



Stable Isotopes Suggest Limited Role of Wetland Macrophyte Production Supporting Aquatic Food Webs Across a Mangrove-Salt Marsh Ecotone

Ronald Baker^{1,2,3} · Kátya Abrantes⁴ · Ilka C. Feller⁵

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Abstract

Mangroves and salt marshes are considered important habitats for a diversity of fishery and other species. One of the key presumed values of these systems is their role in fuelling aquatic food webs that support many fisheries species. The mangrove-salt marsh ecotone along the NE Atlantic coast of Florida provides a natural experiment to examine the relative importance of mangrove and marsh production in supporting aquatic food webs. Representative food web components comprising key functional groups were sampled across the ecotone to test the prediction that species or functional groups that rely on the dominant wetland producers should show large differences in carbon stable isotope values across sites that span C4-dominated *Spartina* marshes in the north to C3-dominated mangrove wetlands in the south. Source contributions were estimated for fishery species (blue crabs, penaeid shrimp), wetland specialists (cyprinodontiformes fishes, grass shrimp, fiddler crabs), zoobenthivores (pinfish, spot), phytodetritivores (mullet) and planktivores (menhaden, anchovy, silversides). The range of wetland macrophyte source contributions had minima < 5% for most groups at most sites, despite the shift from C3- to C4-dominated wetlands, suggesting that *Spartina* and mangroves contributed minimally to the trophic support of these groups. Spatial correlations between sources and individual consumer species that spanned the ecotone showed the strongest correlations with micro-algal sources (microphytobenthos/phytoplankton), weak correlations with a ‘wetland’ source reflecting the transition from *Spartina* to mangroves across the ecotone, and no correlation with either mangrove or *Spartina* sources. These findings suggest a limited role of mangrove or *Spartina* production in supporting the aquatic consumers examined.

Keywords Fisheries · Production estimates · Habitat value · Climate change · Food webs

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✉ Ronald Baker
rbaker@disl.org

- ¹ Department of Marine Sciences, University of South Alabama, Mobile, AL, USA
- ² Dauphin Island Sea Lab, Dauphin Island, AL 36528, USA
- ³ Smithsonian Marine Station at Fort Pierce, Fort Pierce, FL, USA
- ⁴ College of Science and Engineering, James Cook University, Townsville, Queensland, Australia
- ⁵ Smithsonian Environmental Research Center, Smithsonian Institution, 647 Contees Wharf Road, Edgewater, MD 21037, USA

Introduction

Vegetated intertidal wetlands are broadly considered to provide aquatic organisms with abundant food and refuge from predation (Boesch and Turner 1984). They appear to be particularly important habitats for the juveniles of many valuable fisheries species and therefore play a role in food security and economies around the world (Blaber 2007; Baker et al. 2020). However, despite their apparent value, the direct mechanisms and processes supporting many fisheries species and other aquatic organisms remain poorly resolved (Lefcheck et al. 2019). For example, while mangroves and salt marshes are widely stated to provide fish and mobile crustaceans with abundant foraging opportunities, few studies have directly demonstrated the consumption of prey from within these vegetated wetlands (e.g. Rozas and LaSalle 1990; Sheaves and Molony 2000).

Vegetated intertidal wetlands are characterised by a conspicuous and high biomass of primary producers in a part of the coastal system that is heavily utilised by fish and crustaceans. That this primary production should provide an important source of nutrition at the base of food webs seems logical (Teal 1962). Yet, findings from stable isotope studies have yielded conflicting results. Some studies indicate that wetland macrophytes make important contributions alongside benthic and planktonic microalgae in supporting aquatic food webs (e.g. Currin et al. 1995; Abrantes et al. 2015), while others suggest a more limited role than anticipated by the widely held paradigm (Galván et al. 2011; Nelson et al. 2012, 2019). This apparent discrepancy may be due in part to the specific goals and experimental design of individual studies, but also arises because the importance of mangrove/salt marsh carbon depends on the relative availability of material from the different origins, i.e. it varies depending on the ecological settings of each system (Polis et al. 1997; Abrantes et al. 2013, 2015).

