



## Fish habitat use in a Caribbean mangrove lagoon system

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### ABSTRACT

One of the most important ecosystem services of mangroves is their role as fish habitat. While this function has been studied in many Caribbean Islands, Indo-West Pacific areas and lagoon systems in the Americas, studies in turbid estuarine lagoon systems in the Caribbean are scarce. We surveyed fish in the Ciénaga Grande de Santa Marta (CGSM), Colombian Caribbean, at five sites which had different mangrove and physicochemical characteristics. Three gillnets, parallel to the mangroves, were set at each site over six sampling cycles ( $n = 84$ ); one in the mangrove, one further (~250 m) from the mangrove and a third one furthest from the mangrove (~400 m). We hypothesized that fish abundance and diversity, would be higher in mangrove habitats compared to mudflats, whereas biomass would be higher away from mangroves. Total fish abundance and juvenile fish abundance differed across habitats and sites, while fish biomass and fish diversity differed across sites, but not across habitats. While mangroves may be critical habitats for fish in the CGSM, mudflats may be of similar importance. Some sites had very high salinity values that together with other anthropogenic activities may limit the benefits of mangrove as critical habitats. The proportion of juveniles (67%) relative to adults of estuarine species is of concern. We recommend urgent implementation of management strategies that focus on maintaining freshwater inputs and mitigate the impact of fisheries the system is suffering.

### 1. Introduction

Mangrove habitats provide a number of different ecosystem services worldwide, including provision services such as food (Carrasquilla-Henao and Juanes, 2017) and wood (López-Angarita et al., 2016), supporting services (e.g. primary productivity), regulating services such as flood and erosion control (Brander et al., 2012), and cultural services (Costanza et al., 1997; Vo et al., 2012). However, despite global decreases in mangrove loss rate, mangroves are still being lost (Friess et al., 2020) primarily due to anthropogenic impacts, such as land-cover change, unsustainable aquaculture, pollution, and overfishing (Lotze, 2006; Halpern et al., 2008).

Juvenile and subadult fish use mangrove habitats as foraging areas (Green et al., 2012), shelter from predators (Laegdsgaard and Johnson, 2001; Nanjo et al., 2011; Grimm et al., 2020) or as nursery grounds, particularly in Caribbean islands (Nagelkerken et al., 2000) or where a mosaic of other habitats such as seagrass and coral reefs occur (Dubuc et al., 2019; Berkström et al., 2020). In contrast, adult fish use mangrove habitats mainly as feeding grounds to forage on juvenile fish prey (Nagelkerken et al., 2008), but also as spawning grounds (Blaber, 2000).

Studies of mangrove fish habitat use in the Caribbean have mainly focused on testing the nursery hypothesis (e.g. Mumby et al., 2004), and have been conducted primarily on Caribbean islands with low mangrove coverage (Castellanos-Galindo and Krumme, 2013), high water visibility, and where a complex seascape exists (e.g. Mumby et al., 2004; Nagelkerken et al., 2017). However, evidence for mangrove use by different fish stages (e.g. subadults and adults) in the Caribbean remain scarce. Mangroves also occur on the continental Caribbean coast, where geomorphological conditions differ from those present on islands. For example, on the Caribbean coast of Colombia, mangrove habitats can be found in lagoon systems, where turbidity is higher due to continental freshwater discharge, salinity fluctuates as a function of precipitation and, unlike on islands, the adjacent habitat mosaic non-existent or limited to one other habitat (Botero and Salzwedel, 1999; Marley et al., 2020). In such cases, mangroves in lagoon systems in the Caribbean share some characteristics with mangroves in the Indo-West Pacific, and other regions such as western Africa, Brazil and the eastern Pacific. Such characteristics include larger mangrove cover, turbid waters, and seasonal variation in salinity. At the same time, mangrove species composition and tidal amplitude in Caribbean lagoon systems resemble those

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of mangroves on Caribbean islands (Spalding et al., 2010). Mangrove habitats in macrotidal regions, such as the Indo-West Pacific, are not available throughout the full tidal cycle; therefore, fish only have limited temporal access to forage and shelter and they need to return to adjacent habitats, such as mudflats (Ellis and Bell, 2008; Igulu et al., 2014). As such, constantly inundated mangroves also provide continuous food accessibility compared to those with high tidal amplitudes (Nagelkerken et al., 2008). Recent studies in microtidal environments have shown the importance of adjacent habitats such as mudflats for both juvenile and adult fish (Marley et al., 2020) and the importance of mangrove habitats to support artisanal fisheries and food security (Sandoval Londoño et al., 2020). Studies conducted in coastal lagoon systems in the neo-tropics such as in Mexico have described fisheries aspects such as bycatch (Amezcuca et al., 2009) and the mangrove-fisheries relationships in several lagoon systems (Aburto-Orpeza et al., 2008; Carrasquilla-Henao et al., 2013), and the fish community structure and its relationship with mangrove ecology in both the Pacific (Flores-Verdugo et al., 1990) and Gulf of Mexico (Yáñez-Arancibia et al., 1988).

In Colombia, the Ciénaga Grande de Santa Marta (CGSM) is the most studied lagoon system from a mangrove ecology and fish ecology perspective (Castellanos-Galindo et al., 2021). In the early 1990s Santos-Martínez and Acero (1991) first studied the fish community of the system. In subsequent years the spatial distribution of fish (Rueda, 2001b), fish community structure (Rueda and Defeo, 2003), and gear selectivity (Rueda, 2007) have been assessed. While the connectivity between mangroves and coral reefs has been well documented and has shown that proximity to mangroves enhances coral reef fish populations (e.g. Nagelkerken et al., 2012; Olds et al., 2012; Martin et al., 2015), the connectivity between mangroves and mudflats in a macrotidal temperate system and a microtidal turbid estuary in Trinidad and Tobago have shown the importance of mudflats as fish habitat (Payne and Gillanders, 2009; Marley et al., 2020). However, trying to disentangle the importance of mangrove habitats and adjacent habitats by consistently sampling at different distances from mangroves remains a priority in microtidal continental tropical Caribbean lagoon systems and has not been investigated in Colombia.

The purpose of this study was to determine fish ecological interactions with mangrove habitats and adjacent habitats within a lagoon system in the Caribbean Coast of Colombia. Specifically, we asked whether fish abundance, fish biomass, fish diversity and fish community structure differ between mangrove habitats and mudflats. We hypothesized that abundance and diversity would be greater in mangrove habitats, since mangroves provide additional structured habitat for estuarine fish and could potentially host a higher density of juveniles (Laegdsgaard and Johnson, 2001). In contrast, we hypothesize that biomass would be higher in adjacent habitats (mudflats) further from mangroves compared to mangrove habitat since mangroves are important nursery habitats that can increase fish survival, growth and recruitment, and therefore enhance productivity in adjacent habitats (Mumby et al., 2004).

