Mangrove and mudflat food webs are segregated across four trophic levels, yet connected by highly mobile top predators

Running page head: Estuarine food web segregation and connectivity

Authors: Guy Marley[1*], Andrew J. Lawrence[2], Dawn A. T. Phillip[1†], Brian Hayden[3]

1. Department of Life Sciences, The University of the West Indies, St. Augustine, Trinidad and Tobago

2. Department of Biological Sciences, University of Chester, Chester, CH1 4BJ, U.K.

3. Stable Isotopes in Nature Laboratory, Canadian Rivers Institute, University of New Brunswick, Fredericton, E3B 5A3, Canada

*Corresponding author: Guy Marley, Email: guidomarley@gmail.com

† Deceased

Abstract

Seascape connectivity is crucial for healthy, resilient ecosystems and fisheries. Yet, our understanding of connectivity in turbid mangrove-lined estuaries - some of the world's most productive ecosystems - is limited to macrotidal systems, and rarely incorporates highly mobile top predators. We analysed $\delta^{13}C$ and $\delta^{15}N$ isotope values of seven primary producers, 24 invertebrate taxa, 13 fishes, four birds and one reptile to reveal trophic interactions within and between a mangrove and adjacent mudflat in a microtidal system of the Gulf of Paria, Orinoco River estuary. Primary producers, invertebrates and fishes collected within the mangrove were significantly depleted in ^{13}C and ^{15}N compared to those collected on the mudflat. Stable isotope mixing models showed that mangrove-derived carbon was predominantly assimilated by invertebrates (78±5%) and fishes (88±11%) sampled in the mangrove. In contrast, invertebrates and fishes sampled in the mudflat derived less than 21% of their carbon from mangrove sources. Instead, microphytobenthos and phytoplankton underpinned the mudflat food web. Scarlet ibis (*Eudocimus ruber*) and night heron (*Nyctanassa violacea*) were also highly associated with mangrove carbon sources. However, osprey (*Pandion haliaetus*), snowy egret (*Egretta thula)*, and caiman (*Caiman crocodilus*) obtained carbon from both mangrove and mudflat sources, effectively integrating the food webs. The present study demonstrates simultaneous aspects of food web segregation and connectivity, as well as the importance of surveying the entire food web across a range of tidal systems when investigating seascape connectivity.

Keywords: estuary, stable isotope, seascape, connectivity, food web, mixing model

1. Introduction

Spatial conservation planning advocates for a seascape based ecological approach which incorporates interactions between neighbouring habitats (Olds et al. 2012, Nagelkerken et al. 2015, Weeks 2017). Connectivity improves ecosystem resilience to climate change and other disturbances by stabilising food web dynamics (Chen & Cohen 2001). Food webs are connected between habitats by the passive exchange of organic matter and animal feeding migrations (Dorenbosch et al. 2004, Igulu et al. 2013). These interactions contribute to the productive fisheries found in tropical estuaries (Rönnbäck 1999, Manson et al. 2005). But there has been little empirical measurement of food web connectivity between turbid habitats of the world's largest tropical estuaries. Furthermore, seascape connectivity is strongly influenced by tidal regime (Krumme 2009, Igulu et al. 2014), yet the few studies in tropical estuaries have been largely limited to macrotidal systems (e.g. Kruitwagen et al. 2010).

An intermediate level of connectivity is predicted to offer the greatest stabilising effect to food webs (LeCraw et al. 2014). 'Spatially coupled' food webs allow 'prey switching', whereby predators diminish prey in one habitat but can switch focus to more abundant prey in another habitat (Murdoch et al. 1975, McCann et al. 2005); and 'rescue effects', whereby predators or prey that are close to extinction in a particular habitat can be 'rescued' by resources from a nearby habitat. However, if connectivity is too high then habitat divisions are blurred and food webs become continuous and synchronised (LeCraw et al. 2014). Conversely, species in isolated food webs are at greater risk of local extinctions (Eklof & Ebenman 2006). If these species are important prey, their loss can lead to cascading secondary extinctions up the food chain (Dunne et al. 2002, Eklof & Ebenman 2006).

In turbid tropical estuaries, mangrove food webs interact with the main estuary channel, rivers, mudflats and the surrounding coastline (Bouillon et al. 2008, Krumme 2009). Fauna that use these habitats must derive their energy from one of three potential sources: 1) in-situ production; 2) passive import from neighbouring habitats; or 3) feeding migrations between habitats. Mangrove leaves were traditionally thought to underpin mangrove food-webs and bolster secondary production in neighbouring habitats via carbon 'outwelling' (Odum & Heald 1975, Lee 1995). However, more recent evidence from stable isotope analysis (SIA) suggests the picture is more complex (see review in Lee 1995). Mangrove-derived carbon underpins mangrove food webs in some circumstances (Rodelli et al. 1984, Vaslet et al. 2012), but imported mudflat and seagrass carbon can be important too (Bouillon et al. 2002, Kruitwagen et al. 2010). As a result, there has been a shift in focus from carbon 'outwelling' to carbon 'inwelling' (Bouillon et al. 2008); and even where mangrove carbon is readily available, consumers may still select more digestible carbon sources (MacIntyre et al. 1996, Underwood & Kromkamp 1999, Melville & Connolly 2005, Shahraki et al. 2014).

Animal migration is a vector for the transport of organic material and nutrients between systems (Sheaves & Molony 2000, Lugendo et al. 2006). Fishes and invertebrates are the best documented vectors in this regard, but the mobility of wetland birds and reptiles introduces new scales of seascape connectivity (Krumme 2009, Buelow & Sheaves 2015). These top predators feed in the mangrove forest and channels, but also undertake regular migrations to forage in other estuarine habitats (Bildstein 1990, Miranda & Collazo 1997). Even though birds and reptiles may fundamentally alter ecosystem functioning (Steinmetz et al. 2003, Schmitz et al. 2010, Valencia-Aguilar et al. 2013, Moss 2017), the degree to which they influence food web dynamics in mangrove-lined estuaries is unknown.