The Florida Atlantic mangrove-salt marsh ecotone provides an ideal natural experiment to examine the importance of wetland production in supporting aquatic food webs and to assess the implications of a climate-driven transition in wetland foundational species on energy flow in these ecosystems (Colombano et al. 2021). Spanning approximately 2° of latitude (~28–30° N), the intertidal wetlands transition from *Spartina alterniflora*- (hereafter *Spartina*) dominated in the north to mangrove-dominated in the south, and mangroves are expanding at their northern range limits (Cavanaugh et al. 2014). *Spartina* is a C4 grass with typical carbon isotopic ($\delta^{13}\text{C}$) values around -13‰ (Currin et al. 1995; Baker et al. 2013) while mangroves are C3 trees with $\delta^{13}\text{C}$ values around -27‰ (Bouillon et al. 2008). As such, this ecotone represents a significant shift in the carbon isotopic value of the dominant wetland macrophytes (mangrove vs. *Spartina*). The aim of this study was to assess the importance of wetland macrophyte production in supporting aquatic consumers in the Florida Atlantic Coast. We predicted that any aquatic consumers relying substantially on either or both of these wetland macrophytes should show significant shifts in their $\delta^{13}\text{C}$ values across sites spanning the ecotone.

Methods

Study Sites We sampled six sites spanning from *Spartina*-dominated salt marshes at Mayport in the north to mangrove-dominated wetlands at Fort Pierce in the south (Fig. 1; Online Resource 1). The mangrove-salt marsh ecotone on Florida's Atlantic coast spans from around Cocoa Beach (28° N) to St. Augustine (30° N) (Fig. 1; Cavanaugh et al. 2019). To the north of St. Augustine, fringing saline marshes are dominated by *Spartina alterniflora*, while south of Cocoa Beach, they are dominated by mangroves. Within the ecotone,

fringing wetlands transition from *Spartina* to mangrove dominance from north to south. Three species of mangroves occur in Florida. *Avicennia germinans* (black mangrove), the most cold tolerant, forms extensive populations as far north as the Matanzas River but also occurs further north in small patches to almost 31° N (Kennedy et al. 2020). *Rhizophora mangle* (red mangrove) dominates mangrove forests south of the ecotone but small stands and vagrant individuals have established as far north as Fort George Inlet (Cavanaugh et al. 2019), just to the north of the Mayport study site (Fig. 1). *Laguncularia racemosa* (white mangrove), also more common southward, has established as isolated individuals as far north as the Matanzas River near the Matanzas Inlet (Kennedy et al. 2020).

Although isolated mangrove plants occur north of Mayport (Kennedy et al. 2020), the sampling site in Chicopit Bay near the mouth of the St. John's River was a *Spartina*-dominated salt marsh with no mangroves. The St. Augustine site was along the *Intracoastal Waterway* (ICW) in the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM NERR), 10–20 km north of the St. Augustine Inlet and 35 km south of Chicopit Bay/Mayport. The wetland was a *Spartina*-dominated marsh with occasional individual *Avicennia*. Sampling along the Matanzas River occurred along a 10 km portion of the ICW from Fort Matanzas south. Merritt Island was approximately 110 km south of Matanzas, and the vegetation fringing the wetlands comprised a mix of succulents (*Sarcocornia perennis*, *Batis maritima*), grasses (*Distichlis spicata*, *Spartina*) and mangroves. The Cocoa Beach site was 55 km further south from Merritt Island, and the wetland fringe was dominated by mangroves. The wetland interior at Cocoa Beach was mixed succulents and mangroves. Fort Pierce was the southernmost site, 90 km south from Cocoa Beach. The entire wetlands were dominated by mangroves. The open waters adjacent to Merritt Island and Cocoa Beach had some seagrass present. Open waters adjacent to the Fort Pierce site have extensive seagrass meadows (Vaslet et al. 2012). Sampling site maps and further details are provided in Online Resource 1 to facilitate comparisons with studies in other regions (Ziegler et al. 2021). Sampling was conducted across all sites during two sampling trips in the spring and summer of 2011, from 7 to 15 April and from 18 June to 1 July.

Field Sampling Design To compare sources of nutrition across the ecotone, we aimed to sample the same species representing key functional groups of consumers at each site. For production sources, our focus was on the dominant wetland macrophytes: *Spartina* and mangroves. Because the $\delta^{13}\text{C}$ values of these aeri ally respiring plants are relatively consistent across wide geographic regions (Currin et al. 1995; Bouillon et al. 2008; Baker et al. 2013), we relied on published mean $\delta^{13}\text{C}$ values for *Spartina* from Baker et al. (2013) (-13.4‰) and mangroves from

