

# **Mangrove or mudflat: prioritising fish habitat for conservation in a turbid tropical estuary**

Running page head: Prioritising mangrove or mudflat fish habitats

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1 **Abstract**

2 Mangrove habitats are typically the focus of conservation efforts in tropical estuaries because  
3 their structural complexity is thought to support greater biodiversity and nursery function than  
4 unvegetated habitats. However, evidence for this paradigm has been equivocal in turbid tropical  
5 estuaries where unvegetated mudflats are also highly productive. The present study compared the  
6 community composition, biodiversity, nursery-role and commercial fish biomass in two  
7 mangrove habitats and one mudflat habitat in the Gulf of Paria, Trinidad. A total of 12 705  
8 fishes, comprising 63 species from 26 families, were sampled in mangrove creeks, seaward  
9 mangrove fringe and the subtidal margin of an intertidal mudflat from June 2014 to June 2015.  
10 The composition of the creek and mudflat communities were distinct, while the mangrove fringe  
11 community resembled the mudflat more than it did the mangrove creeks. Mean species richness  
12 (MSR), total species richness (TSR) extrapolated from species accumulation curves, and juvenile  
13 species richness (JSR) were significantly greater in the mudflat (MSR =  $11.4 \pm 1.0$ ; TSR =  $75 \pm 14$ ;  
14 JSR =  $9.1 \pm 0.8$ ) than mangrove creeks (MSR =  $9.0 \pm 0.5$ ; TSR =  $49 \pm 3$ ; JSR =  $6.1 \pm 0.4$ ) and the  
15 seaward mangrove fringe (MSR =  $6.4 \pm 0.7$ ; TSR =  $58 \pm 14$ ; JSR =  $5.2 \pm 0.4$ ). Meanwhile, Shannon  
16 Weiner diversity, juvenile fish abundance and commercial fish biomass were comparable  
17 between habitats. These findings caution against the generalisation that mangroves are the most  
18 important habitat for fishes in turbid tropical estuaries. There is now a growing body of evidence  
19 that mudflats warrant consideration as important repositories of biodiversity and nursery function  
20 for juvenile fishes.

21 **Keywords:** Biodiversity, commercial, nursery, community, juvenile, Caribbean

22

23

24 **1. Introduction**

25 Estuaries have the greatest economic value of all the world's ecosystems (Costanza et al. 1997),  
26 with mangroves being the most productive of estuarine habitats. Yet, mangrove-lined estuaries  
27 are in severe decline, and coastal managers and scientists are prioritising areas for conservation  
28 (Beck et al. 2001, Sheaves et al. 2015). Conservation priorities have focused on the provision of  
29 nursery habitat for coral reef fish (Nagelkerken et al. 2008) and commercial fisheries (Manson et  
30 al. 2005). However, tropical estuaries are also excellent feeding grounds for adult fish (Baker &  
31 Sheaves 2006), harbour rich and diverse communities where specialised species complete their  
32 life cycles (Blaber 2007, Elliott et al. 2007), and have economic value to subsistence and  
33 artisanal fishermen (Blaber 2013). Much of our understanding of tropical estuaries has centred  
34 on clear water habitats associated with coral reefs (Nagelkerken et al. 2008, Blaber 2013).  
35 Whereas, turbid-water estuaries of large rivers support a distinct suite of species whose ecologies  
36 are based on a different group of habitats (Blaber 2008). Here, mangroves and mudflats are  
37 prominent features, but our understanding of how these habitats compare and contrast in their  
38 biodiversity and role as nursery habitats is currently limited.

39

40 Vegetated habitats, such as mangroves and seagrasses, have often been valued above  
41 unvegetated open flats (Nagelkerken & Van der Velde 2002). The architectural complexity of  
42 mangroves helps juveniles to evade predators and offers a substrate for invertebrate prey  
43 (Laegdsgaard & Johnson 2001). However, the ebbing tide forces fish out of mangroves and into  
44 surrounding areas for substantial parts of the day, thus negating some of this value (Igulu et al.  
45 2014). Even when mangroves are flooded, many species still migrate to feed in adjacent habitats  
46 at night or as they mature (Laegdsgaard & Johnson 1995, Hammerschlag & Serafy 2010).

47 Clearly, the resource needs of all fishes are not accommodated by mangroves. Meanwhile,  
48 mudflats are productive systems in their own right, where highly digestible microphytobenthos  
49 underpins an abundant and diverse food supply for fishes (MacIntyre et al. 1996, Sheaves et al.  
50 2016a). There is a growing body of evidence suggesting that mudflats have been undervalued in  
51 their biodiversity and nursery function (Sheridan & Hays 2003, Sheaves et al. 2016a).  
52 Furthermore, in microtidal systems, where interactions between mangroves and adjacent habitats  
53 are diminished (Igulu et al. 2014), each habitat may harbour distinct communities reliant on  
54 specific components of habitats that are not ubiquitous. Such communities will warrant  
55 individual conservation measures.

56  
57 Many of the arguments used for conserving estuaries are based on the predominance of  
58 commercially valuable fish (Blaber 2007). Estuarine fisheries can be divided between “within  
59 mangrove” fisheries - where artisanal or subsistence fishermen target valuable adult fish; and  
60 “offshore of mangrove” fisheries - which are reliant on mangroves as nursery areas for  
61 commercially valuable juveniles (Blaber 2007). However, few studies have compared the role of  
62 different habitats for commercially valuable species, even though juveniles of several  
63 commercial species rely on mudflats rather than mangroves (Ray 2005, Tanaka et al. 2011).

