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Mangrove-associated fish assemblages off the southern Panama Bight region (tropical eastern Pacific)

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The Panama Bight ecoregion (PBE) in the eastern Pacific contains probably the best developed mangrove forests in the American continent. Fishes inhabiting the mangrove-estuary mosaic play fundamental ecological roles and sustain the artisanal fishery operating there. Here, using data collected along ~300 km between 2012 and 2017, we examine the spatial dynamics of mangrove fish assemblages that undertake intertidal migrations in the southern part of the PBE (southern Colombian Pacific coast), where the largest and least disturbed mangroves of Colombia are located. Sixty-one fish species used intertidal mangrove habitats in these areas, constituting ~30% of all fishes inhabiting the whole mosaic of mangrove habitats in this ecoregion. Species within Clupeidae, Ariidae, Centropomidae and Tetraodontidae, all common in mangroves of the eastern Pacific, were the most dominant. Half of the fish species found are commercially important to the artisanal fishery. Differences in fish community structure could be related to salinity differences, but other environmental and ecological factors could also play a role in explaining these differences. A better understanding of the ecological role of mangrove fishes in the region could be gained by examining the ichthyofauna of other habitats within the mosaic and their trophic relationships.

Keywords: Colombia, Community ecology, Estuarine fishes, Macrotidal estuaries, Mangroves fishes.

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La ecorregión del Panama Bight (EPB) en el océano Pacifico oriental contiene probablemente los bosques de manglar más desarrollados de America. Los peces que habitan el mosaico estuario-manglar juegan papeles ecológicos fundamentales y sostienen las pesquerías artesanales que operan allí. Usando datos colectados a lo largo de ~300 km entre 2012 y 2017, examinamos la dinámica espacial de ensamblajes de peces de manglar que realizan migraciones intermareales en el EPB sur (costa sur del Pacífico colombiano), donde se encuentran los manglares más grandes y menos intervenidos de Colombia. Sesenta y un especies de peces ingresaron en zonas intermareales de manglar, constituyendo ~30% de todos los peces que pueden ser encontrados en el mosaico de hábitats de manglar de esta ecoregión. Especies de Clupeidae, Ariidae, Centropomidae y Tetraodontidae, todas comunes en manglares del Pacífico oriental, fueron las más dominantes. La mitad de los peces encontrados son importantes comercialmente para la pesquería artesanal. Las diferencias en la estructura de la comunidad pueden estar relacionadas con diferencias en salinidad, pero otros factores ambientales y ecológicos podrían también jugar un rol explicando las diferencias encontradas. Un mejor entendimiento del rol ecológico de los peces de manglar de la región podría alcanzarse examinando la ictiofauna de otros hábitats de este mosaico y sus relaciones tróficas.

Palabras clave: Colombia, Ecologia de comunidades, Estuarios macro-mareales, Peces de manglar.

INTRODUCTION

More than 20% of mangrove areas in the world are located in Latin America and the Caribbean (Bunting *et al*., 2018). These mangroves belong to the Atlantic-East Pacific mangrove biogeographic region (AEP), which is considered low in species richness if compared with the Indo-Pacific mangrove region (Lee *et al*., 2017). Nevertheless, mangroves in the AEP are still important habitats for a diverse range of coastal taxa that are threatened by various human-related stressors acting at different scales (*e.g*., urban expansion; Castellanos-Galindo *et al*., 2017). A conspicuous part of this biodiversity is represented by fishes that play key ecological roles like transporting energy within mangroves and adjacent shallow-water ecosystems (Nagelkerken *et al*., 2015). Many of these fishes are often targeted by coastal small-scale or industrial fisheries providing food for people and income to local and national economies (Aburto-Oropeza *et al*., 2008, Herrón *et al*., 2019).

In the Latin American and Caribbean region, Colombia ranks 4th in mangrove areal extent after Brazil, Mexico, and Venezuela (Hamilton, Casey, 2016; Mejía-Rentería *et al*., 2018). Having coasts in both Caribbean and Pacific coasts, the country harbors different mangrove ecosystem types, being the ones in the Pacific the most extensive. These mangroves are undisturbed compared to the ones located close to the few large cities in this coast, and at the same time they poorly studied due to their difficult accessibility (*i.e*., no coastal road connecting them to the rest of the country;

Castellanos-Galindo *et al*., 2015, 2021). Mangroves in the Pacific coast of Colombia are predominately distributed in the southern 2/3 of the extremely rainy (~3000 mm annual rainfall) macro and mesotidal coastline where extensive alluvial plains and two major deltas occur, *i.e*., The Patía and Mira River deltas (Correa, Morton, 2010). It is in this ~500 km coastal stretch where the tallest mangroves of the American continent are located with tree heights reaching almost 60 m (Simard *et al*., 2019; Castellanos-Galindo *et al.,* 2021).

A long-standing paradigm, but one with poor scientific support, has claimed that 75 % of all commercially caught fish depend directly on mangrove ecosystems (Sheaves, 2017). This has driven the conservation agenda and has helped to make the case for mangrove protection worldwide in recent years. However, more careful examinations of the dependence of fish on mangroves and specially those fish targeted by fisheries restrict the number of mangrove-associated fish well below the 75 % number (*e.g*., Aburto-Oropeza *et al*., 2008). This confusion is partly due to the difficulties in differentiating what constitutes a mangrove-dependent fish (see Zu Ermgassen *et al*., 2020). Coastal fishes occupy a mosaic of habitats that could be defined as a seascape nursery (Nagelkerken *et al*., 2015). In this seascape, mangroves may play an important role for certain fish species whereas for others not. Differentiating and understanding how different habitats within a certain seascape nursery benefit fishes can bring valuable insights for habitat conservation or even for fisheries management in mangrove areas (Brown *et al*., 2018).