## 2. Methods

### 2.1. Study area

Ciénaga Grande de Santa Marta (CGSM) is a coastal estuarine lagoon complex, located on Colombia's Caribbean coast and it is part of the Magdalena river delta (Fig. 1). It is the largest lagoon of its type in the country, with an area of 1280 km<sup>2</sup>, and has historically been highly productive by sustaining artisanal fisheries (Botero and Salzwedel, 1999; Rueda and Defeo, 2003). However, catches have been decreasing over time due to higher fishing pressure and deteriorating conditions (Torres-Guevara et al., 2016; Rodríguez-Rodríguez et al., 2018). CGSM contains three main mangrove species, *Rhizophora mangle* (Red mangrove), *Avicennia germinans* (Black mangrove) and *Laguncularia*

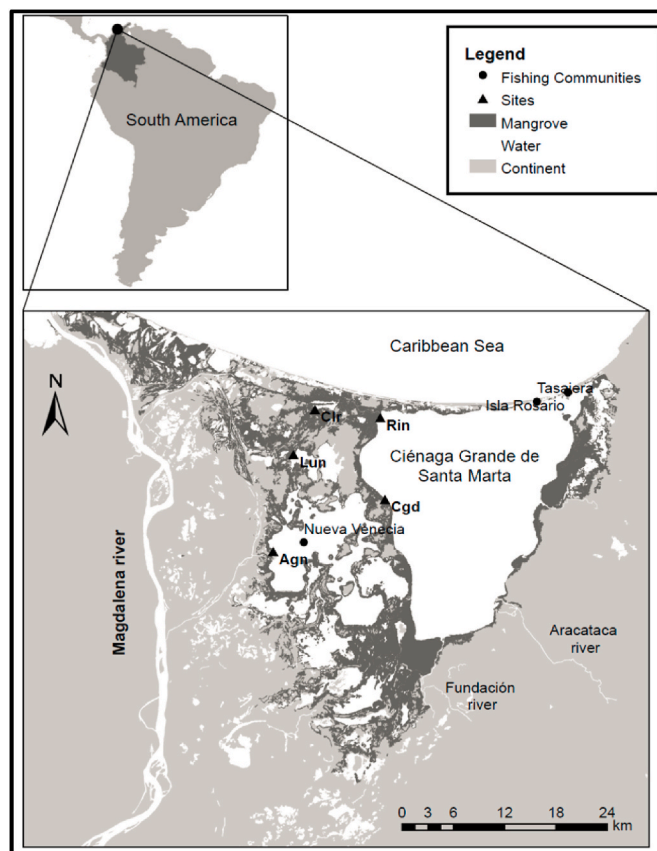


Fig. 1. Map of Ciénaga Grande de Santa Marta (CGSM) showing the five sampling sites (▲): Cgd = Caño Grande; Rin = Rinconada; Agn = Aguas Negras; Lun = Luna; and Clr = Ciénaga La Redonda.

*racemosa* (White mangrove) that surround the system almost entirely (Fig. 1). Mangrove cover was as high as 51,100 ha in the 1950s (Perdomo et al., 1999), but after a massive mortality event (see below) the coverage has only risen to ca. 39,500 (Ibarra et al., 2014). The system exchanges marine water through a mouth to the north, while fresh water enters the lagoon system from rivers that drain from a coastal mountain, Sierra Nevada de Santa Marta, and the Magdalena river from the east and southeast (Botero and Salzwedel, 1999). This ecosystem was declared a Biosphere Reserve by UNESCO and was included in the RAMSAR convention (Vilardy et al., 2011). Despite the importance of this ecosystem, it has been subject to a variety of anthropogenic disturbances, with negative impacts. Connections between the lagoon and the ocean, and the lagoon and the rivers, were temporarily interrupted by building a highway from Ciénaga to Baranquilla and by blocking freshwater flow from streams that fed the lagoon. As a result, the lagoon suffered hypersalinization, which in turn, caused high mangrove and fish mortality (Botero and Salzwedel, 1999; Perdomo et al., 1999). CGSM is also subject to high nutrient concentration runoff due to intensive agriculture surrounding the system, and has recently been strongly impacted by the lack of fresh water entering the system (INVEMAR, 2017). Although considerable effort has been put into restoration projects (Botero and Salzwedel, 1999), the system is continuously under anthropogenic pressure.

### 2.2. Sampling

Five study sites were selected (Fig. 1), all of which had mangroves, Caño Grande (Cgd), Rinconada (Rin), Ciénaga La Redonda (Clr), Aguas Negras (Agn) and Luna (Lun). Mangrove structure has been monitored for over a decade at four of these sites (Cgd, Rin, Agn, and Lun) by the

Institute of Marine and Coastal Research (INVEMAR) as part of the CGSM restoration program (Botero and Salzwedel, 1999).

Fish sampling occurred from May to August 2015. Cgd, Rin and Clr were sampled six times each; Agn and Lun were sampled five times each. A cycle (where all sites were sampled) lasted three consecutive days, whereby two sites were sampled per day. At each site three lines were set parallel to the edge of the mangroves at different distances to assess how fish abundance, biomass and diversity differed while moving away from mangrove habitats. Line one (Mangroves) was set at the edge of the mangroves, line two was set further (~250 m) away from mangroves and the third line was set even further (~400 m), the latter two were both mud habitats. These distances were chosen because many estuarine and mangrove related fish species have home ranges that do not go beyond 200 m and thus differences in habitat use may be observed at this scale, and because mangroves closer than 250 m from reefs enhance fish abundance relative to reefs further away from mangroves (Olds et al., 2012). Thus, over the field season, 15 lines were set in Agn and Lun and 18 in the remaining three sites for a total of 84 lines (sampling units).

A line consisted of three contiguous gillnet panels of different mesh sizes, small, medium and large, to control size and species selectivity. Each panel measured about 50 m in length and 1.5 m in height for a total length of 150 m. For sites Cgd, Rin and Clr, small, medium and large mesh sizes were 5.4 cm, 6.3 cm and 7.6 cm while for Agn and Lun mesh sizes were 5.1 cm, 6.9 cm and 7.6 cm. The slight differences in mesh sizes were due to two different fishing crews whom, given their geographic location within the lagoon, own nets with different mesh sizes. We intentionally opted to work with the mesh sizes available from the fishers' gears to engage them and provide additional income to the crews who helped throughout the sampling season.

Lines were soaked for six continuous hours from 7:00am to 1:00pm, but were checked and fish collected every 2 h. At each line, dissolved oxygen (DO), salinity, temperature, pH and turbidity (Secchi disk depth) were measured. All fish samples were stored in separate bags depending on site and habitat (Mangroves, 250 m or 400 m), and preserved in ice until stored and frozen in INVEMAR's facilities for later processing. Fish were identified to the lowest taxonomical level following [Carpentere's \(2002\)](#) keys for the Western Central Atlantic. In the lab, each individual was measured (Total length,  $\pm 0.1$  cm) and weighed (grams,  $\pm 0.1$  g). We classified fish as juveniles or adults based on length at maturity from local studies and/or reports when available, or from the database by [Froese and Pauly \(2021\)](#). Individuals that could not be measured because they were missing part of their bodies were classified as undetermined for maturity and were included in abundance and diversity analyses, but not in biomass data because measuring or weighing an organism with missing parts does not accurately represent its metrics and can cause biases in the dataset.