64  
65 Mangroves are heterogenous environments, yet studies typically target only one type of  
66 mangrove habitat: e.g. submerged forest (Sheaves et al. 2016b), creeks (Giarrizzo & Krumme  
67 2007), or the seaward fringe (Hindell & Jenkins 2004). Studies that addressed multiple habitats  
68 have been compromised by employing different gears in the different habitats (e.g. Thayer et al.  
69 1987, Robertson & Duke 1990). Spatially explicit assessment - incorporating multiple mangrove

70 habitat types surveyed in the same manner - will better reflect the diversity of mangrove  
71 communities and provide more meaningful comparisons with alternative habitats.

72

73 The present study compared fish communities with fyke nets in three habitats of a mangrove-  
74 lined estuary, namely, mangrove creeks, seaward mangrove fringe (hereon 'fringe') and the  
75 subtidal margin of an intertidal mudflat. We posed two questions: 1) do these habitats have  
76 similar community compositions; and 2) which habitats harbour greater fish biodiversity, nursery  
77 role for juvenile fishes, and commercial fish biomass? It was hypothesised that feeding and  
78 ontogenetic migrations between habitats would be reflected in an overlap of species composition,  
79 and that mangrove habitats would support higher biodiversity, nursery-function and commercial  
80 value compared with mudflats due to their structural complexity offering food and refuge.

81

## 82 **2. Materials and method**

### 83 *2.1. Study area*

84 The Gulf of Paria is a highly turbid and estuarine environment due to discharge from the Orinoco  
85 and Amazon rivers (Hirst 1962). The eastern margin of the gulf is impounded by the island of  
86 Trinidad and a 52.6 km<sup>2</sup> mangrove-dominated wetland known as the Caroni Swamp (Fig. 1). The  
87 mangrove is comprised predominantly of the species *Rhizophora mangle*, *Avicennia germinans*  
88 and *Laguncularia racemose* (Juman & Ramsewak 2013). A tidal range of approximately 1 m on  
89 spring tides is sufficient for mangrove creeks to remain flooded at low tide. The seaward  
90 mangrove fringe extends for 21.7 km with roots and dead vegetation providing potential habitat  
91 for fish. The swamp is bordered to the north by the Caroni River which empties the largest  
92 watershed in Trinidad and forms an intertidal mudflat at its mouth. All habitats have a soft mud

93 substrate. A part of the mudflat and mangrove has been designated as a RAMSAR site of  
94 international importance but the fish communities are poorly characterised in the mangrove and  
95 uncharacterised in the mudflat.

96

## 97 *2.2. Study design*

98 For open habitats, i.e. the mangrove fringe and mudflat, the only prerequisite for site selection  
99 was 1.5-3 m depths at high spring tide to accommodate the minimum fishable depth of the nets  
100 and to prevent fish passing above the net. As such, the mudflat was sampled along its deeper,  
101 subtidal edges. The closest mudflat site was approximately 400 m from the mangrove, while  
102 fringe sites were within 10 m of the mangrove. Additional criteria were required to maintain  
103 consistency and sampling efficiency across mangrove creek sites: 1) similar current; 2) creek  
104 width did not exceed the width of the net (i.e. 8-10 m); 3) no obstructions to access or net  
105 deployment; and 4) nets were obscured from passing boats. Few locations met these criteria and  
106 creek site selection was limited to the sites used in this study. Due to differences in area of the  
107 three habitats, an unbalanced design was adopted to encompass spatial variation within habitats:  
108 12 creek sites, two fringe sites and two mudflat sites (Fig. 1). Sites were sampled around spring  
109 tides on at least three occasions in both the dry season (June 2014, May and June 2015) and the  
110 wet season (August, October and December 2014). Early June sampling targeted the very end of  
111 the dry season. Strong tides caused the nets to fail on three occasions in the creeks. Hence, the  
112 number of successful fyke net deployments was 69 in the creeks, 17 in the fringe and 14 in the  
113 mudflat.

114

## 115 *2.3. Field sampling*

116 Fyke nets were custom modified with three 3×8 m wings (1.6 cm mesh), and a 1.1 m diameter,  
117 5-hoop cod end (1.25 cm mesh). One net was set concurrently in each of two sites (> 1 km apart  
118 to maintain independence) from a boat at low tide and orientated to catch fish with the rising  
119 tide. Nets were deployed for 24 hrs but emptied at sunset to minimise escapes and consumption  
120 by trapped predators. Stomach contents of trapped predators were checked for prey but predation  
121 was largely limited to *Batrachoides surinamensis* and infrequent. Specimens were processed in  
122 the field whenever possible or otherwise in the lab. Specimens were identified to species level  
123 before measuring standard length (mm) and wet weight (g). Juveniles were defined based on  
124 literature values of size at maturity, and commercial species identified from dialogue with  
125 fisherman, grey literature on Trinidad and Tobago's fisheries, FAO reports and peer-reviewed  
126 literature from the wider area (e.g. Chan A Shing 2002, Mangal 2008, Mohammed et al. 2011,  
127 IMA 2016). Only species that are commercially valuable in Trinidad and Tobago or the central  
128 western Atlantic were designated as such. Physiochemical parameters (salinity, water  
129 temperature, dissolved O<sub>2</sub> and turbidity) were assessed midwater at each site using a YSI  
130 multiparameter probe and a secchi disk before setting and emptying the nets.

