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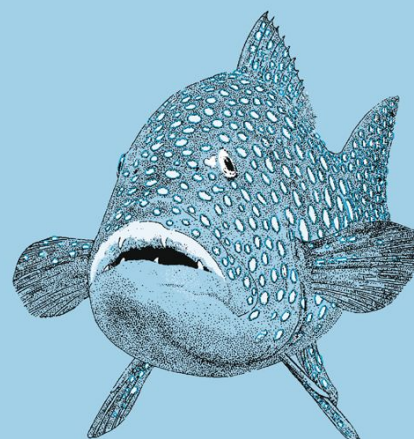
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Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean

Gustavo A. Castellanos-Galindo · Uwe Krumme · Efrain A. Rubio · Ulrich Saint-Paul

Abstract Mangroves in the tropical eastern Pacific (TEP) constitute a dominant coastal ecosystem that harbours diverse and economically important fish assemblages. We describe here regional scale patterns in the composition of this poorly documented mangrove ichthyofauna. A review of available studies (including own data) from five countries covering the entire region was performed. Species abundance distribution curves were constructed and compared among studies. Relative abundance data of fish species and families were analysed with classification and ordination techniques. Common species and families responsible for differences among localities were identified. Overall, 315 fish species associated to mangroves of the TEP were identified. Fifteen fish families accounted for 80 % or more of the relative abundance of all studies. Despite the use of different sampling techniques, common features arose for most of the mangrove fish assemblages. Clupeidae were numerically dominant throughout the region, while Gerreidae were particularly dominant in the northern mangroves. The catch mass contributions of families from studies where these data were available indicated a dominance of Ariidae, Centropomidae, Lutjanidae and Tetraodontidae. A relatively uniform composition at the family (and sometimes species) level supports recent claims to merge the Panamic with the Mexican province in the TEP according to the distribution of the shore fish fauna. Similarities found with other estuarine-mangrove ichthyofaunas in the Neotropics may be related to the connectedness of these regions in past geological times. Quantitative assessments of mangrove fish communities in four areas of the TEP would improve further zoogeographic analyses and facilitate the development of conservation strategies.

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Introduction

Mangrove ecosystems dominate many of the coastal landscapes across tropical and subtropical regions. The existence of these ecosystems is, however, threatened by a number of human activities such as conversion into aquaculture ponds or coastal development (e.g. Valiela et al. 2001) and has resulted in a ca. 35 % decline in mangroves over the past two decades (Alongi 2002). This decline is reflected by a loss in the ecological functions that this ecosystem provides. Mangroves provide habitat for a wide spectrum of marine and terrestrial organisms, which spend part of their life cycles in these areas. The paradigm of mangroves as nurseries has been argued in several academic and conservation forums for a long time. At the same time, a number of direct and indirect evidences support the idea that mangroves increase the biomass of fishes and fisheries yields in adjacent habitats (Manson et al. 2005; Aburto-Oropeza et al. 2008).

Mangroves in the tropical eastern Pacific (TEP) region are extensive in area and represent a highly threatened ecosystem (Polidoro et al. 2010). The second largest mangrove area in the Neotropics is located in the TEP totalling 1.21 million ha and representing 26.6 % of the New World mangroves (Lacerda et al. 2002). Moreover, several small-scale artisanal fisheries operate within these mangroves increasing fisheries yields in adjacent coastal areas and producing important revenues for local economies (see Aburto-Oropeza et al. 2008, for an example in the Gulf of California).

Quantitative comparisons of fish assemblage compositions from tropical mangrove-dominated estuaries over large geographical areas are rare. Exceptions are comparisons made in tropical Australia (Robertson and Blaber 1992; Ley 2005; Sheaves and Johnston 2009) and northern Brazil (Giarrizzo and Krumme 2008). Robertson and Blaber (1992), compared mangrove fish assemblages in different habitats of four relatively arid estuarine systems in northern Australia and concluded that the number of microhabitats present at each area had a major influence on fish community structure and that species richness was a function of tidal amplitude, water clarity and salinity fluctuations. Along 1,400 km adjacent to the Great Barrier Reef in Australia, Ley (2005) employed gillnets of different mesh sizes to compare the fish

fauna of 11 mangrove estuaries. She concluded that tide and wave dominated systems were clearly discriminated by the presence of specific fish families and that the variation in fish assemblages was explained mainly by a combination of physical attributes of the estuaries (e.g. catchment hydrology, substrate, mangrove area). Finally, Sheaves and Johnston (2009) compared small mesh cast nets' fish catches compositions of 21 estuaries over 650 km at the north eastern coast of Australia, finding that differences in faunal composition were better explained by estuary-level ecological variables (e.g. intertidal, subtidal or mangrove areas, sediment index) than by differences in climatic zones or the estuaries' position relative to other estuaries. In northern Brazil, where ca. 650 km of macrotidal coastline comprise the largest contiguous mangrove area of the world, Giarrizzo and Krumme (2008) found similarities at the family and species level in the intertidal mangrove fish composition using block nets. Nevertheless, the species and family contributions (catch mass) differed among sites as a function of their relative distance to the Amazon River mouth.

There are about 1,300 near-shore fish species in the TEP region, which is low compared to other tropical regions (Zapata and Robertson 2006). A great proportion of these species is considered to be endemic to the region (ca. 72 %). Shore fish diversity gradients for the entire endemic species in the TEP show two peaks: between 8° and 10° N (Panama-Costa Rica) and 23°–29° N (lower Gulf of California; Mora and Robertson 2005a). Robertson and Cramer (2009), based on the overall near-shore fish species distribution, redefined the biogeographical subdivisions within the area in three main provinces: The Cortez (Gulf of California and lower Pacific Baja), the Panamic (southward) and the Ocean Island province (comprising five sets of islands including the Galapagos islands), merging the previously defined Mexican province with the Panamian province (Fig. 1). Previous studies of the shallow-water fish fauna in the TEP have used the category "soft bottom fishes", which includes species associated to mangrove, estuarine and mud/sandy bottoms up to 100 m depth (ca. 375–487 species) (Mora and Robertson 2005b; Zapata and Robertson 2006). However, a further distinction of this category into more habitat-specific fish assemblages, explicitly referring to mangrove-associates, does not yet exist in the literature.

This study fills a gap, acknowledged in the literature (Faunce and Serafy 2006), in documenting the mangrove fish composition of this region. Although a number of studies dating back to the late 1970s on mangrove-associated fish assemblages in the region are available in the published and grey literature, no attempts have been made to synthetize this knowledge. We combine previous studies with our own information to examine if general patterns on this specific portion of the shore fish fauna can be derived. The present study aims to identify general patterns in mangrove fish assemblage composition for the TEP region using a compilation of ecological studies that cover most of the geographic range where mangroves occur.