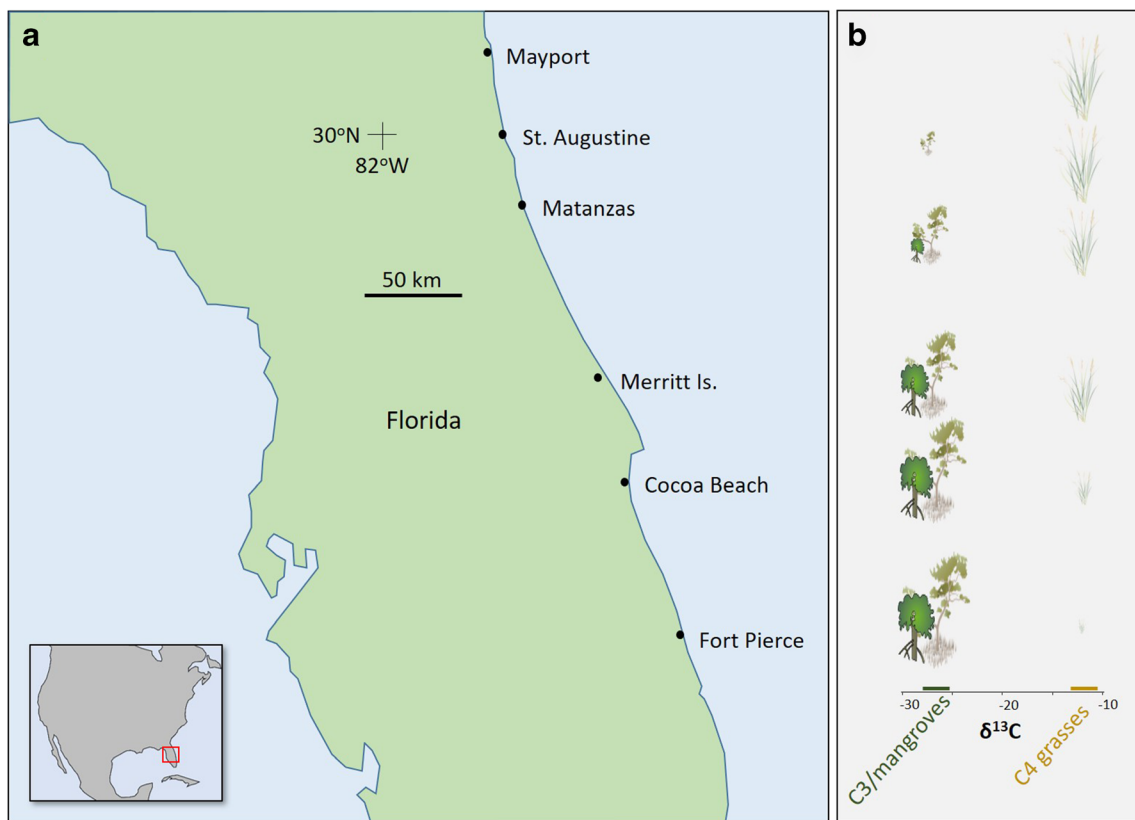


Fig. 1 **a** Study sites along the Florida Atlantic mangrove-salt marsh ecotone, **b** where the fringing tidal wetlands transition from C4 *Spartina* dominated in the north to C3 mangrove dominated in the south. Images

in **b** from Diana Kleine, Tracey Saxby, Kim Kraeer and Lucy van Essen-Fishman, Integration and Application Network, University of Maryland Center for Environmental Science

Bouillon et al. (2008) (-27‰), together with preliminary samples, which verified consistency in $\delta^{13}\text{C}$ with published values (Table S2). We collected up to three replicate surficial (top 1–3 mm) sediment samples to represent microphytobenthos (MPB) (see “Sample Processing” below). To represent phytoplankton, we sampled sessile filter-feeding invertebrates (see below) and subtracted 1.1‰ from the mean site $\delta^{13}\text{C}$ values for these consumers as a proxy for phytoplankton $\delta^{13}\text{C}$ (Post 2002; McCutchan Jr et al. 2003). Although more extensive sampling and replication of the key production sources and inclusion of $\delta^{15}\text{N}$ data (see data analysis below) may have provided more precise source value estimates and better resolution in our multi-source mixing models, the resulting models would still be under-resolved (Fry 2013a). We anticipated that any substantial shifts in the contributions of the extreme end-members of *Spartina* and mangrove should be evident regardless.