SIA is a useful tool with which to estimate the degree of connectivity between estuarine food webs (Mallela & Harrod 2008, Kruitwagen et al. 2010). Differential fractionation of carbon and uptake of nitrogen during primary production in these habitats results in distinct stable isotope signatures of primary producers (Lugendo et al. 2006, Vaslet et al. 2012). The limited carbon fractionation between trophic levels, and the contrasting trophic enrichment in nitrogen isotope ratios, means that isotope ratios of consumers reflect the primary producers that underpin their food web (France 1995). Stable isotope mixing models can then be used to estimate the relative contribution of different primary producers to consumers diet (Post 2002). As such, primary producers and 42 consumer taxa covering four trophic levels were sampled in mangrove and mudflat habitats of the Gulf of Paria in the Orinoco River estuary. $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios and mixing models were used to answer the question ‘Are mangrove and mudflat food webs connected through passive carbon exchange or animal migrations in microtidal estuaries?’.

2. Materials and methods

2.1. Study area

The Caroni Swamp covers 52.63 km^2 on the Gulf of Paria coast of Trinidad and Tobago in the Orinoco River estuary (Juman & Ramsewak 2013). It is characterised by an estuarine mangrove forest dominated by *Rhizophora mangle*. A tidal range of roughly 1 m on spring tides is sufficient for the under-canopy benthos to be exposed at low tide but with channels, creeks and lagoons remaining flooded. The swamp is bordered to the north by the Caroni River which drains the largest watershed in Trinidad and forms an intertidal mudflat at its merger with the Gulf of Paria (Fig. 1). An area encompassing part of the mangrove and mudflat was designated a RAMSAR site in 2005 to reflect its internationally important bird communities, especially the scarlet ibis *Eudocimus ruber* (Bildstein 1990, Juman & Ramsewak 2011).

2.2. Sample collection

Samples were collected in the dry season in March 2016 and 2017 at two sites in both the mangrove and the mudflat (Fig. 1). Samples from each habitat were pooled across years and sites so that they incorporated spatial and temporal variability in diets and isotope values.

2.2.1. Primary producers

Primary producers and other potential carbon sources were collected in the mangrove: *R. mangle* leaves (live and senescent yellow), microphytobenthos (MPB), benthic and prop-root macroalgae (*Ulva intestinalis*, *Caulerpa verticiliata, Caloglossa leprieurii* and *Polysiphonia* sp.), sediment and particulate organic matter (POM); and the mudflat: MPB, macroalgae, sediment, phytoplankton and POM. MPB was scraped off the sediment surface from conspicuous microalgal mats under the canopy of the mangrove and from the exposed mudflats. Sediment was taken from 2 cm below the surface to avoid contamination with MPB and rinsed with 0.1 M hydrochloric acid to remove carbonates. POM was isolated by filtering 20 L of water through a 63 μ glass microfiber filter. Phytoplankton could not be isolated from the mangrove POM due to low densities and an overwhelming abundance of mangrove fragments. As such, we used a global mean for marine phytoplankton in data analyses ($\delta^{13}C$=-21.3±0.15‰, $\delta^{15}N$=8.6±0.5‰; Newell et al. 1995). Although phytoplankton was isolated in the mudflat, isotope values were markedly depleted compared to any mudflat consumers and mudflat POM (Table 1). Presumably, mudflat phytoplankton was influenced by a nearby sewage treatment plant at the time of collection, and so were omitted from further analyses. Instead, the mudflat POM signature ($\delta^{13}C$ = -20.2±0.6, $\delta^{15}N$ = 8.5±1.0; collected within one week of other samples) was considered a suitable proxy for mudflat phytoplankton as it closely aligned with a global mean for marine phytoplankton (as above) and with mudflat consumers - especially planktivores.

2.2.2. Consumers

Invertebrates were sampled from mangrove prop-roots, dead vegetation and from the sediment surface, while benthic meiofauna were isolated from MPB samples (see below) and squid

(Loliginidae) from trawls in the mudflat. Invertebrates (excluding meiofauna and squid) were kept in filtered seawater for 24 hours to evacuate guts. Fish were collected using fyke and trawl nets, and a baited palangue for stingray, *Dasyatis americana*. Fish were measured, weighed and similar sizes selected within species (Supplement S1). As most fish species were predominantly represented by juveniles in the Caroni Swamp, specimens were generally large juveniles with the exception of the Ariidae and *S. testudineus* which were adults. The 13 fish species accounted for 84% of approximately 15 000 individuals surveyed in a wider community study (Marley unpublished). Two caiman (*Caiman crocodilus*) were caught in fyke nets during the mangrove sampling, and a third, recently deceased carcass found in the mangrove was also sampled. Feathers of scarlet ibis (*Eudocimus ruber*), snowy egret (*Egretta thula*) and night heron (*Nyctanassa violacea*) were collected from a roosting site in the mangrove, while feathers of osprey (*Pandion haliaetus*) were dropped from birds perched in the mangrove.

2.3. Sample processing

Samples were kept on ice until returned to the lab, then frozen pending preparation for isotope analysis. Muscle tissue was sampled from bivalves, decapods, fishes and caiman, and nondescript tissue from sponge and tunicates. Phytoplankton, MPB and meiofauna were separated by centrifugation and stepwise decanting after buffering with Ludox solution (Levin & Currin 2012). Samples were then microscopically inspected for purity. All samples were washed with distilled water and dried at 40°C for 48 hours, ground into a fine powder, and weighed into tin capsules (1-1.2 mg for animals and 3-3.5 mg for plants, algae, sediment and POM). $\delta^{13}C$ and $\delta^{15}N$ compositions were measured with a FlashEA 1112 elemental analyser coupled to a Thermo Finnigan DELTA^{PLUS} Advantage mass spectrometer at Stable Isotopes in Nature Laboratory at the University of New Brunswick, Canada. Experimental error, based on the repeated analysis of in-house laboratory standards bovine liver tissue ($\delta^{13}C$: -18.8‰; $\delta^{15}N$: 7.1‰) and muskellunge liver tissue ($\delta^{13}C$: -22.3‰; $\delta^{15}N$: 14.1‰) was estimated as 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

2.4. Data analysis

2.4.1. Stable isotope values

All statistical analyses were performed using the R statistical software (R-Core-Team 2018). Isotope values of taxa were compared between habitats with a student's t-test where data met assumptions of normality and homogenous variances, with Welch's t-test when variances were heterogenous, and with the non-parametric Wilcoxon signed rank test when data could not be log transformed to normality (only *Balanus* sp. data was transformed). Assumptions of parametric methods were validated with Shapiro-Wilke's test for normality and Levene's test for variances.