Materials and methods

Study area

The tropical eastern Pacific extends from $\sim$25°N to $\sim$5°S along the western coast of the Americas (Robertson and Cramer 2009) (Fig. 1). The coastline is ca. 12,000 km long, dominated by a mosaic of rocky shores, sand/mud bottoms and mangrove habitats and a very marginal representation of corals and seagrasses (Glynn and Ault 2000; Santamaría-Gallegos et al. 2006). The coasts in the TEP are dominated by mountain ranges and an alternation of narrow coastal plains and steep sectors. The climatic conditions in the region range from arid areas at the limits of the region
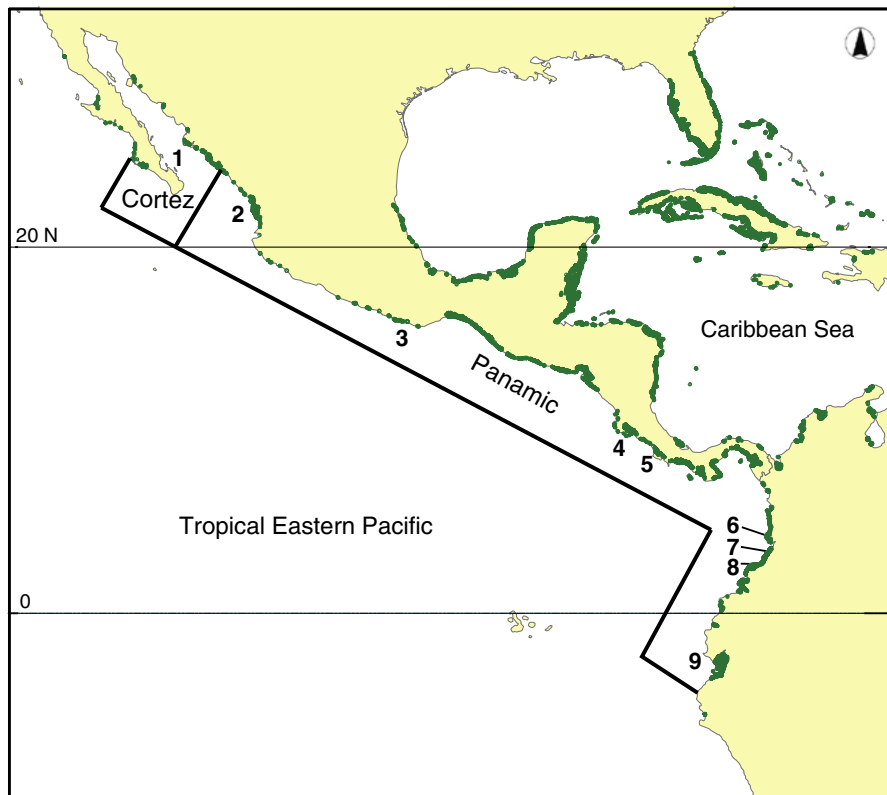

Fig. 1 Map of the tropical eastern Pacific region showing mangrove distribution (*source*: UNEP-WCMC; http://data.unep-wcmc.org/datasets/6) and the localities where the mangrove fish fauna studies used in the present analysis were carried out. *1* El Conchalito, La Paz Bay, Baja California Sur, Mexico (MEX LP), *2* Teacapán-Agua Brava Lagoon, Mexico (MEX-TL), *3* Chacahua Lagoon, Oaxaca State, Mexico (MEX-CL), *4* Golfo de Nicoya, Costa Rica (COS-GN), *5* Golfo Dulce, Costa Rica (COS-GD), *6* Bahía Málaga, Colombia (COL-BM), *7* Bahía de Buenaventura, Colombia (COL-BB), *8* Sanquianga, Colombia (COL-SA) and *9* Palmar, Ecuador (ECU-PA). Tropical eastern Pacific subdivisions according to shore fish fauna distribution are shown (Robertson and Cramer 2009)

(Baja California and southern Ecuador) with precipitations of 200 mm year^{-1}, to extremely rainy areas at the central and northern Colombian coast where mean rainfall can reach 8,000 mm year^{-1} (Table 1). In the southern part of the TEP, rivers drain the steep slopes of coastal ranges carrying large amounts of sediments (i.e. Colombia), whereas coastal lagoons, with sometimes hyper-saline conditions and virtually no freshwater input during dry seasons are common in northern areas of the region (i.e. Mexico). Macrotides are common in Colombia, Panama and the Gulf of California, whereas mesotides occur on the other coasts of the TEP.

Mangrove forest structure and physiognomy in the region are specially regulated by climatic conditions, with less structurally developed (basal areas = 4–30 m^2 ha^{-1}) and smaller mangroves (less than 20 m in height) in dry environments and well developed (basal areas = 20–30 m^2 ha^{-1}) fringe or riverine mangroves reaching heights of 30 m, partially >40 m and belt widths of up to 24 km inland at extremely humid coastal areas (West 1956; Jiménez 1990). Colombia and Mexico rank first and second in terms of their mangrove extension. The Mexican coastline (ca. 6,500 km) harbours extensive mangrove areas, especially in the northern portion (Nayarit and Sinaloa) where coastal lagoons are common features (CONABIO 2009). In Colombia, the central and southern alluvial coast give rise to large mangrove forests that grow behind sand/mud barrier islands and along deltas. The smallest mangrove area is located in

north Peru at the southern limit of mangrove distribution in the Eastern Pacific (see Table 1).

Data analyses

Mangrove fish studies carried out in the region were compiled from scientific publications available in local and international journals from 1984 to 2010 and our own unpublished data from Colombia were also used. The selected studies employed different fishing gears (trawls, gillnets, blocknets, flownets, beach seines) (Table 2). These gears were mainly employed along the main channels of estuarine systems containing mangroves (subtidal) or in close proximity to intertidal mangroves. All these studies sampled at least two locations during wet and dry seasons. Studies that contained only species lists or collected at single locations with no temporal replicates were not considered. Nine studies from Mexico, Costa Rica, Colombia and Ecuador were compiled (Table 2). A matrix of the species found in all the studies was constructed and the validity of scientific names was checked using the web resource Catalog of Fishes (http://www.calacademy.org/research/ichthyology/catalog). For all but one study (Rojas et al. 1994; Costa Rica) a measure of relative abundance for each species was available (i.e. percentage of individuals) in order to account for possible differences in sampling intensities among studies. Species abundance distribution models (SADs; log-abundance vs. Rank plots) were constructed to obtain a general description

Table 1 Characteristics of mangrove forests of countries with coasts in the Eastern Pacific region

Country	Mangrove area (ha)	Mean annual rainfall (mm)	Tidal range (m)[a]	References
Mexico	261,864	200–2,000	0.2–2.5[b]	CONABIO (2009)
Guatemala	16,086	1,000–2,000	1.5–2.0[c]	Jimenez (1992)
Salvador	35,235	1,000–2,000	2.0–3.0[c]	Jimenez (1992)
Honduras	46,869	1,000–2,000	4.0[c]	Jimenez (1990)
Nicaragua	39,310	1,000–3,000	2.0–3.0[c]	Jimenez (1990)
Costa Rica	41,292	1,000–5,500	2.5–3.0[c]	Jiménez (1994)
Panama	164,968	∼1,000–3,000	4.5–6.0[c]	D'Croz (1993)
Colombia	283,000	∼2,000–8,000	3.5–4.5[c]	Sánchez-Páez et al. (1997)
Ecuador	149,688	400–2,000	2–3.6[c]	Sanchez and Moran (1999)
Peru	4,550	>200	∼1.0[c]	FAO (2007)

[a] Tidal ranges taken from Bird (2010)

Tidal types: [b] Mixed semi-diurnal, [c] Semi-diurnal

Table 2 Mangrove fish fauna studies carried out in the tropical eastern Pacific region where quantitative data was available (1984–2010). Except for Rojas et al. (1994), where catch weight was used, all other studies show dominant species in terms of relative abundance