Consumers were sampled from the vegetation-open water boundary of each site using a combination of cast nets, dip nets, minnow traps and hand collection. We targeted penaeid shrimps (brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus*) and blue crabs (*Callinectes sapidus*) as two key groups of fishery species, three groups

of wetland specialists (*Palaemonetes* grass shrimp, *Uca* fiddler crabs and cyprinodontiformes fishes), planktivorous fish (menhaden, anchovies, silversides), zoobenthivores (spot, pinfish), phytodetrivores (mullet), as well as sessile filter feeding invertebrates (mussels, oysters, barnacles) that were used to define the phytoplankton end-member (Table 1). The target sample size for each consumer species at each site was three spatially separate (10’s to 1000’s m) replicates, each comprising up to 15 pooled individuals. Pooling individuals within each replicate increases precision of the mean isotopic value for a site, while minimising analytical costs (Fry et al. 2008). The full target sample size and suite of species were not collected in all locations (Table 1).

Although the functional groupings included species with somewhat varying trophic ecologies, species within each group tend to have similar carbon isotopic values at any particular site (Baker et al. 2013). Although variability among species within a group would add noise to our spatial comparisons, we predicted large shifts in $\delta^{13}\text{C}$ across the ecotone, which should be clearly apparent despite such variability. Additionally, grouping species into these functional groups allowed us to make more robust comparisons across all sites in the ecotone when each individual species was not sampled at all sites (Table 1).

Table 1 Sample size and spatial distribution of samples of consumers collected from fringing tidal wetlands at each site. Values indicate the number of replicate samples used for isotope analysis, followed in parenthesis by the total number of individuals pooled within those replicates

| Consumer functional group | Penaeid | Blue crab | Wetland fish | Wetland shrimp | Wetland crab | Zoobenthivore | Phyto detritivore | Planktivorous fish | Filter-feeding invertebrate | | | | | | | |
|---------------------------|--------------------------------|------------------------------|----------------------------|------------------------------|--|----------------|---------------------------|---------------------------|-----------------------------|----------------------------|------------------------|------------------|--------|--------|--------|--------|
| Site | | | | | | | | | | | | | | | | |
| | <i>Farfantepenaeus aztecus</i> | <i>Litopenaeus setiferus</i> | <i>Callinectes sapidus</i> | <i>Cyprinodon variegatus</i> | <i>Palaemonetes grandis/latipinna</i> spp. | <i>Uca</i> sp. | <i>Lagodon rhomboides</i> | <i>Mugil cephalus</i> sp. | <i>Anchoa mitchilli</i> sp. | <i>Balanus crassostrea</i> | <i>Menidia demissa</i> | <i>virginica</i> | | | | |
| Mayport | 5 (14) | 3 (35) | 4 (4) | 4 (28) | 1 (1) | 5 (39) | 6 (37) | 3 (3) | 2 (9) | 4 (4) | 4 (6) | 1 (15) | 5 (18) | 3 (12) | 4 (6) | 3 (5) |
| St Augustine | 6 (15) | 2 (42) | 10 (10) | 6 (27) | - | 5 (31) | 6 (21) | 5 (7) | 6 (20) | 6 (8) | 3 (9) | - | 6 (32) | 6 (18) | 6 (19) | 6 (25) |
| Matanzas Inlet | 4 (6) | 1 (8) | 4 (11) | 6 (26) | - | 3 (20) | 5 (24) | 4 (7) | 3 (15) | 4 (8) | 4 (15) | - | 5 (21) | 4 (23) | 3 (8) | 6 (8) |
| Merritt Island | - | - | 1 (1) | 5 (12) | 6 (18) | 1 (7) | 3 (3) | - | 5 (7) | 6 (8) | - | - | 4 (18) | 3 (8) | - | - |
| Cocoa Beach | 4 (12) | - | - | - | - | 3 (3) | - | 2 (2) | - | 4 (7) | 3 (3) | 1 (7) | 3 (3) | 1 (1) | - | - |
| Fort Pierce | 5 (5) | - | - | 6 (6) | 5 (5) | 6 (6) | 3 (3) | 6 (6) | 1 (1) | 1 (1) | 6 (6) | 4 (4) | - | 4 (9) | 6 (6) | 6 (6) |