2.4.2. Trophic mixing models

The trophic position of consumers were calculated using the package tRophicPosition (Quezada-Romegialli et al. 2018)(Supplement S1). Bi-plots of $\delta^{13}C$ against $\delta^{15}N$ of all samples were used to inform the selection of baselines for estimating trophic positions. For mangrove specimens (including birds and caiman), mangrove leaves and phytoplankton were used as the benthic and pelagic baselines respectively. For mudflat specimens, MPB and POM were the benthic and pelagic baselines. Trophic enrichment factors (TEFs) were 1.3±0.3‰ and 2.9±0.3‰ for carbon and nitrogen respectively (McCutchan et al. 2003).

Two-source Bayesian mixing models (MixSIAR; Stock & Semmens 2016) determined the relative reliance of each consumer on two distinct sources of primary production: mangrove or mudflat. In the mangrove, carbon sources with similar isotope values were pooled together as composite sources representing 1) *mangrove leaves*: live and senescent mangrove leaves, mangrove POM and mangrove sediment; and 2) *macroalgae*: *U. intestinalis, C. leprieurii* and *Polysiphonia* sp.. *C. verticiliata* was omitted from the *macroalgae* source as it bore little relation to consumer isotope signatures (see Table 1 for isotope values of all sources). The mangrove source was then calculated as a weighted mean and SD of isotope values from *mangrove leaves*, *macroalgae,* MPB and phytoplankton[1]. Meanwhile, the mudflat source was a weighted mean and SD of MPB, POM, sediment, *U. intestinalis* and mixed macroalgae. The weightings gave each source an equal contribution to the overall mean and SD, and were calculated by $\bar{x}_w = \sqrt{\frac{\sum_{i=1}^{N} w_i x_i}{\sum_{i=1}^{N} w_i}}$ and $sd = \sqrt{\frac{\mathrm{N}\sum_{i=1}^{N} w_i (x_i - \bar{x}_w)^2}{(\mathrm{N}-1)\sum_{i=1}^{N} w_i}}$, where N is the number of observations, x_i are the observations, and w_i are the weights calculated by $w_i = \frac{total\ number\ of\ observations}{number\ of\ observations\ in\ source}$. Calculated median trophic positions and TEFs of McCutchan et al. (2003) were used in mixing models. Mangrove and mudflat source values were compared with a weighted Mann-Whitney-U test.

3. Results

[1] The only exceptions were for *Aratus pisonii* and *Littorina angulifera* which had isotope values highly specific to mangroves leaves and thus mangrove leaves alone were used as the mangrove source to avoid violating conditions of the mixing models.

A total of 305 samples were collected and processed for SIA. These included nine potential carbon sources (seven primary producers, sediment and POM), 24 taxa of invertebrate consumers, 13 fishes, four birds and one reptile (Table 1).

3.1. Stable isotope values

Primary producers sampled in the mangrove were ^{13}C depleted (range: -42.3 to -18.4‰) relative primary producers in the mudflat (-23.4 to -15.8‰; Table 1). Of the four sources collected in both habitats, *Ulva intestinalis*, sediment and POM were significantly ^{13}C depleted in the mangrove relative to the mudflat, whereas MPB was comparable between habitats. Mean $\delta^{15}N$ values were similar in the mangrove (range: 1.2 to 8.6‰) and the mudflat (1.1 to 8.5‰), but with significant differences for POM (enriched in the mudflat) and MPB (enriched in the mangrove). There was a clear segregation in $\delta^{13}C$ and $\delta^{15}N$ values of consumers in the mangrove and the mudflat (Fig. 2). $\delta^{13}C$ values of mangrove invertebrates (mean across taxa = -24.6±0.3‰) were significantly different to mudflat invertebrates (-17.0±0.3‰)($t_{df=113}$ = -15.52, $p < 0.001$). Likewise, $\delta^{13}C$ values of mangrove fishes (mean across taxa = -23.9±0.4‰) were significantly different to mudflat fishes (-16.6±0.3‰)($t_{df=75}$ = -13.746, $p < 0.001$). Of the five invertebrate species collected in both habitats, four were significantly depleted in ^{13}C in the mangrove relative to the mudflat (i.e. *Melongena* sp., *Crassostrea rhizophorae*, *Thais rustica* and *Balanus* sp.; Table 1). Meanwhile, all five fish species collected in both habitats were significantly depleted in ^{13}C in the mangrove relative to the mudflat. $\delta^{15}N$ values of mangrove invertebrates (mean across taxa = 6.5±0.3‰) were also significantly different to mudflat invertebrates (8.9±0.3‰)($W_{df=113}$ = 621, $p < 0.001$), and $\delta^{15}N$ values of mangrove fishes (mean across taxa =

10.0±0.2‰) were significantly different to mudflat fishes (12.9±0.2‰)($t_{df=75}$ = -10.782, $p < 0.001$). Of the species collected in both habitats, *T. rustica*, *Balanus* sp. and all five fish species were significantly depleted in ^{15}N in the mangrove relative to the mudflat (Table 1).

3.2. Trophic mixing models

There were significant differences in $\delta^{13}C$ values of mangrove (mean = -24.5±0.7‰) and mudflat primary producers (-19.8±0.7‰) used in two-source mixing models ($\chi^2_{df=69}$ = 3.31, $p < 0.001$). These models revealed a segregation of resource-use between habitats by both invertebrates and fishes (Fig. 3). Of the taxa collected in the mangrove, the median mangrove carbon utilisation averaged 78±5% across invertebrate taxa and 88±11% across fish taxa. Only *Balanus* sp. and nematoda exhibited isotope signatures indicative of mudflat carbon sources (Fig 3). For mudflat taxa, median mangrove carbon utilisation averaged 21±5% across invertebrate taxa and 19±2% across fish taxa. Only mudflat nematoda showed evidence of assimilating a mangrove carbon component of the mudflat sediment. This component was apparent in the ^{13}C depleted values of mudflat sediment (Table 1).