Country	System	Sampling intensity	Sampled habitats	Sampling gear	Number of species	Dominant species	Rainfall (mm year^{-1})	References
Mexico	El Conchalito, Baja California 24° 08'–24° 07'N; 110° 21'–110° 20'	1 year (1996–1997; four seasons)	Mouth of a tidal channel	Flow net (30 × 2 m, 6 mm mesh size)	34	*Eucinostomus currani, Anchoa ischana, Diapterus peruvianus, E. entomelas, E. gracilis*	219	González-Acosta et al. (2005)
Mexico	Teacapán-Agua Brava (22° 04'–22° 35'N; 105° 50'W)	1 year (1979–1980; four samplings)	Main channel along 20 stations	Trawling and monofilament nets, beach seine	75	*Lile stolifera, Cathorops liropus, Mugil curema, Hyporhamphus* sp., *Eucinostomus dowii*	1,000–1,500	Alvarez-Rubio et al. (1986)
Mexico	Chacagua Lagoon (15° 58'–16° 00'N, 97° 42'–97° 39'W)	1 year (1992–1993; five every 2 months)	Lagoon surrounded by mangroves	Trawl net (5 m length, 2.5 m mouth opening, 20 mm mesh size)	33	*Diapterus peruvianus, Centropomus robalito, Anchovia macrolepidota, Lile stolifera, Lutjanus novenfasciatus*	700–2,500	Mendoza et al. (2009)
Costa Rica	Golfo de Nicoya (9° 52'–10° 15'N; 84° 42'–85° 15'W)	15 months (1992–1993; Three sites)	Sandy and mud bottoms adjacent to mangroves	Beach seine (25 × 1.80, 2.5 cm mesh size), 50 × 5 net (mesh size (8.75 cm)	75	*Ariopsis seemani, Notarius osculus, Sciades dowii, Lutjanus colorado, Centropomus robalito*	~1,600	Rojas et al. (1994)
Costa Rica	Gofo Dulce (8° 22'–8° 45'N, 83° 05'–83° 30')	2005 rainy and 2007 dry season (10 sites)	Sandy and mud bottoms adjacent to mangroves	Gillnets, beach seine, cast net	82	*Anchoa mundeola, Mugil curema, Diapterus peruvianus, Sphoeroides* sp., *Centropomus armatus*	4,500–5,500	Feutry et al. (2010)
Colombia	Bahía Málaga (3° 56'–4° 05'N and 77° 19'–77° 21'W)	1 year (2009–2010; four sites, monthly)	Intertidal mangrove creeks	Block nets (20 × 4 m, 12 mm mesh size)	50	*Lile stolifera, Centropomus armatus Lutjanus argentiventris, Diapterus peruvianus, Ariopsis seemani*	7,435	Castellanos-Galindo and Krumme (unpublished data)
Colombia	Bahía de Buenaventura (3° 54'N and 79° 5'W)	Three stations between 1978 and 1980	Intertidal mangrove and adjacent soft bottoms	Block nets, beach seines, gill nets, cast nets	178	*Lile stolifera, Sphoeroides annulatus, Anchoa panamensis, Mugil cephalus, Anchoa nasus*	~6,000	Rubio (1984)
Colombia	Sanquianga National Park (2° 40'N and 78° 28'W)	1980 (three sampling sites)		Block nets, gill nets, beach seines	150	*Lile stolifera, Mugil cephalus, Ophistonema libertate, Lutjanus guttatus, Sphoeroides annulatus*	4,000	Rubio and Estupiñan (1992)

Table 2 continued

Country	System	Sampling intensity	Sampled habitats	Sampling gear	Number of species	Dominant species	Rainfall (mm year^{-1})	References
Ecuador	Palmar (2° 01′S and 80° 44′W)	2003 Dry and 2004 wet seasons	Main channel, 2 creeks and adjacent river	Bag seine (7 × 2 m, 3 mm mesh size)	36	*Mugil curema, Atherinella serrivomer, Ctenogobius sagittula, Evorthodus minutus, Lile stolifera*	250–300	Shervette et al. (2007)

of each of the assemblages avoiding the loss of information that occurs when employing other univariate descriptors of community structure (i.e. Shannon, Simpson; McGill et al. 2007). Classification analyses (hierarchical agglomerative clustering) from a similarity matrix that used untransformed relative abundance data at the fish species and family level were carried out. For this purpose, Bray-Curtis similarity metric was used, as it does not treat absences to derive similarity between groups (Clarke 1993). Nonmetric mutidimensional scaling (nMDS) ordination was used to inspect data in two dimensions. A permutation procedure, the similarity profile routine (SIMPROF), was used to test the null hypothesis of no multivariate structure in the data being analysed (Clarke et al. 2008). Pearson correlations with MDS1 and MDS2 in nMDS plots were carried out to identify species and families related to the different studies analysed. All analyses were carried out with the VEGAN and BiodiversityR packages of the R programme (Oksanen 2010) and with the PRIMER 6 software (Clarke and Gorley 2006).

Results

A total of 315 fish species from 69 families and 162 genera inhabiting mangroves in the TEP were identified. Twelve families and 23 species were cartilaginous fishes (Chondrichthyes) and the remaining species and families corresponded to bony fishes (Osteichthyes). The most speciose families were Sciaenidae (39 species). Carangidae and Ariidae ranked second (each with 21 species). Other important families were Engraulidae, Gobiidae (both with 17 species), Haemulidae (16) and Gerreidae (13) (Table 3).

Studies with the greatest species richness (150–178 species) were located in the central and southern Colombian coasts (Table 2; Fig. 2), where large areas of mangrove forests are present. In contrast, studies with <40 species and the lowest species richness were identified for two areas in Mexico (MEX-LP, MEX-CL) and Ecuador (ECU-PA) which generally presented very low mangrove area coverage (Table 4; Fig. 2). All SADs for the eight studies showed a lognormal distribution shape, reflecting the dominance of very few abundant species and a predominance of rare species. This was especially evident for two studies in

Table 3 Contribution of the 15 most abundant families (% number of individuals) across eight mangrove fish fauna studies carried out in the tropical eastern Pacific region; the five most important families of each study in bold

Family	Species[a]	MEX-LP	MEX-TL	MEX-CL	COS-GD	COL-BM	COL-BB	COL-SA	ECU-PA
Gerreidae	13	**64.83**	**12.96**	**56.90**	**10.37**	**7.73**	2.81	**7.24**	0.46
Clupeidae	8	**1.36**	**42.48**	**6.51**	3.32	**34.91**	**14.32**	**16.76**	**3.60**
Engraulidae	17	**30.24**	0.87	**5.78**	**15.71**	0.03	**17.40**	4.24	1.53
Mugilidae	4	**1.39**	**9.07**	0.18	**10.94**	0.74	**5.80**	**7.81**	33.46
Centropomidae	6	–	2.19	**16.68**	**10.37**	**15.20**	2.49	4.97	0.42
Gobiidae	17	**0.97**	0.18	1.61	0.25	1.67	4.22	3.46	**28.08**
Atherinopsidae	5	–	–	0.00	2.39	1.40	3.75	0.30	**28.37**
Lutjanidae	7	0.03	1.88	**5.44**	6.66	**11.85**	1.19	**8.02**	–
Ariidae	21	–	**12.07**	1.68	7.73	5.00	2.66	2.70	–
Carangidae	21	0.08	**4.48**	1.68	**7.80**	**5.80**	5.14	4.82	0.56
Sciaenidae	39	0.05	1.38	0.00	6.72	0.97	**5.47**	**9.98**	0.00
Tetraodontidae	9	0.07	0.10	0.11	7.29	3.60	**6.51**	4.02	**2.42**
Haemulidae	16	0.61	1.32	0.95	5.08	0.70	1.33	6.51	–
Paralichthyidae	7	–	0.87	1.56	1.07	1.50	3.38	1.51	0.09
Hemiramphidae	5	0.06	4.81	0.04	–	0.17	3.08	0.45	–
Total	195	99.69	94.66	99.12	95.70	91.27	79.55	82.79	98.99

1. El Conchalito, La Paz Bay, Baja California Sur, Mexico (MEX LP), 2. Teacapán-Agua Brava Lagoon, Mexico (MEX-TL), 3. Chacahua Lagoon, Oaxaca State, Mexico (MEX-CL), 4. Golfo Dulce, Costa Rica (COS-GD), 5. Bahía Málaga, Colombia (COL-BM), 6. Bahía de Buenaventura, Colombia (COL-BB) 7. Sanquianga, Colombia (COL-SA) and 8. Palmar, Ecuador (ECU-PA). Studies are sorted by latitude (from north to south)

[a] Sum of all species occurring across the eight studies

Mexico (MEX-LP, MEX-CL) and Ecuador (ECU-PA) where evenness was lower. In contrast, studies with the highest evenness were found in Colombia (COL-BB, COL-SA) and in Costa Rica (COS-GD). In these studies the slopes of the plots were less pronounced indicating more diverse fish assemblages (Fig. 2).

