



Effects of a no-take reserve on mangrove fish assemblages: incorporating seascape connectivity

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ABSTRACT: No-take reserves (NTRs) have been effective at conserving fish assemblages in tropical systems such as coral reefs, but have rarely been evaluated in turbid tropical estuaries. The present study evaluated the effect of a mangrove NTR on the conservation of juvenile fish abundance, commercial fish biomass and biodiversity at the assemblage level, and the abundance of juveniles, target and non-target adults at the family level. The evaluation incorporated one aspect of seascape connectivity, namely proximity to the sea, or in this case, the Gulf of Paria. Linear mixed models showed that the NTR had a positive effect only on species richness at the assemblage level. However, juvenile fish abundance, commercial fish biomass, taxonomic distinctness and functional diversity were not enhanced in the NTR. The inclusion of connectivity in these models still failed to identify any positive effects of the NTR at the assemblage level. Yet, there were significant benefits to juvenile fish abundance for 5 of 7 families, and for 1 family of non-target adults. Possible explanations for the limited success of the NTR for fish assemblages include failing to account for the ecology of fish species in NTR design, the drawbacks of 'inside–outside' (of the NTR) experimental designs and the fact that fishing does not always impact non-target species. It is important to recognise that mangrove NTRs do not necessarily benefit fish assemblages as a whole, but that finer-scale assessments of specific families may reveal some of the proclaimed benefits of NTRs in tropical estuaries.

KEY WORDS: Estuarine · MPA · Conservation · Management · Caribbean · Habitat

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1. INTRODUCTION

No-take reserves (NTRs) are a widely implemented tool in biodiversity conservation, fisheries management and building ecosystem resilience to climate change (Roberts & Hawkins 2000, Elmqvist et al. 2003, Folke et al. 2004). Their success has been well established in coral and rocky reefs (Gell & Roberts 2003, Halpern 2003, Kelaher et al. 2014). In contrast, only 2 evaluations of NTRs in tropical estuaries (i.e. Johnson et al. 1999, Ley & Halliday 2003) are referenced in multiple reviews on fish conservation (Halpern 2003, Barletta et al. 2010, Chong et al. 2010, Whitfield & Cowley 2010, Blaber 2013), while more recent studies have been limited to Australia

and West Africa (e.g. Sadio et al. 2015, Gilby et al. 2017). Tropical estuaries are some of the most productive ecosystems on earth, with invaluable fishery resources (Faunce et al. 2002, Ley et al. 2002, Gilby et al. 2017). Yet, the paucity of empirical assessments in these systems hinders our ability to advocate different design and management approaches.

Fisheries typically target the largest specimens, and so restricting their removal in NTRs has a positive effect on target fish biomass and fish size (Halpern 2003). The benefit of NTRs to the nursery role of ecosystems is less clear, because protecting large piscivores potentially elevates predation on small juveniles (Polunin & Roberts 1993). Likewise, the benefit to the conservation of wider biodiversity

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and non-target species is equivocal (e.g. Rolim et al. 2019). Given that tropical estuaries, and in particular mangroves, are highly regarded for their biodiversity and provision of nursery habitat (Faunce & Serafy 2006), understanding the value of NTRs to these attributes is especially important. However, detecting the effects of fishing in estuaries is complicated, because estuaries are naturally high-stress environments (Elliott & Quintino 2007). In this 'estuarine quality paradox', a combination of structural and functional indices are needed to evaluate the health of the system (Elliott & Quintino 2007).

Estuaries suffer from the intense spatial demands of multiple users, at times forcing NTRs into ecologically unimportant locations (Gilby et al. 2017). Meanwhile, NTRs designed around the ecology of 'umbrella' or surrogate taxa, such as birds, do not necessarily conserve wider marine communities (Andelman & Fagan 2000, Ludynia et al. 2012, Ronconi et al. 2012). In these circumstances, NTRs create sociological issues without meeting their biodiversity objectives (Vanderklift & Ward 2000). More recent approaches to NTRs recognise the importance of seascape connectivity, i.e. the access to resources in or from different habitats (Olds et al. 2012, Nagelkerken et al. 2015). Greater connectivity supports the early settlement of eggs and larvae, facilitates inter-habitat foraging migrations and reduces the risk of predation during ontogenetic migrations (Little et al. 1988, Koenig et al. 2007, Hammerschlag & Serafy 2010). As such, connectivity structures fish assemblage composition, abundance and diversity (Nagelkerken et al. 2012, Olds et al. 2012, Martin et al. 2015). Previous studies have quantified connectivity according to the edge-to-edge distance between habitats, and have demonstrated that NTRs are more effective when nurseries are within reach of adult habitats (e.g. Olds et al. 2012, Martin et al. 2015). However, connectivity is not homogeneous across habitats, particularly large habitats (Dorenbosch et al. 2005, Nagelkerken et al. 2015), and so incorporating spatial variation in connectivity across habitats should also improve the veracity of NTR evaluations.

The Caroni Swamp, Trinidad, contains an NTR that was established to protect waterfowl, but fish extraction is also prohibited (Marley et al. 2019). There was no quantitative characterisation of fish assemblages prior to its implementation, and its effectiveness at conserving fish assemblages has not been tested. The present study applied an 'inside–outside' experimental design which incorporated the spatial variation in connectivity across the swamp by characterising sampling sites by their proximity to the Gulf of

Paria. Using a combination of assemblage- and family-level assessments, we posed the following questions: (1) Has the NTR, connectivity or their interaction altered fish assemblages relative to fished areas in terms of their composition, nursery role (juvenile fish abundance), commercial fish biomass and structural and functional biodiversity? (2) Has the NTR enhanced the abundance of juveniles, target adults and non-target adults from specific fish families? We hypothesised that the NTR, or an interaction between the NTR and connectivity with the gulf, alters the composition of fish assemblages and improves structural and functional diversity (FD), because it maintains a state closer to a natural ecosystem and facilitates access to gulf resources. However, we also hypothesised that the NTR has a negative effect on juvenile fish assemblages due to increased predation, and that these effects will be family specific.

