the estuarine morphology and degree of connection with the ocean have been reported in other geographical locations like the Gulf of Mexico, Australia and South Africa (Strydom et al., 2003; Vorwerk et al., 2003; Valesini et al., 2014; Vasconcelos et al., 2015; Schrandt et al., 2018). The dynamics of the estuarine mouth affected the local abundance and diversity of fish as well, with the greatest diversity during the open-mouth phase of the system. In contrast, no clear differences in fish abundance and diversity were observed statistically between estuarine lagoons and estuaries with permanently open mouths. The same pattern has been observed in warm and cold temperate regions of South Africa (Whitfield and Kok, 1992; James et al., 2007). The higher species richness observed in permanently open estuaries is attributed to the increase in marine straggler species (Bennett, 1989) and species having year-round access (Vorwerk et al., 2003). In contrast, the low species richness in TOCEs is partly attributed to the closed period of the estuarine mouth, which acts as an environmental filter regulating recruitment opportunities, thus affecting the structure of the fish community (James et al., 2007; Vasconcelos et al., 2015).

The fish species in the estuarine systems of the Honduran MBRS region show differences in their degree of occupancy of different estuaries and estuarine lagoons. Only one species, *Caranx latus*, was present in all but one estuarine system (Table 3, Fig. S2). *C. latus* is a widely distributed fish in the Caribbean and western Atlantic coast with considerable diet plasticity (Berry et al., 1981; Novak et al., 2020; González et al., 2021). In contrast, 49 species (32 % of total) were present in just one system. More than half of them were marine stranglers and freshwater stranglers (19 and 8 species, respectively), which are found typically in low abundances in estuaries, in the more saline and less saline areas, respectively (Potter et al., 2015). Most likely, their low numbers and sporadic presence explain why they were found in only one estuarine system. These species tend to be ecological generalists with wide physiological ranges, suggesting that they can occur in different coastal environments at diverse scales of space and time (da Silva et al., 2022). Similarly, marine estuarine-opportunist are not restricted to just one estuary by environmental filtering, given that they are mainly marine species able to use estuarine systems facultatively. Therefore, random dispersion due to mass effects from adjacent habitats is likely more important than habitat filtering as an explanation of the presence of these species in a single system (Mouquet and Loreau, 2003). In general, all the species found just in one of the estuarine system were found in very low abundances, except *Sicydium plumieri*, an obligate estuarine user with an amphidromous life cycle, which was found in the Chachaguala estuary in relatively high numbers. In contrast, the rest of species with a single occupancy (about 24 %) were obligatory estuarine species (5 amphidromous, 2 estuarine-marine, 2 estuarine-fresh water) and 3 freshwater estuarine-opportunists, which could be more prone to be present in just one estuarine system due to habitat selection (Alofs et al., 2004).

4.2. SCBD and LCBD contributions to β-diversity

The contribution of each species to the overall β-diversity was inversely related to occupancy in the estuarine systems of the MBRS region, with the species with single occupancy being the major contributors (Fig. S3). The inverse statistical relationship observed between SCBD and occupancy contrasts with the positive or unimodal (humped) relationships observed for different taxonomic groups in the limited available studies (Heino and Grönroos, 2017; de Silva et al., 2018; Xia et al., 2022). The relationship between SCBD and occupancy might be complex and system dependent as it has been shown to change with abundance, functional traits, niche availability, and niche breadth (Heino and Grönroos, 2017), making intersystem comparisons difficult.

Local contribution to the overall β-diversity denotes the ecological uniqueness of an estuarine system compared to other estuaries within the studied region (Legendre and De Cáceres, 2013; Xia et al., 2022). LCBD was highest in estuarine systems located in the east and west extremes of the studied region. This edge effect has been observed in fish metacommunity studies at river basin scale due to dispersal limitation from the middle to the margins (Shao et al., 2019; Borges et al., 2020; Xia et al., 2022). However, this is not comparable with our study, where different estuarine systems, not directly connected, have been studied. In the MBRS region, systems with high LCBD tended to have higher fish abundance, α-diversity, and more exclusive species as well (Table 3, Fig. 4, Fig. S3). However, an inverse relationship between LCBD and species richness with total fish abundance was observed in the riverine fish metacommunity at a basin scale (Xia et al., 2022). Likely, these differences are due to a lower range of environmental variability at the river basin scale and to spatial factors. Local fish communities within a basin are spatially connected in a directional way along the river, while the connectivity between different estuaries of the MBRS region occurs mainly through the species that can thrive or survive in the marine environment along the 682–km coastline.