Two bird species and the caiman connected the two habitats (Fig. 3). The six *Egretta thula* collected in the mangrove had a median mudflat resource use of 46% (28-63% BCI), but this reached 66% (47-82%) for two of those individuals. Only two *Pandion haliaetus* were collected in the mangrove, but they also divided their resource use between the two habitats (Fig. 3): one individual had isotope signatures indicative of feeding in the mangrove ($\delta^{13}C$ = -21.3; $\delta^{15}N$ = 11.91), while the other clearly fed in the mudflat ($\delta^{13}C$ = -15.5; $\delta^{15}N$ = 15.4). Similarly, there were individualistic feeding behaviours of *Caiman crocodilus*. Two individuals were predominantly reliant on mangrove carbon (median mangrove source 75%, 60-87%), whereas the third individual showed evidence of feeding in the mudflat (median mudflat source 59%, 34-78%). In contrast, *Eudocimus ruber* and *Nyctanassa violacea* were highly reliant on mangrove sources. *E. ruber* in particular, were almost entirely dependent on mangrove derived prey (median mangrove source 98%, 97-99%).

4. Discussion

Seascape connectivity should be an integral component of spatial conservation planning (Weeks 2017). Mangrove ecosystems have been at the forefront of seascape connectivity concepts for the role they play as nursery habitats, foraging habitats and potential sources of organic carbon (Mumby et al. 2004, Mumby & Hastings 2008, Nagelkerken et al. 2012). However, the present study found that connectivity between food webs in adjacent habitats of a turbid mangrove-lined estuary was very limited for invertebrates and fishes in the dry season of consecutive years. There was little evidence that mangrove carbon was imported into mudflat food webs, that mudflat carbon was imported into mangrove food webs, or that invertebrates and fishes migrate between the two habitats to feed. Only *Balanus* sp. and nematoda collected in the mangrove appeared to rely on mudflat carbon sources. However, this was more likely due to specific assimilation of mangrove MPB and/or phytoplankton which had $\delta^{13}C$ values equivalent to mudflat sources. The habitats were however connected by highly mobile top predators, including two species of birds and one species of reptile. Thus, this study reveals simultaneous aspects of segregation and connectivity in turbid estuarine seascapes. The segregation of communities and processes has important implications for the resilience of ecosystems; while top predators have the potential to connect and influence the functioning of tropical seascapes (Sheaves 2005, LeCraw et al. 2014, Moss 2017).

4.1. Passive carbon exchange

Mangrove food webs are generally underpinned by organic carbon from the decomposition of mangrove leaves (Kristensen et al. 2008). Imported carbon from neighbouring mudflats is also significant in ‘open’, macrotidal systems, with strong mixing between surrounding coastal waters (Bouillon et al. 2002, Kruitwagen et al. 2010). However, the Gulf of Paria is a microtidal system with a tidal amplitude of only 1 m. Tidal mixing is relatively limited, and any imported carbon seems to be diluted by the strong mangrove signal. This is reflected in the POM and sediment isotope values being closely aligned to those of mangrove leaves; as well as the visible concentration of mangrove fragments in the POM. An overwhelming predominance of mangrove carbon in the system clearly displays its incorporation throughout the mangrove food web.

As a global average, about half of all the carbon produced by leaflitter is exported into coastal waters - amounting to 11% of all terrigenous carbon entering the oceans (Jennerjahn & Ittekkot 2002). How far this carbon is transported is still debated, but is generally being revised down (Kristensen et al. 2008). In the Caroni Swamp, mangrove carbon is not incorporated into the adjacent mudflat food web, and there have been similar observations in other habitats adjacent to mangroves (Rodelli et al. 1984, Newell et al. 1995, Lugendo et al. 2006, Kruitwagen et al. 2010). Such findings could be attributed to three major processes. 1) *Hydrodynamics*: mangrove carbon does not reach the mudflat. Rodelli et al. (1984) reported that mangrove-derived carbon was only important for secondary production within 2km of the mangrove/sea boundary. Still, proximity is unlikely to be a limiting factor in our study area as the two habitats are only 10s–100s of meters apart. The $\delta^{13}C$ depleted values of mudflat sediment and nematodes are testament to a sizeable mangrove carbon constituent of the mudflat sediment and its availability to consumers, at least to nematodes. While mudflat POM isotope values showed little evidence of mangrove POM, mangrove POM can have considerable exchange with surrounding habitats (Hemminga et al. 1994). A tidally explicit sampling of the mudflat POM may yet reveal a mangrove carbon element. 2) *Mineralisation rate*: mangrove carbon is mineralised too fast or too slow to be available to mudflat consumers. As much as 40% of leaflitter carbon is leached as dissolved organic carbon (DOC) in the first 8h after falling into mangrove waters (Benner et al. 1986). Estimates of DOC mineralisation vary widely. While some fractions may be incorporated rapidly into microbial biomass (Benner & Hodson 1985), more refractory fractions are washed far offshore before being mineralised (Dittmar et al. 2006). 3) *Selective feeding*: mudflat consumers avoid mangrove carbon. MPB production can be five times higher in mudflats than in mangroves, and along with phytoplankton, is generally the primary carbon source to mudflat food webs (MacIntyre et al. 1996, Li & Lee 1998, Nascimento et al. 2008). These highly digestible algae are preferred to nutritionally poor mangrove leaves (Nicotri 1980, Bouillon et al. 2002). Even though mudflat nematoda assimilated mangrove carbon, this signal was not apparent in meiobenthic predators or other detritivorous and omnivorous invertebrates. Thus, nematodes do not appear to be important prey for the higher trophic taxa examined herein, and mangrove carbon would seem to be selectively avoided by detritivores such as *Clibanarius vittatus* and *Litopenaeus schmitti*. Ultimately, passive carbon exchange does not connect these food webs in the same ways that have been observed for macrotidal systems (Kruitwagen et al. 2010).