131

#### 132 *2.4. Data analysis*

133 All statistical analyses were performed using the R statistical software (R-Core-Team 2018).  
134 PERMANOVAs tested for significant differences in community composition (by abundance)  
135 between habitats, seasons and their interaction, followed by pairwise PERMANOVAs for each  
136 habitat combination. Rare species (fewer than three individuals) were removed to focus  
137 differences on regular habitat users. Heteroscedastic variances were diminished with a log(x+1)  
138 transformation, but still remained. Therefore, differences in community composition were  
139 substantiated with non-metric multidimensional scaling (NMDS) based on a Bray-Curtis

140 dissimilarity matrix in the metaMDS function of the Vegan package (Oksanen et al. 2019).  
141 SIMPER analysis identified the most important species contributing to differences in  $\log(x+1)$   
142 transformed community compositions. Species accumulation curves were extrapolated to 10 000  
143 individuals sampled (aligning sampling across the three habitats) to estimate total species  
144 richness in the package iNext (Hsieh et al. 2019). This sampling effort was a good reflection of  
145 the empirically measured species richness in the creeks. Species richness, Shannon Weiner  
146 diversity, juvenile fish abundance, juvenile species richness and commercial fish biomass were  
147 standardised per catch and square-root (richness) or log transformed (abundance and biomass) to  
148 meet assumptions of two-way ANOVAs (habitat and season as orthogonal fixed factors) and  
149 post-hoc pairwise t-tests for significant effects (Holm-Bonferroni's correction). Physiochemical  
150 parameters were compared between seasons for each habitat and between habitats with one-way  
151 ANOVAs (log and square-root transformations), Welch's t-tests for data with unequal variances  
152 and Kruskal-Wallis tests where data did not meet assumptions of the model. Temperature and  
153 dissolved O<sub>2</sub> were not significantly different between seasons for any habitat and so data were  
154 pooled across seasons for these two parameters.

155

### 156 **3. Results**

#### 157 *3.1. Community composition*

158 A total of 12 705 fishes were sampled in the mangrove creeks (9258; no. of catches = 69)  
159 mangrove fringe (1135; n = 17) and subtidal mudflat (2311; n = 14) of the Gulf of Paria between  
160 June 2014 and June 2015. Fish community compositions were significantly different between  
161 habitats ( $p < 0.001$ ) and seasons ( $p < 0.01$ ), with pairwise tests showing that each habitat was  
162 distinct from the others (Table 1). However, the fringe community was more similar to the



163 mudflat community than it was to the creek community (Fig. 2). Communities were largely  
164 distinguished by the relative importance of *Diapterus rhombeus*, *Bairdiella ronchus*,  
165 *Centropomus ensiferus* and *Sciades herzbergii* (Table 2). *D. rhombeus*, *C. ensiferus* and *S.*  
166 *herzbergii* accounted for 61% of total abundance in the creeks (Supplement), whereas *B. ronchus*  
167 alone accounted for 67% of total abundance in the mudflat. Dominant species in the fringe  
168 overlapped with the creeks and the mudflat, i.e. *B. ronchus*, *C. ensiferus* and *D. rhombeus*  
169 together comprised 73% of total abundance.

170

### 171 3.2. Biodiversity

172 Field sampling recorded 63 species from 26 families, with 48 species in the creeks, 31 species in  
173 the fringe and 42 species in the mudflat (Supplement S1). Of these, 21 species were observed in  
174 all three habitats and 24 rare species were represented by just one or two individuals. Species  
175 accumulation curves, extrapolated to 10 000 individuals sampled, attained  $49 \pm 3$  ( $\pm 1$  SD) species  
176 in the creeks,  $58 \pm 18$  species in the fringe, and  $75 \pm 14$  species in the mudflat (Fig. 3). Mean  
177 species richness per catch was higher in the creeks than the fringe ( $p < 0.05$ ), but the mudflat  
178 supported greater species richness than both the creeks ( $p < 0.05$ ) and the fringe ( $p < 0.01$ ; Table  
179 3 & Fig. 4). In contrast, species diversity was not significantly different between any habitat ( $p >$   
180 0.05).

181

### 182 3.3. Nursery value

183 Juveniles accounted for 73% of all individuals in the creeks, 97% in the fringe and 91% in the  
184 mudflat. Juvenile abundance was 2.8-fold higher in the mudflat than the creeks in the wet season  
185 (Fig. 4), largely due to abundant *B. ronchus*. However, juvenile abundance per catch was not

186 significantly different between habitats ( $p > 0.1$ ; Table 3). Juvenile stages were identified for 42  
187 species, 10 of which were common as adults and thus deemed to not use the habitats specifically  
188 as nursery grounds (see Beck et al. 2001). Still, the creeks were a nursery habitat for 27 species,  
189 the fringe for 18 species and the mudflat for 21 species. Mean juvenile species richness was  
190 significantly higher in the mudflat than both the creeks ( $p < 0.01$ ) and the fringe ( $p < 0.01$ ; Table  
191 3).

192

### 193 *3.4. Commercial biomass*

194 In the creeks, 91% of fish were commercially valuable, 94% in the fringe and 84% in the  
195 mudflat. The commercial species *S. herzbergii*, *B. ronchus*, *B. surinamensis*, *C. ensiferus* and *C.*  
196 *spixii* were generally the most important across habitats (Supplement S1). The average catch of  
197 commercial biomass was 5.2-fold higher in the creeks than the fringe ( $p < 0.01$ ; Table 3 & Fig.  
198 4). However, commercial biomass varied considerably between creeks, ranging from  $2.1 \pm 0.5$  kg  
199 per catch at the most landward creeks to  $14.4 \pm 5.1$  kg in creeks where the catfish *S. herzbergii*  
200 were particularly abundant. Mudflat sites were at the lower end of this range ( $2.8 \pm 0.6$  kg), and  
201 differences between mudflat and creeks were not significant ( $p > 0.1$ ). The mudflat did support a  
202 2.4-fold greater biomass of commercial fish than the fringe, but differences were not significant  
203 ( $p > 0.05$ ).

