Estuaries and Coasts (2024) 47:1637–1649
https://doi.org/10.1007/s12237-024-01389-w

Foundation Species Shift Causes a Partial Loss of Functional Support for Benthic Coastal Consumers

Janelle A. Goeke[1,3] · **Thomas W. Boutton**[2] · **Anna R. Armitage**[1]

Received: 5 September 2023 / Revised: 13 June 2024 / Accepted: 17 June 2024 / Published online: 2 July 2024

Abstract

Foundation species support highly productive and valuable ecosystems, but anthropogenic disturbances and environmental changes are increasingly causing foundation species shifts, where one foundation species replaces another. The consequences of foundation shifts are not well understood, as there is limited research on the equivalency of different foundation species and the functions they support. Here, we provide insight into community-level consequences of foundation shifts in the Gulf of Mexico, where the typical marsh foundation species (*Spartina alterniflora*) is being replaced with a mangrove foundation species (*Avicennia germinans*), forcing marsh fauna to rely on *Avicennia* for foundational support. We evaluated the interactions of two common and ecologically valuable basal consumers, fiddler crabs (*Uca* spp.) and marsh periwinkle snails (*Littoraria irrorata*), with both foundation species across sites with different levels of mangrove encroachment. By investigating both physical support, measured as habitat association and co-occurrence, and trophic support, as basal resource diet contributions, we found that *Avicennia* can physically replace *Spartina* for some consumers, but is not providing equivalent trophic support. *Uca* and *Littoraria* commonly occupy encroached sites and associate with mangroves but incorporate almost no mangrove plant matter into their diets. The ultimate consequences of a foundation shift in the case of mangrove encroachment may include shifting energy flows and resource use and decreased populations of basal consumers. Looking at interactions with foundation species from multiple perspectives is necessary to obtain a complete picture of the effects that foundational shifts are having, especially as such shifts are becoming increasingly common.

Keywords Mangrove encroachment · Coastal wetlands · Stable isotopes · Food web shifts · Foundation species

Introduction

Foundation species structure communities both physically and functionally by facilitating the growth and survival of other species (Dayton 1972; Reid and Lortie 2012; Osland et al. 2013; Bittick et al. 2019). The occurrence of foundation species in systems can be impacted by, among other things, changing environmental conditions (Osland et al. 2016), invasive species, pests and disease (Ellison et al. 2005), and anthropogenic impacts such as deforestation and eutrophication (Youngquist et al. 2017). Often these factors lead to foundation species disappearances, but in some cases there is instead a foundational shift, when one foundation species (often an exotic species or one undergoing climate change induced range expansion) replaces another (O'Brien et al. 2013; Saintilan et al. 2014; Vergés et al. 2014; Bittick et al. 2019). Changes in foundation species occurrence can have cascading effects on the biodiversity, ecosystem service provision, and faunal resource use patterns in a system (Boesch and Turner 1984; Peters and Yao 2012; Baiser et al. 2013; Youngquist et al. 2017). When a new foundation species appears in a system, it can alter the available physical resources by introducing habitat of a different structural complexity or prey refuge value (Bittick et al. 2019; Glazner et al. 2020), and the available trophic resources by introducing a novel food source or changing food availability (O'Brien et al. 2013; Harris et al. 2020).

Communicated by James Allen Nelson

✉ Janelle A. Goeke
janelle.goeke@maine.edu

[1] Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553, USA

[2] Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX 77843-2258, USA

[3] Casco Bay Estuary Partnership, University of Southern Maine, Portland, ME 04101, USA

This altered resource provision can cause changes in species distribution and survival within a system, leading to community level responses that may have consequences for the ecosystem health and service provision of shifting systems.