The measurement and analysis of LCBD is important, because it can have practical applications in the selection of specific areas for the implementation of cost-efficient conservation measures of biodiversity due to the ecological uniqueness of their biological community (rare species, endemisms, endangered species, etc.) (Heino and Grönroos, 2017; da Silva et al., 2018; Nakamura et al., 2020; Xia et al., 2022; Heino et al., 2022), or the detection of anthropogenic impacts (Vilmi et al., 2017). LCBD likely depends on the balance between the sorting of species due to local conditions (environmental conditions and biotic interactions) and the dispersal rate (spatial isolation, mass effect, etc.), with the trade-off between these complementary drivers being system-dependent (da Silva et al., 2018; Maloufi et al., 2016; Tonkin et al., 2016). The large abundance of marine guilds in the estuaries and estuarine lagoons of the MBRS region seems to indicate a strong mass-effect from the fish community of the coastal marine environment.

4.3. Differences in fish communities from estuaries and estuarine lagoons

Fish communities compared by either taxonomic composition or functional groups was statistically different between estuarine lagoons and estuaries according to the multivariate analysis (Fig. 2b, Fig. 6a, b). Marine and estuarine fish showed higher numbers in estuarine lagoons, while diadromous and freshwater fish in estuaries. Within each type of system, species belonging mainly to the marine category and the marine-estuarine-opportunist guild contributed most to the similarity between estuarine lagoons, whereas species in the freshwater category and the freshwater-estuarine-opportunist guild contributed most to the similarity between estuaries. Despite evident differences in fish communities between estuaries and estuarine lagoons, there were a number of species (56.5 % of total) present in both environments. These were species with a wide distribution, such as *A. milleri, V. maculicauda, C. latus,* and *P. orri*, which have most likely high dispersion rates and, therefore, contribute to homogenize the fish communities in the estuarine systems of the MBRS region. However, the relative abundance of these species in estuaries and estuarine lagoons was different indicating a certain degree of habitat preference as well.

On the other end, we detected 13 species contributing to the dissimilarity between estuaries and estuarine lagoons, such as *A. lyolepis*, *S. testudineus*, *D. rhombeus*, *D. monticola* and *P. gillii* (33.9 % to the total dissimilarity). This difference in the fish community between estuaries and estuarine lagoons is due probably to some degree of environmental filtering since the environmental conditions in both types of environments were statistically different (Fig. 2a, Table 2, Table S1). Nonetheless, differences between local systems related to connectivity, geomorphology, hydrology, mouth open/closed stages, and species-dependent differences in the dispersion rates contribute to shaping the local fish communities and of the MBRS region's metacommunity. The connection of estuarine systems with the sea (open or closed mouth) is an important determinant for the fish community assemblage (Schallenberg et al., 2010). In addition to a direct effect on the dispersion and migration of the marine and diadromous categories from the presence of a physical barrier, other fish categories are also affected, most likely, due to environmental changes occurring in TOCE systems depending on the mouth status (Schallenberg, 2010; França et al., 2012; Romero-Berny et al., 2020). For instance, changes associated to mouth dynamics such as salinity, pH, or DO, affect physiological characteristics or primary production and the trophic status, affecting food availability among other variables (Carrasco et al., 2020; Nunes et al., 2022), are known to affect fish abundance and community composition (Potter et al., 2015; Capuzzo et al., 2018; Bélanger and Rodríguez, 2002).

4.4. Environmental variability and changes in the fish metacommunity

The sixteen estuarine systems investigated in Honduran coast of the MBRS region encompass a wide range of environmental conditions. Ecological variables such as salinity, temperature, DO, pH, and turbidity varied within the same system, between systems, and seasonally (Table 1, 2, Fig. S1), affecting the structure of fish communities as shown in other tropical and subtropical estuaries (Winemiller and Leslie, 1992; Borges et al., 2020; Xia et al., 2022). The analysis of the environmental variability using nMDS found a significant separation between estuaries and estuarine lagoons, along the first axis. This axis was strongly correlated with salinity, pH, DO, bottom vegetation, and sediment type (Fig. 2) that were significantly different in estuarine lagoons and estuaries (Table 2). Turbidity was generally high in most systems, limiting the presence of benthic vegetation to a few estuarine lagoons. Estuarine lagoons had mostly mud-silty sediments, while estuaries had predominantly sandy sediments. These differences in the environmental conditions between estuarine lagoons and estuaries of the Honduran MBRS region likely affected the fish assemblages by environmental filtering due to physiological and/or behavioral trade-offs of the different species (Leibold et al., 2004; Mouillot et al., 2007). This hypothesis was confirmed by the nMDS ordination analysis of the estuarine systems based on their fish communities. Estuaries and estuarine lagoons harbored clearly different fish assemblages independently of whether the fish metacommunity was characterized in terms of taxonomic composition or functional groups, both at the category and guild level (Fig. 2, 7).