2. MATERIALS AND METHODS

2.1. Study area

The Caroni Swamp occupies 52.6 km² on the west coast of Trinidad, where it fringes the Gulf of Paria in the Orinoco River estuary (Fig. 1). A 20.9 km² NTR was established in 1987, with finfish still targeted in the channels bordering the reserve on a daily basis by recreational, artisanal and subsistence fishermen. The fish assemblage was qualitatively characterised by Bacon (1970) and Deonarine (1980). However, these data are unsuitable as a baseline for subsequent NTR appraisals.

2.2. Survey design

Survey sites were small creeks adjoining the 3 largest channels draining the mangrove forest and 2 small creeks which empty directly into the Gulf of Paria. Sites had to meet several criteria: (1) depth of 1.5–3 m at high spring tide; (2) width of 8–10 m so nets could close off creeks; (3) similar flow rate; (4) no obstructions to accessing the site or deploying the net; and (5) nets could be obscured to avoid possible tampering from passing boats. Only 10 sites met these criteria, so an unbalanced design employed 6 sites in the fished area and 4 sites in the NTR (Fig. 1). Sites were also categorised based on their proximity to the Gulf of Paria: near (<2 km; 6 sites) and far (3.5–4.5 km; 4 sites). The near and far categories were considered to be the maximum distance beyond which juvenile and

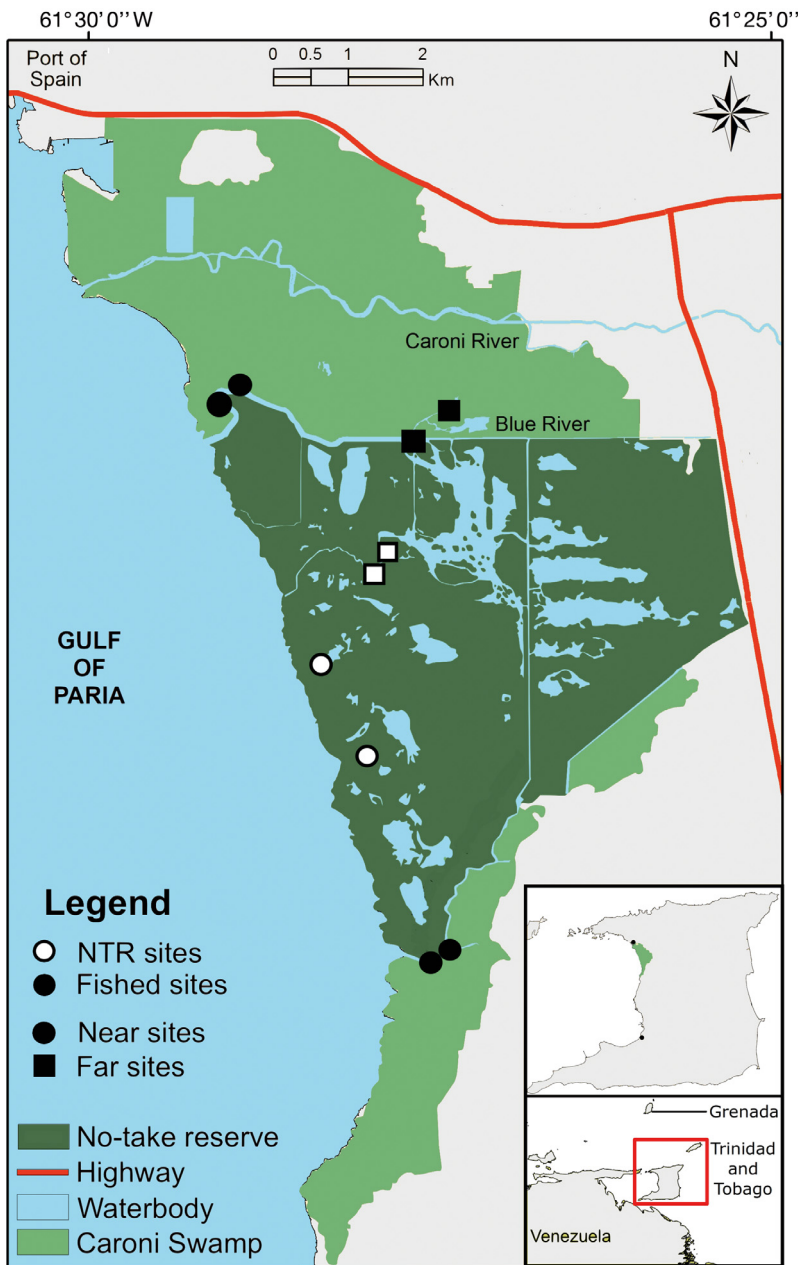


Fig. 1. Caroni Swamp, Trinidad, showing the no-take reserve (NTR) and fished area survey sites categorised by their proximity (connectivity) to the Gulf of Paria (near/far). Inset shows the swamp's location relative to Trinidad and South America

adult fish, respectively, were unlikely to make daily feeding migrations to the gulf (Krumme 2009, Berkström et al. 2013). Sampling took place around full moon spring tides between June 2014 and June 2015. All 10 sites were sampled 6 times: 3 times in the wet season (late June to December 2014) and 3 times in the dry season (early June 2014 and January to early June 2015), but the nets failed on 3 occasions in fished

area sites. Abiotic conditions (water temperature, salinity, dissolved oxygen and turbidity) were assessed midwater when setting and emptying the nets using a YSI multiparameter probe and a Secchi disk.