The study of the relationship between mangroves and fish has significantly increased in the last two decades. A couple of reviews in the last ~15 years ago summarized our understanding of this relationship at the global level (see Faunce, Serafy, 2006; Nagelkerken *et al*., 2008). At local scales, salinity has been frequently identified as a major driver of fish community organization in mangroves (Ley *et al*., 1999). Salinity can also interact with physical and seascape characteristics of mangroves settings explaining much of the variability observed at the community level (Castellanos-Galindo, Krumme, 2015; Bradley *et al*., 2021) Considering larger scales, Sheaves (2012) compiled 76 studies from around the world to understand the functional characteristics of mangrove fishes. These overviews have helped to identify geographical data gaps and also to motivate research in those areas less well studied (*e.g*., Eastern Pacific – Castellanos-Galindo, Krumme, 2013a; Castellanos-Galindo *et al*., 2013; Western Atlantic – Vilar *et al*., 2013). Nevertheless, several gaps in the understanding of regional ecological patterns persist in areas of the Eastern Pacific like Central America and the southern portion of Panama Bight mangroves including Colombia, Ecuador and Peru.

This manuscript presents data on mangrove fish assemblages of the Panama Bight mangrove eco-region collected between 2012 and 2017 that help to fill in a gap in the knowledge of mangrove-associated fish communities in the Eastern Pacific region (West coast of the American continent). We specifically examined the small-scale variability (10s of km) in fish community structure and its relation to salinity in an area dominated by highly developed mangrove forests (southern Colombian Pacific coast).

MATERIAL AND METHODS

Study area. The Panama Bight mangrove eco-region includes the coasts of Panama, Colombia, and Ecuador in the western coast of the Americas and is part of the larger tropical eastern Pacific region that spans the continental shores of Mexico to Peru plus five oceanic islands (Robertson, Cramer, 2009). The Colombian Pacific is inserted in these two regions and extends for *ca*. 1400 km between Panama and Ecuador. The southern 2/3 of the coast are dominated by mangrove forests that thrive within a matrix of alluvial plains and barrier islands (Martinez *et al*., 1995). Mangrove extent in this part of the coast ranges between 110000 and 130000 ha (Mejía-Rentería *et al*., 2018) and represent more than 70% of all mangrove area in the whole country. *Rhizophora* spp. mangrove trees of up to 55 m heights (Simard *et al*., 2019) are the dominant species but at least five more mangrove tree species can be found in this coast. Most artisanal fisheries in the Colombian Pacific coast operate in these mangrove-dominated areas and target several resources that can live in close proximity to mangrove areas (Castellanos-Galindo, Zapata, 2019; Herrón *et al.,* 2019). Salinities in this meso and macrotidal coast are typically < 30 psu and precipitation is extremely high with annual rainfall ranging from *ca*. 8 m in the central coast to 3 m in the southern coast close to the border with Ecuador. Primary data for this manuscript were collected in the southernmost province of the Colombian Pacific (Nariño) bordering the Ecuadorian coast (Fig. 1).

Data collection. Fish sampling in intertidal mangrove creeks was carried out between 2012 and 2017 at seven different localities in the southern Colombian Pacific coast (Fig. 1). Sampling in all locations followed the methodology described in Castellanos-Galindo, Krumme (2013b), where small intertidal mangrove creeks (mouths ~10 m, internal lengths ~100 m) were blocked with nets (20 m x 4 m, stretch mesh size 12 mm) at high tide. After blocking the small creeks at high tide with the nets, fishes that enter with the rising tide into the mangroves are captured on the next low tide after ~6 h. This methodology allows effectively sampling the part of the fish community that exploits intertidal mangrove habitats in meso and macro-tidal regimes. During each sampling, surface salinity at high tide was measured at the entrance of each mangrove creek. Mulatos and Iscuande localities were more intensely sampled than the rest of the other localities (total n = 18 block net samplings from 2012 to 2015), whereas due to logistical constraints the other five localities were only sampled in 2017 (n = 2 per sampling locality) (see Tab. **S1**). These seven localities cover almost the whole southern mangrove-dominated coast of the Colombian Pacific where the tallest mangrove forests of the Americas are located (Fig. 1). For data analyses, these localities were grouped into high salinity (> 20 psu: Boca Grande, Chontal, Mulatos, and Teheran), medium salinity (15–20 psu: Curay and Trujillo) and low salinity (< 15 psu: Iscuandé) sites (Fig. 1).

After capture, fishes were identified, measured (total length, TL), and weighed wet (g ± 0.1). Each fish species was also assigned to one spatial and trophic guild group according to collected stomach content information or derived from Elliott *et al*. (2007), Froese, Pauly (2021) and Robertson, Allen (2015).

