



## Linking mangroves and fish catch: a correlational study in the southern Caribbean Sea (Colombia)

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**ABSTRACT.**—Mangroves provide habitat to a variety of fish species, potentially enhancing fish production in small-scale fisheries. Fish production ecosystem services have been correlated with mangrove area and perimeter in many tropical locations; however, nothing has been published linking small-scale fish catch and mangrove attributes in the southern Caribbean Sea. We correlated environmental variables with experimentally-derived catch per unit effort (CPUE) and richness of fishes in the Colombian southern Caribbean Sea, an area not directly connected with other productive coastal habitats. Concurrently, we measured mangrove attributes (area, perimeter, above-ground carbon), water quality (salinity, total dissolved solids), and water column productivity parameters (chlorophyll *a*, seston, zooplankton biovolume). Mangrove area and zooplankton biovolume were the main factors influencing fish species richness. Mangrove area was positively correlated with catches for three of the most common fish species in the local artisanal fishery: *Ariopsis canteri* Acero P, Betancur-R, and Marceniuk, 2017, *Mugil incilis* Hancock, 1830, and *Sciades proops* (Valenciennes, 1840), which represent about 22% of the total regional annual catch. Our results suggest causal links between mangrove habitat and fishery production through a mangrove trophic contribution. *Ariopsis canteri* appears to be a mangrove-dependent species and *M. incilis* a mangrove-associated species. These results support managing or preserving mangroves in the most extensive areas in the southern Caribbean to sustain small-scale fishery resources used mainly for community sustenance where alternative resources are limited.



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Mangroves provide a number of valuable ecosystem services, such as fish production, coastal protection, carbon storage, and sediment trapping (Lee et al. 2014). Given the role of mangroves as nursery habitats for marine and estuarine species, the mangrove-fishery linkage has been widely studied (Manson et al. 2005a, Blaber 2007, Carrasquilla-Henao and Juanes 2016). Various studies report positive correlations between mangrove extent and catches in nearby fisheries, suggesting that

the former translates into the secondary production of fishes and ultimately into commercial resource capture (Manson et al. 2005a). According to government and nongovernment documents, an estimated 75% of commercially caught fishes and prawns depend directly on mangroves, but this is debatable (Sheaves 2017) because other factors influence catches, such as river discharge, connectivity with surrounding habitats, and diverse food source availability (Manson et al. 2005a, Blaber 2007, Carrasquilla-Henano and Juanes 2016).

Most studies on the mangrove-fishery linkage have been performed in the Indo-West Pacific and fewer in the Atlantic-Caribbean and eastern Pacific (Carrasquilla-Henano and Juanes 2016). Much of the evidence has been obtained from studies on penaeid prawns in the Gulf of Mexico (Turner 1977), Indonesia (Martosubroto and Naamin 1977), India (Kathiresan and Rajendran 2002), Australia (Staples et al. 1985), and the Philippines (Primavera 1998), with positive correlations between commercial offshore prawn catches and total area of adjacent mangroves. Additionally, positive correlations between commercial finfish catches and mangrove area have been reported in Australia (Manson et al. 2005b, Meynecke et al. 2008), the Gulf of Mexico (Yáñez-Arancibia et al. 1985), the Gulf of California (Aburto-Oropeza et al. 2008, Carrasquilla-Henao et al. 2013), and the Philippines (Paw and Chua 1991).

Recently, Carrasquilla-Henao and Juanes (2016) conducted a global meta-analysis providing strong evidence on the links between mangrove attributes and fisheries in a variety of mangrove settings. Their results agreed with other studies (Manson et al. 2005a, Sheaves 2017) that future investigations should focus on the reasons behind the use of mangroves by different species at different life stages. This is necessary to understand the derived benefits and to identify mangrove attributes that contribute to greater fish abundance.

Furthermore, Manson et al. (2005a) recommended fine-scale mangrove-fishery analyses for predicting the effects of habitat loss. Hutchison et al. (2015) expanded on this idea by developing a preliminary global model of the spatial distribution of benefits to fisheries from mangroves. Although the model was based on expert knowledge of mangrove ecology and fisheries biology, it was not parameterized with field data and was, therefore, qualitative.

For the Atlantic-Caribbean and eastern Pacific regions, most mangrove-fishery databases originate from Mexico (Yáñez-Arancibia et al. 1985, Aburto-Oropeza et al. 2008, Carrasquilla-Henao et al. 2013), while the majority of field studies linking fishes with mangroves, seagrasses, and coral reefs have been conducted in the Caribbean islands (Mumby et al. 2004, Nagelkerken and Van Der Velde 2004, Serafy et al. 2015). Despite having a wide range of mangrove settings along the Caribbean coast of Colombia, there are no such studies carried out there (Carrasquilla-Henao et al. 2013). Most Colombian systems are not directly connected with other highly productive coastal habitats, such as coral reefs and seagrasses (e.g., Ciénaga Grande de Santa Marta and Gulf of Urabá).