Coastal ecosystems are ideal for examining the consequences of foundational shifts on fauna while minimizing geographic variation, as there can be rapid changes in foundation species occurrence across small geographic ranges when the abiotic factors that structure coastal systems (e.g., temperature, precipitation, and sea level) cross certain thresholds (Osland et al. 2016, 2020; Saintilan et al. 2018). One such foundational shift is the shift from *Spartina alterniflora* (marsh cordgrass, synonym *Sporobolus alterniflorus*, hereafter *Spartina*; other species in the genus are referred to by the entire scientific name) to *Avicennia germinans* (black mangrove, hereafter *Avicennia*) dominance in the Gulf of Mexico, USA (Osland et al. 2013, 2014; Cavanaugh et al. 2019). *Avicennia* has the northernmost range limits of all North American mangrove species and is common in southern Gulf of Mexico wetlands, but has historically occurred along the western (Texas and Louisiana) Gulf of Mexico coast in small, scattered stands due to periodic mortality from low winter temperatures (Osland et al. 2013; Cavanaugh et al. 2014). From 1990 to 2021, temperatures in the northern Gulf of Mexico rarely dropped below the *Avicennia* mortality threshold, allowing mangroves to encroach into wetlands previously dominated by *Spartina* and expand into large stands (Saintilan et al. 2014; Armitage et al. 2015).

Dayton (1972) defined foundation species as “those which have a disproportionately important influence on the structure of the community.” While *Spartina* and *Avicennia* are both foundation species, they differ in the ecological roles they perform and the services they support. For example, *Spartina* is a better choice for quickly establishing physical structure and reducing erosion in recently restored sites (Yando et al. 2019), but large areas of *Avicennia* are more effective at protecting shorelines from hurricane induced erosion (Armitage et al. 2020; Pennings et al. 2021). Insight into these ecosystem-level effects of mangrove encroachment is undoubtedly important, but work going forward must examine community-level responses as well, especially as there now exists a small but growing body of literature demonstrating that *Avicennia* and *Spartina* do not fill similar foundation roles for fauna. However, existing studies vary widely in the trophic level, taxa, and response metrics they examine, making it difficult to detect general patterns (e.g., Kelleway et al. 2017; Yando et al. 2019; Osland et al. 2022). We sought to better understand consumer responses by separating the ways in which foundation species can influence faunal resource use into two dimensions of foundational support: physical (providing habitat, physical structures, and influencing the distribution of species in a system) and functional (providing food and supporting organism growth and survival), evaluated here as trophic support.

Short-term effects of a foundational shift from *Spartina* to *Avicennia* are likely to be most apparent at lower trophic levels and in low mobility benthic consumers, as they rely heavily on foundation plants for both food and shelter. In Gulf Coast salt marshes, common consumers that occupy this niche are *Uca* spp. (fiddler crabs, hereafter *Uca*) and *Littoraria irrorata* (marsh periwinkle snails, hereafter *Littoraria*). Both taxa have documented physical associations with the structure provided by *Spartina* stems, with *Uca* using them to support burrows and *Littoraria* vertically migrating along stems to escape predation (Bertness and Miller 1984; Vaughn and Fisher 1992). Additionally, both taxa regularly consume *Spartina*, although *Littoraria* are typically considered *Spartina* specialists while *Uca* are more generalist feeders (Teal 1962; Currin et al. 1995; Silliman and Ziemann 2001). The relationships of these benthic taxa with *Avicennia* are not fully understood in the region, though recent work suggests there are negative consequences of *Avicennia* consumption for both species (Goeke and Armitage 2021; Goeke et al. 2023). Therefore, in this study, we investigated their physical and trophic reliance on foundational plants across a gradient of mangrove encroachment in order to gain insight into how basal consumers may respond to shifts in foundation species. Specifically, we sought to evaluate **1)** the physical association of both consumers with the rigid vertical structures that both *Spartina* and *Avicennia* possess and **2)** dietary resources utilized by each consumer as marshes undergo a foundational shift from *Spartina* to *Avicennia* dominance.