The most common mangrove fish species in terms of relative abundance was the Pacific piquitinga *Lile stolifera* (Clupeidae), which was the most abundant species in 50 % of the studies (Fig. 2). Catfishes (*Ariopsis* spp.), snooks (*Centropomus* spp.), mojarras (*D. peruvianus*) and pufferfishes (*Sphoeroides* spp.) were present in most of the studies in significant proportions (Fig. 2; Table 2). In all the studies, 15 common families accounted for 80 % or more of the total fish abundance (Table 3). Gerreidae, Clupeidae, Engraulidae, Mugilidae and Centropomidae were the most abundant components of the fish assemblages in almost all the studies. Based on the mean relative abundance expressed in percentages, Gerreidae was the most important family in the area ($\overline{X} = 20.4$ %), mainly driven by their numerical dominance in two Mexican studies (i.e. MEX-LP, MEX-CL; Table 3).

Clupeidae and Engraulidae ranked second and third with a mean relative abundance of 15.4 and 9.5 %, respectively. The contribution of Clupeidae was especially high for a study in Mexico (MEX-TL) and one in Bahía Malaga, Colombia (COL-BM). The relative abundance of Engraulidae was high (>15 %) for the studies in the Gulf of California (MEX-LP), Colombia (COL-BB) and Costa Rica (COS-GD).

For all the classification and ordination analyses at the family and species level, the studies with the greatest similarities were those carried out in the central and southern Colombian coast (COL-BB and COL-SA). These two studies shared several species, which were only found at these sites (Figs. 3, 4).

Using the species relative abundance of each study, four clusters were formed according to the SIMPROF test: (1) an isolated study from Ecuador (ECU-PA), (2) two studies from Mexico (MEX-LP and MEX-CL), (3) the two closely related studies from Colombia (COL-BB, COL-SA), and (4) the remaining studies from Costa Rica (COS-GD), Mexico (MEX-TL) and Colombia (COL-BM). These same groups were also observed and supported in the nMDS representation
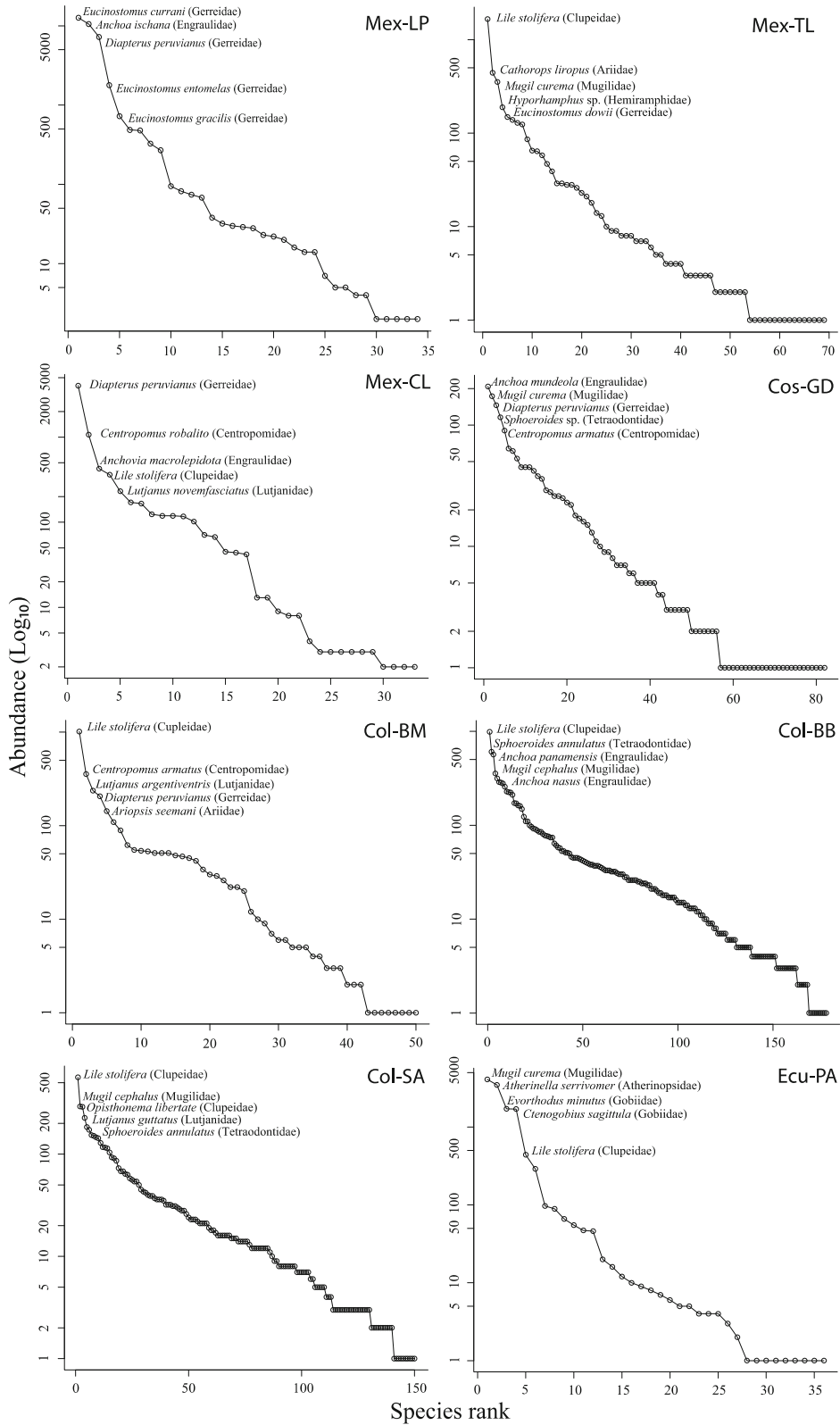
◄ **Fig. 2** Rank-abundance ($\log_{10}$ transformed) plots for eight mangrove fish studies carried out along the tropical eastern Pacific Ocean. *1* El Conchalito, La Paz Bay, Baja California Sur, Mexico (MEX LP), *2* Teacapán-Agua Brava Lagoon, Mexico (MEX-TL), *3* Chacahua Lagoon, Oaxaca State, Mexico (MEX-CL), *4* Golfo Dulce, Costa Rica (COS-GD), *5* Bahía Málaga, Colombia (COL-BM), *6* Bahía de Buenaventura, Colombia (COL-BB), *7* Sanquianga, Colombia (COL-SA) and *8* Palmar, Ecuador (ECU-PA). The five most abundant species are given

(Fig. 3). Cluster (1) was characterized by *Mugil curema* (Mugilidae), *Atherinella serrivomer* (Athesinopsidae), and *Ctenogobius sagittula* (Gobiidae) (Fig. 2). These species were exceptionally abundant and represented ca. 75 % of the relative abundance in this study. Cluster (2) was characterized by *D. peruvianus*, which occurred in similar relative abundances at both sites. Both studies of cluster (3) shared three of their five most abundant species in similar proportions (*L. stolifera*, *Sphoeroides annulatus*/Tetraodontidae and *Mugil cephalus*/Mugilidae) (Fig. 2). The arrangement of this group was supported by the large amount of common and unique species shared by these studies (Fig. 3). Cluster (4) was characterized by the great dominance of *L. stolifera* at MEX-TL and COL-BM and the large contribution of *D. peruvianus* and *Lutjanus argentiventris* (Lutjanidae).