Current knowledge on estuarine fisheries along the Caribbean coast of Colombia has been obtained mostly from Ciénaga Grande de Santa Marta, a large coastal lagoon located east of Barranquilla (Blaber and Barletta 2016). The Gulf of Urabá, located near the western border of northern Colombia next to Panama, is another major estuary with extensive mangrove areas and artisanal fisheries for local commerce and subsistence, but information concerning these mangroves and local fisheries is limited. Recent studies suggest that most of the Gulf of Urabá commercial

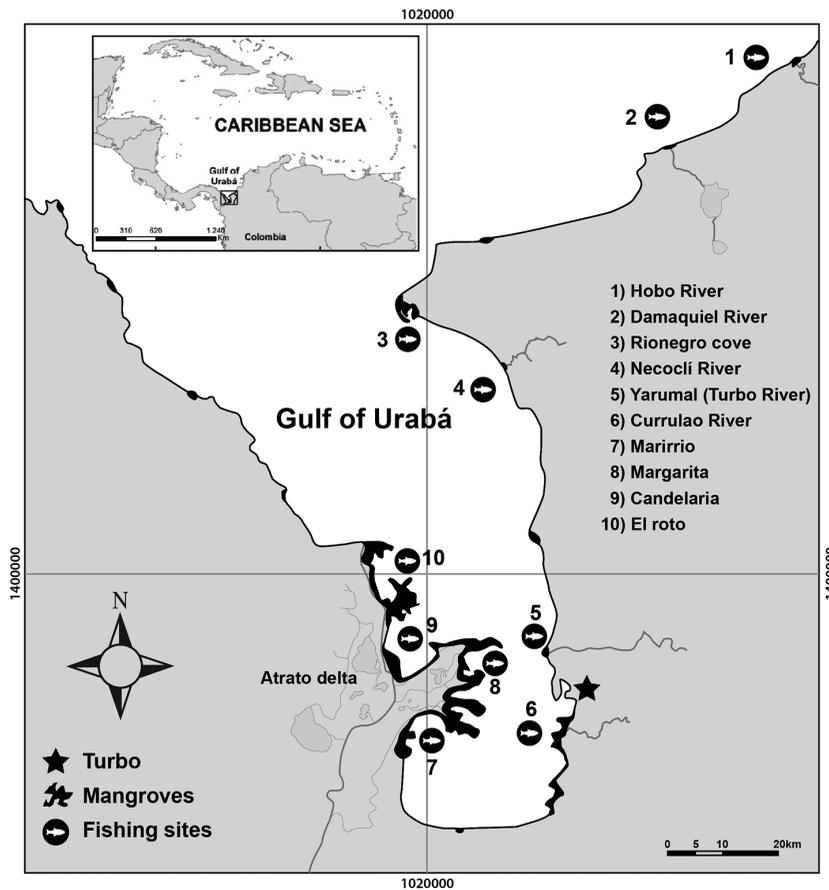


Figure 1. Map of the study area showing the 10 sites where experimental fishing was conducted, location of mangrove areas, and a major human settlement (port city of Turbo).

fish species use mangroves and mangrove lagoons at least during their early life cycle stages (Sandoval et al. 2014, LOPEGU 2017).

The aim of this study was to examine the importance of mangroves for CPUE (catch per unit effort) in the Gulf of Urabá and its vicinity, an area not directly connected with other highly productive coastal habitats. We investigated the linkages between CPUE and species richness using several environmental variables: mangrove attributes (area, perimeter, above-ground carbon), water quality (salinity, total dissolved solids), and water column productivity parameters (chlorophyll *a*, seston, zooplankton biovolume).

## METHODS

**STUDY AREA.**—The Gulf of Urabá is the largest estuary along the Caribbean coast of Colombia (7°50'N–8°56'N, 77°22'W–76°25'W). It is a semienclosed water body (length: 80 km, width: 6–45 km; Fig. 1) and has a microtidal regime (<40 cm amplitude). The largest freshwater input to the southern Caribbean is the Magdalena River, followed by the Atrato River which discharges into the western coast of the

gulf (García 2007). Additional freshwater is received from small rivers located along the southeastern coast. Extensive mangrove forests (approximately 5688 ha) can also be found along the different deltas and river mouths. The red mangrove *Rhizophora mangle* L. is the dominant mangrove species (>80% by area), followed by white mangrove *Laguncularia racemosa* (L.) Gaertn (f.) and black mangrove *Avicennia germinans* (L.). The largest mangrove areas are located on the Atrato River delta where most stands are monodominant (Blanco-Libreros 2016). The artisanal fishery is practiced only for local commerce and/or subsistence. It is the main income and food source for many poor communities and is mostly associated with fringe mangroves (Sandoval et al. 2014, LOPEGU 2017). This situation is similar to other locations observed along the Colombian Caribbean and elsewhere in the tropics (Hutchison et al. 2014, Saavedra-Díaz et al. 2015). We examined the importance of mangroves to CPUE in the Gulf of Urabá and its vicinity extending approximately 514 km, including protected coast and mangrove-dominated sites (the Gulf of Urabá) and open coast sites not dominated by mangroves.