4.2. Animal movement

We found little evidence that invertebrates or fishes make inter-habitat feeding migrations between mangrove and mudflat habitats on time scales of weeks to months across consecutive years. Two-source mixing models - distinguishing mangrove and mudflat sources of energy - showed a clear segregation of the communities, even segregating populations of the same species in each habitat. The only exception was one of ten *Centropomus ensiferus* individuals surveyed in the mudflat, but which had isotope values indicative of feeding in the mangrove.

Habitat connectivity between mangroves and adjacent habitats is less emphatic where small tidal amplitudes do not force animals into surrounding habitats at low tide, where beneficial habitats are unavailable nearby, or where the cost to benefit ratio of the journey is unfavourable (Lugendo et al. 2006, Dorenbosch et al. 2007, Hammerschlag et al. 2010, Igulu et al. 2014). The effect is that home range of fishes in microtidal systems could be an order of magnitude smaller than conspecifics from macrotidal systems, and are rarely more than 2 km (Krumme 2009). As mangrove creeks in the Caroni Swamp remain flooded at low tide, and weak tides do not expedite fish movement, the incentive to migrate to feed in adjacent habitats may fail to offset the energetic cost and risk of predation (Nøttestad et al. 1999, Hammerschlag et al. 2010). We collected mangrove fish specimens at 2-5 km from the Gulf of Paria, and even further from the mudflat. Presumably, this is beyond a reasonable distance at which fish could regularly migrate to other habitats, and our findings may have been different if fish were collected from within 2 km of the gulf. However, the Caroni Swamp is approximately 8 km from sea to land, meaning that fish residing in the vast majority of mangrove habitat do not connect habitats through regular feeding migrations. While connectivity studies have recognised the importance of distance between mangroves and adjacent habitats (Dorenbosch et al. 2007, Jelbart et al. 2007), and tidal regime (Krumme 2009, Igulu et al. 2014), rarely have studies incorporated spatial variation in connectivity across the mangrove forest. The 13 fish species in this study accounted for a substantial proportion (84%) of individuals in the Caroni Swamp (Marley unpublished), and are important members of mangrove communities in the region (e.g. Giarrizzo 2007, Bouchereau et al. 2008, Arceo-Carranza & Vega-Cendejas 2009). As such, these findings have considerable importance to ecosystem functioning in microtidal estuaries.

Fish collected in the mudflat showed no evidence of feeding in the mangrove, even though the mangrove was easily accessible and mangroves are perceived as good feeding habitats for juveniles (Laegdsgaard & Johnson 2001). Invertebrate densities are often greater in mudflats than in mangroves, and peak in the lower inter-tidal area in front of mangroves (Dittmann 2001, Alfaro 2006, Sheaves et al. 2016). There may be little incentive to feed in the mangrove if food resources are plentiful in the mudflat. Mudflat fishes may still take advantage of the mangrove root architecture as a safe resting place during the day, as coral reef fishes do (Verweij et al. 2006, Verweij & Nagelkerken 2007). Even so, the data presented here strongly suggests they return to feed in the mudflat.

Fish size is also an important determinant of migratory behaviour (Nøttestad et al. 1999, Hammerschlag et al. 2010). Juveniles, including *Lutjanus griseus* and *Anchovia clupeoides* that were reported in the present study, do make regular feeding migrations in micro- and meso-tidal systems (Starck & Davis 1966, Giarrizzo 2007, Verweij & Nagelkerken 2007). However, some species may prefer to remain in the safety of mangrove prop-roots rather than move into open feeding areas (Thayer et al. 1987, Laegdsgaard & Johnson 2001). Most fish in the present study were juveniles, and the findings herein might be different if more mobile fishes such as large snappers, groupers and tarpon were included (Koenig et al. 2007, Meyer et al. 2007).

The realisation that coral reefs and fisheries are enhanced when connected to mangroves has encouraged a fish-centric approach to seascape connectivity (Mumby et al. 2004, Mumby & Hastings 2008, Nagelkerken et al. 2012). Meanwhile, the roles of birds and reptiles in connecting seascapes has been neglected. The present study is the first to incorporate these top predators when evaluating the connectivity of food-webs between habitats of a mangrove-lined estuary. *P. haliaetus*, *E. thula* and *C. crocodilus* that were sampled in the mangrove, fed in the mangrove, but also fed in the mudflat. These mobile predators translocate organic material and nutrients through their foraging migrations and return to roosting/resting sites (Schmitz et al. 2010, Valencia-Aguilar et al. 2013, Buelow & Sheaves 2015, Moss 2017). The faeces of birds and caiman at roosting/resting sites subsidise the nutrient load in what are often nutrient-limited mangroves (Fittkau 1970, Adame et al. 2015, Alongi 2018). Such nutrient subsidies can be strong enough to fundamentally alter ecosystem functioning (Fittkau 1970, Powell et al. 1991, Maron et al. 2006, Graham et al. 2018), yet we have little understanding of these processes in mangrove-lined estuaries. The influence of predators in top-down control of food-webs is better understood, but birds and reptiles have generally been overlooked as top predators in aquatic food webs, especially in mangroves (Steinmetz et al. 2003, Valencia-Aguilar et al. 2013, Buelow & Sheaves 2015).

4.3. Limitations of the study

We calculated trophic positions (TPs) of taxonomic groups to more accurately model their resource use - selecting benthic and pelagic baselines that reflected the different feeding guilds of our taxa. However, TPs may be under- or overestimated if resource use is highly specific to either baseline. While we verified TPs of each species with dietary information from the literature, TPs of below two for some primary consumers were obvious underestimates (Supplement S1). As this only affected a small number of consumers, and because the sources in mixing models were separated by $\delta^{13}C$ which only has a small fractionation between trophic levels, this was unlikely to have an impact on our overall findings.