At the fish family level three significant groups were formed in the cluster dendrogram according to the SIMPROF test (Fig. 4): (1) The study from Ecuador (ECU-PA), (2) two studies from Mexico (MEX-CL and MEX-LP) and (3) the remaining fives studies (MEX-TL, COS-GD, COL-BB, COL-BM and COL-SA; Fig. 4). The study in Ecuador was clearly separated from the rest by the dominance of species from Mugilidae, Atherinopsidae and Gobiidae, with

the last two families being extremely dominant only in this study. The separation of the two studies from Mexico (second cluster) from the rest of studies is attributed to the disproportionately high contribution of Gerridae to relative abundance (>55 % in each study). Finally, the third cluster was comprised by five of the eight studies (Fig. 4). Fifteen families accounted for >80 % of the total abundance in these studies (Table 3). Carangidae characterised these five studies with a correlation > 0.75 with the MDS2 axis (Fig. 4) and contributed a relatively high proportion to the total abundances. Carangidae were almost absent from the studies of Ecuador and Mexico (ECU-PA, MEX-CL and MEX-LP). Similarly, Ariidae and Tetraodontidae were abundant families in terms of individuals in at least four of these five studies (Table 3). Finally, these five studies were also the ones having relatively high number of families represented in their assemblages (>25). This feature clearly differentiated this cluster from the other two clusters which were poorer in the number of families (<20 families).

Discussion

The shore fish fauna in the TEP region has been relatively well documented in terms of its overall composition (but see Zapata and Robertson (2006), for an account of the shore fish species yet to be described). However, detailed studies documenting patterns in the structure and composition of mangrove fish assemblages along the entire region do not exist. This information can prove valuable when identifying ecological functions of mangrove ecosystems in the

Table 4 Mangrove fish fauna studies carried out in the tropical eastern Pacific Ocean with environmental characteristics of the specific study sites

| Study	Mangrove area (ha)	Tidal amplitude (m)	Rainfall (mm year^{-1})
Conchalito, La Paz, Baja California, Mexico—MEX-LP	18.5	1.0–1.3	219
Teacapán Agua Brava Lagoon, Mexico—MEX-LT	80,000	0.9–1.3	1,000–1,500
Chacahua Lagoon, Oaxaca State, Mexico—MEX-CL	2,550	0.9–1.3	1,300
Golfo de Nicoya, Costa Rica—COS-GN	15,176	3.0	1,800
Golfo Dulce, Costa Rica—COS-GD	2,000	1.76	4,500–5,500
Bahía Málaga, Colombia—COL-BM	4,400	4.0	7,345
Bahía de Buenaventura—COL-BB	9,709.2	3.7	4,700
Sanquianga, Colombia—COL-SA	70,000	3.5	3,000–3,500
Palmar, Ecuador—ECU-PA	30	2.5–3.0	250–300
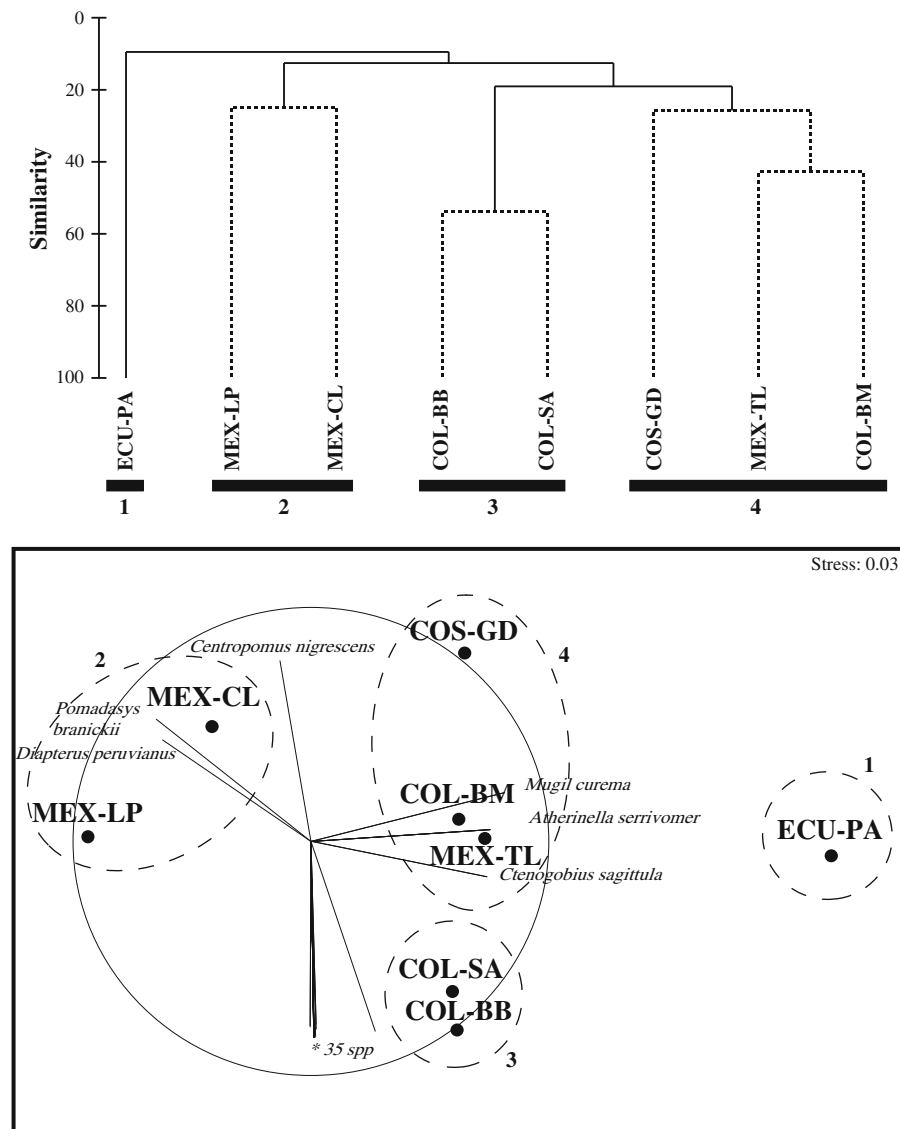
Fig. 3 Cluster dendrogram and nMDS ordination plot of data (% abundance of species; Bray–Curtis metrics and average linkage algorithm) from eight mangrove fish studies in the tropical eastern Pacific. *Dotted lines* in dendrogram represent groups where no further internal structure can be found according to the SIMPROF test. Species with correlation with MDS1 and MDS2 axes (Pearson) >0.75 are shown. *Aetobatus narinari, Anchoa nasus, Bathygobius ramosus, Batrachoides pacifici, Cerdale ionthas, Chaenomugil proboscideus, Chaetodipterus zonatus, Cynoponticus coniceps, Diplectrum rostrum, Dormitator latifrons, Epinephelus analogus, Haemulon sexfasciatum, Hemicaranx leucurus, Hemieleotris latifasciata, Hyporhamphus gilli, Ilisha fuerthii, Menticirrhus nasus, Mugil cephalus, Myrophis vafer, Narcine entemedor, Nebris occidentalis, Notarius troschelii, Opisthopterus equatorialis, Ophichthus remiger, O. zophochir, Paralonchurus dumerilii, Parapsettus panamensis, Polydactilus opercularis, Prionotus horrens, Rhinobatos planiceps, Sphoeroides annulatus, Sphyrna tiburo, Syngnathus* sp., *Trinectes fonsecensis, Urotrygon aspidura*

TEP (e.g. nursery function). The present analysis constitutes a first attempt to understand how mangrove ichthyofaunas may be structured in this marine biogeographical region.