**FISHING DATA.**—Although the Gulf of Urabá is a designated area for monitoring of fish landings by the National Aquaculture and Fisheries Authority (Autoridad Nacional de Acuicultura y Pesca, AUNAP), spatial and temporal coverage is still limited. For this reason, data from experimental fishing campaigns conducted between 2015 and 2016 were used during a project aimed at providing guidelines for small-scale fisheries management in the area [hereafter LOPEGU project (Lineamientos Prioritarios para la Formulación de un Ordenamiento Pesquero del Golfo de Urabá)]. We used information from 10 sites, representing the most important gulf fishing grounds (LOPEGU 2017). The focus of experimental fishing was to provide baseline information on fish catches from the most representative fishing grounds along the gulf's mangrove coastlines and the outer northeastern coastline where mangroves are less extensive and patchily distributed.

There were seven fishing campaigns included: four in 2015 (March, August, October, December) and three in 2016 (February, April, August). Operations were performed using two fishing boats in the southern sites and northern gulf sites, respectively (Table 1, Fig. 1). At each of the 10 sites, two gillnets set side by side were deployed during the daytime (07:00 to 11:00 hrs) and nighttime (18:00 to 22:00 hrs); day and night samples were treated as replicates for each campaign in subsequent analyses. Gillnets were similar to those used by local fishermen (800 m long and 7 m high, with mesh sizes of 7, 7.6, 10.2, and 12.7 cm). Gillnet hauls per site ranged from 14 to 29 (Table 1), depending on the weather. The gillnets were set approximately 0.8 to 1.9 km away from mangroves (Table 1). The distance to the nearest sampling site ranged between 12 and 40 km (Table 1).

Fishes were transported on ice and identified to the species level at the Marine Ecology Laboratory of the Universidad de Antioquia (Marine Sciences Campus). A reference collection was sent to the National Museum of Marine Natural History (Museo de Historia Natural Marina de Colombia, MHNMC; collection code PEC9038). Species richness was estimated as the total number of species from 14 random hauls at each site, because fishing effort differed among sites. Fish catch was expressed as CPUE and estimated as mass (kg) per number of hauls at each site.

Table 1. Fishing effort summary: fishing effort (number of hauls) over seven campaigns at each study site. Estimated distance between fishing site and mangroves (MA-Fishing), and estimated distance between fishing sites (Fishing-Fishing).

Fishing sites	Hauls						Total fishing effort	MA-fishing (km)	Fishing-fishing (km)	
	April 2015	August 2015	October 2015	December 2015	February 2016	April 2016				August 2016
Northern sites										
Hobo River	0	4	4	4	0	2	0	14	1.9	---
Damaquiel River	0	0	4	4	2	4	2	16	1.5	15
Rionegro Cove	0	4	4	4	4	4	4	24	1	40
Necocli River	0	4	4	4	4	4	4	24	1	17
Southern sites										
Yarumal	0	4	4	2	2	4	3	19	1.3	38
Currulao River	4	4	4	4	4	4	4	28	0.8	13
Marirrio	0	4	4	4	4	4	3	23	1.3	17
Margarita	4	4	4	4	3	4	4	27	0.7	13
Candelaria	4	4	4	4	4	4	4	28	1.5	12
El Roto	4	4	4	4	4	4	4	28	1	12

**MANGROVE DATA.**—We examined mangrove forest attributes within the coastal segments coinciding with fishing sites (bays and river deltas along the Gulf of Urabá and the open coast; Fig. 1). Mangrove area (MA, in ha) was obtained from a technical report based on high-resolution aerial imagery (Blanco et al. 2013). Mangrove perimeter (MP, in km) was computed from that mosaic using ArcGIS 9.3; MP was estimated as the length of the mangrove fringe in contact with open water (interior perimeter in contact with terrestrial vegetation or wetlands was not considered).

To estimate carbon accumulated in aerial biomass (CAB), we first estimated aerial biomass (AB) using the following equation for *R. mangle* reported by Fromard et al. (1998):

$$W = 0.178 (\text{DBH})^{2.47}$$

where  $W$  is tree weight and DBH is diameter at breast height. This equation was selected as equations based on locally logged trees were not available. We used mean DBH and tree density per hectare in each area from Blanco et al. (2013). AB was calculated by multiplying mean tree weight and tree density for each site; tree densities were preobtained using sampling plots (10 × 10 m; Blanco et al. 2013). Finally, CAB was estimated as 50% of the AB as suggested by Bouillon et al. (2008) and expressed in Tg after multiplying by the MA corresponding to each of the 10 study sites.