Phytoplankton densities are highly variable in mangrove ecosystems, probably due to the high turbidity and an inhibiting effect of tannins (Kristensen et al. 2008). Given their low densities in the mangrove, it is unlikely that phytoplankton are important to the largely $\delta^{13}C$ depleted mangrove food web, and isotope values of *Balanus* sp. would suggest that resuspended MPB may be more important than phytoplankton. Still, to be thorough, we used literature values of marine phytoplankton in the composite mangrove source as phytoplankton could not be isolated from the POM. Literature values have the advantage that they incorporate the high spatial and temporal variability of phytoplankton isotope values. However, estuarine phytoplankton may be more $\delta^{13}C$ depleted than marine phytoplankton (Bouillon et al. 2008). If this were the case, it would serve to improve the separation of our composite mangrove and mudflat sources - further differentiating the mangrove and mudflat food webs and strengthening our conclusions. Still, marine phytoplankton isotope values were likely to be applicable in our study as 1) they were highly similar to those of mudflat POM and mudflat planktivores; and 2) salinity – an important determinant of $\delta^{13}C$ of estuarine phytoplankton (Bouillon et al. 2007) – was higher in the mangrove than the mudflat and close to that of seawater (25-35 ppt).

Conclusions

Despite their close proximity, mangrove and mudflat food webs within the Gulf of Paria were highly segregated, each supporting invertebrate and fish assemblages in their own right, and warranting distinct management approaches to conserve ecosystem functioning. These findings are likely due to the small tidal amplitudes in this region, which constrain tidal mixing and fish migrations. As such, spatial variation in seascape connectivity across mangrove forests may be even more important in microtidal than macrotidal systems. While the segregation of habitats makes management somewhat simpler, it also increases vulnerability - whereby local disturbances may have greater impact if they are not buffered by interactions with adjacent habitats. Highly mobile top predators however, can connect habitats through their feeding migrations and return to roosting/resting sites. The significance of this trophic coupling is still unknown. As birds and reptiles can fundamentally alter the nutrient dynamics of other tropical systems, further work is needed to address the importance of these mobile predators in turbid estuarine mangroves where bird and reptile communities are probably more common than non-estuarine fringing mangroves. Special attention is also needed to their role as top-down controllers of estuarine food-webs, as apex predators are most at risk from habitat loss and climate change.

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Table 1. Mean (±SE) stable isotope values of primary producers and consumers in the mangrove and mudflat habitats of the Gulf of Paria, Trinidad and Tobago. P shows the outcome of t-tests and Wilcoxon Signed Rank tests (*) with bold values highlighting significant differences. NAs given when insufficient samples for a statistical test. n=sample size. Species IDs provided for Fig. 2.

Taxa	δ^{13}C (n)			δ^{15}N		
	Mangrove	Mudflat	P	Mangrove	Mudflat	P
Carbon sources						
Caulerpa verticiliata	-42.3±0.4 (6)			4.4±0.5		
Ulva intestinalis	-33.9±0.1 (2)	-15.8±0.6 (3)	**<0.001**	7.2±0	7.2±1.1	>0.1
Caloglossa leprieurii	-30.1±1.5 (3)			7.3±0.2		
Polysiphonia sp.	-30.1±1.2 (6)			8.2±0.1		
Rhizophora mangle	-27.8±0.2 (12)			1.2±0.9		
Sediment	-27±0 (11)	-23.4±0.4 (4)	**<0.01**	2.9±0	3.9±1.5	>0.1*
POM	-26.9±0.1 (7)	-20.2±0.6 (5)	**<0.001**	2.6±0.2	8.5±1	**<0.01**
Phytoplankton	-21.3±0.2 (56)[a]	-31.7±0.2 (3)[b]		8.6±0.5 (4)[a]	6.6±0.4[b]	
Mixed macroalgae		-22.9±0.5 (5)			5.8±0.1	
Microphytobenthos (MPB)	-18.4±0.7 (4)	-16.6±0.5 (4)	>0.1*	5.1±0.2	1.1±0.4	**<0.001**
Meiofauna						
Root meiofauna	-28.1±0.8 (2)			6.4±0.2		
Nematoda	-23.1±0.3 (3)	-24.2±0.7 (2)	>0.1	5.1±0.2	5.1±0.2	>0.1
Copepoda		-17.4±0.9 (3)			4.0±1.1	
Porifera/Tunicata						
Botryllus planus	-27.5±0.1 (4)			4.9±0.1		
Distaplia bermudensis	-25.9±0 (1)			6.2±0		
Sponge unidentified	-27.9±0.3 (6)			5.8±0.3		
Bivalvia						
Brachidontes exustus	-23.8±0.1 (5)			5.7±0.2		

Table 1. cont.

Taxa	δ13C (n)			δ15N		
	Mangrove	Mudflat	P	Mangrove	Mudflat	P
Crassostrea rhizophorae	-23.6±0.2 (8)	-18.2±0.1 (3)	**<0.001**	7.5±0.5	8.4±0.2	>0.1
Codakia orbicularis		-19.1±0 (1)			7.3±0	
Polychaeta						
Sabellidae	-24.9±0.5 (2)			5.7±0.6		
Gastropoda						
Nassarius antillarium	-28±0 (1)	-16.1±0.2 (4)	NA	8.4±0	9.3±0.1	NA
Melongena sp.	-24.1±0.7(4)	-16±0.2 (4)	**<0.001**	8.1±0.1	8.9±0.5	>0.1
Thais rustica	-21.8±0.2 (4)	-15.4±0.3 (4)	**<0.001**	8±0.2	10.2±0.5	**<0.05**
Decapoda						
Callinectes sapidus	-27.3±0.7 (6)			6.7±0.3		
Pachygrapsus gracilis	-24.3±0 (3)			8.1±0.1		
Panopeus sp.	-24.2±0 (1)			8.2±0		
Petrolisthes amatus	-23.1±0 (1)			6.4±0		
Clibanarius vittatus		-16.4±0.5(4)			7.1±0.3	
Macrobrachium acanthurus	-26±0 (1)			9.7±0		
Litopenaeus schmitti		-16.1±0.7(10)			9.4±0.2	
Other invertebrates						
Littorina angulifera (Littorinidae)	-25.2±0.1 (5)			1.2±1.5		
Aratus pisonii (Sesarmidae)	-25.8±0.6 (3)			1.7±1.6		
Balanus sp. (Balanidae)	-20.3±0.3 (10)	-18.3±0.2(6)	**<0.05**	8.9±0.1	9.8±0	**<0.005**
Loliginidae		-15.5±0.2(3)			14.1±0	
Fishes (Benthivores)						
Diapterus auratus	-28±1.8 (3)	-17±0.4(4)	**<0.005**	10.1±0.3	11.9±0.3	**<0.05**
Centropomus ensiferus	-24.5±0.5 (7)	-20±1.7(4)	**<0.05**	8.6±0.2	11.9±0.5	**<0.001**
Bairdiella ronchus	-23.2±0.5(7)	-15.4±0.2(7)	**<0.001**	11.4±0.2	13.8±0.1	**<0.001**

Table 1. cont.