### 2.3. Site characteristics

The five sites differed in mangrove characteristics and water parameters. Mangrove density at each site was obtained from mangrove surveys conducted by [Ibarra et al. \(2014\)](#), the most updated data prior to our fish surveys.

The highest mangrove density was observed at Luna with 6425 trees  $\text{ha}^{-1}$  while Caño Grande had the lowest density (1533 trees  $\text{ha}^{-1}$ ). Caño Grande was dominated by *R. mangle*, while Rinconada, Cienaga La Redonda and Aguas Negras were dominated by *A. germinans* trees. In contrast, Luna was dominated by individuals of *L. racemosa* (Table 1).

We conducted nested (habitat within sites) linear models to determine whether water parameters varied across sites and between habitats within sites. A model validation process was conducted for each model ([Zuur et al., 2009](#)) and if necessary the response variable (i.e. environmental variable) was log10 transformed to normalize the residuals. No water parameters differed between habitats within sites, and only salinity and turbidity differed across sites. Salinity was lowest in Agn

**Table 1**

Mean ( $\pm$ SD) of the water parameters sampled over the sampling season and species specific mangrove density and total mangrove density at the five different sites. Cgd = Caño Grande; Rin = Rinconada; Clr = Ciénaga la Redonda; Agn = Aguas Negras; Lun = Luna. Superscripts show statistical differences across sites for the water parameters. All statistical differences where  $p < 0.001$ .

Sites	Cgd	Rin	Clr	Agn	Lun
<b>Water properties</b>					
Salinity (PSU)	36.70 <sup>c</sup> (0.66)	36.41 <sup>c</sup> (0.95)	37.73 <sup>c</sup> (5.62)	8.55 <sup>b</sup> (2.88)	51.88 <sup>a</sup> (5.42)
DO (mg/l)	6.96 (1.32)	6.59 (1.53)	7.1 (1.46)	6.86 (1.07)	6.8 (1.38)
Temp (°C)	31.78 (1.10)	30.82 (0.89)	31.44 (0.95)	32.36 (1.43)	32.77 (0.99)
Turbidity (cm)	30.00 <sup>c</sup> (6.64)	30.55 <sup>c</sup> (7.45)	28.33 <sup>c</sup> (5.69)	13.33 <sup>b</sup> (3.62)	19.33 <sup>a</sup> (1.76)
pH	8.71 (0.21)	8.75 (0.22)	8.5 (0.16)	8.88 (0.24)	8.42 (0.13)
<b>Mangrove density (trees <math>\text{ha}^{-1}</math>)</b>					
<i>R. mangle</i>	793	71	13	15	712
<i>A. germinans</i>	420	1193	1833	1885	213
<i>L. racemosa</i>	320	936	213	377	5500
<b>Total density</b>	<b>1533</b>	<b>2200</b>	<b>2059</b>	<b>2277</b>	<b>6425</b>

and highest in Lun, while turbidity was lowest in Rin, and highest in Lun and Agn, respectively (Table 1). Since the environmental characteristics of each site were unique we decided to use site and habitats within sites as our explanatory variables for all statistical models.

### 2.4. Data analysis

We used fish abundance, fish biomass, species richness and Shannon diversity as our response variables for both total fish and juvenile fish. Juveniles were subsetted by selecting all fish that were classified as juveniles from the complete dataset. We calculated fish abundance and juvenile abundance as the number of fish caught over a period of 6 h for each line. Similarly, we calculated total fish biomass and juvenile fish biomass per line as the total weight of all fishes caught during the 6-h period for each line. Total fish diversity and juvenile fish diversity were calculated based on the Shannon diversity index because it is less sensitive to rare species than other diversity indices ([Morris et al., 2014](#)). Finally, total species richness and juvenile species richness were calculated as the number of species present in each line.

#### 2.4.1. Statistical models

Fish abundance was modeled with a negative binomial distribution to account for the overdispersion in the count data which cannot be captured by the Poisson distribution ([Zuur et al., 2009](#)). Fish biomass and Shannon diversity were modeled with linear models, but biomass was log transformed to account for the right skewness. Species richness was modeled using a Poisson distribution as species richness are count data and we did not find evidence of overdispersion.

In all cases we first constructed a full model that included both explanatory variables and an interaction term. The significance of the interaction was evaluated in each model and discarded if no interactions between variables were found. To finalize the modeling process we verified that the model was a good fit by plotting the residuals against fitted values and against all covariates and assessed the patterns in the plots ([Zuur and Ieno, 2016](#)). All models and statistical analyses were conducted in the statistical package R ([R Core Team, 2020](#)).

#### 2.4.2. Multivariate analysis

We used PERMANOVA with site and habitat as fixed effects to determine how fish community structure differed across these two variables. The interaction between site and habitat was not significant

and thus removed from the analysis. Prior to analyzing the fish abundance matrix we eliminated the rare species (i.e. abundance <5) from the dataset and conducted a Hellinger transformation on the abundance data because this transformation reduces the effect of low abundance species relative to the higher abundance species and accounts for differences in sample sizes, both of which were present in our dataset. (Legendre and Gallagher, 2001; Juniper et al., 2013). Next, we calculated pairwise comparisons in sites and habitats separately to determine where the fish composition differed and used non-metric multidimensional scaling (NMDS) to visualize the ecological distances within sites and habitats. Finally, a similarity percentage analysis (SIMPER), after calculating Bray Curtis dissimilarity, was used to determine the species that had the highest contributions for the differences in sites and habitats respectively. All multivariate analysis were done using the 'Vegan' package (Oksanen et al., 2020) in the R statistical package (R Core Team, 2020).

### 3. Results

#### 3.1. Fish abundance

A total of 1459 individuals from 33 different species and 19 families were caught throughout the sampling season, 67.38% of which were classified as juveniles according to their length at maturity. *Anchovia clupeioides* (32.2%), *Cathorops mapale* (20.6%), *Elops saurus* (11.8%), *Megalops atlanticus* (8.4%) and *Mugil incilis* (7.7%), were the five most abundant species across all sites and together represented ~80% of the

total catches in the lagoon system. All the species caught except for one (*Lutjanus* sp.) were either marine-estuary (98%) or freshwater (2%) species (Table 2).