2.3. Sampling method

Fyke nets were custom modified with three 3×8 m wings (1.6 cm mesh) and a 1.1 m diameter, 5-hoop cod end (1.25 cm mesh). Similar nets have been effective in targeting small fishes in the range of 5–30 cm where active and visual sampling is not feasible (McInerny & Cross 2004, Clement et al. 2014, Smith & Simpkins 2017). Although fyke nets are typically orientated upstream to catch fish leaving the mangrove on the falling tide, they were trialled in this orientation and substantial drifting leaf litter would clog and dislodge the nets. Therefore, nets were orientated downstream to catch fish moving into the creeks and forest with the rising tide. Two sites were sampled simultaneously (>1 km apart to maintain independence) with 1 net per site deployed from a boat at low tide. Nets were set for 24 h but emptied at sunset to minimise escapes and consumption by trapped predators. Specimens were identified to species level before standard length and wet weight measurements were taken.

2.4. Data analysis

Statistical analyses were performed using R statistical software (R Core Team 2018) with the exception of permutational multivariate ANOVAs (PERMANOVAs) and canonical analysis of principal coordinates (CAP), which were performed in PRIMER (Clarke & Gorley 2015). A mixed effects PERMANOVA (Anderson 2001) based on a Bray-Curtis dissimilarity matrix, with protection and connectivity as fixed factors, and site and time (sampling month) as random factors, tested for significant differences in assemblage com-

position. A log transformation limited the effect of exceptionally abundant species and heteroscedastic variances. The effect of these independent variables on assemblage composition was visualised using CAP (Anderson & Willis 2003).

Juveniles were defined based on values of size at maturity reported in the primary literature wherever possible and otherwise reported in Fish-Base (Froese & Pauly 2018). Species that are commercially valuable in Trinidad and Tobago or the central western Atlantic were designated as such. Structural diversity was evaluated with species richness and taxonomic distinctness (Δ^*). Δ^* uses a Linnaean classification tree to determine the average taxonomic distance between pairs of species in an assemblage/sample (Clarke & Warwick 1999). Here the sample is 1 fyke net catch. To evaluate FD, species were assigned to ecological and trophic guilds based on Potter et al. (2015), with information on life history and feeding guilds of each species sourced from peer-reviewed literature wherever possible, and otherwise using Fish-Base (Froese & Pauly 2018). The Caroni Swamp fish assemblage constituted 9 different ecological guilds and 8 trophic guilds (Table A1 in the Appendix), which were crossed to make 72 possible functional combinations, although the Caroni Swamp assemblage represented only 29 of those combinations. Simpson's index ($D_1 = 1 - \sum_{i=1}^S p_i^2$, where p_i is the proportion of species i , and S is the number of species) was then used to determine the FD in each catch.

Assemblage-level indices of juvenile fish abundance, commercial fish biomass and Δ^* were log transformed, species richness was square-root transformed, and FD was square transformed to meet parametric model assumptions. Transformed indices were analysed using Gamma distributed linear mixed models (LMMs) with fixed effects of protection, connectivity and their interaction, and random effects of site and time. Family-level fish abundance was assessed using Gamma distributed generalised linear mixed models (GLMMs) with the same factors as LMMs. Post hoc least square means tests (Tukey's adjustment) were made for significant effects of interaction terms in family-level assessments. Abiotic conditions were compared between protection levels in a season-specific manner using 1-way ANOVAs and Welch's test where variances were not homogeneous (turbidity was square-root transformed), and similarly compared between levels of connectivity. Assumptions of LMMs and ANOVAs were verified with histograms, Shapiro-Wilk tests and Levene's tests, and models were visu-

alised with residual and qqnorm plots. GLMM assumptions were verified with histograms, residual and qqnorm plots.

3. RESULTS

3.1. Assemblage composition

A total of 9740 fishes belonging to 47 species and 23 families were sampled in the Caroni Swamp between June 2014 and June 2015. Of these, 29 species were new records for the Caroni Swamp (Table A1). Six species accounted for 81% of total abundance: *Diapterus rhombeus*, *Centropomus ensiferus*, *Sciades herzbergii*, *D. auratus*, *Anchovia clupeioides* and *Rypticus saponaceus*. Meanwhile, 5 species accounted for 83% of total biomass: *S. herzbergii*, *Batrachoides surinamensis*, *C. ensiferus*, *Sphoeroides testudineus* and *R. saponaceus*. Most fishes were juveniles (74%), but they comprised only 14% of total biomass. Commercially valuable species accounted for 89% of all fishes and 88% of all biomass.

PERMANOVA results revealed significant differences in fish assemblage composition due to both main effects, with F -values indicating that protection and connectivity were responsible for similar amounts of variation (Table 1, Fig. 2). However, there were no significant interactive effects on assemblage composition.

3.2. Assemblage indices

Juvenile fish abundance, commercial fish biomass, Δ^* and FD were not affected by the main factors protection or connectivity, nor by their interaction (Table 2, Fig. 3). Although the average catch of commercial biomass in the fished area (9.5 ± 2.6 kg per catch) was more than double that recorded in the

Table 1. PERMANOVA for the fixed effects of protection, connectivity with the Gulf of Paria and interactions (site and time as random effects), on the composition of fish assemblages in the Caroni Swamp, Trinidad. **Bold:** significant ($p < 0.05$)

Variable	df	MS	F	p
Protection (P)	1	8248	2.22	<0.05
Connectivity (C)	1	8194	2.31	<0.05
P × C	1	2483	0.70	0.719

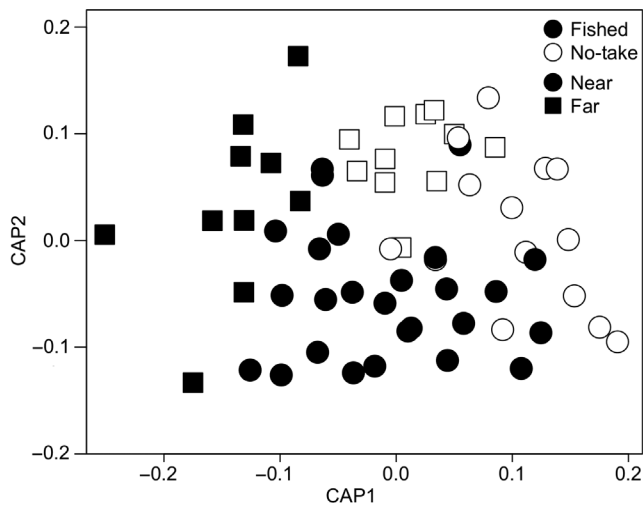


Fig. 2. Canonical analysis of principal coordinates (CAP), showing the dissimilarity in assemblage composition between protection levels (fished area/no-take reserve) and between levels of proximity (connectivity) with the Gulf of Paria (near/far)