**QUALITY AND PRODUCTIVITY OF THE WATER COLUMN.**—We measured the quality and productivity of the water column at the 10 sites where experimental fishing was conducted. Four sampling campaigns were included: one in 2015 (December) and three in 2016 (February to March, April to May, August). There were fewer water column sampling campaigns than fishing campaigns due to logistical difficulties. Nevertheless, water column sampling was conducted during the major fishing time, allowing for the examination of water column variables among sites throughout the year. We determined salinity (SAL) and total dissolved solids (TDS,  $\mu\text{g L}^{-1}$ ) in situ using a multiparameter probe, while water samples were taken to determine seston and chlorophyll *a* in the laboratory. We measured seston [total suspended solids

(TSS,  $\text{g L}^{-1}$ ) according to USEPA (1999) and chlorophyll *a* (CHL,  $\mu\text{g L}^{-1}$ ) according to Strickland and Parson (1972). We obtained zooplankton samples from surface net tows (net mesh of 300  $\mu\text{m}$  over 6 min at 2 knots), with a flow meter fixed to the plankton net to record the filtered volume. Subsequently, we estimated zooplankton biovolume (ZB,  $\text{ml } 1000 \text{ m}^{-3}$ ) using the displaced volume method (Escarria et al. 2005).

**DATA ANALYSIS.**—Given that water column sampling campaigns were fewer than fishing campaigns, our explanatory variables corresponded to the mean values for the entire study period for each of the 10 fishing sites. Additionally, the absolute values of mangrove attributes were used for each site. The dependent variables describing fish catches were CPUE (total and species-specific) and species richness (total number of species). We tested each variable distribution for normality (as a prerequisite for regression analyses), and all of them were rank-transformed to satisfy the normality assumption (Conover 2012). We performed Spearman rank correlation (SRC) analysis between explanatory variables to explore colinearity, using XLSTAT software (Addinsoft 2019). Then, we then ran multiple linear regression with backward elimination to determine the best environmental variables to predict CPUE and species richness, using the same software. In each step, we checked the model fit and significance of each covariate and manually eliminated nonsignificant terms. We examined the CPUE of the most common species collected where data were normally distributed. We considered  $P < 0.1$  as a significant correlation. Nonparametric Kruskal–Wallis (H) test in R Studio v3.5.3 was used to assess for the differences in water column variables, species richness, total fish CPUE, and species-specific CPUE among sites.

## RESULTS

**FISHING DATA.**—We captured 77 species belonging to 30 families. Rionegro Cove and Marirrio Bay showed the highest species richness (32 and 30 species, respectively). Hobo River had the lowest species richness with 13 species (Fig. 2A). However, species richness among sites did not differ (Kruskal–Wallis test,  $P = 0.28$ ,  $\text{df} = 9$ ). The total catch from all 10 sites in the Gulf of Urabá was 870 kg. Nearly 40% of the biomass comprised three species: common snook, *Centropomus undecimalis* (Bloch, 1792) (Centropomidae), 0.44 kg haul<sup>-1</sup>; New Granada sea catfish, *Ariopsis canteri* (Ariidae), 0.36 kg haul<sup>-1</sup>; and Serra Spanish mackerel, *Scomberomorus brasiliensis* Collette, Russo, and Zavala-Camin, 1978 (Scombridae), 0.31 kg haul<sup>-1</sup>. The following species were secondarily abundant: tarpon, *Megalops atlanticus* Valenciennes, 1847 (Megalopidae), 0.27 kg haul<sup>-1</sup>; sauteur, *Oligoplites saliens* (Bloch, 1793) (Carangidae), 0.22 kg haul<sup>-1</sup>; gafftopsail sea catfish, *Bagre marinus* (Mitchill, 1815) (Ariidae), 0.21 kg haul<sup>-1</sup>; coco sea catfish, *Bagre bagre* (Linnaeus, 1766) (Ariidae), 0.21 kg haul<sup>-1</sup>; Atlantic bumper, *Chloroscombrus chrysurus* (Linnaeus, 1766) (Carangidae), 0.18 kg haul<sup>-1</sup>; and largehead hairtail, *Trichiurus lepturus* (Trichuridae), 0.14 kg haul<sup>-1</sup> (Fig. 3A).

The average CPUE was 3.74 kg haul<sup>-1</sup>. CPUE ranged from 6.68 to 1.64 kg haul<sup>-1</sup> for Damaquiel River and Necoclí River, respectively (Fig. 2B). *Scomberomorus brasiliensis* and *C. undecimalis* were the most important species in Damaquiel River. *Oligoplites saliens* and *S. brasiliensis* were the most important species in Yarumal. *Megalops atlanticus* was the most important species in Margarita. *Oligoplites saliens*,