Fish abundance was considerably higher in Agn relative to the other four sites for both total fish ( $\bar{x} = 50.7 \pm SE = 6.46$  fish/net) and juvenile fish ( $\bar{x} = 29.5 \pm SE = 2.69$  fish/net) while the fewest fish were caught in Clr with an average of 3.06 fish/net (SE = 0.51) for total fish and 2.62 fish/net (SE = 0.55) for juveniles fish, respectively (Fig. 2A and B). In both cases the average number of fish caught in Cgd and Rin was not statistically different, but Clr and Agn did show statistical differences in total fish abundance ( $p < 0.05$ ). Average fish abundance in Lun ( $\bar{x} = 9.4 \pm SE = 1.8$  fish/net) was significantly lower than Cgd ( $\bar{x} = 16.1 \pm SE = 2.77$  fish/net,  $p = 0.01$ ) for total fish, but not when accounting only for juveniles ( $\bar{x} = 8.8 \pm SE = 1.72$  fish/net,  $p = 0.29$ ). Although there was a strong site effect in fish abundance, a habitat effect was also present at most sites for total fish. In general, fish abundance was not statistically different in Mangrove relative to 250 m. However, fish abundance in Mangrove was significantly lower than in 400m. Fish abundance was 45% higher in 400m than in Mangrove for total fish, and 42% higher for juveniles. Higher fish abundance in 400m compared to Mangrove was observed and significant for total fish in Cgd ( $\bar{x}_{total} = 23.2 \pm SE = 5.82$  fish/net vs  $\bar{x}_{total} = 9.83 \pm SE = 1.92$  fish/net), Lun ( $\bar{x}_{total} = 13 \pm SE = 4.23$  fish/net vs  $\bar{x}_{total} = 7 \pm SE = 1.3$  fish/net), and Rin ( $\bar{x}_{total} = 16.8 \pm SE = 4.23$  fish/net vs  $\bar{x}_{total} = 10.3 \pm SE = 2.79$  fish/net) while not significant in Agn and Clr. Although 250m was captured as significantly different to 400 m by the negative binomial model for total fish, this was

**Table 2**

Total fish abundance, relative abundance, total weight and minimum and maximum length by species and maturity stage (i.e. Adults and Juveniles) collected across all sites during the sampling season in Ciénaga Grande de Santa Marta, Colombian Caribbean. Environment categories are as follows ME = Marine-estuarine, M = Marine and F = Freshwater. Undetermined are those individuals that were counted, but not measured because they were missing parts of their body.

Species	Family	Environment	Adults		Juveniles		Undetermined	Total abundance	Total weight (g)
			Abundance	Length	Abundance	Length			
				(cm)		(cm)			
				min - max		min - max			
<i>Anchovia clupeioides</i>	Engraulidae	ME	219	15.5–19.9	230	2.2–15.4	21	470	9667.3
<i>Cathorops mapale</i>	Ariidae	ME	163	16.4–26.8	135	11.1–16.3	3	301	14183.7
<i>Elops saurus</i>	Elopidae	ME			171	14.1–45.8	1	172	15095
<i>Megalops atlanticus</i>	Megalopidae	ME			123	18–55.1		123	28668
<i>Mugil incilis</i>	Mugilidae	ME	2	30.6–32.3	110	2.7–28.8	1	113	10065.2
<i>Ariopsis</i> sp	Ariidae	ME	20	30–37.4	63	13.1–29.9		83	16161
<i>Micropogonias furnieri</i>	Sciaenidae	ME			34	10.5–21.8		34	2473.2
<i>Oligoplites palometa</i>	Carangidae	ME	14	17.2–26.5	10	13.5–25.7		24	2040.4
<i>Strongylura marina</i>	Belonidae	ME	20	32.5–62.5				20	3442.4
<i>Eugerres plumieri</i>	Gerreidae	ME	9	20.1–25.1	10	11.5–19		19	1790.6
<i>Cetengraulis edentulus</i>	Engraulidae	ME			12	13.6–15.6		12	611.9
<i>Stellifer venezuelae</i>	Sciaenidae	ME	4	10.8–14.7	5	12.5–16.1	1	10	251.7
<i>Mugil liza</i>	Mugilidae	ME	3	36.7–47.1	6	11.9–34.5		9	2745.6
<i>Achirus lineatus</i>	Achiridae	ME	5	9.9–18.1	3	9–13.2		8	393.8
<i>Trachelyopterus insignis</i>	Auchenipteridae	F	1	17.6–17.6	7	14.5–18		8	329.2
<i>Leporinus muyscorum</i>	Anostomidae	F	1	26.3–26.3	6	22–26.8		7	991.2
<i>Caranx hippos</i>	Carangidae	M			7	13.1–17.9		7	448.4
<i>Bairdiella ronchus</i>	Sciaenidae	ME	3	16.7–19.9	4	12.4–13.7		7	336.2
<i>Diapterus rombeus</i>	Gerreidae	ME			6	12–13.1		6	171.1
<i>Ctenolucius hujeta</i>	Ctenoluciidae	F	4	17.9–22.2	1	13.1–13.1		5	208.2
<i>Gerres cinereus</i>	Gerreidae	ME	1	17.2–17.2	4	15.7–19.6		5	361.8
<i>Oligoplites saurus</i>	Carangidae	ME	1	23.2–23.2	1	22.5–22.5		2	155
<i>Caquetaia kraussii</i>	Cichlidae	F	1	14.1–14.1	1	15.8–15.8		2	128.8
<i>Oreochromis niloticus</i>	Cichlidae	F			2	19.2–19.5		2	343
<i>Centropomus undecimalis</i>	Sciaenidae	ME			2	22–22.2		2	199.6
<i>Astyanax fasciatus</i>	Characidae	F	1	16.2–16.2				1	66
<i>Curimata mivartii</i>	Curimatidae	F			1	21.4–21.4		1	95.2
<i>Prochilodus magdalenae</i>	Prochilodontidae	F	1	26.6–26.6				1	253.6
<i>Mugil curema</i>	Mugilidae	ME			1	16.7–16.7		1	34.9
<i>Oreochromis</i> spp	Cichlidae	F	1	20.3–20.3				1	147.7
<i>Diapterus auratus</i>	Gerreidae	ME			1	13.8–13.8		1	42.5
<i>Lutjanus</i> sp	Lutjanidae	M	1	22.2–22.2				1	145.7
<i>Pimelodus blochii</i>	Pimelodidae	F			1	17.5–17.5		1	33.3