Table 2. Linear mixed model results for the fixed effects of protection (P) and connectivity with the Gulf of Paria (C), and their interactions (site and month as random effects), on juvenile fish abundance, commercial fish biomass and diversity metrics. **Bold** indicates significance ($p < 0.05$)

Parameter	df	MS	F	p
Juvenile abundance				
Protection	1	5.65	5.15	0.060
Connectivity	1	4.45	4.06	0.085
P × C	1	0.50	0.46	0.522
Commercial biomass				
Protection	1	0.10	0.16	0.706
Connectivity	1	0.14	0.21	0.660
P × C	1	0.10	0.16	0.701
Species richness				
Protection	1	4.64	14.17	<0.001
Connectivity	1	0.36	1.11	0.296
P × C	1	1.02	3.12	0.083
Taxonomic distinctness				
Protection	1	0.01	0.02	0.906
Connectivity	1	0.25	0.46	0.521
P × C	1	0.60	1.13	0.328
Functional diversity				
Protection	1	0.03	1.08	0.303
Connectivity	1	0.01	0.37	0.545
P × C	1	0.02	0.76	0.387

NTR (4.5 ± 0.7 kg), high variation within protection levels precluded significant differences. However, species richness per catch was significantly higher in the NTR.

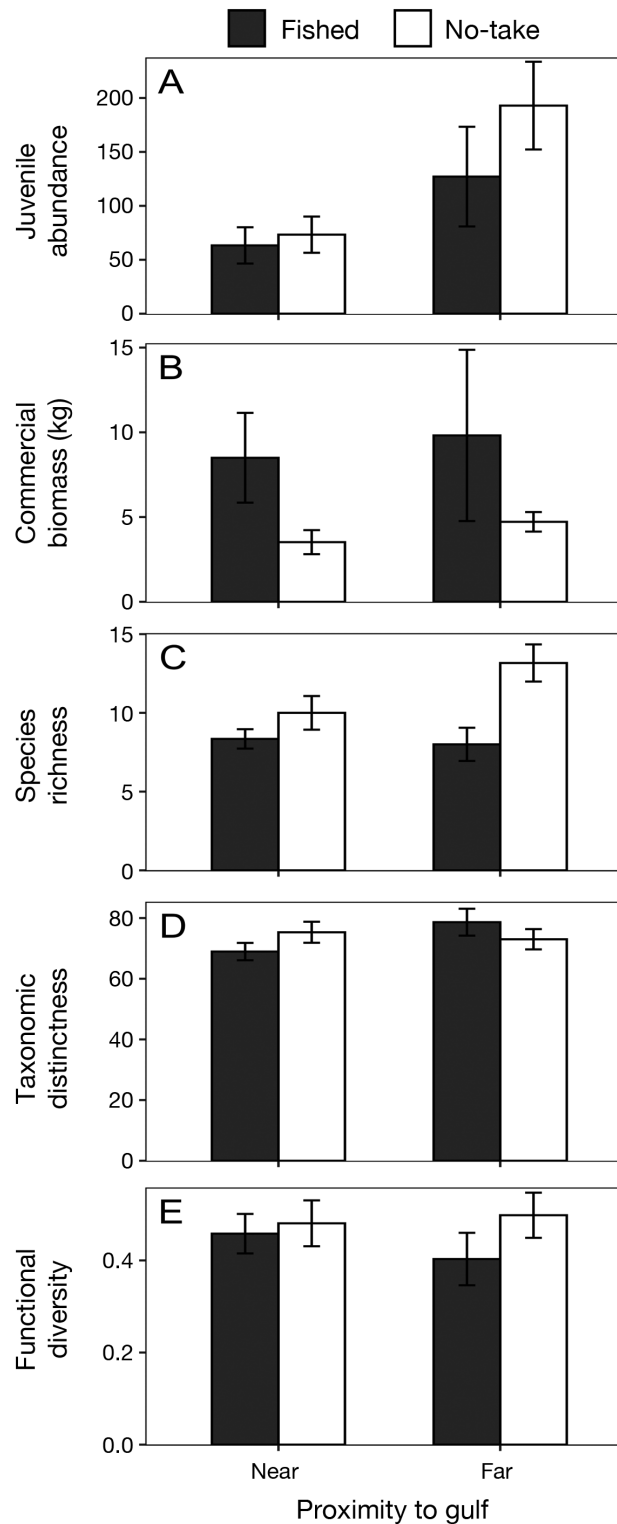


Fig. 3. Mean fish abundance, biomass and diversity indices (\pm SE) per catch in the fished area and no-take reserve of the Caroni Swamp at 2 levels of proximity (connectivity) with the Gulf of Paria: (A) juvenile fish abundance; (B) commercial fish biomass; (C) species richness; (D) taxonomic distinctness; and (E) functional diversity

3.3. Family abundance

The NTR had a positive impact on juveniles from 5 of 7 families. The NTR significantly enhanced the abundance of juveniles of Gerreidae, Haemulidae and Carangidae, regardless of connectivity with the Gulf of Paria (Fig. 4). Furthermore, the interaction term ‘protection × connectivity’ was significant for Centropomidae and Lutjanidae, with juveniles being more abundant in the NTR than in the fished area, but only at far sites. The interaction term also had a significant effect on juveniles of Sciaenidae, but in this case, juveniles were more abundant in the fished area than in the NTR at far sites. Juveniles of Engraulidae were not affected by the NTR. For adults targeted by the fishery, Ariidae and Sparidae were significantly affected by protection status, but were more abundant in the fished area than the NTR. These 2 families

showed little evidence of being influenced by connectivity with the gulf. Large variation in abundance of Batrachoididae precluded significant differences between protection levels (Fig. 4). The Serranidae, composed entirely of the non-target species *R. saponaceus*, were significantly more abundant in the NTR relative to the fished area, especially at far sites. In contrast, the other non-target family, Tetraodontidae, was not affected by the NTR.