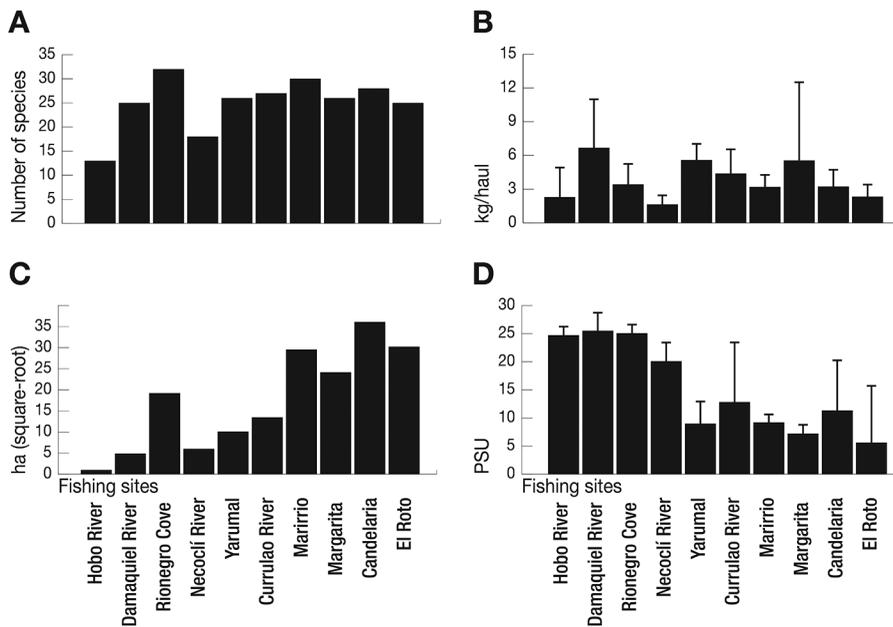


Figure 2. Main results of total catch and environmental variables at each study site. (A) species richness (number), (B) total CPUE (kg/haul), (C) mangrove area (MA,  $\sqrt{\text{ha}}$ ), and (D) salinity (SAL). Error bars in (B) and (D) represent standard deviations.

*T. lepturus*, and *A. canteri* were the most important species in Currulao River (Fig. 3B). There was no significant difference in total CPUE among sites (Kruskal–Wallis test,  $P = 0.47$ ,  $df = 9$ ). Significant differences in CPUE of *A. canteri* ( $P = 0.03$ ,  $df = 9$ ), *B. bagre* ( $P < 0.01$ ,  $df = 9$ ), and *O. saliens* ( $P = 0.04$ ,  $df = 9$ ) among sites were suggested. However, subsequent pairwise comparisons among sites using Wilcoxon rank sum test revealed no significant differences.

**ENVIRONMENTAL DATA.**—The magnitude of mangrove variables (MA, MP, CAB) varied considerably among sites along the Gulf of Urabá and the open coast. Values of all three variables were higher on the western coast of the Gulf of Urabá (Marirrio, Margarita, Candelaria, and El Roto) where mangroves are more extensive (e.g., MA exceeded 20 ha; Table 2, Fig. 2C). However, Rionegro Cove, a coastal lagoon located in the northeastern tip of the Gulf of Urabá, exhibited higher MA, MP, and CAB values than the rest of the sites along the southeastern and northeastern coasts (Table 2, Fig. 2C). The average water column variables (TDS, CHL, SAL, TSS, ZB) also varied considerably among sites (Table 2). For instance, salinity exceeded 20 in the northeastern sites (Hobo River, Damaquiel River, Rionegro Cove, Necocí River), while it was persistently lower at sites in the interior of the gulf (Table 2, Fig. 2D). The Kruskal–Wallis test suggested significant differences in TDS ( $P < 0.01$ ,  $df = 9$ ), TSS ( $P = 0.02$ ,  $df = 9$ ), and SAL ( $P < 0.01$ ,  $df = 9$ ) among sites. However, pairwise comparisons among sites using Wilcoxon rank sum test revealed no significant differences.

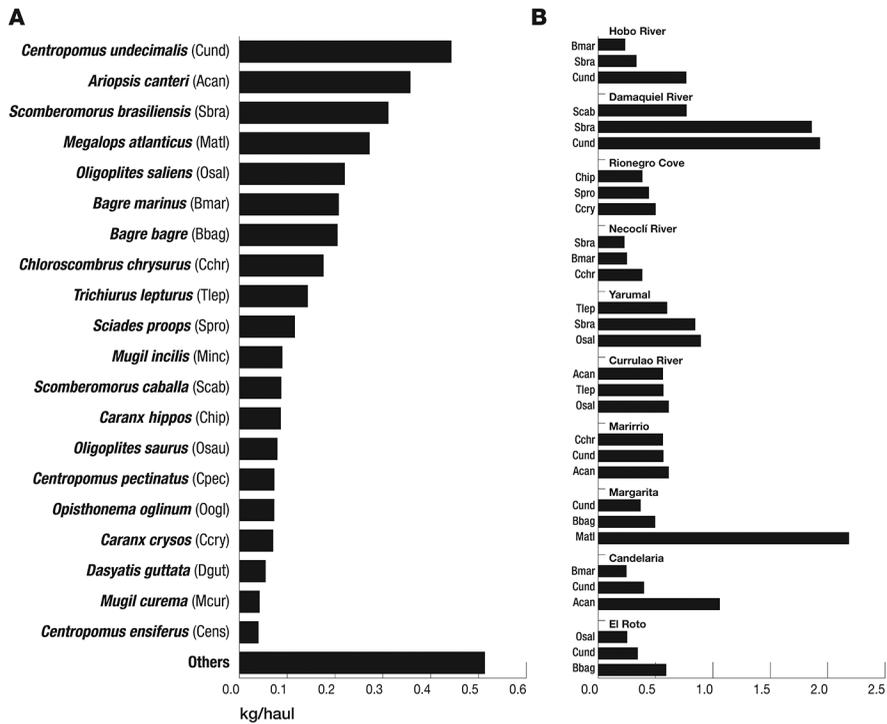


Figure 3. Total fish CPUE (kg haul<sup>-1</sup>) for the most common species collected (A) in the study and (B) at each study site.