204

### 205 *3.5. Physiochemical environment*

206 All physiochemical characteristics had the greatest range across mangrove creeks which spanned  
207 10 km from sea to land (Table 4). Temperature and DO were not significantly different between  
208 seasons for any habitat (Supplement S2), and so seasonal data were pooled for these two

209 variables. Mangrove creek and fringe habitats exhibited salinities close to seawater in the dry  
210 season, while lower salinity in the mudflat was due to freshwater input from the Caroni River  
211 ( $F_{df=2,21} = 49.1$ ,  $p < 0.001$ ). Salinities declined in all habitats in the wet season - particularly in the  
212 creeks and fringe - rendering them similar across habitats ( $\chi^2_{df=2} = 3.8$ ,  $p > 0.1$ ). Temperature was  
213 not significantly different between habitats (Welch's test  $F_{2,37} = 0.59$ ,  $p > 0.1$ ), however, DO was  
214 significantly lower in the creeks than the other habitats ( $F_{2,120} = 39.6$ ,  $p < 0.001$ ), averaging  
215  $2.9 \pm 0.2$  mg l<sup>-1</sup> in both seasons, but dropping below 1 mg l<sup>-1</sup> on several occasions. Turbidity in the  
216 mudflat was diminished by the outflow of the Caroni River in the dry season ( $F_{2,20} = 15.5$ ,  $p <$   
217  $0.001$ ), but the creeks and fringe declined to similar levels in the wet season ( $F_{2,40} = 0.04$ ,  $p >$   
218  $0.1$ ).

219

## 220 **4. Discussion**

### 221 *4.1. Habitat conservation priorities*

222 Mangrove-lined estuaries represent one of the world's most productive ecosystems but they are  
223 also one of the most threatened (Valiela et al. 2001). Spatial conservation planning in these  
224 systems has to balance the demands of multiple users, and as such, must prioritise areas with the  
225 greatest conservation value (Beck et al. 2001). Our findings showed that subtidal mudflat can  
226 support comparable species diversity and juvenile fish abundance to two types of mangrove  
227 habitat, and even surpass their species richness of the whole community, and, more specifically,  
228 of the juvenile fish community. Mangrove creek, mangrove fringe and mudflat habitats also  
229 harboured distinct community compositions, thus warranting separate consideration in  
230 conservation planning. These communities may be less inclined to mix as fish have access to  
231 creeks throughout the tidal cycle, rather than being forced into surrounding habitats in more

232 tidally-governed systems (Igulu et al. 2014). However, commercial fish biomass was markedly  
233 higher in the mangrove creeks than the other two habitats, largely due to the predominance of the  
234 catfish *Sciades herzbergii* in the creeks.

235

236 Extrapolation of species accumulation curves showed that the 48 species recorded in mangrove  
237 creeks of the Caroni Swamp was a good reflection of the total species richness for this habitat.  
238 Comparable observations of 34, 40, 49, 65 and 70 species have been made in Brazilian estuaries  
239 much larger than the Caroni Swamp (see meta-analysis in Giarrizzo & Krumme 2008). In  
240 contrast, the species richness of the mudflat (42) was almost certainly an underestimate due to  
241 insufficient sampling, and the extrapolated estimate may surpass 75 species. While this  
242 extrapolation has large potential errors without further sampling, these estimates for total species  
243 richness align with 80 species observed in a Brazilian tidal flat (da Silva et al. 2018), and  
244 extrapolations of 45-90 species for upper subtidal communities in four Brazilian estuaries (Vilar  
245 et al. 2013), but falls short of the 133 species reported in tidal sandflats (Spach et al. 2004).  
246 Higher species richness per catch and juvenile species richness per catch in the mudflat relative  
247 to the two mangrove habitats also supports the importance of the mudflat for biodiversity and  
248 juvenile fishes. Previous studies have reported fish abundance and diversity to be greater in  
249 mangroves compared to unvegetated flats (Robertson & Duke 1987, Chong et al. 1990,  
250 Laegdsgaard & Johnson 1995), relatively similar (Hindell & Jenkins 2004, Tse et al. 2008, Payne  
251 & Gillanders 2009), or superior in mudflats relative to mangroves (Blaber et al. 1989). However,  
252 these studies either 1) do not use the same fishing gears in all habitats (Robertson & Duke 1987,  
253 Blaber et al. 1989, Chong et al. 1990); or 2) sample the pneumatophore zone of the seaward  
254 fringe (Robertson & Duke 1987, Laegdsgaard & Johnson 1995, Hindell & Jenkins 2004, Tse et

255 al. 2008, Payne & Gillanders 2009). Employing different gears can cause considerable sampling  
256 bias (Smith & Hindell 2005, Wang et al. 2009), and our findings support previous assertions that  
257 the mangrove fringe community may reflect open water habitats more than the mangrove forest  
258 (Huxham et al. 2004). Studies that avoided these shortcomings reported findings similar to the  
259 present study. Fish abundance was comparable in mangrove creek and mudflat habitats (Wang et  
260 al. 2009), and species richness was superior in mudflats and open areas compared to submerged  
261 forest (Sheridan 1992, Huxham et al. 2004, Wang et al. 2009).

262

263 Given the number of sub-habitats that were omitted in this study, particularly in the mangroves,  
264 it would be presumptive to conclude that, as a whole, the mudflat supports greater species  
265 richness than the mangroves in this study area, and thus should be prioritised over mangroves in  
266 fish conservation agendas. It is also important to qualify here that this study assessed the relative  
267 nursery ‘potential’ of mangrove and mudflat habitats based on juvenile fish abundance and  
268 juvenile species richness. Identifying valuable nursery habitats ultimately requires determining  
269 the relative contributions of recruits from all habitats to adult populations (Dahlgren et al. 2006).  
270 Nevertheless, our findings add to an accumulating body of evidence challenging the perception  
271 that mangroves are always the habitat with the greatest biodiversity and nursery value within the  
272 seascape (Sheridan 1992, Huxham et al. 2004, Wang et al. 2009). Mangroves are thought to  
273 harbour more abundant and diverse fish communities, and support a greater nursery role than  
274 unvegetated habitats because they offer superior feeding and refuge resources (Laegdsgaard &  
275 Johnson 2001). Clearly, there is sufficient ambiguity in the relative biodiversity and nursery  
276 function of habitats in turbid tropical estuaries to revisit whether these hypotheses are applicable  
277 in such systems.