3.4. Abiotic environment

Salinity in the Caroni Swamp was close to that of seawater in the dry season (mean 32.2 ± 0.5 SE) but declined in the wet season (24.4 ± 0.5). Physiochemical variables were not significantly different between the NTR and the fished area in either season, with

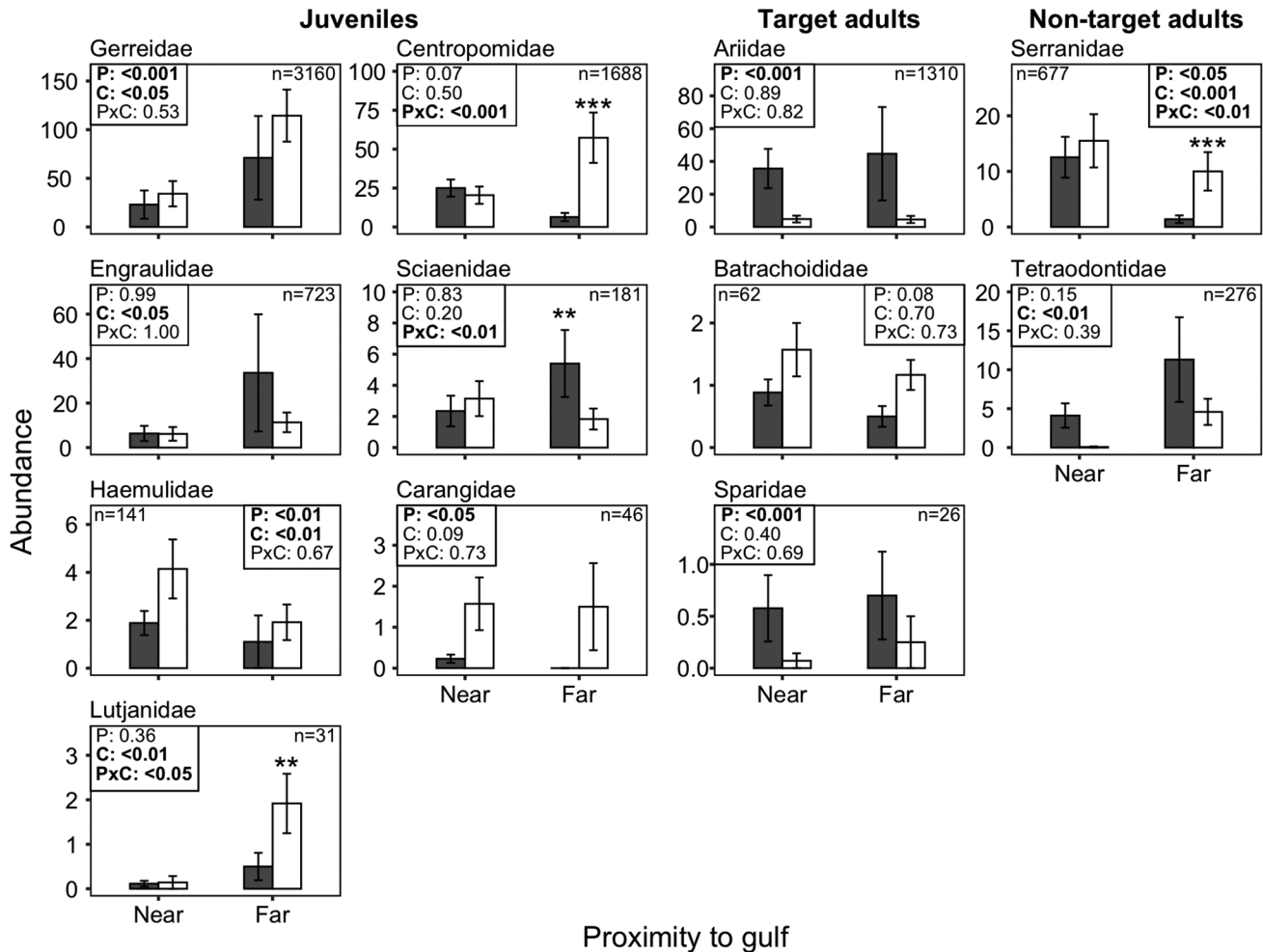


Fig. 4. Mean family abundance (\pm SE) per catch of juveniles, target and non-target adults, in the fished area (grey) and no-take reserve (white) of the Caroni Swamp at 2 levels of proximity (connectivity) with the Gulf of Paria. GLMM p-values in **bold** indicate significance ($p < 0.05$), and pairwise least square means tests where interaction terms were significant are shown as ****** $p < 0.01$ and ******* $p < 0.001$. P: protection, C: connectivity

the exception of salinity being significantly lower in the fished area (23.6 ± 0.7) than the NTR (25.6 ± 0.4) in the wet season (Table 3). There were further physiochemical differences between creeks, according to their connectivity to the Gulf of Paria. Temperatures in far creeks (mean $28.8 \pm 0.5^\circ\text{C}$) were significantly higher than near creeks ($27.2 \pm 1.1^\circ\text{C}$) in the wet season, but with little difference in the dry season. Meanwhile, DO was diminished in far creeks ($2.3 \pm 0.3 \text{ mg l}^{-1}$) relative to near creeks ($3.3 \pm 0.2 \text{ mg l}^{-1}$) in the dry season, but with no significant difference in the wet season. Turbidity was low in both the fished area and the NTR in both seasons, but consistently lower at near ($0.9 \pm 0.2 \text{ m}$) than far sites ($0.5 \pm 0.1 \text{ m}$). Other parameters were not significantly different between connectivity levels in either season.