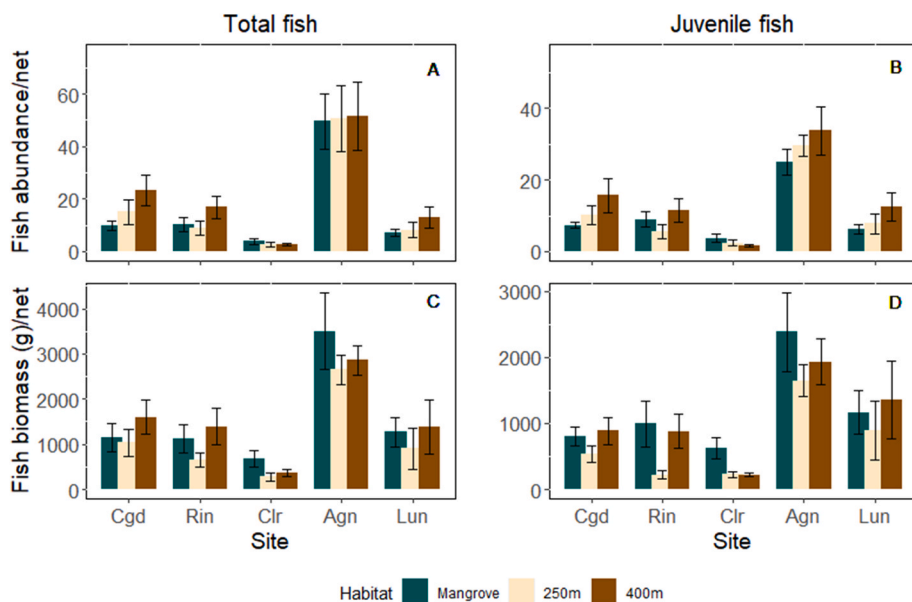


Fig. 2. Mean fish abundance for total fish (A) and juvenile fish (B) and mean fish biomass for total fish (C) and juvenile fish (D) for the three sampled habitats across the five sites. Error bars represent estimated standard errors. Cgd = Caño Grande; Rin = Rinconada; Agn = Aguas Negras; Lun = Luna; and Clr = Ciénaga La Redonda. Habitats are defined as: Mangrove = lines set at the edge of the Mangrove; 250 m = lines set approximately 250 m away from Mangrove; 400 m = lines set approximately 400 m away from Mangrove.

driven by Rin whereby 250m had fewer fish ( $\bar{x}_{\text{total}} = 6.17 \pm \text{SE} = 2.18$  fish/net) than 400m ( $\bar{x}_{\text{total}} = 11.8 \pm \text{SE} = 3.39$  fish/net) (Fig. 2A and B).

### 3.2. Fish biomass

The total fish biomass collected throughout the field season was 112.08 kg while juvenile biomass was 78.55 kg or about 70% of the total weight of the fish caught. Mean fish biomass from all samples ( $n = 84$ ) was  $1.35 \text{ kg} \pm (\text{SE} = 0.11)$ . However, a large variation was observed across lines ranging from 12.2 g in 400 m habitat to 64.46 kg in Mangrove habitat. Tarpon (*M. atlanticus*) was the species with the highest total biomass (28.67 kg) representing 25.6% of the total biomass. *Ariopsis* sp. (14.4%), *E. saurus* (13.5%), *C. mapale* (12.7%), *M. incilis* (8.9%), and *A. clupeioides* (8.6%) together with Tarpon accounted for 83.81% of the total biomass across all samples.

Fish biomass differed across sites, but there were no significant differences between habitats in any of the sites for both total fish and juvenile fish. Agn had the highest biomass in both cases ( $\bar{x}_{\text{total}} = 3002 \text{ g} \pm \text{SE} = 316 \text{ g}$  and  $\bar{x}_{\text{juvenile}} = 1990 \text{ g} \pm \text{SE} = 239 \text{ g}$ ) and was significantly different than the other four sites. In contrast, Clr had the lowest average fish biomass over the sampling period with 444 g ( $\text{SE} = 83.1$ ) and 374 g ( $\text{SE} = 77.3$ ) respectively. For total fish, Cgd presented higher fish biomass than Clr ( $p < 0.05$ ), but this same pattern was not observed for juvenile fish. Although not statistically significant fish biomass was usually higher in Mangrove and 400 m relative to 250 m for both total fish and juvenile fish (Fig. 2C and D).

### 3.3. Fish diversity

Species richness by net ranged from 1 to 12 species for total fish and from 1 to 9 species for juvenile fish, suggesting that some species were only present as adults in the system. Similarly, Shannon diversity values ranged from 0 (multiple lines) meaning that only one species was reported for a given line to 2.11 for total fish and 2.03 for juvenile fish. Fish diversity (richness and Shannon) differed across sites, but not across habitats for both total fish and juvenile fish. Species richness was highest in Agn ( $\bar{x}_{\text{total}} = 8.07 \pm 0.55$  and  $\bar{x}_{\text{juvenile}} = 6.73 \pm 0.42$ ) and lowest in Clr ( $\bar{x}_{\text{total}} = 2 \pm 0.26$  and  $\bar{x}_{\text{juvenile}} = 1.81 \pm 0.42$ ). Agn species richness was significantly higher compared to all other sites except for Cgd, while Clr and Lun where significantly lower than Cgd, Rin and Agn, but not between them for total fish and juvenile fish.

Shannon diversity index showed similar results to species richness

with Agn having the highest values ( $\bar{x}_{\text{total}} = 1.56 \pm 0.12$  and  $\bar{x}_{\text{juvenile}} = 1.55 \pm 0.09$ ) and Clr the lowest ( $\bar{x}_{\text{total}} = 0.53 \pm 0.12$  and  $\bar{x}_{\text{juvenile}} = 0.44 \pm 0.12$ ). However, Lun also presented low and similar values to Clr. As a result, in both cases Agn, Cgd and Rin were not significantly different among them, but were significantly higher than Clr and Lun (Fig. 3).

### 3.4. Fish community structure

The PERMANOVA results revealed that the fish community structure differed among sites and habitats ( $p < 0.05$ ). Although there was a lot of overlap amongst samples and thus in species composition across sites (Fig. 4A), a pairwise comparison showed significant differences across all sites, except for Clr and Lun, which suggests that both sites had similar fish communities. Average dissimilarity across sites varied from 72% between Cgd and Rin to 87% between Rin and Clr according to the SIMPER analysis. *C. mapale* contributed highly to the dissimilarities of Cgd and Rin (26.9%) and Cgd and Clr (32.9%) given its higher abundance in Cgd with respect to the other sites. In contrast, *A. clupeioides* was the most important species driving community differences in all Agn comparisons due to its overwhelmingly higher abundance at this site relative to the other four sites. The Tarpon, *M. atlanticus*, contributed to the dissimilarity between Lun and Cgd (20%) and Rin (22.6%) given the higher number of individuals caught in Lun compared to the other two sites (Table 3 and Supplemental material).

Mangrove and 250 m habitats ( $df = 1$ ,  $f = 2.35$ ,  $p < 0.05$ ) and Mangrove and 400 m habitats ( $df = 1$ ,  $f = 2.25$ ,  $p < 0.05$ ) showed significantly different fish species composition according to the pairwise comparisons while 250 m and 400 m had similar fish community structure ( $p > 0.05$ ). Despite the high degree of overlap in species composition for each sample (Fig. 4B), some species contributed to the dissimilarity across habitats. Tarpon, which had higher abundance in Mangrove, contributed to 16% and 15.4% of the dissimilarity between Mangrove and 250 m and Mangrove and 400 m, respectively. Conversely, *A. clupeioides* had a higher abundance away from mangroves and as a result also contributed to the differences in community structure between Mangrove and the two mud habitats (Table 3).