Table 2. Environmental variables [mean (standard deviation)], including water quality, water column productivity, and mangrove attributes of 10 study sites. Quality-water and productivity means were computed from four ( $n = 4$ ) campaigns: December 2015, February 2016, April 2016, and August 2016, except for Hobo River, where samples were obtained with three ( $n = 3$ ) campaigns. TDS = total dissolved solids, CHL = chlorophyll  $a$ , SAL = salinity, TSS = total suspended solids (sestion), ZB = zooplankton biovolume, MA = mangrove area, MP = mangrove perimeter, CAB = carbon accumulated in aerial biomass.

Site	TDS ( $\mu\text{g L}^{-1}$ )	TSS ( $\text{g L}^{-1}$ )	SAL	CHL ( $\mu\text{g L}^{-1}$ )	ZB ( $\text{ml } 1,000 \text{ m}^{-3}$ )	MA (ha)	MP (km)	CAB (Tg)
Northeastern coast								
Hobo River	21.36 (0.9)	0.01 (0)	24.78 (1.01)	1.46 (1.36)	185.95 (112.26)	1	0.38	0.19
Damaquiel River	21.62 (2.16)	0.01 (0)	25.5 (4.96)	5.37 (2.9)	192.86 (180.37)	24	0.19	4.83
Southeastern coast								
Rionegro Cove	21.25 (1.05)	0.01 (0)	25.07 (0.44)	0.9 (1.46)	126.53 (107)	369	30.61	5.87
Necocli River	17.55 (2.17)	0.01 (0)	20.11 (1.07)	1.47 (2.98)	35 (32.31)	36	1.93	0.65
Yarumal	8.2 (3.02)	0.01 (0)	8.99 (3.4)	4.46 (3.52)	79.76 (70.14)	102	20.72	0.8
Currulao River	11.35 (7.6)	0.03 (0.01)	12.82 (4.77)	3.87 (9.32)	48.54 (56.86)	182	10.24	0.71
Western coast								
Marirrio	8.49 (1.28)	0.02 (0)	9.2 (1.6)	2.53 (1.36)	159.65 (212.25)	873	60.23	82.86
Margarita	6.69 (1.27)	0.02 (0.01)	7.13 (1.69)	2.81 (1.48)	37.14 (29.94)	584	32.45	31.85
Candelaria	10.12 (6.63)	0.02 (0.01)	11.33 (1.39)	2.06 (7.83)	40.37 (39.63)	1,303	102.1	93.01
El Roto	4.84 (7.44)	0.09 (0.07)	5.63 (8.55)	7.17 (8.85)	39.59 (45.95)	913	89.31	40.73

Table 3. Spearman's rank correlation matrix for explanatory variables ( $n = 10$ , for all variables). \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . TDS = total dissolved solids, TSS = total suspended solids (seston), SAL = salinity, CHL = chlorophyll  $a$ , ZB = zooplankton biovolume, MA = mangrove area, MP = mangrove perimeter, CAB = carbon accumulated in aerial biomass.

	TDS ( $\mu\text{g L}^{-1}$ )	TSS ( $\text{g L}^{-1}$ )	SAL	CHL ( $\mu\text{g L}^{-1}$ )	ZB ( $\text{ml } 1,000 \text{ m}^{-3}$ )	MA (ha)	MP (km)	CAB (Tg)
TDS	<b>1</b>							
TSS	-0.82*	<b>1</b>						
SAL	0.99**	-0.79*	<b>1</b>					
CHA	-0.44	0.49	-0.46	<b>1</b>				
ZB	0.59	-0.57	0.56	0.01	<b>1</b>			
MA	-0.70	0.76*	-0.64	0.13	-0.42	<b>1</b>		
MP	-0.75*	0.70	-0.70*	0.06	-0.42	0.98**	<b>1</b>	
CAB	-0.53	0.52	-0.47	0.19	-0.13	0.90**	0.87**	<b>1</b>

RELATIONSHIPS BETWEEN MANGROVE, WATER COLUMN, AND CPUE DATA.—Based on SRC results, four environmental variables were retained for inclusion in regression analyses: MA, SAL, CHL, and ZB (Table 3). Regression analyses revealed that total CPUE was not correlated to any variable, and that species richness was correlated to MA and ZB ( $R^2 = 0.56\%$ ). Two species were positively associated with MA (*A. canteri*,  $R^2 = 0.50$ ; *Mugil incilis*,  $R^2 = 0.38$ ), while one species was negatively associated with MA (*S. brasiliensis*,  $R^2 = 0.77$ ). Several species were consistently associated with SAL (*B. bagre*,  $R^2 = 0.45$ ; *O. saliens*,  $R^2 = 0.52$ ; *Oligoplites saurus*,  $R^2 = 0.42$ ), and water column productivity variables (*Centropomus ensiferus* with CHL,  $R^2 = 0.47$ ; *Centropomus pectinatus* with SAL and CHL,  $R^2 = 0.84$ ; *C. undecimalis* with ZB,  $R^2 = 0.77$ ). *Sciades proops* CPUE was consistently associated with MA, CHL, and ZB ( $R^2 = 0.83$ ; Table 4).