4. DISCUSSION

Very few evaluations of NTRs have been conducted in estuaries. Some suggest that estuarine fish assemblages have benefited from the protection of NTRs (Johnson et al. 1999, Ley et al. 2002), but there are also examples where NTRs have been ineffective (Sadio et al. 2015, Gilby et al. 2017). Here we found that a mangrove NTR enhanced species richness and altered the composition of fish assemblages relative to fished areas. However, at the assemblage level, it did not enhance juvenile fish abundance or commercial fish biomass relative to fished areas, nor did it harbour superior Δ or FD, which are some of the purported benefits of NTRs (Halpern 2003). Olds et al. (2012) proposed that reserves are most effective when mangroves are in close proximity to adult habi-

tats. As such, the present study modelled the interaction of protection and connectivity with the Gulf of Paria to test for such an effect. Even then, most assemblage-level indices failed to detect a positive impact of the NTR, and similar findings have been reported in NTRs in other systems (Polunin & Roberts 1993). However, evaluating the effectiveness of the NTR at the assemblage level missed positive effects for the abundance of juveniles from 5 of 7 families, and for 1 family of non-targeted adult fishes (Serranidae). In contrast, adults of the targeted families Ariidae and Sparidae were more abundant in the fished area.

4.1. Driving factors in assemblage-level effects

Fishing can lead to localised extinctions, and so species richness has been recommended as a metric for detecting the effects of fishing restrictions on biodiversity (Halpern 2003, Pelletier et al. 2005). In a review of 89 marine reserves, species richness was superior in reserves relative to fished areas in 59% of cases, and enhanced by a total of 20–30% (Halpern 2003). There are several possible explanations for why the NTR does not appear to have substantially enhanced other assemblage-level metrics.

4.1.1. Fishing pressure

It may be that fishing pressure is not sufficient outside the NTR to have a discernible impact on the whole assemblage. Ramdial (1975) reported 40 full-time and 29 part-time fishermen removing an estimated $357 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in the Caroni Swamp—comparable to other overfished estuaries (Laë 1997). However, the study by Ramdial (1975) is dated, used questionnaire data that can exaggerate landings (Bochenek et al. 2012), and was conducted before the expansion of the NTR to its current size. NTRs historically force fishermen out of fisheries (Ban et al. 2017), and socioeconomic development drives a movement away from artisanal and subsistence fishing (Kronen et al. 2010). During the present study, we observed up to 3 fishing boats active in the fished area on weekdays and up to 5 boats on weekends. This suggests that the area is moderately fished but is unlikely to return the landings reported by Ramdial (1975). Ultimately, although some impact would be expected from the observed fishing pressure, the absence of recent fishing effort and landings data makes this point difficult to reconcile.

Table 3. ANOVA in season-specific comparisons of physiochemical characteristics between protection levels and connectivity levels. **Bold:** significant ($p < 0.05$); *Welch's test; DO: dissolved O_2

Variable/ Parameter	df	Dry		Wet	
		F	p	F	p
Protection					
Salinity	1	1.33	0.256	6.12	<0.05*
Temp.	1	0.14	0.715	0.16	0.695
DO	1	0.00	0.976	1.01	0.322
Turbidity	1	0.11	0.740	0.26	0.614
Connectivity					
Salinity	1	0.25	0.617	2.62	0.142
Temp.	1	2.99	0.091	29.87	<0.001
DO	1	5.84	<0.05	0.11	0.748
Turbidity	1	5.96	<0.05	6.54	<0.05

4.1.2. Compliance

It is likely that fishers do not comply with the restrictions of the NTR. Lack of compliance by artisanal fishers has undermined NTRs elsewhere (Fiske 1992). While patrols and enforcement are inconsistent in the Caroni Swamp, in 100 field days for this study, the only evidence of illegal finfishing was a few fixed lines attached to trees. Nonetheless, illegal fishing in the NTR may be more discreet or may have been more pervasive in the past.

4.1.3. Indirect fishing effects

Indirect effects of fishing on non-target species may not be evident in assemblage-level abundance and diversity indicators. While fishing may disrupt food webs (Pauly et al. 2000), there are cases where fishing effects and the benefits of protection were limited to target species even under intense exploitation (Jennings & Kaiser 1998, Abesamis et al. 2006). Restricting the removal of large piscivores potentially increases the predation of juveniles and small fishes (Polunin & Roberts 1993, Daan et al. 2005, Olds et al. 2012). Important piscivores were more abundant in the NTR, i.e. *Batrachoides surinamensis* (2.2-fold), *Lutjanus griseus* (3.1-fold) and piscivorous *Centropomus* spp. >60 mm (2.3-fold). However, other large predators, such as groupers, jacks and tarpon (reported by Ramdial 1975), were poorly represented by our fyke net sampling, and it is unclear what effect they may have on small fishes inside and outside of the NTR.

4.1.4. Reserve size

It is possible that the Caroni Swamp NTR is too small to be effective. NTR size needs to correspond to the scale of fish movements, and may have limited benefit if fish are highly mobile (Gell & Roberts 2003). Unfortunately, there have been few fish movement studies in mangroves, especially for the dominant species in the Caroni Swamp. Small fishes are certainly capable of migrating up to 2 km, and even 5 km for large-bodied species (Krumme & Saint-Paul 2010, Berkström et al. 2013). However, in microtidal systems such as the Caroni Swamp, home ranges are probably an order of magnitude smaller than in macrotidal systems (Krumme 2009), and so should be easily encompassed by the 30 km² NTR. In Florida, a 40 km² mangrove NTR was effective when it pro-

tected 22% of the system (Johnson et al. 1999). Models show that most NTRs benefit fish assemblages when 20–40% of the system is closed to fishing (Roberts & Hawkins 2000). Yet, the Caroni Swamp NTR encompasses >50% of the mangrove area—considerably exceeding the proportional coverage of other successful NTRs.