Material and Methods

Site Descriptions

Sites with different levels of mangrove encroachment were selected along the Texas coast of the Gulf of Mexico. On the Upper Coast, three *Spartina* dominated sites (hereafter “marsh” sites, SA1-3) without mangroves present and three sites with both *Spartina* and *Avicennia* present (hereafter “mixed” sites, Mix1-3) were selected on Galveston Island (Figs. 1 and 2). Mangroves in the Upper Coast region are sparsely distributed but have formed a patchy mix of mangroves and marsh vegetation in some areas (Fig. 2) between the last freeze-induced dieback in 1989 (Everitt et al. 1996) and 2019 when this study was performed. In the Coastal Bend region 1.5° latitude farther south, three *Avicennia*-dominated sites where *Spartina* was rare or absent (hereafter “mangrove” sites, AG1-3) were selected on Mustang Island, near Port Aransas (Figs. 1 and 2), which has many sites that have been mangrove-dominated for decades. The Port

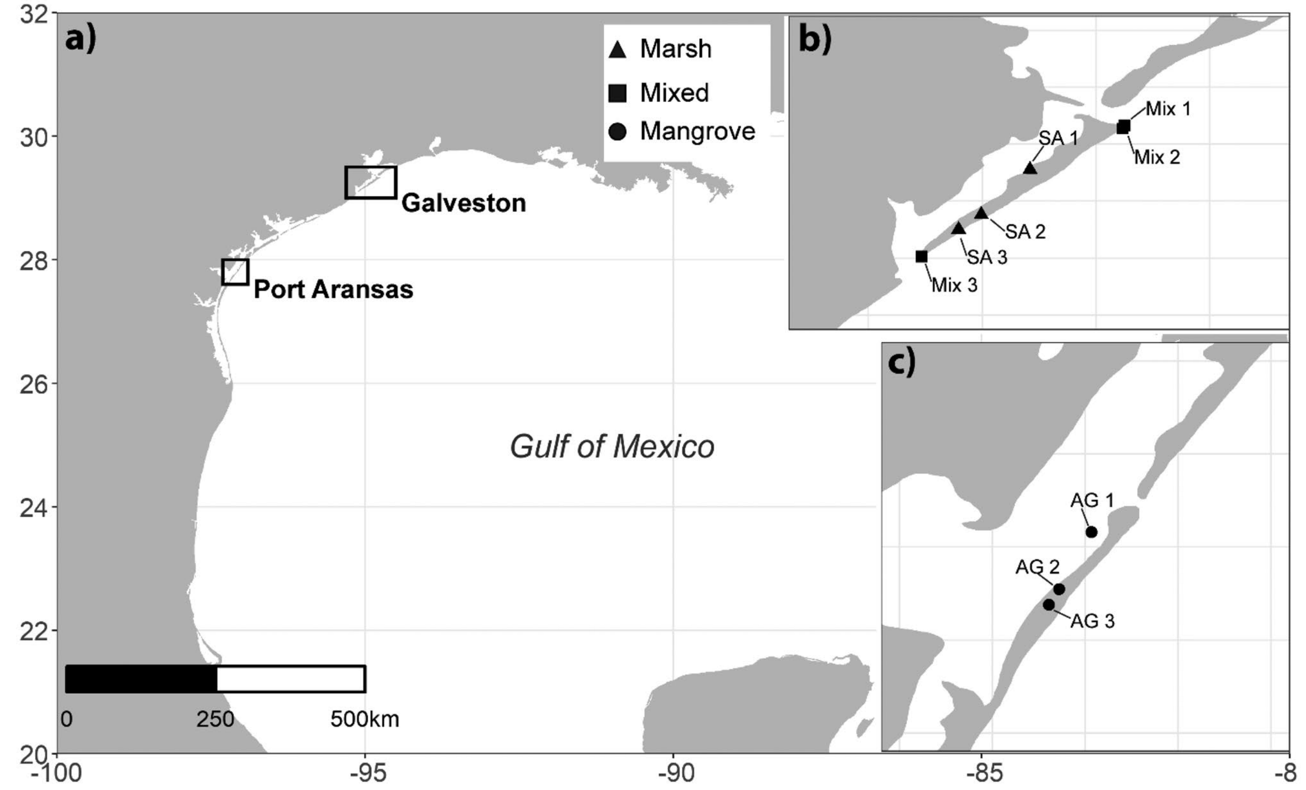

Fig. 1 Map of study areas showing **a** the two regions of the Texas coast where study sites were located, **b** Galveston Island (Upper Coast) study sites locations and site types, and **c** Port Aransas (Coastal Bend) area study site location and site types

Aransas area also has sites that are dominated by salt marsh vegetation in inland bays behind the barrier islands, where mangrove absence is likely due to dispersal limitations. Our original intent was to collect consumers from these sites for comparison with those from encroached sites, but very few consumers could be located at the time of sampling, despite previous records of presence. We were unable to include these Port Aransas marsh consumers as part of this study because of low sample size, but previous work found a high degree of dietary similarity between consumers sourced from Galveston and Port Aransas salt marshes without mangroves present (Goeke 2021).