Taxa	δ^{13}C (n)			δ^{15}N		
	Mangrove	Mudflat	P	Mangrove	Mudflat	P
Cathorops spixii	-20.9±0.5(5)	-16.1±0.1(6)	**<0.001**	10.4±0.2	13.1±0.1	**<0.001**
Diapterus rhombeus	-25.1±0.2(9)	-17±0(1)	NA	9±0.1	14±0	NA
Sciades herzbergii	-27.7±0(1)			10.2±0		
Lutjanus griseus	-23.6±0.2(3)			8.4±0.5		
Pomadasys crocro	-21.4±0.5(3)			11.2±0.2		
Stellifer venezuelae		-15.9±0(3)			13.1±0.1	
Sphoeroides testudineus		-15.6±0.1(3)			11.8±0.2	
Dasyatis americana		-13.4±0(1)			14.2±0	
Fishes (Planktivores)						
Anchovia clupeoides	-22.9±1.6(4)	-16.4±0.1(3)	**<0.05**	11.1±0.4	13.1±0.1	**<0.05**
Cetengraulis edentulus		-17.8±0.3(3)			11.9±0.1	
Birds and reptile						
Eudocimus ruber (Ibis)	-25.5±0.3(21)			7.7±0.1		
Egretta thula (Egret)	-22.5±1.4(6)			9.1±0.2		
Caiman crocodilus (Caiman)	-21.1±1.5(3)			12.6±1.4		
Nyctanassa violacea (Heron)	-20.4±0.6(4)			12.5±0.3		
Pandion haliaetus (Osprey)	-18.3±2(2)			13.6±1.2		

a. Literature values from Newell et al. (1995).

b. Omitted from data analyses.

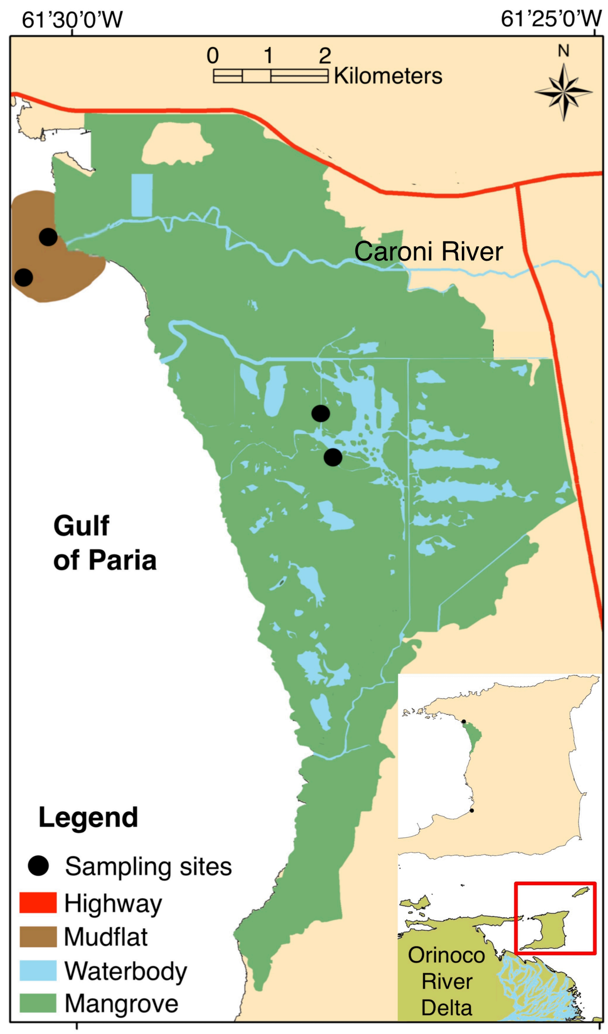

Fig. 1. Location of sampling sites in the Caroni Swamp mangrove and mudflat; and the swamp’s situation relative to Trinidad and the Orinoco River Delta, Venezuela.