4.1.5. Reserve design

NTRs have failed to conserve biodiversity and target species when they were not placed in ecologically important habitats (Gilby et al. 2017). While little is known about the specific habitat requirements of the most common species in the Caroni Swamp, the NTR does possess habitats typically considered superior: i.e. it has a greater diversity of meandering channels and connected lagoons compared to the fished area, and its embankments have not been deforested (Marley et al. 2020). The 2 areas are also distinguished by wider river mouths in the fished area (Blue River = 100 m and Madame Espagnole River = 60 m) than in the NTR (Catfish Channel = 30 m and two 5 m wide creeks connecting directly to the gulf). Characteristics of the river mouth define the downstream connection with the gulf, regulating the exchange of eggs, larvae and migratory fishes (Ley 2005). Greater fish abundances have been found in estuaries with deeper mouths and wider openings to the sea (Monaco et al. 1992, Gilby et al. 2017). While we endeavoured to standardise survey creeks across the 2 areas, their connection with the Gulf of Paria may be greater in the fished area. Proximity to the gulf is just 1 measure of seascape connectivity, and including features of the main channel mouth, flow rate and any barriers to connectivity may reveal effects not found in the present study. Unfortunately, the geography of the Caroni Swamp does not replicate different sized river mouths inside and outside of the NTR.

The availability of macrobenthic invertebrate prey is also spatially variable in the Caroni Swamp (Kanhai & Juman 2018). However, it is difficult to make inferences about prey effects with the different sites used by Kanhai & Juman (2018). Still, variation in abundance and diversity of potential prey could be an important factor in fish distribution in the Caroni Swamp.

4.1.6. Study design

Fish assemblages are not always characterised prior to implementing NTRs, prompting appraisals to

make 'inside–outside' comparisons (e.g. Polunin & Roberts 1993, Kamukuru et al. 2004). Such comparisons are criticised because some NTRs are initially designated for their special biodiversity or habitats, and subsequent appraisals cannot separate the effects of the reserve from its initial superior state (Gell & Roberts 2003). However, the Caroni Swamp NTR was designed to protect bird assemblages rather than fish assemblages, and our findings do not show superior fish assemblages in the NTR. The geography of the Caroni Swamp also prevents a reserve–adjacent–control experimental design that negates the effects of spillover (Gell & Roberts 2003). Fished area creeks had to be situated at the boundary of the NTR, and fish may spillover directly from the NTR. Furthermore, prominent species in the Caroni Swamp spawn outside of mangroves (Targett 1979, Chaves 1995, Chaves & Otto 1998, Chaves & Bouchereau 2000), and eggs and larvae drifting back into the mangrove are more likely to enter the large channels of the fished area.

4.2. Driving factors in family-level effects

The family-specific responses to the NTR are difficult to explain given that little information is available on the ecology of the dominant species in this system and the factors influencing their distribution. Despite the lack of regulation on landing sizes in the Caroni Swamp, juveniles in this study were generally too small to be of value to fishermen (i.e. <10 cm). Other possible explanations include complex fishing effects that extend beyond target species and sizes, such as selective predation, family-specific habitat preferences influencing the recruitment and survival of juveniles, and other factors affecting connectivity with the Gulf of Paria that were not measured in this study.

4.3. Seascape connectivity

The effects of connectivity were not apparent at the assemblage level, but were demonstrated for 6 of 12 fish families, although 4 of these families were more abundant at sites farther away from gulf. These results question a generalised concept of greater seascape connectivity positively affecting juvenile fish abundance, commercial fish biomass and fish diversity, despite near creeks having easier access to feeding grounds in the gulf and presumably a better supply of eggs and larvae (Little et al. 1988). Differences

in abiotic conditions are unlikely to explain these findings, as they were broadly similar across proximity levels, with only small differences in temperature, dissolved O₂ and turbidity. It is plausible that regular feeding migrations may not structure fish assemblages in microtidal mangrove systems where fish have access to flooded creeks throughout the tidal cycle. Alternatively, superior feeding opportunities in the seaward fringes of mangroves are moderated by the need for small fishes to move further into mangroves to avoid predators (Vance et al. 1996, Sheaves et al. 2016). This would explain why juvenile fish abundance was 2.4-fold higher in far than near creeks, and why juveniles of several families were more abundant at far sites.

4.4. Recommendations

NTRs need to be evaluated in more turbid tropical estuaries which are amenable to robust experimental designs, such as variations of the before–after–control–impact or reserve–adjacent–control, incorporating interactions with connectivity (Osenberg et al. 2011). Factors that may confound any observed effects need to be accounted for, e.g. habitat differences, fishing pressure, compliance and connectivity. Further understanding is needed of how target and non-target taxa are predisposed to NTR effects depending on their specific life-history characteristics, behaviour or morphological attributes. More specifically to the Caroni Swamp, behavioural and life-history investigations are needed for the most common species using these habitats. The hydrology of the swamp is already heavily modified; however, meandering channels constitute just a small fraction of the aquatic habitat in the NTR, and there is only 1 opening to the gulf (Juman & Ramsewak 2011). Additional habitat modifications, whereby isolated lagoons are connected to the Gulf of Paria, could improve critical fish habitat in the Caroni Swamp. However, careful consideration is needed of all potential ecological consequences.