Data analyses. Rank abundance plots (RADs) for each individual sampled

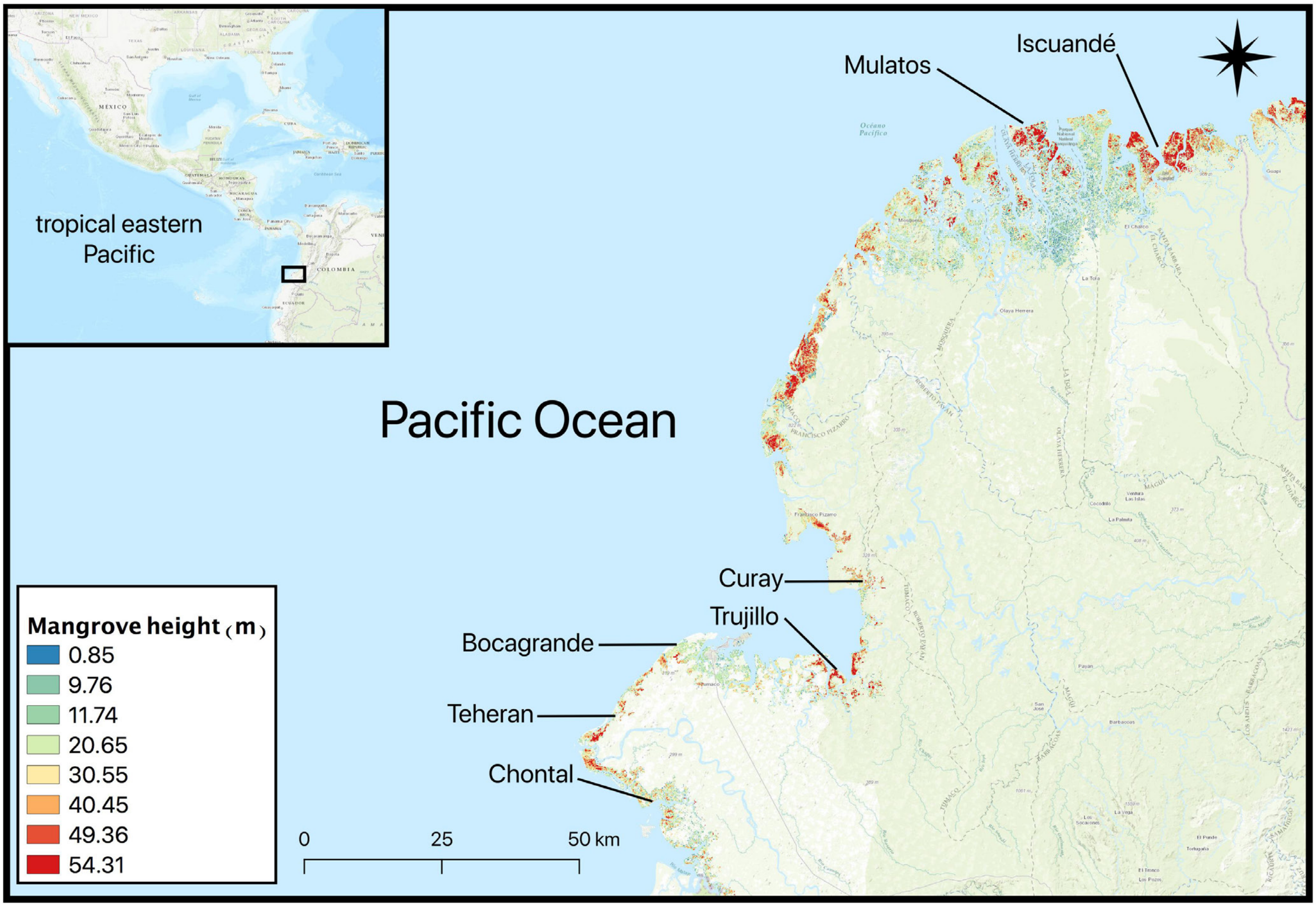

FIGURE 1 | Southern Colombian Pacific (Nariño province) coast with the seven mangrove sampling sites of this study. Mangrove tree height estimates were derived from Simard *et al.* (2019b). The five southernmost localities lie within the Tumaco-Cabo Manglares area.

locality were used to visualize species abundance distributions. Multivariate statistic techniques were employed to analyze data related to fish assemblage organization. A PERMANOVA test (permutational multivariate analysis of variance, Anderson, 2001) was used to evaluate differences in fish assemblages between localities and salinity zones (fixed factor with 3 levels: low, medium and high). To visualize multivariate patterns revealed by PERMANOVA, constrained (canonical analysis of principal coordinates, CAP) ordination techniques were used (Anderson, Willis, 2003). All multivariate analyses were based on Bray-Curtis distances calculated from square root transformed abundance data and conducted using the Vegan and BiodiversityR packages of the R statistical environment (Oksanen *et al.*, 2017).

RESULTS

A total number of 61 (+10) morphotypes and 10987 individuals were sampled at the seven localities examined (Tab. 1; Tab. **S2**). These corresponded to 30 fish families. Sixty three percent of the total abundance was composed by species within the

Clupeidae (sardines) and Ariidae (sea catfishes). *Lile stolifera* (Jordan, Gilbert, 1882) (Pacific piquitinga) and *Ariopsis simonsi* (Starks, 1906) (Tete sea catfish) constituted 99% of this 63%. Other families that were also abundant were Centropomidae (9 %), Tetraodontidae (4 %), Sciaenidae (3 %), Gerreidae (3 %), Atherinopsidae (3 %), Haemulidae (2 %), Serranidae (2 %), Mugilidae (2 %), Engraulidae (2 %), and Lutjanidae (2 %). All these families accounted for 32% of the total abundance. However, the dominance of each family and species varied in each assemblage according to the locality (Fig. 2). For example, rank-abundance plots showed the sea catfish *A. simonsi* as the most dominant species in four of the seven localities. *Centropomus armatus* Gill, 1863 (Centropomidae) was present in all localities within the top five species. Similarly, *L. stolifera* was among the most abundant species in five of the seven localities, and *Sphoeroides rosenblatti* Bussing, 1996 (Tetraodontidae) was among the most abundant in four of the seven localities Despite the differences in sampling intensity, species richness at each locality was generally between 20 and 40 (Fig. 2). In terms of the trophic and spatial guilds that were represented in these intertidal mangrove fish communities, zoobenthivores and benthopelagic – demersal fish were clearly dominant in number of species and abundance (Tab. 1).