Our analysis showed that the greatest mangrove fish species richness occurred at the central and southern coast of Colombia, coinciding with the most extensive mangrove areas in the whole TEP region. This pattern
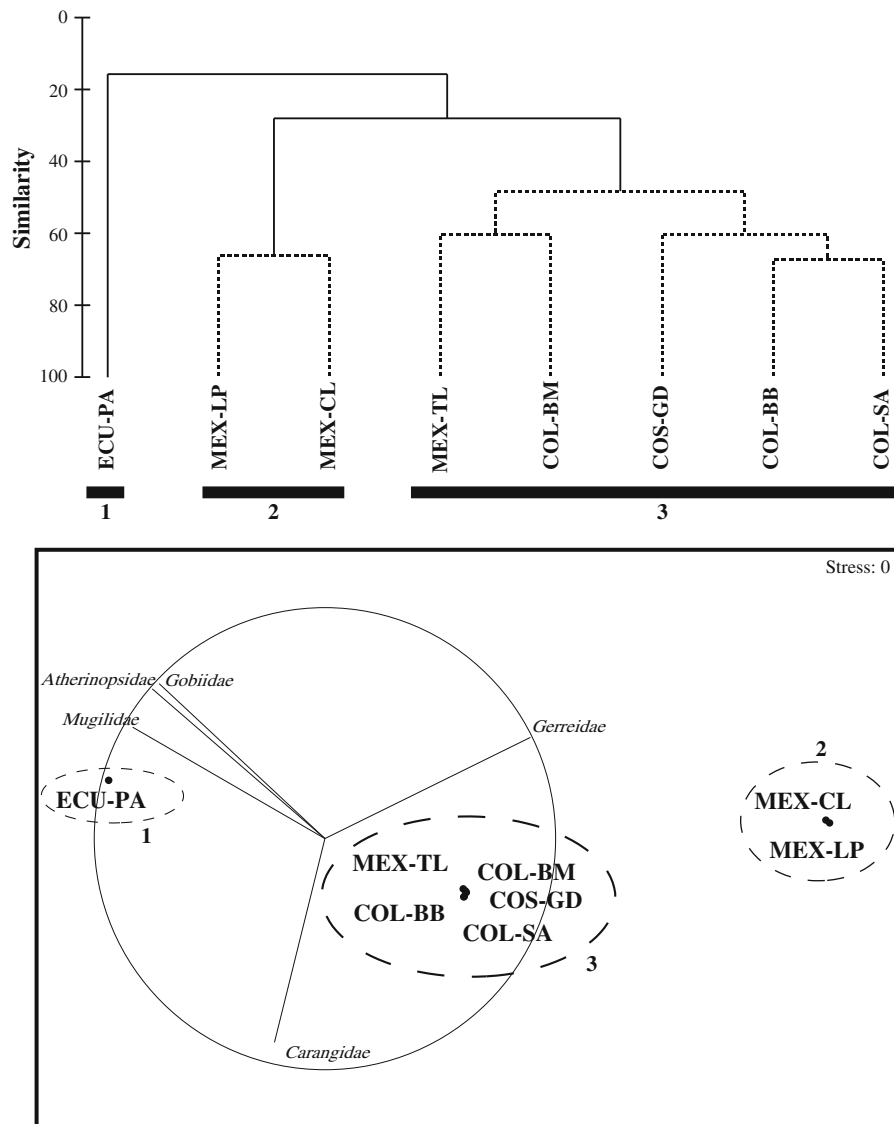
Fig. 4 Cluster dendrogram and nMDS ordination plot of data (% abundance of families; Bray–Curtis metrics and average linkage algorithm) from eight mangrove fish studies in the tropical eastern Pacific. *Dotted lines* in dendrogram represent groups where no further internal structure can be found according to the SIMPROF test. Families with correlation with MDS1 and MDS2 axes (Pearson) >0.75 are shown

requires an examination of the mangrove ichthyofauna in Pacific Panama where a great diversity in environmental conditions (Robertson and Cramer 2009) might favour the presence of species-rich assemblages similar to those of Pacific Colombia.

Low similarity values among studies at the species level (except for the two most speciose assemblages in Colombia) indicate that considerable variability exists among mangrove fish assemblages in the region. This may be influenced by the specific seascape characteristics of each system as identified in other biogeographical regions (Giarrizzo and Krumme 2008; Sheaves and Johnston 2009). It would have been expected that studies carried out in proximate areas along the Pacific coast of Colombia were more related to each other in their fish composition. However, a study carried out in Bahía Málaga (COL-BM) showed little association at the species level with the remaining studies carried out in Colombia (COL-BB and COL-SA, ca. 30 and

180 km south of Bahia Malaga, respectively). Bahía Málaga is located in a previous valley of the San Juan River which was flooded after a tectonic uplift of the northwest part of Bahía de Buenaventura (COL-BB) and further tectonic events associated to active faults. These events took place from the late Miocene to the Holocene Epochs (Martínez and López-Ramos 2011) giving rise to a mosaic of rocky, sandy and muddy habitats including well-developed mangrove areas. The presence of this diversity of habitats favours species from families such as Lutjanidae that undertake ontogenetic migrations between mangroves and rocky habitats (Aburto-Oropeza et al. 2009). This contrasts with the geological setting in Bahía de Buenventura (COL-BB) and Sanquianga (COL-SA) where there is an almost complete absence of rocky substrates and small rivers have extremely high water discharge and sediment load. These seascape differences among nearby locations are likely to explain the differences in the mangrove fish faunas in the Colombian Pacific. Nevertheless, the fact that the species composition of a study in Mexico (MEX-TL) was very similar to one in Colombia (COL-BM) indicates that despite the considerable differences in mangrove configuration and environmental conditions among the two areas (e.g. in terms of tidal regime and rainfall) (Table 1), a common fish species composition might be encountered at distinct mangrove areas of the TEP. Further explanations for the spatial variability in mangrove fish composition along the region could be rooted in the different energy flows and food web structures among estuarine/mangrove systems.

It is unclear if the dominance of Gerreidae in the northern portion of the TEP constitutes a consistent element in the composition of the mangrove fish fauna of this area, or if this is just an artefact of the sampling methodology employed in these studies (flow and trawl nets).

Despite Sciaenidae being the most speciose fish family in mangrove fish studies in the TEP (39 species), their average contribution to the number of individuals in all studies was only 3 %. Only the studies carried out in Costa Rica (COS-GD) and Bahía de Buenaventura and Sanquianga in Colombia (Rubio 1984; Rubio and Estupiñan 1992) had slightly higher proportions of individuals within this family (5–10 %). In these studies, species from the genera *Cynoscion*, *Bairdiella*, *Larimus* and *Ophioscion*

contributed ca. 1–2 % each to the total number of individuals, with the remaining species within the family representing very marginal numbers. Giarrizzo and Krumme (2008) argued that the contribution of Sciaenidae in intertidal mangrove creek fish assemblages of northern Brazil might be influenced by the presence of stronger marine conditions at the specific sampling sites. Increased marine influence in Sanquianga National Park suggests that this may also be the case in the TEP where the highest contribution of Sciaenidae to the overall mangrove ichthyofauna of the region was found. Sanquianga National Park is a deltaic system with relatively close contact to fully marine conditions in spite of a recent human-made river diversion that is increasing the freshwater influence of this system (Restrepo and Cantera 2011). Apparently, Sciaenidae are not common inhabitants of semi-enclosed and intermittently hypersaline lagoon systems of Pacific Mexico as their contribution to these assemblages was negligible. Mangroves may be a rather marginal habitat for Sciaenidae being more abundant and occurring in higher biomasses in adjacent soft bottom assemblages in the area (e.g. Bianchi 1991).