278

279 *4.2. Feeding and refuge hypotheses*

280 Comparisons of food resources and their effect on growth rates in mangroves and mudflats are  
281 sparse (Sheridan & Hays 2003, Lee 2008, Sheaves et al. 2016a), while comparisons of gut  
282 fullness have been inconsistent across species and sizes (Laegdsgaard & Johnson 2001, Tse et al.  
283 2008). Most fish in the present study were juvenile benthic invertivores - particularly favouring  
284 microcrustaceans (Marley unpublished). While microcrustaceans are abundant components of  
285 the epibiota of prop roots (Silva-Camacho et al. 2017), their density and diversity in mangrove  
286 sediments are compromised by the poor digestibility of mangrove leaves and anoxic conditions  
287 (Sheridan 1997, Dittmann 2001). In contrast, macroinvertebrate abundances peak in the  
288 sediments of the lower intertidal area in front of mangroves, and this could be a critical hotspot  
289 in ecological processes of tropical estuaries (Sheaves et al. 2016a). The fact that many species  
290 make perilous migrations from mangroves to feed in surrounding habitats would suggest that  
291 mangrove prey are inadequate (Sheaves 2005, Ley & Halliday 2007, Hammerschlag & Serafy  
292 2010). Such species presumably use mangroves for refuge rather than feeding (Laegdsgaard &  
293 Johnson 2001).

294

295 The predator-refuge hypothesis has been widely used to promote the nursery value of mangrove  
296 habitats (see review in Whitfield 2017), even though not all mangroves provide the same level of  
297 protection (Rönnbäck et al. 1999, Chittaro et al. 2005). Moreover, the shallow, turbid waters of  
298 estuarine mudflats also provide protection from predators (Abrahams & Kattenfeld 1997,  
299 Paterson & Whitfield 2000), and the predator-refuge hypothesis may not favour mangroves when  
300 they are adjacent to other potential nursery habitats (Huxham et al. 2004, Smith & Hindell 2005).

301 The premise that mangroves have fewer predators has also been refuted (Baker & Sheaves 2006,  
302 Dorenbosch et al. 2009). In the present study, piscivores, such as *Centropomus* spp. and *B.*  
303 *surinamensis*, were more abundant in mangrove creeks than the mudflat. However, large  
304 transient piscivores, such as lutjanids, serranids and *Megalops atlanticus*, were likely to be  
305 underestimated by the size-selective fyke nets, and it is unclear what effect these predators have  
306 on prey fish assemblages.

307

#### 308 4.4. Physiochemical environment

309 Abiotic conditions are some of the most important structuring forces in tropical estuaries  
310 (Nagelkerken et al. 2008). Conditions in the three focal habitats were relatively similar. Salinities  
311 were generally close to seawater, turbidity was low, and temperatures averaged 27-28°C.  
312 However, DO was significantly lower in the creeks than the other habitats. Mean DO  
313 concentrations in this study were around half of those reported in mangrove creeks elsewhere  
314 (Giarrizzo & Krumme 2007, Shervette et al. 2007), and extreme lows (<1 mg l<sup>-1</sup>) could have  
315 been fatal to fish (Shimps et al. 2005). DO influences fish community composition in tropical  
316 estuaries (Vaslet et al. 2010), and potentially exerts a stronger influence on Caribbean mangrove  
317 fish communities than salinity (Bouchereau et al. 2008). DO also affects the distribution of taxa  
318 that were important components of the Caroni Swamp community: Gerreidae (Ramos et al.  
319 2016), Ariidae (Dantas et al. 2012) and *Epinephelus itajara* (Koenig et al. 2007). More accurate  
320 assessments of DO concentrations throughout the tidal cycle, rather than the snapshot  
321 measurements of this study, are required to fully evaluate its structuring influence. Nonetheless,  
322 it has the potential to structure fish communities and be a limiting factor for many species in our

323 mangrove creeks. In contrast, the ability of Ariidae to tolerate low DO levels (Dantas et al. 2010)  
324 explains their high biomass in mangrove creeks and the greater commercial value of this habitat.

325

#### 326 *4.3. Sampling effects*

327 Fish community surveys can be considered qualitative when the sampling volume of water, and  
328 thus fish densities, are not calculated (Sheridan & Hays 2003). Sampling volume could not be  
329 calculated with the fyke net method used in this study. However, sampling volume was likely to  
330 be largest in mangrove creeks where water funnelled into the forest on the rising tide, and  
331 weakest in the fringe which was far from any major channels. The nets would have also been  
332 most effective in mangrove creeks where they closed-off the channel - preventing fish from  
333 navigating around the net. As such, sampling artefacts fail to explain the relatively high  
334 abundance and species richness found in the mudflat. On the contrary, the mudflat community  
335 may have been underestimated. In contrast, the depauperate communities observed in the  
336 mangrove fringe may be better explained by sampling artefacts since other studies have  
337 documented more abundant and diverse assemblages in this habitat (Hindell & Jenkins 2004,  
338 Bouchereau et al. 2008). Deploying nets parallel to the forest edge in the fringe may have been  
339 more successful, but would have been inconsistent with sampling in the other habitats.

340

#### 341 *4.5. Seascape connectivity*

342 Although this study has assessed three estuarine habitats in a relatively isolated manner, their  
343 ecologies are surely entwined within a mosaic of interconnected coastal habitats (Sheaves et al.  
344 2015). Mangroves enhance fish abundance and diversity in adjacent habitats (Dorenbosch et al.  
345 2005, Jelbart et al. 2007), mudflats serve as low tide feeding areas when the mangrove is  
346 inaccessible (Sheaves 2005), and as intermediate habitats for juveniles migrating from



347 mangroves to offshore adult habitats (Laegdsgaard & Johnson 1995), and adjacent habitats  
348 exchange organic matter (Marley et al. 2019). The Gerreidae, Centropomidae, and Sciaenidae  
349 were almost entirely represented by juveniles in this study area, and are known to use these  
350 habitats as nurseries in other systems and then ontogenetically migrate offshore (Chaves 1995,  
351 Aliaume et al. 1997, Chaves & Otto 1998, Chaves & Bouchereau 2000). However, studies of  
352 seascape nurseries and habitat shifts in turbid tropical estuaries have been limited to only small  
353 proportions of fish communities in Brazil (Dantas et al. 2012) and the Gulf of Mexico (Mohan &  
354 Walther 2018). As such, there are huge gaps in our understanding of how different species use  
355 tropical estuarine habitats during their lifecycles, despite this information being crucial to guide  
356 spatial conservation planning.