Sample Processing Macrophyte leaves were scraped with a scalpel to remove any epiphytes or debris. White muscle tissue was dissected from the dorsal side of fishes, the abdomen of shrimps and the legs of crabs. The adductor muscle was removed from bivalves and the muscular foot from gastropods. The soft tissues of barnacles were removed from their shells and analysed whole after testing for carbonate contamination with 1N HCl. If contamination was found, the sample was acidified overnight and re-dried. All samples were rinsed in tap water and soaked for > 30 min in deionised water to remove salts. Samples were dried for 48 h at 60 °C and homogenised using a bead-beater grinding mill. MPB sediments were extracted with acetone and the extracted pigments analysed as a proxy for MPB isotopic values, following the methods described in Demopoulos et al. (2008) and Baker et al. (2013). A comparison of $\delta^{13}\text{C}$ values of acetone extracts to whole cell samples, obtained from field collected sediments via the migration method described by Abrantes and Sheaves (2009), and to whole cells from cultured algal samples, revealed a $3.3 \pm 0.11\text{‰}$ (mean \pm 1 SE, $n = 12$) depletion in the extracts relative to the whole cells (Baker unpubl. data). These data are being replicated for publication, but for the current study, 3.3‰ was added to each acetone extract value to obtain the $\delta^{13}\text{C}$ value for MPB used in the mixing models (Table S2).

As a proxy for changes in dissolved inorganic carbon (DIC) $\delta^{13}\text{C}$ across the ecotone, barnacle-shell carbonate $\delta^{13}\text{C}$ was analysed. After tissues were removed, shell fragments were soaked in sodium hypochlorite for 48 h to remove any residual organic tissues. Bleached shells were then triple rinsed in tap water and triple rinsed in deionised water before drying and grinding for analysis.

$\delta^{13}\text{C}$ was measured at the Smithsonian Institution's Stable Isotope Mass Spectrometry Laboratory, using a Thermo Scientific Delta V Advantage mass spectrometer coupled to a C-N-S Costech ECS 4010 Elemental Analyser. Vienna Pee Dee Belemnite (VPDB) was used as standard, and the precision of the system was $\leq 0.2\text{‰}$. Isotopic ratios are expressed in standard delta notation.

Data Analysis For each site, Bayesian mixing models were used to estimate the contribution of mangrove, *Spartina*, plankton and MPB to each consumer group, using the R package SIMMR (Stable Isotope Mixing Model in R; Parnell et al. (2013)). We were unable to quantify $\delta^{15}\text{N}$ for each source across each site (particularly MPB and phytoplankton), so our mixing model was based on $\delta^{13}\text{C}$ alone. A $\delta^{13}\text{C}$ trophic discrimination factor (TDF) of $+1.1\text{‰}$ was used in the models (McCutchan Jr et al. 2003), while taking into account the different groups' trophic levels. Wetland crabs, phytodetritivores and filter-feeding invertebrates were considered to be of trophic level 2, penaeid shrimp and wetland fish of trophic level 2.5, wetland shrimp and

blue crabs of trophic level 2.7, and planktivorous fish and zoobenthivores of trophic level 3, based on the estimates of Baker et al. (2013) from multiple salt marshes across the SE USA. To account for the uncertainty in TDFs (McCutchan Jr et al. 2003) and consumer trophic levels, a large TDF standard deviation (SD) of 1.5‰ was used. Similarly, because MPB and plankton $\delta^{13}\text{C}$ values were not directly measured, large source SDs of 1.5‰ were used to address the uncertainty in sources' $\delta^{13}\text{C}$ values. The large TDF and source SDs used in the mixing models will lead to conservative results regarding the importance of the different producers.

To avoid over interpreting under-resolved mixing models, we present the 95% credibility intervals (CI) from the mixing models to reflect the range of possible contributions of each source (Fry 2013a, b). When the lower bound of the 95% CI was > 5%, we interpreted this as a non-zero contribution indicating probable importance of a source to consumers. We predicted that consumers which rely on wetland macrophyte production should have source contributions that shift from zero (< 5%) to non-zero across the ecotone as the wetland becomes dominated by that source.

To examine spatial patterns across the ecotone in individual consumer species, we tested for spatial correlations between the different consumer and source $\delta^{13}\text{C}$ values (Currin et al. 2003; Melville and Connolly 2003). To account for any consumer that relied on the dominant wetland macrophytes that transition from *Spartina* to mangroves across the ecotone, we included in the correlations a computed “wetland” source reflecting this transition. This wetland source was calculated as a simple two-source mixing model of *Spartina* and mangrove based on the proportions of each along the fringe of each site, estimated from contemporary Google Earth imagery and ground truthed at each site (Online Resource 1).