## DISCUSSION

This is the first study of mangrove-fishery relationships in the southern Caribbean and northern South America. By testing the relative contribution of environmental variables (water column quality and productivity, and mangrove metrics) for an area not directly connected with other highly productive coastal habitats, we demonstrated that MA predicted the catch for four of the most common fish species in local artisanal fisheries. This suggests mangrove shorelines contribute to fish catches in this part of the Caribbean Sea.

The partial contribution of MA and ZB to species richness variability suggests food availability in the water column plays a complementary role for mangrove-associated fishes. Food and refuge are the beneficial aspects of mangroves to fishes (Sheaves 2017). The lack of correlation between fish species richness and salinity may suggest a species turnover of the entire fish community along the geographic gradient observed between the Gulf of Urabá and the open coast to the Caribbean Sea. Salinity may be one of the most important physical factors affecting estuarine fishes (Blaber 2013). For instance, in more constrained estuarine environments such as tropical coastal lagoons, higher species richness has been recorded under low salinity (Sosa-López et al. 2007). However, CPUE of some species was correlated with salinity as discussed below.

Table 4. Environmental variables significantly explaining species richness and CPUE for 10 fish species, identified using Multiple Linear Regressions by backward elimination;  $n = 10$  for all variables ( $R^2$  and  $P$ -values are included). MA = mangrove area, CHL = chlorophyll  $a$ , SAL = salinity, ZB = zooplankton biovolume.  $P < 0.1$  was considered significant correlation.

	Coefficient	$P$	$F$	$R^2$
Species richness				
Step 3 (MA + ZB)	---	---	0.06	0.56
ZB	0.60	0.06	---	---
MA	0.76	0.03	---	---
<i>Ariopsis canteri</i>				
Step 4 (MA)	0.70	0.02	0.02	0.50
<i>Bagre bagre</i>				
Step 4 (SAL)	-0.67	0.03	0.03	0.45
<i>Centropomus ensiferus</i>				
Step 4 (CHL)	0.66	0.03	0.03	0.47
<i>Centropomus pectinatus</i>				
Step 3 (SAL + CHL)	---	---	0.00	0.84
SAL	-0.48	0.03	---	---
CHL	0.58	0.01	---	---
<i>Centropomus undecimalis</i>				
Step 4 (ZB)	0.76	0.01	0.01	0.57
<i>Oligoplites saliens</i>				
Step 4 (SAL)	-0.72	0.02	0.02	0.52
<i>Oligoplites saurus</i>				
Step 4 (SAL)	-0.65	0.04	0.04	0.42
<i>Mugil incilis</i>				
Step 4 (MA)	0.61	0.06	0.06	0.38
<i>Scomberomorus brasiliensis</i>				
Step 4 (MA)	-0.88	0.00	0.00	0.77
<i>Sciades proops</i>				
Step 2 (MA + CHL + ZB)	---	---	0.01	0.83
CHL	-0.45	0.04	---	---
ZB	0.90	0.00	---	---
MA	0.54	0.03	---	---

Similar to previous studies, positive correlations between mangroves and fish catches have been obtained in a variety of mangrove settings globally, suggesting that mangroves have a strong effect on fisheries. However, most studies do not explain the causal relationship between mangroves and fisheries (Blaber 2007, Lee et al. 2014, Carrasquilla and Juanes 2016). Mangroves may serve as a nursery for fishes (Nagelkerken 2009, Serafy et al. 2015) and make trophic contributions, i.e., litterfall detrital-based and/or attached algae-based food webs (Hyndes et al. 2014, Serafy et al. 2015), but past studies are primarily correlative.

MA partially predicted catches of *A. canteri* and *M. incilis* (Table 4). Such correlations may be a result of benthic feeding habits of both species associated with mangrove fringes (*see below*), where other highly productive coastal habitats are absent. Only small coral reef patches are found to the northwest of the Gulf of Urabá in the vicinity of Panama, about 50 km from the study sites (Díaz et al. 2000). Moreover, soft bottoms in the Gulf of Urabá are presumably low in productivity. Contrary to our findings, most studies in the Caribbean have linked mangrove habitats to fish

abundance, due to enhancement by adjacent coral reefs, serving as juvenile habitat (Mumby et al. 2004, Serafy et al. 2015). In our study area, in addition to mangrove extent, other environmental factors may influence fish catches, such as rainfall, water temperature, and extent of shallow waters, as reported elsewhere (Manson et al. 2005b). Future attempts to predict catches would benefit from more rigorous collection of climatic and oceanographic data. However, in this study, MA rather than water column variables best predicted catches of *A. canteri* and *M. incilis*, suggesting a greater relative contribution.