357

## 358 **Conclusion**

359 Tropical estuaries are the focus of intense modification, exploitation and pollution. In spatial  
360 conservation planning, some habitats are prioritised while others are effectively sacrificed. This  
361 study adds to the growing body of literature challenging the paradigm that mangroves are the  
362 only priority habitat for conservation in turbid tropical estuaries. Our findings emphasise the  
363 potential role of mudflats as nursery habitats, biodiversity hotspots and as critical components of  
364 ecological systems, and that their loss will have wide-ranging consequences. Therefore, it is vital  
365 that we abandon the preconception that vegetated habitats are the only priority in estuary  
366 conservation, and adopt a more integrated seascape perspective that focuses on the habitat  
367 mosaic and the interactions between habitats.

368

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376

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584

585 Table 1. PERMANOVA results for the  
 586 effect of habitat, season and their  
 587 interaction on the composition of fish  
 588 communities in three habitats of the Gulf  
 589 of Paria, Trinidad. Post-hoc pairwise  
 590 habitat PERMANOVAs also given. **Bold**  
 591 indicates significance at  $p < 0.05$ .

| Parameters       | Df | F     | p                |
|------------------|----|-------|------------------|
| Habitat          | 2  | 9.32  | <b>&lt;0.001</b> |
| Season           | 1  | 2.45  | <b>&lt;0.01</b>  |
| Habitat x Season | 2  | 1.34  | 0.119            |
| Pairwise tests   |    |       |                  |
| Creeks v Fringe  |    |       |                  |
| Habitat          | 1  | 13.02 | <b>&lt;0.001</b> |
| Season           | 1  | 3.44  | <b>&lt;0.01</b>  |
| Habitat x Season | 1  | 1.20  | 0.279            |
| Creeks v Mudflat |    |       |                  |
| Habitat          | 1  | 12.40 | <b>&lt;0.001</b> |
| Season           | 1  | 2.69  | <b>&lt;0.01</b>  |
| Habitat x Season | 1  | 0.86  | 0.609            |
| Fringe v Mudflat |    |       |                  |
| Habitat          | 1  | 1.85  | <b>&lt;0.05</b>  |
| Season           | 1  | 1.87  | <b>&lt;0.05</b>  |
| Habitat x Season | 1  | 1.73  | 0.073            |

592

Table 2. SIMPER analysis showing the proportional contributions of species to the dissimilarity in community composition between habitats. Only the most influential species shown.

| Habitat comparison | Most influential species (left to right) |                             |                              |                               | Cumulative proportion |
|--------------------|--|-----------------------------|------------------------------|-------------------------------|-----------------------|
| Dry season         |  |                             |                              |                               |                       |
| Creeks v Fringe    | <i>B. ronchus</i><br>0.31                | <i>D. rhombeus</i><br>0.17  | <i>C. ensiferus</i><br>0.13  | <i>R. saponaceus</i><br>0.08  | 0.69                  |
| Creeks v Mudflat   | <i>B. ronchus</i><br>0.27                | <i>D. rhombeus</i><br>0.15  | <i>C. ensiferus</i><br>0.13  | <i>R. saponaceus</i><br>0.08  | 0.63                  |
| Fringe v Mudflat   | <i>B. ronchus</i><br>0.47                | <i>D. rhombeus</i><br>0.10  | <i>S. colonensis</i><br>0.09 | <i>S. testudineus</i><br>0.07 | 0.73                  |
| Wet Season         |  |                             |                              |                               |                       |
| Creeks v Fringe    | <i>B. ronchus</i><br>0.22                | <i>C. ensiferus</i><br>0.20 | <i>S. herzbergii</i><br>0.13 | <i>S. colonensis</i><br>0.11  | 0.66                  |
| Creeks v Mudflat   | <i>C. ensiferus</i><br>0.36              | <i>B. ronchus</i><br>0.09   | <i>S. herzbergii</i><br>0.08 | <i>D. rhombeus</i><br>0.07    | 0.60                  |
| Fringe v Mudflat   | <i>B. ronchus</i><br>0.38                | <i>C. ensiferus</i><br>0.11 | <i>S. colonensis</i><br>0.10 | <i>C. spixii</i><br>0.09      | 0.68                  |

595 Table 3. Summary results of two-way ANOVAs for biodiversity indices, abundance and commercial  
 596 biomass of fishes between three estuarine habitats of the Gulf of Paria, Trinidad. Post-hoc pairwise t-tests  
 597 given for significant factors. C = Creeks, F = Fringe, M = Mudflat. **Bold** indicates significance at p <  
 598 0.05.