Results

Across the ecotone, and for the great majority of consumer groups, the contribution of both C3 and C4 had wide 95% credibility intervals (CI), with lower bounds < 5% (Table 2). This suggests the potential for minimal contributions of wetland production to the trophic support of these consumers. The mixing model results were largely under-resolved, with the lower bounds of the 95% CIs of all four sources < 5% for most consumer groups across most sites (Table S3). The most substantial contributions of wetland sources were C4 production to phytodetritivores across all sites, which reached a maximum of 65–92% at Fort Pierce, the mangrove-dominated southern site (Table 2). Other important wetland contributions included C4 sources to wetland crabs (26–68%) and wetland shrimp (7–60%) at Mayport, C4 sources to wetland fish at

Merritt Island (34–75%) and C3 sources to planktivorous fish at Matanzas (16–50%).

The $\delta^{13}\text{C}$ values of the consumer species that were sampled widely across the ecotone tended to be highly correlated with micro-algal sources (MPB, phytoplankton), weakly correlated with the computed wetland source and not correlated with either mangrove or *Spartina* alone (Table 3). *Farfantepenaeus aztecus*, *Fundulus grandis/heteroclitus*, *Palaemonetes* and *Leiostomus xanthurus* $\delta^{13}\text{C}$ values were highly correlated ($r \geq 0.94$) with the aquatic sources MPB or phytoplankton values (Table 3). The strongest correlation for the pinfish *Lagodon rhomboides* was a weak correlation ($r = 0.63$) with MPB, and a weak correlation for *Anchoa* sp. with the computed wetland source ($r = 0.54$). The strongest correlation with the computed wetland source was for *Palaemonetes* ($r = 0.68$), but this was weaker than the correlation with either phytoplankton ($r = 0.81$) or MPB ($r = 0.94$). The spatial patterns in the phytodetritivore mullet, *Mugil cephalus*, $\delta^{13}\text{C}$ values were not positively correlated with any of the primary producer source values and were negatively correlated with the computed wetland source ($r = -0.8$) (Table 3).

Aquatic producers and most consumers had the lowest $\delta^{13}\text{C}$ values at Fort Pierce, the mangrove-dominated southern site (Fig. 2; Table S4). Barnacle-shell carbonates showed a similar trend in $\delta^{13}\text{C}$ among sites, with higher values at the three northern sites and lower values at Fort Pierce, spanning a range of 2.9‰ (Fig. 2). Barnacle carbonate $\delta^{13}\text{C}$ values were most strongly correlated with MPB values ($r = 0.83$).

Discussion

Across the studied mangrove-salt marsh ecotone, there were no shifts in consumer $\delta^{13}\text{C}$ that suggest significant contributions of wetland production to the consumers examined. We sampled a variety of consumers, including several known to be strongly associated with the vegetated wetlands, such as penaeid shrimps, cyprinodontiformes fishes and blue crabs (Kneib 1997; Minello et al. 2008). We hypothesised that for functional groups that rely on either C3 or C4 wetland producers, the transition from *Spartina*-dominated wetlands in the north to mangrove-dominated in the south should have led to substantial shifts in consumer $\delta^{13}\text{C}$ values and in contributions of wetland producers. However, for most groups across most sites, the lower bounds of the 95% CIs of the C3/C4 contributions were very low (< 5%), suggesting the potential for minimal contributions of these sources to the consumers examined.

Under-resolved mixing models are common for estuarine food web studies (Fry 2013a). We used relatively large standard deviations to account for the uncertainty and natural variability in source values and TDFs. The effect of this would be

Table 2 Estimated source contributions (95% CI range) for C3 (mangrove) and C4 (*Spartina*) sources across the mangrove-marsh ecotone of the Atlantic Coast of Florida. Full mixing model outputs are provided in Online Resource 3

| Site | Penaeid | | Blue crabs | | Wetland fish | | Wetland shrimp | | Wetland crab | | Zoobenthivore | | Phytodetritivore | | Planktivorous fish | |
|----------------|---------|------|------------|------|--------------|-------|----------------|------|--------------|-------|---------------|------|------------------|-------|--------------------|------|
| | C3 | C4 | C3 | C4 | C3 | C4 | C3 | C4 | C3 | C4 | C3 | C4 | C3 | C4 | C3 | C4 |
| Mayport | 2–30 | 4–55 | 2–38 | 3–59 | 2–31 | 5–55 | 2–29 | 7–60 | 2–22 | 26–68 | 4–58 | 2–45 | 2–23 | 17–79 | 5–45 | 2–38 |
| St Augustine | 1–22 | 5–78 | 3–29 | 4–55 | 3–27 | 5–59 | 2–24 | 4–68 | 2–23 | 4–71 | 3–34 | 3–52 | 1–13 | 37–86 | 9–43 | 3–40 |
| Matanzas Inlet | 2–28 | 5–78 | 5–38 | 3–47 | 2–25 | 5–59 | 2–31 | 4–70 | 2–34 | 3–63 | 2–30 | 3–55 | 1–21 | 13–86 | 16–50 | 2–39 |
| Merritt Island | | | 2–29 | 4–59 | 2–18 | 34–75 | 2–44 | 3–61 | | | 2–29 | 5–69 | 1–29 | 7–85 | 3–46 | 2–54 |
| Cocoa Beach | 2–35 | 4–71 | | | | | 2–32 | 4–60 | | | 2–55 | 3–68 | 1–39 | 5–93 | 3–41 | 3–52 |
| Fort Pierce | 3–54 | 3–57 | | | 3–45 | 3–41 | 3–52 | 3–46 | 2–50 | 3–60 | 3–44 | 3–41 | 1–13 | 65–92 | 4–57 | 3–33 |