Marsh sites ranged from 49 to 57% *Spartina* cover, and mangrove sites ranged from 54 to 72% *Avicennia* cover. Mixed sites differed in the relative abundance of *Avicennia* and *Spartina* (Goeke 2021), but we selected

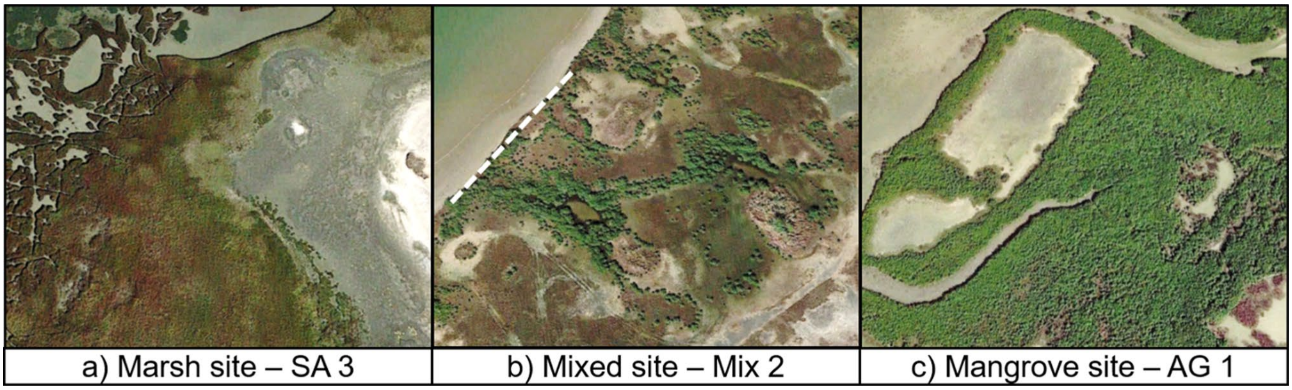
a) Marsh site – SA 3
b) Mixed site – Mix 2
c) Mangrove site – AG 1

Fig. 2 Examples of marsh and mangrove survey sites from the Port Aransas and Galveston regions. **a** A marsh site from Galveston. **b** A mixed site from Galveston with a patchy mix of marsh and mangroves and an example transect location. **c** A mangrove site in Port Aransas. Satellite imagery of sites obtained from Google Earth sites that contained at least 5 mature *Avicennia* individuals (> 1 m in height and reproductive) in our survey area on the basis that this duration and level of mangrove presence would be sufficient to impact site consumers, as levels of mangrove cover as low as 11% can affect faunal physiology (Goeke et al. 2023). Apart from differences in *Spartina* and *Avicennia* abundance, all sites had similar plant communities consisting of a small number of graminoid and succulent species with low cover (< 5% cover at mangrove/mixed sites and < 25% at marsh sites) (Goeke 2021). We aimed to select sites with similar physical characteristics, and all sites were saline wetlands on the bay side of barrier islands, had shallowly sloping elevation gradients, and had similar sediment properties (Armitage et al. 2021; Thompson 2022).