## 4. Discussion

We tested the hypothesis that fish abundance and diversity would decrease, while biomass would increase, as we sampled mud habitats

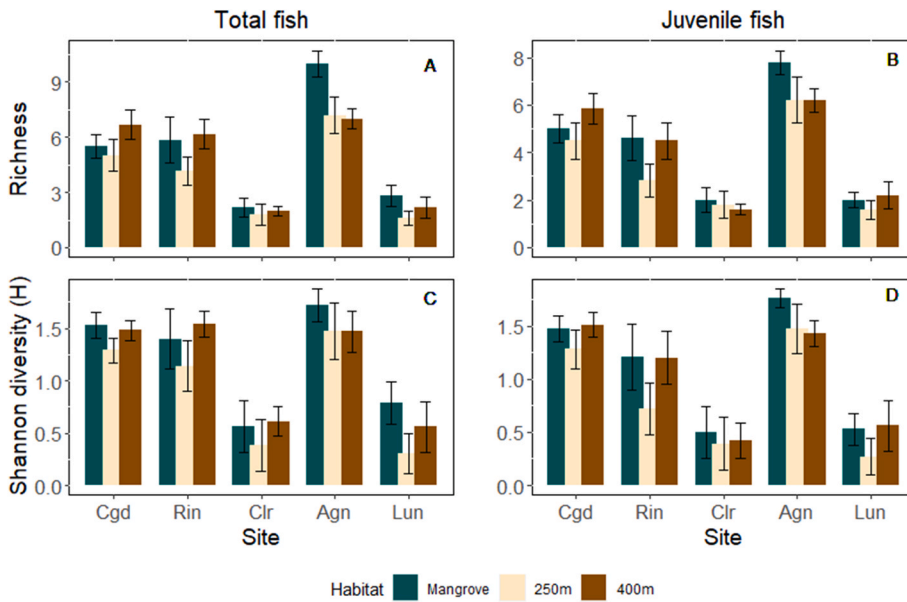


Fig. 3. Mean species richness for total fish (A) and juvenile fish (B) and mean Shannon Diversity for total fish (C) and juvenile fish (D) for the three sampled habitats across the five sites. Error bars represent estimated standard errors. Cgd = Caño Grande; Rin = Rinconada; Agn = Aguas Negras; Lun = Luna; and Clr = Ciénaga La Redonda. Habitats are defined as: Mangrove = lines set at the edge of the Mangrove; 250 m = habitat lines set approximately 250 m away from Mangrove; and 400 m lines set approximately 400 m away from Mangrove.

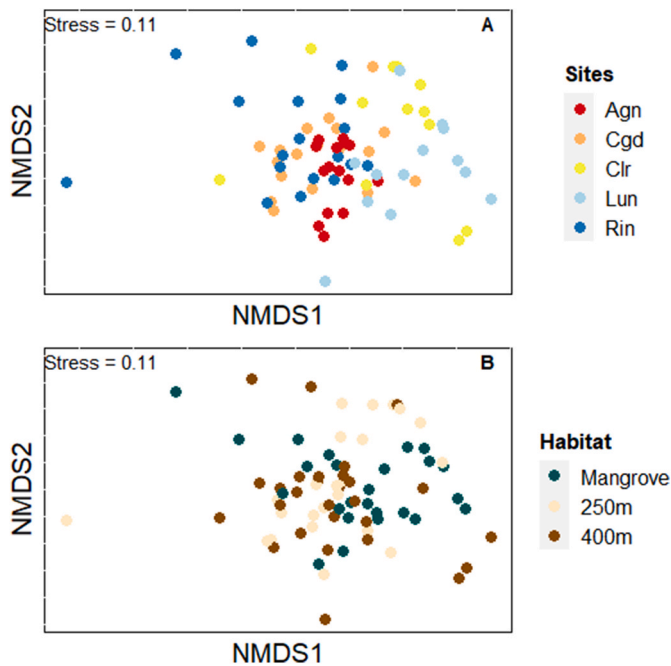


Fig. 4. Non Metric Multidimensional Scaling of fish abundance excluding rare species (i.e. abundance <5) for sites (A) and habitats (B) in Ciénaga Grande de Santa Marta. Cgd = Caño Grande; Rin = Rinconada; Agn = Aguas Negras; Lun = Luna; and Clr = Ciénaga La Redonda. Habitats are defined as: Mangrove = lines set at the edge of the Mangrove; 250 m = habitat lines set approximately 250 m away from Mangrove; and 400 m lines set approximately 400 m away from Mangrove.

further away from mangroves. These predictions were based on the assumption that mangrove habitats are more structurally complex (Cocheret de la Morinière et al., 2004) and provide better feeding grounds and protection than adjacent mudflats and thus should be more highly used by fish, especially juveniles. However, we found the opposite trend for fish abundance, whereby there was a slight increase in fish abundance of total fish and juvenile fish from mangrove to the mudflat habitats further away from mangroves. Our results agree with findings in two other study areas with similar turbid conditions to CGSM. In Gazi

Bay, Kenya fish density was lower in mangrove habitats compared with mudflats (Huxham et al., 2004), and in the Gulf of Praria in the eastern Caribbean the abundance of juvenile fish was higher in mudflats compared to mangroves (Marley et al., 2020). Like in our study, these sites had low visibility and thus the advantages of enhanced structure provided by mangroves as a mechanism to avoid predators could be offset by lower visibility further away from mangroves (Huxham et al., 2004). Similarly, in an estuary in Thailand, Ikejima et al. (2003) found no differences in fish density between mangrove habitat and sandy habitats while Payne and Gillanders (2009) found that fish abundance varied across estuaries but not between mangrove and mudflats. Conversely, our findings differ from others in close geographic regions in the Caribbean where fish abundance has been found to be higher in mangroves compared with adjacent habitats on an island (Nagelkerken et al., 2001) and in Australia where marine reserve performance is enhanced when reef proximity to mangroves is 250 m (Olds et al., 2012) and 500 m (Martin et al., 2015). Our results also differ from a study conducted in Tanzania where fish density was found to be higher in mangroves than in adjacent habitats (Laegdsgaard and Johnson, 2001). Thus, despite our geographical proximity to the study by Nagelkerken et al. (2001), their mangrove geomorphological settings differed from ours because the mangroves found on islands are non-estuarine and not under seasonally varying hydrological conditions. Indeed, the importance of coastal habitats for fish must always be put into context as geomorphology and environmental variables can define how habitats are used by fish (Bradley et al., 2020). While research in more stable conditions can partially explain why clear water non-estuarine mangroves on Caribbean islands have been classified as important nurseries for reef species and support higher abundance of fish relative to other habitats (Barnes et al., 2012), other factors such as proximity to the mouth of the estuary, the size of the estuary and the catchment can explain fish composition in turbid estuaries (Henderson et al., 2021).