Distance-based multivariate linear model marginal tests showed that salinity, pH, bottom vegetation, and DO explained individually a significant fraction of the variability of the fish metacommunity, both when the metacommunity was characterized by taxonomic composition and by functional groups (Tables 4, 6). When more variables were added, results showed that the most parsimonious models solutions included a combination of the same variables, i.e. salinity, pH, and bottom vegetation, as explanatory variables of the changes in the taxonomic composition and functional groups of the fish metacommunity (Tables 5, 7). The importance of these variables for the structure of the fish metacommunity in this study coincide with studies in other geographical areas. In Iranian subtropical estuaries, pH and salinity were the two main variables influencing the fish community structure (Kamrani et al., 2015), whereas salinity was the main environmental driver of the estuarine fish community structure in tropical estuaries of the Gulf of Mexico, Brazil, and India (Alves et al., 2020, Roshni et al., 2022; Garwood et al., 2023). The importance of bottom vegetation for fish has been highlighted in different studies. Submerged plants and algae increase habitat complexity, generate better conditions, offer shelter for fish larvae and juveniles, and contribute to a higher diversity of resources, thus leading to higher abundance, diversity, and biomass of fish (Pogoreutz et al., 2012; Whitfield, 2017). The reduction and disappearance of bottom vegetation is a very evident signal of anthropogenic impact on aquatic environments in general and has been shown to affect negatively fish communities (Sobocinski et al., 2013).

5. Conclusions

This first large-scale study along the Honduran coast of the MBRS region revealed a highly diverse estuarine fish fauna highlighting the region as a noteworthy fish biodiversity "hot-spot". However, the conservation status of most of these species is unknown at both local and regional scales. The high fish diversity is attributed to the wide variety of environmental conditions, including different mouth dynamics (POE and TOCE systems) and habitat characteristics, between and within estuarine systems. Salinity, pH, bottom vegetation, and DO were the main factors explaining the fish metacommunity structure. Mouth dynamics also played a crucial role, with higher abundance and diversity of fish observed in POE with respect to TOCE systems and during the open mouth phase in the latter, suggesting that dispersal between estuarine systems and the sea is important for maintaining local fish communities.

The fish communities in estuarine lagoons and estuaries differed significantly, both in terms of taxonomic composition and functional groups, as a result of their different environmental conditions. Estuarine lagoons communities were dominated by the marine category and the marine-estuarine-opportunist guild, whereas those of estuaries were primarily characterized by the freshwater category and the freshwater-estuarine-opportunist guild. The presence of these marine and freshwater functional groups and their respective opportunist guilds emphasizes the crucial connections between estuaries and adjacent ecosystems.

The occupancy of fish species in local systems varied strongly, with one species present in as many as 15 estuarine systems, while 49 species were found only in one system. Typically, low occupancy is associated with rare or specialist species with narrow niches. However, this does not seem to be the case for most of the species with single occupancy in our study. Many of these species belong to functional groups like marine and freshwater straglers, which are usually widely distributed but found in low abundances within estuarine systems, and to the marine estuarine-opportunist guild, which are likely generalists as well. Obligate estuarine species and freshwater estuarine-opportunist species with single occupancy (12 species) may be more prone to inhabit only one estuarine system due to habitat selection. Understanding why there is a relatively high number of species found in only one system is important because their species contribution (SCBD) accounted for 38.7 % of the total β-diversity collectively.

The evaluation of the local systems contribution to the total β-diversity (LCBD) showed that estuarine lagoons contributed more compared to estuaries. In addition, just three systems (Chachaguala and

Karataska estuarine lagoons and Kruta estuary) accounted for over 41 % of the total β-diversity. These systems were characterized by high species richness and a relatively high proportion of exclusive species. Understanding the structure of the fish metacommunity in the MBRS estuarine systems and the contribution of each system is crucial for developing regional management and conservation strategies from the hydrographic basins to the coastal waters. While the importance of estuaries for coastal fish communities has been documented in other regions, there is currently no information available regarding the potential relationships between estuarine fish communities and those inhabiting the coral reefs of the MBRS.

CRediT authorship contribution statement

Juan C. Carrasco: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization, Resources, Validation, Writing – review & editing. **Sokratis Papaspyrou:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Formal analysis, Conceptualization, Investigation. **Wilfredo A. Matamoros:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Verónica Caviedes:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Alfonso Corzo:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.111765.

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