Physical Association of Consumers with Plants

To characterize the physical association of basal consumers with mangrove and marsh vegetation, site surveys were performed in summer 2019. All sampling started at approximately 8 AM, and while the distance between sites and our rigorous sampling schedule did not provide us the flexibility to adjust our sampling based on tides, the Gulf of Mexico is a microtidal system with tidal levels primarily influenced by prevailing wind conditions. Tidal exchange was therefore minimal during field expeditions and unlikely to influence consumer distributions. At each of the nine sites, the length of a 100-m transect parallel to the water line and set 2 m from the water's edge was sampled with adjacent 1 m^2 quadrats ($n = 100$ per site). Within each quadrat, we recorded canopy cover (%) of each plant species present and basal consumer abundance. *Littoraria* were counted directly, and the location of each snail (on the ground, on plant species A, on plant species B, etc.) was recorded. Due to the highly mobile nature of *Uca* crabs, we were unable to count them directly and instead recorded the number of burrows present within each quadrat as a proxy for relative crab abundance (Schlacher et al. 2016). Burrow counts and counts of *Littoraria* on the ground were not possible in all quadrats, as some locations were inundated, obscuring the ground or softening the structure of burrows beyond recognition. Flooded quadrats were excluded from analyses of *Uca* occurrence. For *Littoraria*, tidal cycle and flooding are more likely to influence snail vertical position (stem height) than horizontal position (location between different stems and/or ground) so we do not believe flooding influenced the associations of visible snails (Vaughn and Fisher 1992). Areas of flooded quadrats that may have obscured *Littoraria* presence were accounted for in analyses of *Littoraria* occurrence as described below.

Trophic Association of Consumers with Plants

The analysis of isotopic ratios of $^{13}C/^{12}C$ ($\delta^{13}C$) and $^{15}N/^{14}N$ ($\delta^{15}N$) in combination can be used to identify trophic relationships between species and make accurate predictions of consumer diets. The $\delta^{13}C$ values of plants are influenced by the photosynthetic pathways they utilize and their specific physiology, and as a result, C_4 photosynthesizers such as *Spartina* have distinctly higher $\delta^{13}C$ values than plants that perform C_3 photosynthesis such as *Avicennia*, allowing detection of their relative contributions to basal consumer diets (Leary 1988). $\delta^{15}N$ values indicate trophic position and increase in higher trophic level organisms and can be used to help separate dietary sources with similar $\delta^{13}C$ values.

To identify dietary sources consumed by *Uca* and *Littoraria*, samples for stable isotope analysis were collected by hand from five pre-determined random points along the length of the survey transect at each site. At each point, samples of *Uca*, *Littoraria*, and all likely end members (potential dietary contributors, see below) were collected. Multiple species of *Uca* are common in Gulf Coast salt marshes (most notably *Uca rapax*, *Uca longisignalis*, *Uca panacea*, and *Uca spinicarpa* in our sites), but the different species have similar diets in this region (Goeke and Armitage 2021), so we did not differentiate among species in our collection. Not all points had consumers present, but we were able to collect each consumer taxa from at least two points in eight of the nine sites. The exceptions were site AG2 for *Littoraria* and site SA2 for *Uca*, where we were only able to locate those consumers at a single point.

Sampled end members were particulate organic matter (POM), benthic organic material (BOM, which includes benthic microalgae and detritus), and any vascular plant species present. Macroalgae was not observed at any site so macroalgae was not included as an end member. At each of the five pre-determined points, 0.5 L of water and a scraping of the top 5 mm of sediment were collected to be processed in the lab for POM and BOM, respectively. Five live and five dead leaves were collected from each plant species present at each point to evaluate isotopic variation between live and senescent plant material. Leaves from plants of the same species in each site were combined to create a single live sample and a single dead sample per species in each site due to funding constraints. BOM and POM samples were not combined as we expected them to have higher spatial variation. A complete list of the sampled end members and sample sizes can be found in Table S1. Following collections, all samples were stored in a cooler with dry ice until they were transferred to a – 20 °C freezer for storage prior to analysis.

Consumer muscle tissue was obtained from the legs and claws of *Uca* and from the muscular foot of *Littoraria*. Tissues from all individuals of a species collected at the same point in a site were combined, resulting in a maximum of five samples per species per site. Combined tissue samples were rinsed in distilled water, dried at 60 °C for 48 h, and then ground to a fine powder with a mortar and pestle. Plant leaves were rinsed thoroughly with distilled water, dried at 60 °C for 48 h, and then ground to a fine powder using a ball mill. Some samples with very small leaves (e.g., *Batis maritima*) were ground with a mortar and pestle to avoid sample loss that can occur with ball mills.