| Parameters                | Two-way ANOVA |       |                 | Pairwise t-tests (p) |                 |                 |
|---------------------------|---------------|-------|-----------------|----------------------|-----------------|-----------------|
|                           | Df            | F     | P               | C x F                | C x M           | F x M           |
| Species richness          |               |       |                 |                      |                 |                 |
| Habitat                   | 2             | 6.10  | <b>&lt;0.01</b> | <b>&lt;0.05</b>      | <b>&lt;0.05</b> | <b>&lt;0.01</b> |
| Season                    | 1             | 0.36  | 0.548           |                      |                 |                 |
| Habitat x Season          | 2             | 0.69  | 0.505           |                      |                 |                 |
| Species diversity         |               |       |                 |                      |                 |                 |
| Habitat                   | 2             | 3.273 | <b>&lt;0.05</b> | 0.064                | 0.573           | 0.064           |
| Season                    | 1             | 3.453 | 0.066           |                      |                 |                 |
| Habitat x Season          | 2             | 0.484 | 0.618           |                      |                 |                 |
| Juvenile abundance        |               |       |                 |                      |                 |                 |
| Habitat                   | 2             | 1.61  | 0.206           |                      |                 |                 |
| Season                    | 1             | 0.84  | 0.363           |                      |                 |                 |
| Habitat x Season          | 2             | 1.31  | 0.276           |                      |                 |                 |
| Juvenile species richness |               |       |                 |                      |                 |                 |
| Habitat                   | 2             | 6.06  | <b>&lt;0.01</b> | 0.554                | <b>&lt;0.01</b> | <b>&lt;0.01</b> |
| Season                    | 1             | 0.35  | 0.56            |                      |                 |                 |
| Habitat x Season          | 2             | 0.18  | 0.84            |                      |                 |                 |
| Commercial biomass        |               |       |                 |                      |                 |                 |
| Habitat                   | 2             | 6.06  | <b>&lt;0.01</b> | <b>&lt;0.01</b>      | 0.499           | 0.081           |
| Season                    | 1             | 0.35  | 0.557           |                      |                 |                 |
| Habitat x Season          | 2             | 0.18  | 0.835           |                      |                 |                 |

599

Table 4. Seasonal variation in physiochemical characteristics of three adjacent fish habitats in the Gulf of Paria, Trinidad. DO=Dissolved O<sub>2</sub>.

| Parameter/<br>Habitat         | Mean±SE (range)   |                   |
|-------------------------------|-------------------|-------------------|
|                               | Dry               | Wet               |
| <b>Salinity</b>               |                   |                   |
| Creeks                        | 32.1±0.4 (24-37)  | 24.0±0.5 (18-29)  |
| Fringe                        | 33.5±0.3 (32-34)  | 25.3±1.0 (22-29)  |
| Mudflat                       | 29.4±0.3 (28-30)  | 26.5±0.4 (25-28)  |
| <b>Temperature (°C)</b>       |                   |                   |
| Creeks                        | 27.2±0.2 (25-30)  | 27.5±0.2 (25-29)  |
| Fringe                        | 27.1±0.2 (26-29)  | 27.9±0.3 (27-30)  |
| Mudflat                       | 27.3±0.1 (27-28)  | 27.7±0.2 (27-28)  |
| <b>DO (mg l<sup>-1</sup>)</b> |                   |                   |
| Creeks                        | 2.9±0.2 (0.4-5.3) | 2.9±0.2 (1.1-5.4) |
| Fringe                        | 5.1±0.2 (4.3-6.0) | 4.7±0.6 (3.3-9.1) |
| Mudflat                       | 5.1±0.3 (4.0-5.7) | 6.4±0.6 (4.8-8.6) |
| <b>Turbidity (cm)</b>         |                   |                   |
| Creeks                        | 74±5 (1-160)      | 58±5 (15-140)     |
| Fringe                        | 77±8 (50-123)     | 51±4 (30-70)      |
| Mudflat                       | 46±3 (40-60)      | 57±15.(25-120)    |

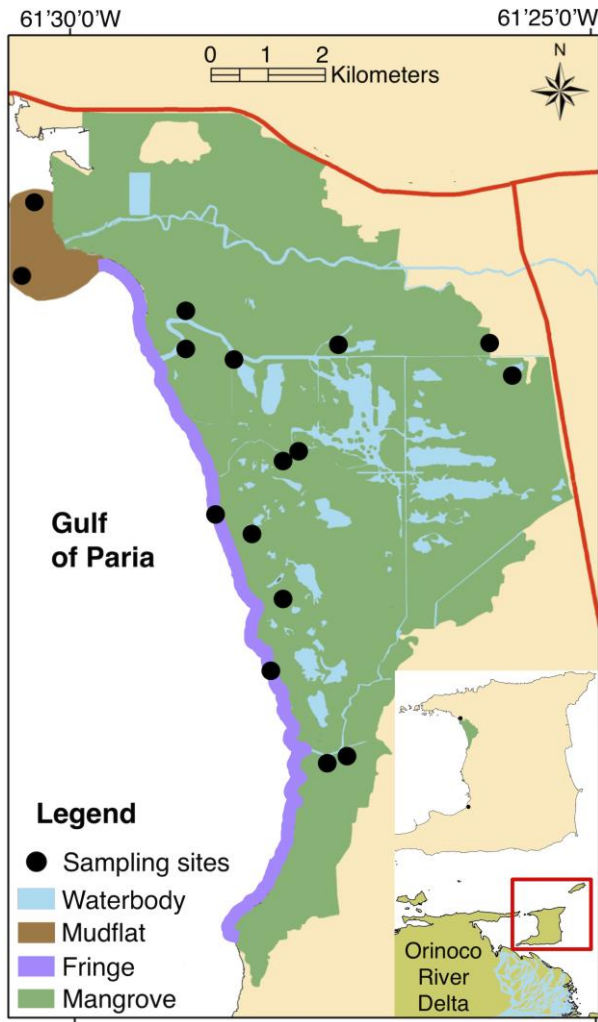


Fig. 1. Survey sites in the Caroni Swamp mangrove and adjacent mudflat habitats, Trinidad, Gulf of Paria.