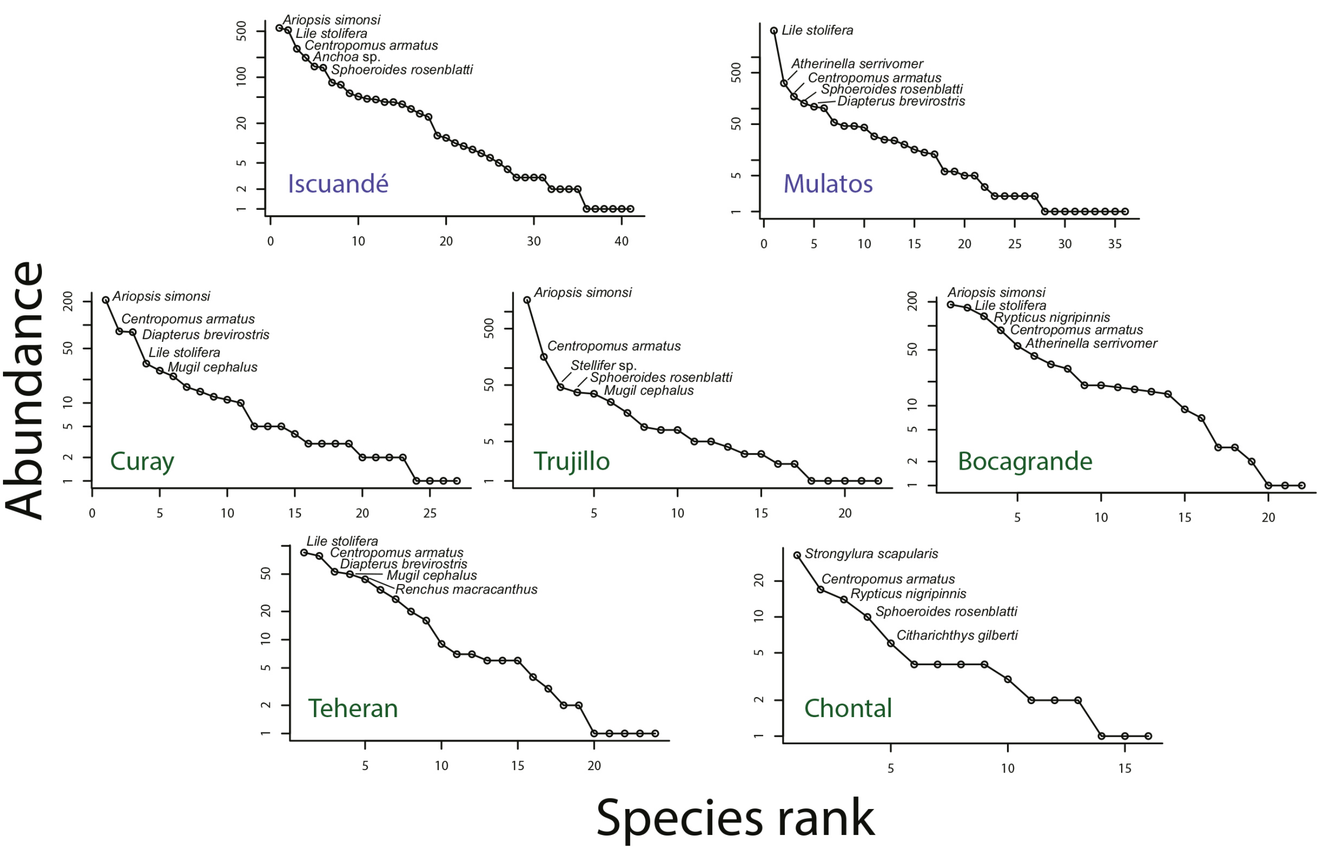

FIGURE 2 | Rank-abundance plots of the intertidal fish communities sampled at different localities in the southern Colombian Pacific between 2012 and 2017. Locality names in purple correspond to the Iscuande-Mulatos region and in green to the Tumaco-Cabo Manglares region.

TABLE 1 | Mangrove fish species captured in intertidal creeks at seven localities of the Colombian Pacific coast during the 2012–2017 period (The Tumaco – Cabo Manglares area includes the five southernmost sampled localities shown in Fig. 1). Spatial guilds (SG): pelagic (P), benthopelagic (BP), demersal (D), reef associated (RA) and freshwater (F) according to Froese, Pauly (2021); and trophic guilds (TG): zooplanktivore (ZP), detritivore (DV), herbivore-phytoplankton (HVP), piscivore (PV), zoobenthivore (ZB), omnivore (OV). Commercially important species for the artisanal fishery are marked with an asterisk.