We found no differences in species richness and diversity in mangroves compared to the mudflat habitats although mangroves have high structural complexity which has been shown to be a good predictor of species richness and abundance (Ferrari et al., 2016). While some studies have shown that mangroves attract more fish and thus increase diversity compared to mudflats that present more predatory risky habitats (Laegdsgaard and Johnson, 2001), other studies in turbid estuaries have shown no differences in diversity between mangroves and mudflat habitats (Payne and Gillanders, 2009; Marley et al., 2020). Since many fish are visual predators and the turbidity in CGSM is high, the use of

**Table 3**

Total fish abundance of the most common species (i.e. total abundance >5) caught in Ciénaga Grande de Santa Marta by site and habitat during the sampling period. Sites are as follows: Cgd = Caño Grande; Rin = Rinconada; Agn = Aguas Negras; Lun = Luna; and Clr = Ciénaga La Redonda. Habitats are defined as: Mangrove = lines set at the edge of the Mangrove; 250 m = habitat lines set approximately 250 m away from Mangrove; and 400 m = lines set approximately 400 m away from Mangrove.

species	Sites					Habitats		
	Cgd	Rin	Clr	Agn	Lun	Mangrove	250m	400m
<i>Anchovia clupeioides</i>	45	41	2	336	46	111	176	183
<i>Cathorops mapale</i>	115	40	2	131	13	74	102	125
<i>Elops saurus</i>	32	31	16	72	21	43	54	75
<i>Mugil incilis</i>	19	11	13	66	4	30	29	54
<i>Megalops atlanticus</i>	8	6	10	43	56	75	22	26
<i>Ariopsis sp</i>	11	18	1	52	1	33	23	27
<i>Micropogonias furnieri</i>	21	13	0	0	0	1	10	23
<i>Strongylura marina</i>	4	14	0	2	0	2	9	9
<i>Cetengraulis edentulus</i>	0	12	0	0	0	0	1	11
<i>Oligoplites palometa</i>	5	11	2	6	0	5	5	14
<i>Eugerres plumieri</i>	8	5	5	1	0	8	2	9
<i>Achirus lineatus</i>	0	0	0	8	0	7	1	0
<i>Trachelyopterus insignis</i>	0	0	0	8	0	4	1	3
<i>Mugil liza</i>	7	0	0	2	0	5	2	2
<i>Leporinus muyscorum</i>	0	0	0	7	0	5	1	1
<i>Stellifer venezuelae</i>	1	1	1	7	0	1	3	6
<i>Diapterus rombeus</i>	6	0	0	0	0	0	3	3
<i>Caranx hippos</i>	1	6	0	0	0	2	2	3
<i>Gerres cinereus</i>	0	5	0	0	0	5	0	0
<i>Bairdiella ronchus</i>	1	1	0	5	0	1	3	3
<i>Ctenolucius hujeta</i>	0	0	0	5	0	3	2	0

mangroves as shelter from predators may not be as important as in clear water mangroves and therefore mudflats may also protect from potential predators (Marley et al., 2020).

The proportion of juvenile fish was high and consistent across habitats likely explaining the lack of relationship between fish biomass and habitats. If fish biomass increased away from the mangrove this would imply that a higher number of adults (larger fish) would also be present in mudflat habitats. Mangrove habitats on Caribbean islands have been shown to be important nurseries for reef fish based on adult fish density in adult habitats (coral reefs) as a function of distance to nursery habitats (Nagelkerken et al., 2017) and to enhance biomass in coral reefs (Mumby et al., 2004). In contrast, and similar to our results, fish biomass in a turbid Caribbean ecosystem was similar between mangrove fringe areas and mudflats suggesting that in turbid conditions mudflats may be as important as more structurally complex habitats (Marley et al., 2020). Similarly, a study in the Gulf of Urabá showed the importance of mangroves for several fish species caught in mudflats at some distance from mangrove, between 800 m and 1500 m (Sandoval Londoño et al., 2020). A possible explanation is that the lagoon system's seascape contains less habitat variability (between mangrove and mudflats) compared to other areas such as Caribbean islands and the Bazaruto archipelago in Mozambique where mangroves, seagrass and coral reefs create a complex habitat mosaic that when in proximity, generates crucial connectivity among habitats for fish (Mumby et al., 2004; Nagelkerken et al., 2017; Berkström et al., 2020). Moreover, environmental conditions where different habitat types are located may have a higher influence on structuring fish assemblages than the habitat itself, especially for juvenile fish (Bradley et al., 2019). Alternatively, the whole lagoon regardless of habitat, may be acting as a nursery for many of the species observed in the study. Previous studies in the CGSM have collected fish larvae of many species caught as sub adults and adults in this study, and have characterized the lagoon as a nursery area (Criales et al., 2002). Nonetheless, some species like *Ariopsis sp.*, *Eugerres plumieri* and *Cathorops mapale* are caught as both adults and juveniles suggesting that the lagoon is also habitat for adult individuals of some species (INVEMAR, 2017).

Our smallest mesh size was larger than many other studies which have used smaller mesh sizes to capture smaller fish (e.g. Green et al., 2012; Marley et al., 2020). As a result, we are missing the lower fish size

end of the spectrum in our study, but this allowed us to closely work with community members and engage them in research activities. Nonetheless the high proportion of juveniles caught provides insight as to how the CGSM lagoon is used by both adults and juvenile fish and highlights the importance of fisheries management to reduce catch of fish prior to maturing as a mechanism to return to sustainable stocks, especially for estuarine species. However, decreasing fishing pressure in the system can be problematic as it is the only way of subsistence for most people who live in the villages surrounding CGSM (Torres-Guevara et al., 2016; Carrasquilla-Henao et al., 2019). Studies that have demonstrated the importance of mangroves as nurseries have used smaller mesh size gears that catch younger fish (Crona and Rönnbäck, 2007) or visual census techniques whereby the size of fish is determined by trained divers (Barnes et al., 2012; Nagelkerken et al., 2017). Such juveniles likely only use these habitats until an ontogenetic shift occurs. While very small fish may not move from their nursery habitat, larger juvenile fish can move among habitats. There has also been some debate on the proper method to sample fishes in mangrove habitat given its structural complexity (Faunce and Serafy, 2006; Wang et al., 2009). Soaking gillnets for 6 h on the edge of the mangrove allows us to capture fish that are moving in and out of the mangroves allowing inferences about the use of mangroves by fish (e.g., as feeding ground or shelter) given the microtidal regime in the Caribbean. In macrotidal mangrove systems different passive fishing gears are deployed at high tide and fish collected when the tide has ebbed (e.g., Green et al., 2012), but this is not possible in microtidal environments where visual censuses are frequently used. Alternatively, sampling with underwater cameras inside the prop-roots can provide valuable information on the abundance and diversity of species that use mangroves (Ellis and Bell, 2013; Sheaves et al., 2016). Recently, underwater video sampling has shown that fish usually use the edge of the mangrove and only move into the prop roots for food or shelter from predators (Dubuc et al., 2019), suggesting that using fishing gear at the edge of the mangroves is an adequate technique to catch fish that use mangrove habitats. Unfortunately, underwater video sampling is ineffective in a high turbid system like CGSM, where visibility is low.