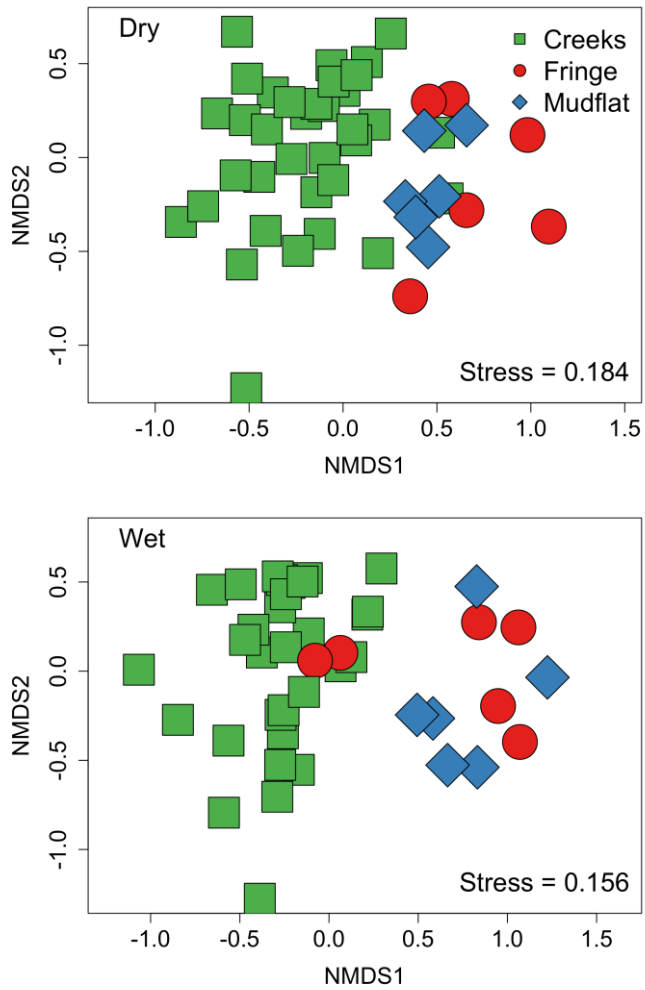
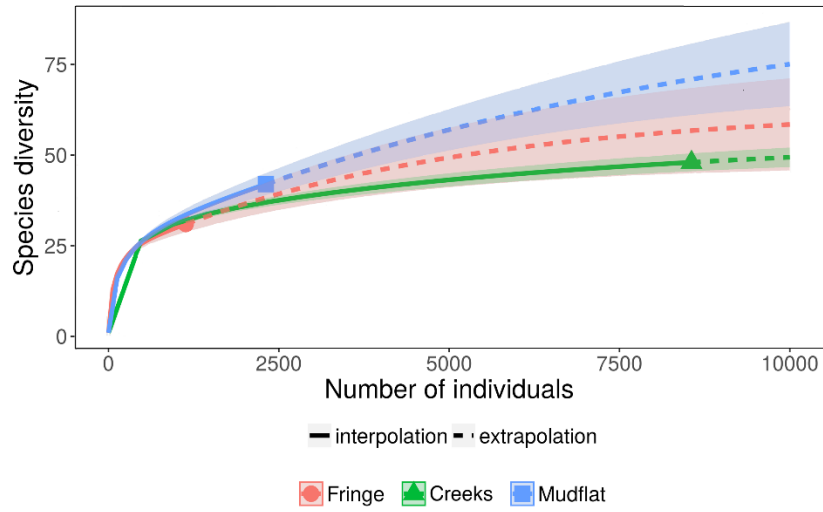


Fig. 2. NMDS plots of species composition (by abundance) of season specific fish communities in three habitats of the Gulf of Paria, Trinidad. Dissimilarity based on a Bray-Curtis matrix. Dimensions = 3.

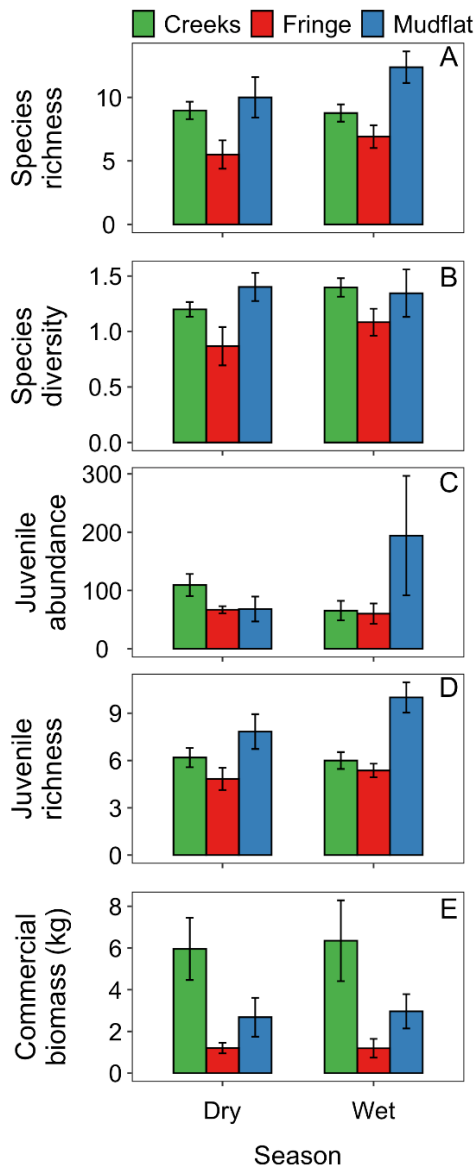
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608 Fig. 3. Species accumulation curves for the accumulation of new species with number of individuals  
609 sampled and individual-based rarefaction and extrapolation to 10,000 individuals sampled ( $\pm 1$  SD).

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611

612 Fig. 4. Mean ( $\pm$ SE) biodiversity indices standardised per catch: A) species richness; B) species diversity  
613 (Shannon Wiener index); C) juvenile fish abundance; D) juvenile species richness; E) commercial fish  
614 biomass in habitats of the Gulf of Paria, Trinidad.

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