Species	Spatial guild	Trophic guild	Iscuandé	Mulatos	Tumaco – Cabo Manglares
Ophichthidae					
1. *Pisodonophis daspilotus* Gilbert, 1898	D	ZB			X
Clupeidae					
2. *Lile stolifera* (Jordan & Gilbert, 1882)	P	ZP	X	X	X
Engraulidae					
3. *Anchovia macrolepidota* (Kner, 1863)	P	ZP, HVP	X	X	
4. *Cetengraulis mysticetus* (Günther, 1867)*	P	ZP, HVP	X		
Pristigasteridae					
5. *Opisthopterus dovii* (Günther, 1868)	P	ZP, HVP		X	
Ariidae					
6. *Ariopsis simonsi* (Starks, 1906)*	D	ZB	X	X	X
7. *Cathorops steindachneri* (Gilbert & Starks, 1904)*	D	ZB	X		
8. *Notarius troschelii* (Gill, 1863)*	D	ZB			X
Synodontidae					
9. *Synodus scituliceps* (Jordan & Gilbert, 1882)	D	ZB	X	X	
Ophidiidae					
10. *Ophidion fulvum* (Hildebrand & Barton, 1949)	D	ZB	X	X	
Batrachoididae					
11. *Batrachoides pacifici* (Günther, 1861)	D	ZB		X	
12. *Daector dowi* (Jordan & Gilbert, 1887)	D	ZB	X	X	X
Trichiuridae					
13. *Trichiurus lepturus* Linnaeus, 1758	P	PV-ZB		X	
Mullidae					
14. *Pseudupeneus grandisquamis* (Gill, 1863)*	BP	ZB		X	
Eleotridae					
15. *Eleotris picta* Kner, 1863	D	ZB	X		
16. *Erotelis armiger* (Jordan & Richardson, 1895)	D	ZB	X		
17. *Gobiomorus maculatus* (Günther, 1859)	D	ZB	X		X
Gobiidae					
18. *Bathygobius andrei* (Sauvage, 1880)	RA	ZB	X	X	X
Centropomidae					
19. *Centropomus armatus* Gill, 1863*	D	ZB	X	X	X
20. *Centropomus medius* Günther, 1864*	D	ZB	X	X	X
21. *Centropomus viridis* Lockngton, 1877*	BP	ZB-PV		X	
Paralichthyidae					
22. *Citharichthys gilberti* Jenkins & Evermann, 1889	D	ZB	X	X	X
Carangidae					
23. *Caranx caninus* Günther, 1867*	P	PV	X	X	X
24. *Oligoplites altus* (Günther, 1868)*	BP	ZB	X	X	X
25. *Oligoplites refulgens* Gilbert & Starks, 1904*	BP	ZB			X
26. *Selene brevoortii* (Gill, 1863)*	BP	ZB	X	X	
27. *Trachinotus kennedyi* Steindachner, 1875*	P	PV			X
Atherinopsidae					

TABLE 1 | (Continued)

Species	Spatial guild	Trophic guild	Iscuandé	Mulatos	Tumaco – Cabo Manglares
28. *Atherinella serrivomer* Chernoff, 1986	P	ZP		X	X
Poecilidae					
29. *Poeciliopsis turrubarensis* (Meek, 1912)	BP	DV	X		X
Belonidae					
30. *Strongylura exilis* (Girard, 1854)	P	PV			X
31. *Strongylura scapularis* (Jordan & Gilbert, 1882)	P	PV	X		X
Hemiramphidae					
32. *Hyporhamphus snyderi* Meek & Hildebrand, 1923	P	ZP	X		X
Mugilidae					
33. *Mugil cephalus* Linnaeus, 1758*	BP	DV	X	X	X
34. *Chaenomugil proboscideus* (Günther, 1861)*	BP	DV			X
Lobotidae					
35. *Lobotes pacificus* Gilbert, 1898*	P	ZB	X		
Chaetodontidae					
36. *Chaetodon humeralis* Günther, 1860	RA	OV		X	X
Diodontidae					
37. *Diodon holocanthus* Linnaeus, 1758	D	ZB			X
Tetraodontidae					
38. *Arothron hispidus* (Linnaeus, 1758)	D	ZB		X	
39. *Sphoeroides rosenblatti* Bussing, 1996*	D	ZB	X	X	X
Serranidae					
40. *Epinephelus quinquefasciatus* (Bocourt, 1868)*	RA	ZB		X	
41. *Mycteroperca xenarcha* Jordan, 1888*	D	ZB		X	X
42. *Rypticus nigripinnis* Gill, 1861	RA	PV	X	X	X
Lutjanidae					
43. *Lutjanus argentiventris* (Peters, 1869)*	RA	ZB		X	X
44. *Lutjanus colorado* Jordan & Gilbert, 1882*	RA	ZB	X	X	X
45. *Lutjanus guttatus* (Steindachner, 1869)*	RA	ZB		X	
46. *Lutjanus jordani* (Gilbert, 1898)*	RA	ZB		X	X
47. *Lutjanus novemfasciatus* Gill, 1862*	RA	ZB		X	X
Gerreidae					
48. *Diapterus brevirostris* (Sauvage, 1879)*	D	ZB, DV	X	X	X
49. *Eucinostomus currani* Zahuranec, 1980*	D	ZB		X	
50. *Eucinostomus dowii* (Gill, 1863)*	BP	ZB			X
51. *Eugerres brevimanus* (Günther, 1864)*	BP	ZB			
Haemulidae					
52. *Haemulopsis axillaris* (Steindachner, 1869)*	BP	ZB			X
53. *Pomadasys branickii* (Steindachner, 1869)*	BP	ZB			X
54. *Rhencus macracanthus* (Günther, 1864)*	BP	ZB	X	X	X
Sciaenidae					
55. *Bairdiella ensifera* (Jordan & Gilbert, 1882)*	BP	ZB	X		
56. *Cynoscion albus* (Günther, 1864)*	BP	ZB			X
57. *Cynoscion phoxocephalus* Jordan & Gilbert, 1882*	D	ZB	X		
58. *Stellifer scierus* (Jordan & Gilbert, 1884)*	BP	ZB			X
59. *Stellifer typicus* (Gill, 1863)*	BP	ZB			X
60. *Umbrina xanti* Gill, 1862*	BP	ZB		X	X
Labridae					
61. *Halichoeres aestuaricola* Bussing, 1972	D	ZB	X		X