Correspondence to the previously defined TEP subdivisions

In the present analysis 64–84 % of the soft-bottom ichthyofauna of the TEP defined by previous macroecological studies were recorded (Mora and Robertson 2005b; Zapata and Robertson 2006). Our results support the recent re-definition of the TEP subdivisions where the Panamic province is proposed as a large unit extending from Mexico to Ecuador (Robertson and Cramer 2009) (Fig. 1). Similarities in mangrove fish species assemblage composition—17 common species, some of them in very similar proportions—between Colombia (i.e. COL-BM) and Mexico (i.e. MEX-TL) support this claim. Moreover, the only study carried out in mangroves of the Cortez province (MEX-LP) did not show any indication, in terms of endemic fish species, for a further separation of the mangrove fish fauna from that of the Panamic province. Of 34 fish species found in MEX-LP, only three were found to be endemic to the Cortez province. The remaining species are well distributed along most of the TEP region. MEX-LP showed the closest association with another study in Mexico (MEX-CL),

which is part of the Panamic province (Fig. 3). This association was largely driven by the dominance of *D. peruvianus*, a widely distributed mojarra in the TEP. Consequently, our comparison suggests that no dispersal barriers affect the distribution and exchange of mangrove fish species along this province, in contrast to what occurs with certain TEP reef fish families (e.g. Chaenopsidae; Hastings 2000).

Number of individuals versus catch mass

It is worth noting that the results of the present study can only be considered preliminary due to the systematic bias caused by the reliance on abundance data in most of the studies. Results based on catch mass are likely to significantly change dominance relationships on all taxonomic levels. For example, in one of the few quantitative studies that generated standardized catch mass estimates, Castellanos-Galindo and Krumme (unpublished data) sampled in intertidal mangrove creeks of central Colombia (COL-BM). They found that Clupeidae, Centropomidae and Lutjanidae dominated the assemblage in terms of relative abundance whereas catch mass was dominated by Lutjanidae, Tetraodontidae, and Ariidae. Similarly, the studies carried out in Costa Rica (COS-GN) and Mexico (MEX-TL; MEX-LP) consistently highlighted the greater contribution in catch mass of Ariidae, Centropomidae, Tetraodontidae, Gerreidae and Mugilidae to their fish assemblages, so that abundance and catch mass-based rankings result in very different dominance structures. Studies in Colombia (COL-BM) and Mexico (MEX-LP), the only ones providing both abundance and catch mass contribution estimates, clearly highlight the importance of Tetraodontidae when catch mass estimates are used. Both studies also show that Gerreidae and schooling species (i.e. Engraulidae, Clupeidae) reduce their contribution to the respective assemblage when catch mass is used instead of abundance (Fig. 5). Even if the relative abundances of Lutjanidae, Tetraodontidae, Ariidae or Centropomidae reach values between 1 and 5 %, it is very likely that these families will dominate the catch mass percentages, downplaying the contribution of schooling species like Clupeidae or Engraulidae. Quantitative studies using relative catch mass from different mangrove areas along the TEP region are needed before a full picture of the spatial patterns in mangrove fish assemblage composition can
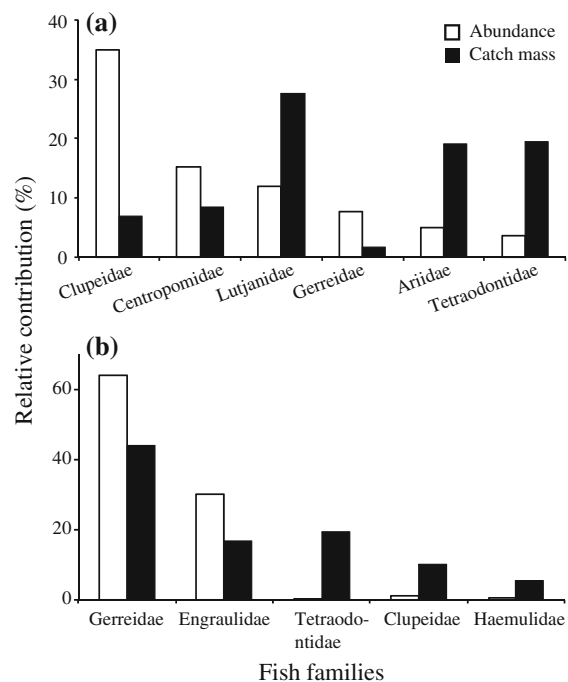

Fig. 5 Examples of asymmetry between the relative total abundance and catch mass of the principal fish families of two mangrove fish studies from the tropical Eastern Pacific. **a** Bahía Málaga, Colombia (COL-BM) and **b** El Conchalito, La Paz Bay, Baja California Sur, Mexico (MEX LP)

be drawn. Yet, we consider that the overall patterns (i.e. species and family compositions) and the possible explanations for spatial variability described here will not change severely.

The mangrove fish fauna of the TEP in comparison to other tropical areas

The overall biogeographical structure of the TEP shore fish fauna seems to be less complex than those of other tropical regions (i.e. Australia, Indo Pacific region) (Allen 2008; Last et al. 2011). This could be explained by the relatively uniform geographic configuration of the continental shelf that despite eustatic changes in sea level has not originated in large barriers. This might have thus influenced the distribution and exchange of demersal soft-bottom fishes, including the mangrove ichthyofauna in the TEP (Robertson and Cramer 2009; Mora and Robertson 2005a).

A few zoogeographical considerations, especially those referring to neotropical mangrove areas, can be drawn from our analysis. As expected, mangrove ichthyofauna from an isolated marine biographical

region like the TEP contains almost 50 % less species than the very rich mangrove fish fauna of the tropical Indo-West Pacific where more than 600 species have been recorded (Blaber 2007). Most studies in the Indo-West Pacific (IWP) have identified Ambassidae, Leiognathidae, Clupeidae and Engraulidae families as the most numerically dominant components of the mangrove fish fauna in that region (i.e. Australia, Malaysia, Philippines; Chong et al. 1990; Blaber and Duke 1990; Sheaves and Johnston 2009). This dominance, however, is likely to change if species were ranked according to catch weight. In Malaysia, for example, family dominance changed to Ariidae, Ambassidae and Mugilidae when catch weights were considered (Chong et al. 1990). Likewise, Blaber and Duke (1990), in mangroves of Alligator Creek (Australia), found Latidae (*Lates calcarifer*) and Sparidae (*Acanthopagrus berda*) to be important components of the fish community using catch weight. The most common families in the IWP such as Leiognathidae and Ambassidae are absent from the Neotropics, however, Gerreidae in the TEP may be an ecological counterpart of the former family. Similarly, the importance of Latidae in some mangrove areas of the IWP may be replaced by the important representation that Centropomidae have in the TEP. Latidae and Centropomidae have been identified as phylogenetically related and may occupy similar ecological niches in estuarine mangrove environments of their respective regions (Li et al. 2011). On the other hand, Ariidae are of minor importance in Australia whereas catfishes are abundant and diverse in the TEP and the Tropical Western Atlantic (TWA). Similarities between the TEP and the IWP can be found when looking at the numerical dominance of the schooling families Clupeidae and Engraulidae in both regions. Blaber (2000, 2002) highlighted the minor importance of Sciaenidae in most mangrove fish assemblages in the IWP region. Although very diverse in the TEP (39 species), Sciaenidae also showed a minor representation in numerical abundance in most of the studies analyzed in this region.