The New Granada sea catfish, *A. canteri*, is an endemic species from Colombia, which is listed as endangered [Colombian fish Red List: national category EN A2d; B1b(iii)c(ii)] due to its degree of endemism and overfishing pressure (Acero et al. 2017). This species inhabits mangrove fringes in coastal lagoons and river deltas. The diet of juveniles and adults is mainly composed of crustaceans and mangrove-related fishes. Males have also been observed incubating eggs for a period, and young fishes remain in mangrove lagoons and creeks possibly as a refuge against predators (Sandoval et al. 2014). Therefore, *A. canteri* appears to be a mangrove-dependent species (Manson et al. 2005a). Mangrove dependence has been associated with several marine-estuarine species having juveniles that are only found among mangroves (e.g., the banana prawn *Penaeus merguensis*; Staples et al. 1985, Manson et al. 2005a). *Ariopsis canteri* appear to use mangroves throughout their life cycle, because juveniles are found exclusively in mangroves, while adults use mangroves alternatively with open waters, but are trophically dependent on mangroves (Sandoval et al. 2014). However, adults have also been recorded entering upriver fresh waters (Acero et al. 2017). Therefore, a more detailed understanding of their life cycle and habitat use is required.

The Parassi mullet, *M. incilis*, is mainly found in brackish estuaries, but also in marine and hypersaline waters (Cervigon et al. 1992). In the Gulf of Urabá, both juveniles and adults feed mainly on diatoms from the seabed near mangroves (Sandoval 2012). Therefore, *M. incilis* appears to be a mangrove-associated species. In the gulf, the Crucifix sea catfish, *S. proops*, was also associated with mangroves; however, its ecology is poorly known, despite it having been documented inhabiting mainly brackish estuaries and lagoons and feeding mainly on fishes (Cervigon et al. 1992).

The CPUE of the Spanish mackerel, *S. brasiliensis*, was negatively correlated with MA ( $R^2 = -0.52$ ; Table 4), consistent with mangrove-independent species or a marine straggler (Manson et al. 2005a). Additionally, catches of seven species were better explained by water column variables than by MA. *Centropomus ensiferus* and *C. undecimalis* CPUE were best explained by CHL + ZB, suggesting a greater dependency on water column productivity. *Oligoplites saliens*, *O. saurus*, *B. bagre*, and *C. pectinatus* catches were best explained by SAL (Table 4), suggesting a distribution mediated by physiological constraints. Yet, we recommend further niche ecology studies to better understand how the biology and life cycle of each species affects their dependence on mangroves and other environmental variables.

Although we did not analyze temporal variability, our results may be useful for predicting the effects of habitat loss on fisheries, as suggested by Manson et al. (2005a), and for generating preliminary local models regarding spatial (geographical) distribution of benefits that mangroves provide to local small-scale fisheries. Specifically, we highlight the importance of the largest MAs (i.e., Atrato River delta) as the major habitats for selected commercially valuable fish species, and we urge for

their conservation within ecosystem-based fishery management or spatial planning frameworks (Pikitch et al. 2004). Ineffective management and planning of small-scale fisheries has resulted in the decline of mangrove-associated fishes (Reis-Filho et al. 2018). Currently, the National Aquaculture and Fisheries Authority is drafting a fishery management plan for the Gulf of Urabá based on the spatially explicit mangrove-fishery linkages reported in the present study.

Our results suggest that the most extensive MA, the Atrato River delta, supports the CPUE for some of the most common fish species in the local artisanal fisheries. For instance, *A. canteri*, *M. incilis*, and *S. proops* positively correlated with MA, which jointly represent about 22% of the total regional annual catch, and are some of the most important species in local trade among approximately 100 registered species of crustaceans and fishes (LOPEGU 2017). Moreover, mangroves located in the Atrato River delta may be important in sustaining fishing livelihoods in the extensive Urabá region, inhabited by 1500 families (in more than 47 villages) engaged in fishing for local commerce and/or subsistence (LOPEGU 2017). Thus, our results suggest that mangrove conservation strategies such as marine protected areas and comanagement would benefit coastal communities through the fisheries provision service.

In summary, MA and food availability in the water column were the main factors explaining fish species richness in the Gulf of Urabá. MA significantly explained catches of three of the most common species in artisanal fisheries. MA, rather than water column variables, was the best predictor of catches of the benthivore species *A. canteri* and *M. incilis*. The former appears to be a mangrove-dependent species and the latter a mangrove-associated species. Our study suggests that the causal links between mangrove habitat and fishery production may be explained through the trophic contribution of mangroves in areas not directly connected to other highly productive coastal habitats (i.e., seagrasses and coral reefs). These results may be useful for designing strategies that jointly address mangrove conservation and management of small-scale fisheries associated with mangroves.

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