The PERMANOVA test showed significant effects for the factor salinity and locality (Tab. 2). The multivariate representation (CAPs) showed clear separation of communities between some localities (Fig. 3A) and across salinity ranges (Fig. 3B). Specially samples from the Iscuandé locality were clearly differentiated from the rest of the samples. Samples from Trujillo, Curay, Bocagrande and Teheran tend to aggregate whereas samples from Mulatos and Chontal grouped together (Fig. 3A). Similarly, samples from low salinity areas (*i.e.*, Iscuandé) were highly dissimilar from

TABLE 2 | Results of a PERMANOVA model testing the effects of salinity and locality on mangrove creek fish assemblages collected between 2012 and 2017 in the southern Colombian Pacific coast. Df = degrees of freedom; Sum of Sqs = sum of squares; Pseudo-F = F value by permutation. Boldface indicates statistical significance. P-values based on 999 permutations.

	Df	Sum of Sqs	R^2	Pseudo-F	Pr(>F)
Salinity	2	1.3966	0.28774	6.1653	**0.001**
Locality	4	1.0786	0.22221	2.3806	0.001
Residual	21	2.3786	0.49005		
Total	27	4.8538	1.00000		

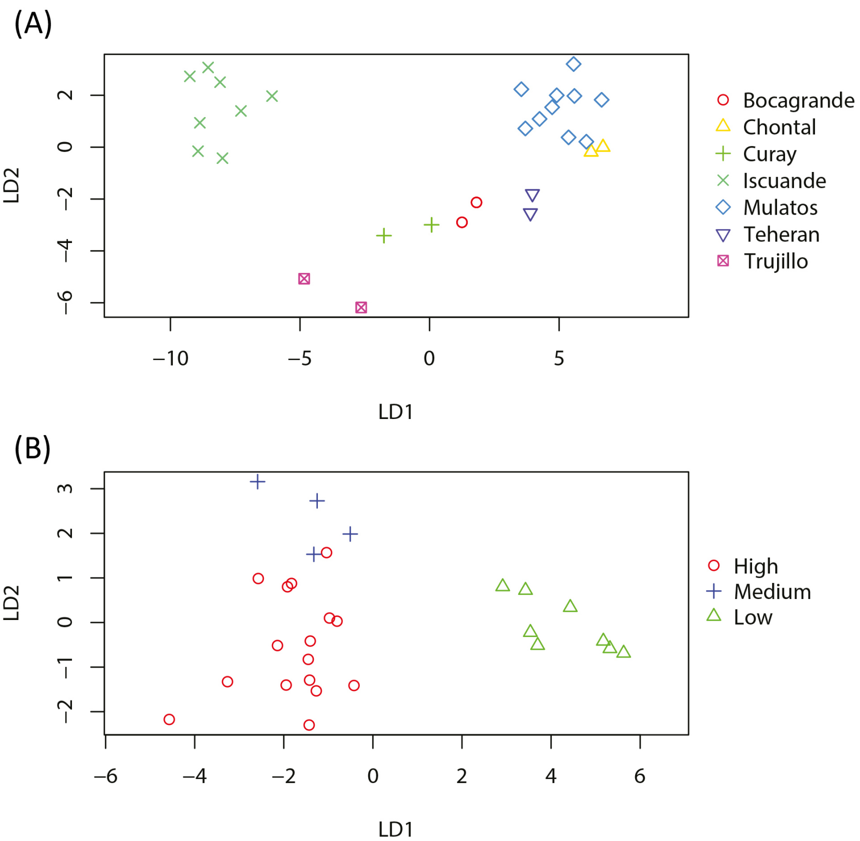

FIGURE 3 | (**A**) Canonical analysis of principal coordinates (CAP) of intertidal mangrove creek fish assemblages taken at different localities and (**B**) Canonical analysis of principal coordinates (CAP) of intertidal mangrove creek fish assemblages taken at different localities with different salinities of the southern Colombian Pacific coast, Panama Bight mangrove eco-region. Symbols represent individual block net catches.