To isolate particulate organic matter, water samples were filtered through a 100-µm sieve onto pre-combusted glass fiber filters. Sieving removed any large detrital plant particles from the sample. Filters were dried in an oven at 60 °C for 48 h and then stored in glass vials. Benthic organic material was separated from the sediment using density centrifugation (Levin and Currin 2012). Briefly, 15 mL of each sediment sample was rinsed twice with an equal amount of distilled water to remove salt. Then, 20 mL of Ludox (1.3 g/mL density) was added, and the sample was homogenized on a vortex mixer. Distilled water was carefully added without disturbing the surface of the Ludox to avoid mixing the Ludox and water layers, and the sample was centrifuged again. Following centrifugation, the organic material from the sediment, including decaying plant matter, microalgae, and benthic meiofauna, were caught at the interface of the water and Ludox layers due to the differential densities of the substances. This layer of organic material was pipetted onto a pre-combusted glass fiber filter through a 100-µm sieve to remove any larger masses of plant matter. Following filtration, the filter was dried at 60 °C for 48 h, and then stored in a glass vial.

Ground plant and animal tissues were weighed into tin capsules, and filters containing POM and BOM were placed in pre-combusted glass vials and cut into fine pieces using a pair of sterilized surgical scissors. The absence of carbonates was verified in a subset of POM and BOM samples via acid fumigation with 36% HCl. Stable isotope (δ^{13}C and δ^{15}N) analysis of most samples was performed at the Stable Isotopes for Biosphere Science (SIBS) Lab at Texas A&M University on a Costech elemental analyzer interfaced with a DELTA V Advantage isotope ratio mass spectrometer. A subset of 50 samples was analyzed by the UC Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer due to an equipment malfunction at the SIBS lab. Analysis of duplicate samples showed no difference in the results produced by the labs. Vienna PeeDee Belemnite and atmospheric nitrogen were used as standards for carbon and nitrogen isotopes, respectively. The accuracy of isotopic measurements was calculated as 0.07‰ for δ^{13}C and 0.03‰ for δ^{15}N. Number of samples analyzed and δ^{13}C and δ^{15}N for each sampled species of end member and basal consumer are reported in Tables S1 and S2. All results are reported in standard delta notation.

Analyses

Analysis of Physical Associations

There was extreme variability in consumer abundances across sites, with one site in particular (Mix-1) having tenfold greater abundances than most other sites. Due to this extreme variability and our limited ability to accurately count consumers at flooded sites, we were unable to directly analyze consumer abundances. Instead, to assess consumer physical associations with *Spartina* and *Avicennia*, we calculated a plant use index, which was based on consumer co-occurrence with each plant species at each site. *Uca* burrow associations were determined based on the dominant plant in the quadrat where they were found. If a plant, such as *Spartina* or *Avicennia*, was the largest contributor to the overall vegetation cover in a quadrat, the burrows were considered to be associated with that plant species. Bare ground was included as a cover type in analyses and *Uca* were considered associated with bare ground when more than 50% of the quadrat was non-vegetated. *Littoraria* were considered associated with *Spartina* or *Avicennia* when they occurred directly on that plant. They could also be associated with the ground or other plants present in the quadrat.

The plant use index (I_p) was calculated following the formula $I_p = \frac{\%C_p}{P}$ as the percent of a consumer associated with a plant in a site ($\%C_p$) divided by the average plant occurrence within the site (P). In the *Uca* use index (I_{pU}), P was the percent of non-flooded quadrats dominated by the plant in question. For *Littoraria* (I_{pL}), P was the percent of the visible (non-flooded) transect area covered by the plant in question. The different metrics of P were necessary because *Uca* association with plants was calculated on the quadrat level while *Littoraria* association was calculated at the plant level.