The estuarine/mangrove fish community of the Tropical East Atlantic Ocean (TEA) was documented by Albaret et al. (2004), in a relatively undisturbed system, the Gambia Estuary. The authors argued that this fish community had the main fish families likely to be found in the TEA (but see, Vidy (2000) for an atypical example of mangrove fish composition in this

region). The system was dominated by five families: Sciaenidae, Clupeidae, Mochokidae, Polynemidae and Ariidae, representing more than 90 % and ca. 95 % of the total fish catch weight and abundance, respectively. Among these families, the relative catch weight and abundance of Sciaenidae and Clupeidae was remarkable (totalling 78 and 86 %, respectively). None of the studies analysed in the TEP region showed the dominance of two single fish families. Clupeidae, however, was in both regions (TEP and TEA) a dominant group of mangrove estuarine ichthyofauna. Nevertheless, the dominance of Sciaenidae in the Eastern Atlantic contrasts with the marginal representation of this family in the TEP. Albaret et al. (2004), found that the dominance of Sciaenidae was due to the disproportionate contribution of *Pseudotolithus elongatus*, a permanent inhabitant of the estuary, occurring in all seasons and all sites. This species was also numerically abundant in mangrove creeks in the same area (Vidy et al. 2004). The TEA mangrove ichthyofauna clearly had an underrepresentation of very important families in the TEP such as Tetraodontidae, Ariidae, Centropomidae and Gerreidae.

The mangrove fish composition of the TEP compared to the IWP and the TEA regions can be considered similar at the family level in terms of the dominance of schooling species of Clupeidae and Engraulidae. However, each mangrove fish fauna has components that are not present in the other regions (Ambassidae and Leiognathidae in the IWP; Mochokidae in the TEA, and Centropomidae in the TEP), which are the result of the particular biogeographic history of each region. Most of these endemic fish fauna components may ocuppy a similar ecological niche as their counterparts in other biogeographical regions.

The mangrove ichthyofauna in non-estuarine areas of the Caribbean is dominated by the families Haemulidae, Scaridae, Lutjanidae and Gerreidae (Acosta 1997). These families, especially Haemulidae, Scaridae and Lutjanidae are found in these systems largely due to the dependence that some species have with the mangrove-seagrass-coral reef continuum present in islands of the Caribbean (Nagelkerken 2007). In contrast, when estuarine mangrove habitats in the Caribbean are analysed, the fish composition shows a dominance of Centropomidae, Ariidae, Gerreidae, Tetraodontidae and Engraulidae (Golfo de Urabá and Ciénaga Grande de Santa

Marta, Colombia and Terminos Lagoon in Mexico) (Rueda and Defeo 2003; Correa-Rendón and Palacio-Baena 2008; Sosa-Lopéz et al. 2010). All these families are also well represented in the mangrove fish fauna of the TEP. Tetraodontidae, Ariidae and Gerreidae have been rarely referred to in most mangrove fish studies from the Caribbean, albeit these families are abundant in catch weights in the estuarine mangrove systems of this region.

The mangrove fish faunas in the TEP and north Brazil in the TWA share the numerical dominance of Engraulidae or Clupeidae at most of the sampling locations. The mean contribution of these two families to the total fish abundance in the TEP was 25 % whereas at some localities in north Brazil this contribution was 16 % (Krumme et al. 2004). In north Brazil, Tetraodontidae (notably *Colomesus psittacus*) is a dominant component (both in number of individuals and catch mass) of mangrove habitats. This is concordant with the dominance (at least in catch weight) of Tetraodontidae in some of the mangrove fish studies of the TEP (e.g. COL-BM, MEX-LP). A clear difference in the mangrove fish assemblages of these two regions is the low contribution of Centropomidae and Gerreidae in the TWA compared to their substantial importance in most of the TEP localities (number of individuals and catch mass). A further difference between these two regions is the greater importance of Ariidae to the total assemblage in the TWA compared to the TEP. Whereas catfish abundances in north Brazil can reach ca. 35 % (Krumme et al. 2004), in the TEP these rarely exceeded 10 % (Table 3). This is also true when catch masses for this family are compared among regions (33 vs. 19 %; Giarrizzo and Krumme 2008, Castellanos-Galindo and Krumme, unpublished data). These differences may be explained by the biotic and ecological characteristics of the mangrove systems present at each biogeographical region. In northern Brazil, mangrove systems have high epifaunal biomass (Wolff et al. 2000; Koch and Wolff 2002), thus, favouring benthophage fish species (i.e. Ariidae). Humid mangrove systems of the TEP influenced by low fluvial sediment input, extremely high precipitation and high amplitude tidal regimes that regularly inundate large intertidal areas and that lack a mangrove plateau, might export most of their primary production to adjacent waters, thereby, sustaining relatively low mangrove epifaunal biomass. In the absence of this important food resource, fish with different feeding strategies (e.g. carnivorous-piscivorous) could thrive (i.e. Centropomidae, Lutjanidae).

Although, the three marine biogeographical regions in the Neotropics (TEP, Caribbean and TWA) share components of their mangrove ichthyofaunas that can be explained by their previous connectedness in geological times, the present composition of these assemblages could be further explained by: (1) the different trajectories (isolation, extinction episodes, environmental changes) characterizing each region once major gaps were formed (i.e. Panama Isthmus closure) and by (2) the local characteristics of mangrove systems within each region, including the interplay of tidal regime, coastal topography, and the productivity of each system.

Caveats of the approach

Although some of the studies analysed here attempted to draw general spatial and temporal patterns within their own locations, it is evident that accurate generalizations about patterns in the whole region are still difficult to draw. This is partly due to the different sampling methodologies employed at each locality and the specific habitats and seascape configurations of the mangroves (Tables 1, 2). For example, the fish composition of the mangrove system in Ecuador (ECU-PA) was consistently different from the other studies examined. This study shared common families with the rest in the TEP (e.g. Mugilidae, Clupeidae), but the disproportionate contribution of Atherinopsidae and Gobiidae may be an artefact of the sampling methodology (small bag seine). Thus, a clearer picture of the variability in fish assemblage composition among mangrove areas in the TEP will be obtained once data from mangrove sites with different seascape settings collected with similar quantitative methodologies are available.

Priority areas pending sampling

At least four areas in the TEP need quantitative examination of their mangrove fish faunas: (1) The Gulf of Fonseca, shared by El Salvador, Honduras and Nicaragua, is one of the largest mangrove areas on the Central American Pacific coast (ca. 60,000 ha) providing important revenues from artisanal fisheries in estuarine areas (Dewalt et al. 1996); (2) mangrove

areas in the Gulfs of Panama, Chiriquí, and San Miguel in Panama constitute > 70 % of the total country mangrove areas. A few published studies and technical reports (e.g. http://www.cathalac.org/manglaresvspesqueria; D'Croz and Kwiecinski 1980) exist on the contribution of mangrove fishes to fisheries, but no quantitative measures of mangrove fish community structure are available; (3) mangroves of the Esmeraldas-Pacific Colombia eco-region (south Colombia and north Ecuador) are recognized as the most structurally complex and best developed mangroves in the Neotropics in terms of leaf area, diameter, height and species diversity (West 1956; Suman 2007); and (4) mangroves of the Guayas estuary (Gulf of Guayaquil, Ecuador) cover an area of 130,000 ha with coastal development and shrimp aquaculture as the main drivers of mangrove loss. Quantitative studies of mangrove fish assemblages in these areas will benefit the understanding of the zoogeographic patterns along the entire TEP region, opening the door to more detailed comparisons as already attempted for fish faunas in other habitats of the region (i.e. Edgar et al. 2011).

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