to widen the 95% CIs; yet, a substantial reliance on either wetland macrophyte would have been evident as a spatial trend across the ecotone. Although in most cases, mixing models did not lead to conclusive results regarding the importance of wetland producers, the lack of spatial correlations between wetland producer and consumer $\delta^{13}\text{C}$ values (Table 3; Fig. 2) suggests minimal input of either mangrove or *Spartina* carbon to most of the consumers examined (Currin et al. 2003; Melville and Connolly 2003). The often strong spatial correlations between consumer and micro-algal sources' $\delta^{13}\text{C}$ suggest that MPB and phytoplankton are much more important in supporting these consumers across the ecotone. This is consistent with recent findings from mixed mangrove-marsh wetlands in Louisiana, where Nelson et al. (2019) found that algae and POM contributed the bulk of production to many of the same species examined in the current study, while *Spartina* and mangroves had moderate and negligible contributions, respectively.

C4 production appeared to be important to the phytodetritivore *Mugil cephalus* at all sites across the ecotone, with the highest importance at Fort Pierce (65–92%), the mangrove-dominated southern site (Table 2). This trend and the negative relationship with the computed wetland source should be interpreted with caution. There are almost no C4 producers in the fringing wetlands at this site; yet, there are extensive seagrass meadows in the subtidal waters adjacent to the wetlands (Vaslet et al. 2012). Seagrass $\delta^{13}\text{C}$ values are

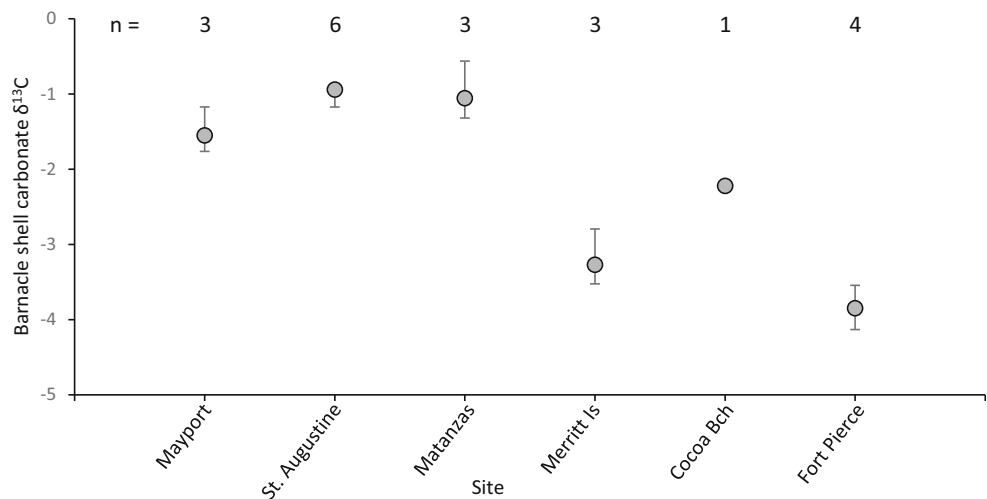
similar to those of *Spartina* (Bouillon et al. 2008), so in this case, seagrass contributions are likely to be confounded with C4 contributions in our mixing models. As such, the high contribution of C4 to phytodetritivores at Fort Pierce and the negative relationship to the computed wetland source probably reflects the importance of seagrass detritus to these consumers at the southern sites. Similarly, the estimated contribution of C4 sources to wetland fish at Merritt Island could include a contribution of either *Spartina* and/or seagrass, both of which were present at that site. The potential confounding of seagrass and *Spartina* contributions in our models is otherwise unimportant since the consumers had negligible C4 contributions at these sites.