5. CONCLUSIONS

This is one of very few studies to have evaluated the effectiveness of NTRs at conserving fish assemblages in mangrove-lined estuaries, and, to our knowledge, is the first to incorporate seascape connectivity, despite recommendations to do so in MPA design. In the Caroni Swamp NTR, where fishing had been prohibited for nearly 30 yr, we found

higher fish species richness compared with the fished areas, but no evidence of benefits in terms of the overall juvenile fish abundance, commercial fish biomass, or increases in Δ or FD, even when accounting for seascape connectivity. Yet, there were benefits to juveniles of specific fish families. These findings emphasise the importance of focussed management measures that are guided by the species-specific ecologies and aligned with the aims of particular MPAs. In the case of the Caroni Swamp NTR, we recommend measures to improve fish habitat and its connectivity with adjacent habitats, so that the benefits of the NTR extend beyond waterfowl and habitat to the entire community. Finally, aside from the question of how successful individual MPAs are at delivering on specific aims, it is important to acknowledge the broader role that MPAs play in restricting mangrove deforestation and alteration on a global scale.

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APPENDIX. Fish assemblages of the Caroni Swamp, Trinidad

Table A1. Species identified in fyke net surveys in the Caroni Swamp, Trinidad, with their ecological groups and feeding guilds (based on Potter et al. 2015) used to calculate functional diversity (see Section 2.4). **Bold:** new species records for the Caroni Swamp; *specimens only identified to genus which were not included in total species or new species counts in Section 3.2

Family	Species	Ecological group	Feeding guild
Achiridae	Trinectes spp.	Estuarine & marine	Benthophagous
Ariidae	<i>Cathorops spixii</i>	Estuarine & marine	Benthophagous
	<i>Sciades herzbergii</i>	Estuarine & marine	Benthophagous
	<i>Sciades passany</i>	Estuarine & marine	Benthophagous
Atherinopsidae	Atherinella brasiliensis	Estuarine & marine	Zooplanktivorous
Batrachoididae	<i>Batrachoides surinamensis</i>	Solely estuarine	Hyperbenthophagous
Belontiidae	Strongylura marina	Marine straggler	Piscivorous
Carangidae	Oligoplites palometa	Estuarine & marine	Piscivorous/Lepidophagous
	Oligoplites saliens	Estuarine & marine	Piscivorous/Lepidophagous
	Oligoplites saurus	Estuarine & marine	Piscivorous/Lepidophagous
	Trachinotus goodei	Marine straggler	Hyperbenthophagous
Centropomidae	<i>Centropomus ensiferus</i>	Estuarine, marine & freshwater	Benthophagous/piscivorous
	Centropomus mexicanus	Estuarine, marine & freshwater	Benthophagous/piscivorous
	<i>Centropomus parallelus</i>	Estuarine, marine & freshwater	Benthophagous/piscivorous
	<i>Centropomus pectinatus</i>	Estuarine, marine & freshwater	Benthophagous/piscivorous
	<i>Centropomus undecimalis</i>	Marine estuarine-dependent	Benthophagous/piscivorous
Characidae	Astyanax bimaculatus	Freshwater straggler	Zooplanktivorous
Cichlidae	<i>Oreochromis niloticus</i>	Freshwater straggler	Herbivorous
Clupeidae	Harengula clupeola	Marine estuarine-opportunist	Zooplanktivorous
Eleotridae	Dormitator maculatus	Freshwater straggler	Omnivorous
	Gobiomorus dormitor	Amphidromous	Piscivorous
Elopidae	<i>Elops saurus</i>	Marine estuarine-dependent	Piscivorous
Engraulidae	Anchoa colonensis	Marine estuarine-opportunist	Zooplanktivorous
	Anchoa trinitatis	Marine estuarine-opportunist	Zooplanktivorous
	<i>Anchoa clupeoides</i>	Marine estuarine-opportunist	Zooplanktivorous
	<i>Anchoa</i> sp.*	Marine estuarine-opportunist	Zooplanktivorous
Ephippidae	Chaetodipterus faber	Marine estuarine-opportunist	Benthophagous
Erythrinidae	Hoplias malabaricus	Freshwater straggler	Piscivorous
Gerreidae	Diapterus auratus	Marine estuarine-dependent	Benthophagous
	<i>Diapterus rhombeus</i>	Marine estuarine-dependent	Benthophagous
	<i>Eucinostomus argenteus</i>	Marine estuarine-dependent	Benthophagous
	<i>Eucinostomus gula</i>	Marine estuarine-dependent	Benthophagous
	Eucinostomus melanopterus	Marine estuarine-dependent	Benthophagous
	Gerres cinereus	Marine estuarine-dependent	Benthophagous
Gobiidae	Gobionellus oceanicus	Estuarine migrant	Hyperbenthophagous
Gobiidae	<i>Gobionellus</i> sp.*	Estuarine migrant	Hyperbenthophagous
Haemulidae	Genyatremus cavifrons	Estuarine & marine	Benthophagous
	Haemulon bonariense	Marine estuarine-opportunist	Benthophagous
	Haemulopsis corvinaeformis	Marine estuarine-opportunist	Benthophagous
	Pomadasys croco	Estuarine, marine & freshwater	Benthophagous
Hemiramphidae	Hyporhamphus sp.	Marine estuarine-opportunist	Zooplanktivorous
Lutjanidae	<i>Lutjanus griseus</i>	Marine estuarine-opportunist	Hyperbenthophagous
Megalopidae	<i>Megalops atlanticus</i>	Marine estuarine-opportunist	Piscivorous
Mugilidae	<i>Mugil curema</i>	Marine estuarine-opportunist	Herbivorous
	<i>Mugil</i> sp.*	Marine estuarine-opportunist	Herbivorous
Sciaenidae	<i>Bairdiella ronchus</i>	Marine estuarine-opportunist	Benthophagous
	Stellifer colonensis	Estuarine & marine	Hyperbenthophagous
	Stellifer venezuelae	Estuarine & marine	Hyperbenthophagous
Serranidae	<i>Epinephelus itajara</i>	Marine estuarine-dependent	Benthophagous
Serranidae	Rypticus saponaceus	Marine estuarine-opportunist	Benthophagous
Sparidae	Archosargus rhomboidalis	Marine estuarine-opportunist	Benthophagous
Tetraodontidae	<i>Sphoeroides testudineus</i>	Estuarine & marine	Benthophagous