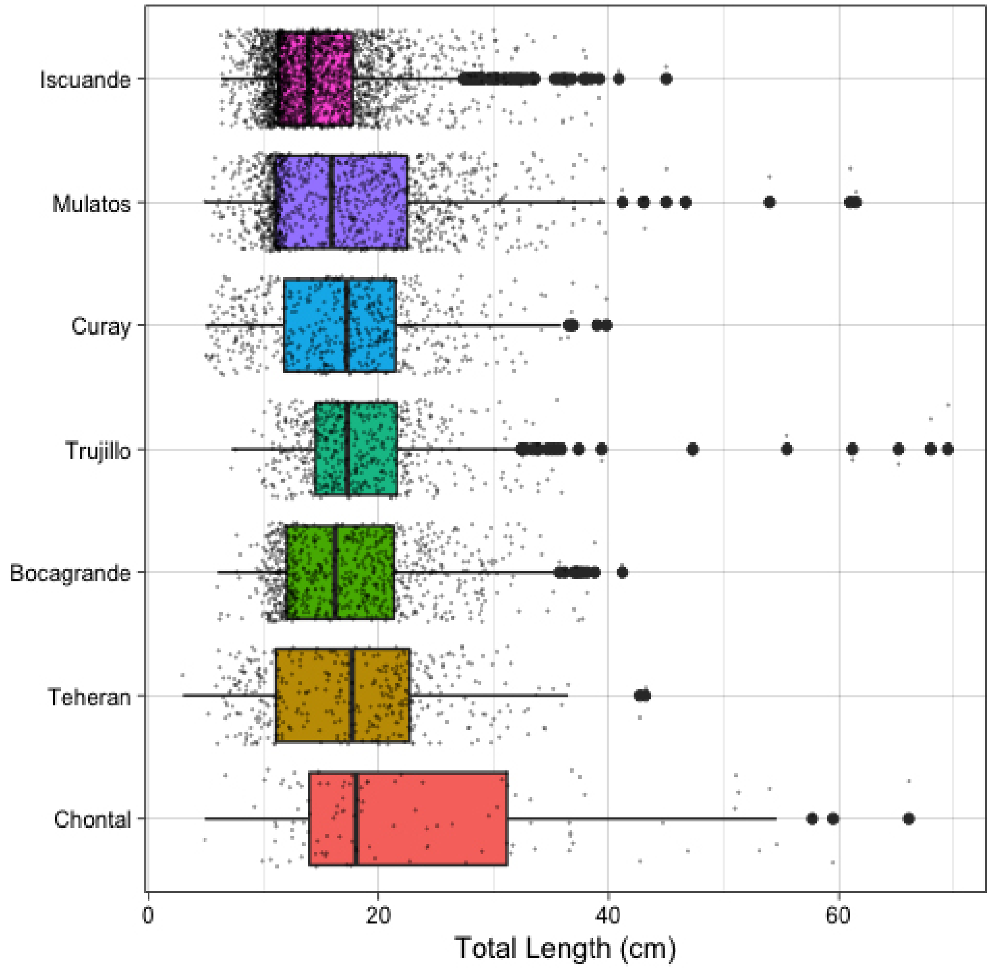

FIGURE 4 | Size distribution of intertidal mangrove fishes captured in the southern Colombian Pacific coast (Panama Bight eco-region) at seven localities between 2012 and 2017.

samples from medium and high salinity areas. The separation between medium and high salinities was less evident but observable along the CAP axis LD2 (Fig. 3B).

Overall fish mean size (TL) at all localities was 16.7 cm (SD ± 6.7). However, fish size in Iscuandé, the locality with the lowest salinities, tended to be lower (mean = 14.9 cm ± 5.0) than in the rest of localities where mean values were > 17.0 cm. Large fish sizes were observed in the Chontal locality probably due to the dominance of the needlefish *Strongylura scapularis* (Jordan, Gilbert 1882) in the samples there (Fig. 4).

DISCUSSION

Our results indicate a fairly similar species composition of fish assemblages in intertidal mangroves in the seven localities examined in the southern Colombian Pacific coast. The species composition is also very similar to that sampled in the same habitats 200 km north of this coast (Bahía Málaga, Castellanos-Galindo, Krumme, 2013b). Likewise, similar fish species composition, with dominance of snooks, marine mojarras (Gerreidae) and croakers (Sciaenidae), has been found in intertidal mangroves of the Gulf of Montijo, Panama (~500 km north) (Castellanos-Galindo *et al.*, unpublished data). This indicates that a specific relatively uniform subset of coastal estuarine fishes (~70 species) is adapted to intertidal migrations throughout the macrotidal Panama Bight eco-region. In northern Brazil (Western Atlantic) and in a similar mangrove-dominated coast (650 km) with a macrotidal regime, Giarrizzo, Krumme (2008), compared studies that used a similar methodology as in the present study and documented a total of 115 fish species inhabiting intertidal mangroves. The similarity in family composition between these two regions is striking, being families like Tetraodontidae and Ariidae common and dominant among the intertidal migrant species in both regions.

Fishes in tropical and subtropical coasts use mosaics of habitats including mangroves (Nagelkerken *et al.*, 2015). These mosaics can include seagrasses and coral reefs in areas of the Caribbean Sea and the Indo-Pacific region, but they include in most of the major mangrove areas of the world, mudflats or other kind of soft-bottom habitats in estuarine and deltaic settings (Twilley *et al.*, 2018) This is the case for most of Panama Bight ecoregion. Of the ~230 fish species that inhabit mangroves and associated mosaic of habitats in this region (see review in Castellanos-Galindo *et al.*, 2013) almost one third undertakes intertidal migrations inside mangroves (Fig. 5). The remaining two thirds of these species rarely enter the intertidal mangrove