The trend for aquatic producers, most consumers and barnacle-shell carbonates to have lower $\delta^{13}\text{C}$ at the southern mangrove-dominated site likely reflects the ^{13}C depletion of the DIC pool caused by the remineralization of mangrove-derived carbon (Lin et al. 1991; Bouillon et al. 2008). Lin et al. (1991) found that mollusc-shell carbonates $\delta^{13}\text{C}$ were 2.9‰ lower at sites near mangroves than at sites further away from mangroves in Florida Bay, an almost identical range to that measured in barnacle carbonates in the current study (Fig. 3). Seagrasses show similar trends in $\delta^{13}\text{C}$ with proximity to mangroves (reviewed by Bouillon et al. 2008). Although data for MPB and phytoplankton are more sparse (Bouillon et al. 2008), there is evidence that these too may show considerable small-scale spatial variability in relation to

Table 3 Correlation coefficients from correlations between $\delta^{13}\text{C}$ of individual consumer species and primary producer source values across the mangrove marsh ecotone

| Source | <i>F. aztecus</i> | <i>F. grandis/heteroclitus</i> | <i>Palaemonetes</i> | <i>L. xanthurus</i> | <i>L. rhomboides</i> | <i>M. cephalus</i> | <i>Anchoa</i> |
|-----------------|-------------------|--------------------------------|---------------------|---------------------|----------------------|--------------------|---------------|
| MPB | 0.98 | 0.72 | 0.94 | 0.74 | 0.63 | 0.08 | 0.50 |
| Phytoplankton | 0.85 | 0.98 | 0.81 | 0.99 | 0.42 | −0.17 | 0.25 |
| <i>Spartina</i> | −0.21 | −0.12 | −0.44 | −0.20 | −0.12 | 0.00 | 0.30 |
| Mangrove | −0.21 | −0.12 | −0.44 | −0.20 | −0.12 | 0.00 | 0.30 |
| Wetland blend | 0.45 | 0.57 | 0.68 | 0.51 | −0.34 | −0.80 | 0.54 |

Fig. 2 Variation in barnacle shell carbonate $\delta^{13}\text{C}$ sampled from fringing tidal wetlands across the mangrove-salt marsh ecotone on the Atlantic coast of Florida. Data are mean values \pm range. Sample size (n) is shown across the top of the plot



proximity to sources of remineralized depleted carbon (Vaslet et al. 2012; Deleon et al. 2019; Curry et al. 2020). Thus, although more extensive sampling of the target production sources would have allowed for a better resolution in our multi-source mixing models, the models would still be under-resolved (Fry 2013a), and the potential for significant small-scale variation in aquatic producer $\delta^{13}\text{C}$ values highlights further challenges in resolving source contributions in estuarine food webs.

Stable isotopes have increasingly highlighted the importance of less conspicuous sources in supporting aquatic consumers in estuarine food webs (Currin et al. 1995, 2011; Galván et al. 2008; Nelson et al. 2019). Significant but inadequately resolved variability in $\delta^{13}\text{C}$ of aquatic producers such as seagrass, MPB and phytoplankton (Bouillon et al. 2008; Currin et al. 2011; Deleon et al. 2019; Curry et al. 2020) could lead to the underestimation of the importance of these sources, if deviations in consumer values are assumed to reflect greater incorporation of more isotopically extreme sources such as mangroves or *Spartina*. Conversely, many of the potential pathways leading from wetland macrophytes to aquatic consumers remain poorly resolved (Bouillon et al. 2008), and the use of assumed but inappropriate trophic fractionation values may lead to the significant underestimation of the importance of wetland macrophytes in specific food chains (Sheaves and Molony 2000; Bui and Lee 2014).

Despite the challenges that remain for resolving estuarine food webs, the current study detected minimal effects of the transition from salt marsh to mangroves on adjacent aquatic food webs. The Florida Atlantic mangrove-salt marsh ecotone represents a relatively small area of tidal wetlands. However, the expansive and highly productive marshes of the northern Gulf of Mexico are also experiencing mangrove expansion (Osland et al. 2013), and similar work there found minimal effect of the wetland plant composition on food web structure (Nelson et al. 2019). Further work on the impacts of wetland

plant composition on aquatic producer distribution, biomass and isotopic values will help to resolve the likely impacts of global change on the ongoing role of these wetlands in supporting fisheries and other aquatic species.

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Authors' Contributions RB and IF designed the project, RB collected and processed the samples, KA and RB analysed and interpreted the data, RB wrote the paper with input from all authors.

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