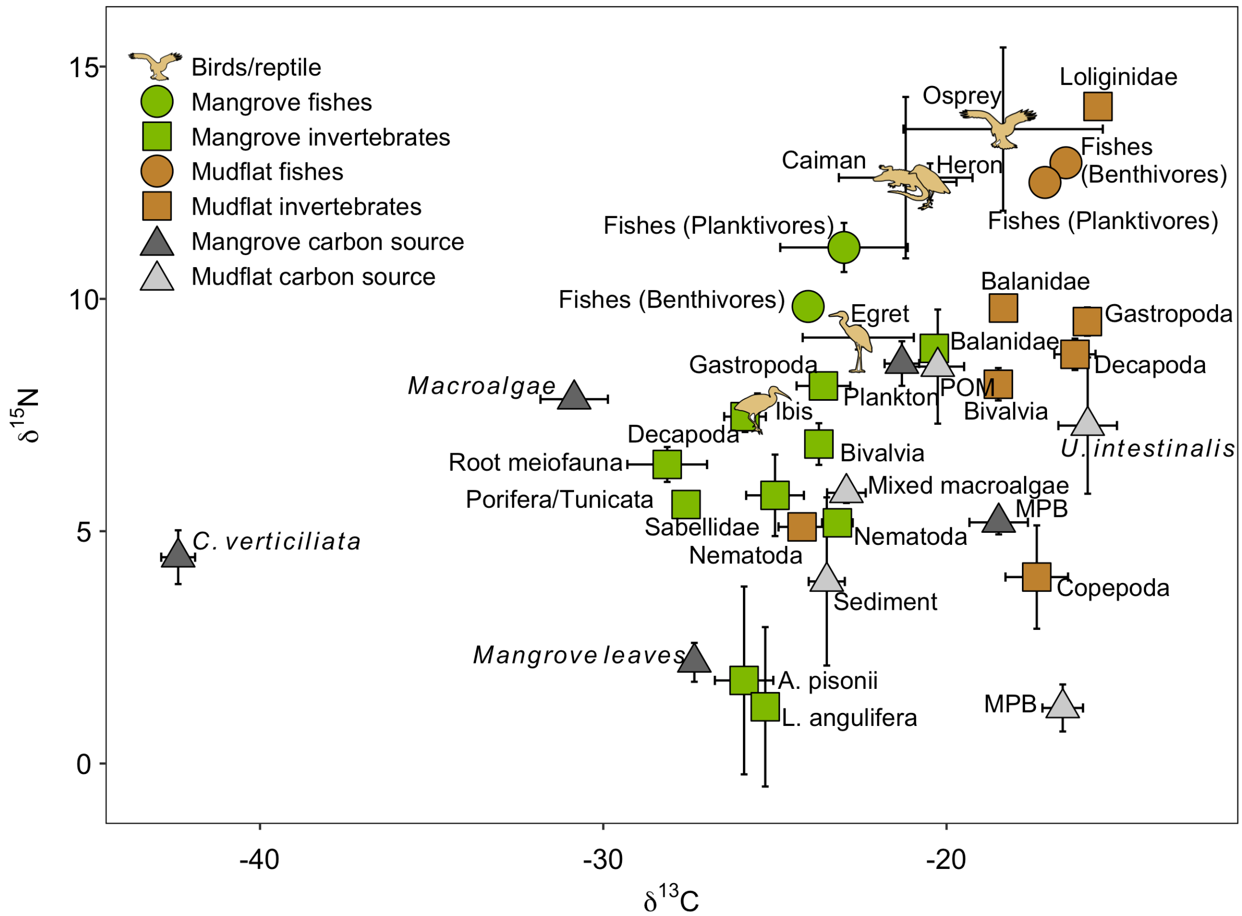

Fig. 2. Biplot of carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope values for carbon sources and consumers (mean±S.E.) in mangrove and mudflat habitats of the Gulf of Paria. Taxonomic groups are described in Table 1.

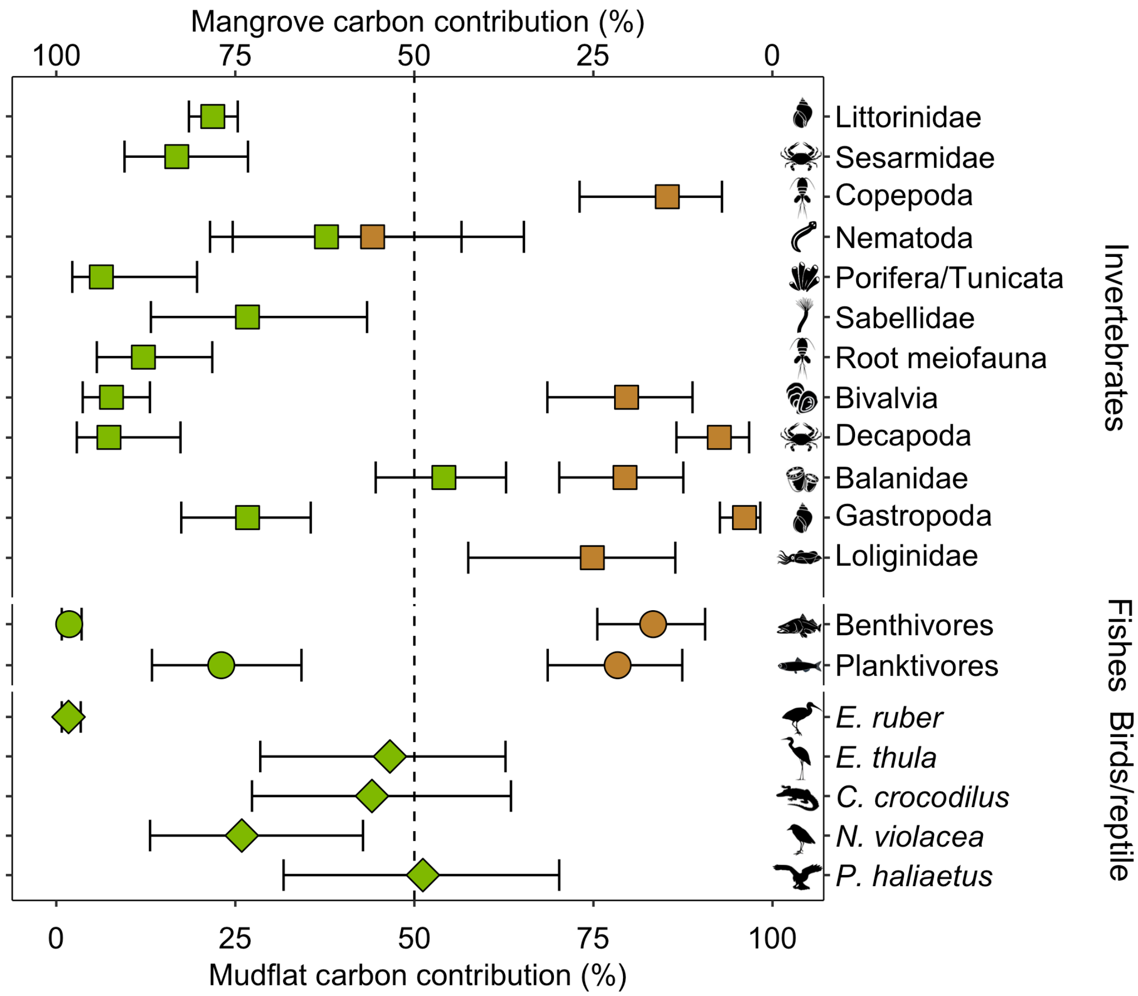

Fig 3. Trophic mixing models of taxa collected in the mangrove (green) and mudflat (brown) habitats of the Gulf of Paria showing their relative reliance (median ± 50% Bayesian credibility intervals (BCI)) on two sources of energy: mangrove or mudflat. Invertebrates (squares); fishes (circles) and birds/reptile (diamonds).