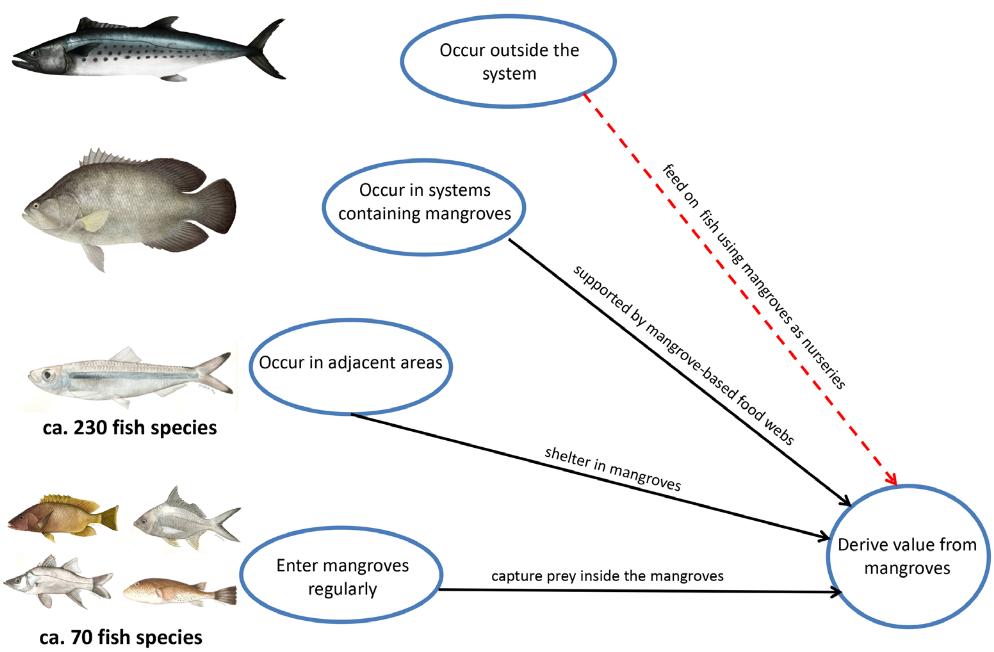

FIGURE 5 | Different ways how coastal fishes may depend on mangrove areas in the Panama Bight ecoregion (adapted from Sheaves, 2017). Species numbers are taken from the compilation of mangrove intertidal samplings and from studies performed in mosaics of estuarine mangrove areas.

area and stays in subtidal habitats such as creeks and submerged sand or mudflats. This habitat partition by fishes does not necessarily implies that those fishes not entering mangroves do not benefit from the energy and food produced in this ecosystem. Instead, these fishes could benefit via trophic transfers from the presence of mangroves (see Fig. 5). A deeper understanding of these trophic links needs to be gained examining other habitats within the mangrove habitat mosaic that were not sampled with our methods.

Comparing our results with the national fishery statistics (SEPEC, 2013), we found that more than half of the total species captured in intertidal mangrove creeks of the southern Colombian Pacific coast are of commercial importance to the artisanal fishery (see Tab. 1). Especially important are the snooks (Centropomidae) and catfishes (Ariidae) that are dominant in the catches of all seven localities examined here (see Fig. 3). In other localities like Bahía Málaga in the central Colombian Pacific coast, snappers are a significant component of the mangrove fish assemblage (in biomass and individual abundance; Castellanos-Galindo, Krumme, 2013b) and are an important part of the artisanal fishery. Other species that do not migrate to intertidal mangrove areas, but that live in close proximity to this habitat are also very important for the artisanal fishery in the central and southern Colombian Pacific coast. Among this group, species of Lobotidae (*Lobotes pacificus* Gilbert, 1898), Scombridae (*Scomberomorus sierra* Jordan & Starks, 1895), Ariidae (*Bagre* spp.), and Centropomidae (*Centropomus* spp.) contribute greatly to the overall fish landings (SEPEC, 2013; Herrón *et al*., 2019) and likely derive some of their food through the trophic mangrove pathway (Fig. 5). Despite it is commonly recognized that this mangrove-dominated coast is crucial in providing habitat for many of the species targeted by the artisanal fishing fleets that operate there, a lack of quantitative knowledge on the relationship between mangrove characteristics and fisheries yields or productivity is lacking. Our results provide initial quantitative information on the fish community that directly use mangroves during tidal inundations.

Data gaps in knowledge of eastern Pacific mangrove fishes. For other ecosystems like coral reefs, small cryptic fishes have been increasingly recognized as significantly important for ecosystem functioning (Brandl *et al*., 2018, 2019). In mangrove ecosystems the biomass and abundances of these fishes is normally underestimated due to the prevailing sampling methodologies used. This is clearly evident in our study, where only a few species of Gobiidae and Eleotridae were sampled with our sampling method. Apart from a few studies in mangroves in northern Brazil (Barletta *et al*., 2000), there is an absence of cryptobenthic fish community studies in mangroves. Preliminary observations of these fauna in the mangroves of the central Colombian Pacific show that they can be abundant and relatively diverse (~20 species of mainly gobids and labrisomids; Castellanos-Galindo *et al*., 2020). They therefore may play an important ecological role transforming energy from within the mangrove systems and being prey for more mobile fishes that move between habitats in the coastal zone.

Some areas in the Panama Bight mangrove eco-region and the rest of the tropical eastern Pacific remain under-studied. These areas contain significant parts of mangrove forests that have been historically inaccessible or of difficult access. These areas include The Gulf of San Miguel in the Darien province of Panama, the Baudó region and the San Juan Delta in the central Colombian Pacific coast and the extensive mangrove area of Esmeraldas in northern Ecuador.

Our study provides for the first time, quantitative information on a portion (the one migrating with the tides to intertidal areas) of the fish community inhabiting the largest and more developed mangrove forest in the Colombian Pacific coast, southern part of the Panama Bight ecoregion. Our results show that this intertidal fish community represents ~1/3 of the whole fish fauna in the mangrove mosaic of this region. Juveniles of many commercially important species for the local fishery are found in these intertidal mangroves and clearly show the importance of this habitat for fishes. Our understanding of the larger role that mangroves play for the other components of the coastal fish fauna of the region continues to be limited and we have delineated here a few themes that could help to fill in those knowledge gaps.

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