Unlike habitats, sites showed differences in abundance, diversity and biomass suggesting the importance of spatial structure in the lagoon system as previously evaluated using a geostatistical approach (Rueda,

2001a). Of the environmental variables measured during fishing, only turbidity and salinity differed significantly across sites (Table 1). Although turbidity was higher in Agn and Lun because of their proximity to freshwater channels (INVEMAR, 2017), turbidity was high across all sites; a common characteristic of mangrove estuaries (Nagelkerken et al., 2008). Turbid waters can protect juvenile fish from predators because of limited visibility (Blaber, 2013), which can explain the high number of juveniles we found across all sites. However, fish abundance across sites differed considerably, especially between the two sites with the highest turbidity (Agn and Lun), but with the highest salinity difference. As a result, we consider salinity to be the major driver of spatial variation. In fact, earlier fish characterizations in the CGSM have shown that salinity was an important driver of abundance and diversity (Santos-Martínez and Acero, 1991). In general, most studies conducted in estuarine-mangrove habitats have found that fish abundance and metrics of fish diversity such as species richness (Sosa-López et al., 2006) and fish biomass (Lorenz, 1999) are negatively related to salinity. The higher abundance and diversity at lower salinities highlights the importance of brackish waters as hotspots for fish in tropical estuaries (Sosa-López et al., 2006) because a number of fish follow freshwater discharges into estuarine habitats (Barletta et al., 2003) as was observed in Agn where freshwater fish were caught. While estuarine fish can tolerate fluctuating salinities given their euryhaline conditions, coping with high salinities (i.e. > 40PSU) generates physiological stress that many fish species avoid by migrating to lower salinities areas (Cowan et al., 2012) which can explain the low abundance of fish found in Lun.

Several fish assemblages have also been found to vary with salinity when analyzed seasonally, where wet and dry seasons alter freshwater inflow generating salinity gradients, including in Brazil (Barletta et al., 2005), the Embley estuary in Australia (Barletta and Blaber, 2007), in Florida (Rehage and Loftus, 2007), and the Terminos lagoon in Mexico (Ramos-Miranda et al., 2005). While a salinity seasonality has been observed in the CGSM and although our study was limited to the minor rainy and minor dry season (Rueda, 2001b), there was little temporal variation in salinity in our results. In contrast, there was substantial spatial variation in salinity whereby Agn had consistently mesohaline conditions (mean = 8.5PSU), Lun hypersaline conditions (mean = 51.9PSU) and marine conditions in the remaining sites (Table 1). The most common species found in hypersaline conditions was *M. atlanticus*, the Tarpon, which has a higher salinity tolerance than other species in the estuary (Adams and Cooke, 2015) and was only found in the juvenile phase therefore contributing to the high overall proportion of juveniles observed. As long as CGSM continues to be under high anthropogenic pressure due to nutrient rich water discharge and an altered hydrological cycle that increases salinity to detrimental levels for fish, the full potential of mangroves as important fish habitats may not be clearly teased apart since the presence of mangrove habitats is not sufficient to ensure healthy fish populations under poor water quality conditions (Vidy, 2000). Moreover, the diversity of meiofauna, food for many estuarine fishes, has been shown to decrease in disturbed mangrove areas compared to undisturbed ones (Carugati et al., 2018).

Fish assemblages across habitats were driven by two species, Tarpon and Anchovy (*A. clupeioides*) which were more frequent in Mangrove, and 250 m and 400 m, respectively. Tarpon have been classified as obligate mangrove users as juveniles in other mangrove settings in the Caribbean (Wilson et al., 2019). The higher abundance of Tarpon in Mangrove combined with the fact that mostly juvenile individuals were captured in our study suggests that the mangroves in CGSM are critical habitats for this species. However, juvenile Tarpon have been reported to use multiple other habitats including salt marshes and stagnant pools amongst others (Adams and Cooke, 2015). Conversely, Anchovy is a more pelagic species that due to its schooling behavior may not require structurally complex habitats like Tarpons do. According to our results other species seem to use mangroves and mudflat habitats in similar ways suggesting some level of connectivity between these habitats. However, the connectivity between mangroves and mudflats in

simplified seascapes with microtidal and turbid conditions requires further research as seascape ecology has focused on more complex habitat arrays. Nonetheless, efforts to conserve mangroves should continue since healthy mangroves maintain high diversity and ecosystem function (Carugati et al., 2018) and contribute to mitigate global climate change by sequestering carbon dioxide (Taillardat et al., 2018). As such, the recent global declines in mangrove loss rate is thus encouraging (Friess et al., 2020). However, efforts to conserve adjoining mudflats, and thus the entire estuary should be equally important to maintain healthy fish communities in estuarine ecosystems (Marley et al., 2020). The CGSM is the largest lagoon system in Colombia and was once highly productive in terms of fish biomass providing subsistence fisheries to many locals who make their living exclusively from the system (Rueda et al., 2011). However, catches and fish sizes have declined over time according to fishers' knowledge (Carrasquilla-Henao et al., 2019). We conclude that ecosystem-level conservation strategies must continue to be implemented in order to preserve fish populations and mangrove habitats.

Since this is one of the first studies to explore the importance of mangrove and adjacent habitats in turbid estuarine lagoon systems in the Caribbean, we recommend more studies in similar settings. For fish in the CGSM, we conclude that mangrove habitats are generally used indistinctly from mudflat habitats, although a few species did show some preference for some specific habitats. Instead, sites, likely driven by salinity differences, are important drivers for fish abundance, diversity, biomass and community structure for both total fish and juvenile fish. Although abiotic conditions in the CGSM vary seasonally, some salinity values observed were higher than previously observed in the system. As a result, these high values coupled with other anthropogenic activities may be hampering our ability to observe the benefits of mangroves as critical habitats for fish. Finally, the high proportion of juveniles relative to adults across the whole system is of concern, particularly for estuarine species that live in the estuary year round. Thus, we suggest implementing fishery management strategies that allow juvenile fishes to reach maturity and reproduce whilst still allowing the resources to be exploited as soon as possible to mitigate the impacts that the system is suffering.

#### CRediT authorship contribution statement

**Mauricio Carrasquilla-Henao:** Writing – original draft, Investigation, Formal analysis, Conceptualization. **Mario Rueda:** Writing – review & editing, Resources. **Francis Juanes:** Writing – review & editing, Supervision, Resources, Funding acquisition.

#### Declaration of competing interest

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

#### Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2022.108090>.

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