An index value of one indicated that the percent of a consumer associated with a plant matched the average occurrence of that plant, which is what would be expected if consumers were randomly distributed among available cover types. A value < 1 indicated avoidance of a plant by consumers, and a value > 1 indicated selective association with a plant by consumers. Plant-use indices were calculated for *Spartina* only in the marsh sites (where no *Avicennia* was present), *Avicennia* only in the mangrove sites (where no or limited *Spartina* was present), and both *Spartina* and *Avicennia* in the mixed sites. Consumers associated infrequently with other plant species or bare ground at each site, so we focused our assessments on associations with foundation plant species (*Spartina* and *Avicennia*). Sites were grouped by site type (marsh, mixed, or mangrove) and a planned contrasts generalized linear model (*glm* function in R) with a Gaussian error distribution followed by a general linear hypothesis test (*glht* function in the *multcomp* package in R, Hothorn et al. 2008) was used to analyze if consumer plant use (I_p values) differed between the same plant at different site types and/or different plants in the same site type.

Stable Isotope Analyses for Trophic Associations

Dietary contributions of sources to consumers at each site type were analyzed using Bayesian mixing models in MixSIAR in R (v 3.1.12, Stock et al. 2018). Two models were run, one for each consumer taxa. Models included site type (marsh, mixed, or mangrove) as a factor. This produced estimates of dietary source contributions to each consumer in each of the three site types.

Live and senescent plant tissues were separately analyzed for stable isotopes, but there were minimal differences in $\delta^{13}C$ or $\delta^{15}N$ isotopic values based on plant condition, so live and senescent samples were not considered separate dietary sources in the mixing model (Table S1). As recommended by the authors of MixSIAR, sources were grouped based on physiological and isotopic similarities to ensure that the model would be able to differentiate between sources and accurately resolve consumer diets. Plants were place into groups of C_4 graminoids (including *Spartina*), C_3 plants (including *Avicennia*), and succulents (*Batis maritima* and *Sarcocornia* spp.). Succulents perform C_3 photosynthesis but were distinct from other C_3 plants in terms of both physiology and $\delta^{13}C$ isotopes. POM and BOM isotopic values overlapped, so these sources were grouped into a single source referred to as fine organic matter (hereafter FOM) (Table S1). The overlap in these sources was unanticipated, but not wholly surprising as the lack of macroalgae or surface algal mats in our sites likely means that POM and BOM were comprised of the same detritus and microalgae and only differed in whether material was suspended (POM) or settled (BOM). All groupings were supported with one-way ANOVA that confirmed the $\delta^{13}C$ and $\delta^{15}N$ isotopic values of the sources within each group could not be distinguished from each other. Our final number of source groups (four) was higher than the best practices of $n+1$ tracers (which would have been three in this case) and may have slightly lowered the certainty of our model results, but all models still successfully converged.

Models were run using habitat-specific raw data for the four source groups. The *Uca* dietary model was run using the "very long" model run in MixSIAR (3 chains, 1,000,000 iterations, burn-in of 500,000, and thinned by 500), and Gelman-Rubin and Geweke diagnostics indicated the model successfully converged. Geweke diagnostics showed not all chains of the *Littoraria* dietary model fully converged with a "very long" model run, so an "extreme" model run (3 chains, 3,000,000 iterations, burn-in of 1,500,000, and thinned by 500) was used instead. This longer run allowed the *Littoraria* model to converge based on evaluation of Gelman-Rubin and Geweke diagnostics. We attribute this difficulty converging to the biomodality of FOM contributions to *Littoraria* at mangrove sites, which we discuss in detail below.

Based on the known dietary habits of these species as basal consumers (Teal 1962; Currin et al. 1995; Silliman and Ziemann 2001), we used trophic discrimination factors (TDFs) of 0.5 (± 1.2) and 2.9 (± 1.8) for $\delta^{13}C$ and $\delta^{15}N$, respectively (Vander Zanden and Rasmussen 2001). These values closely matched preliminary TDFs that we estimated from stable isotope analysis of *Littoraria* individuals restricted to *Spartina* or *Avicennia* diets for 60 days (Goeke et al. 2023). The large standard deviations of these TDFs were used to account for uncertainty in estimated values and potential differences in TDFs between consumers. The

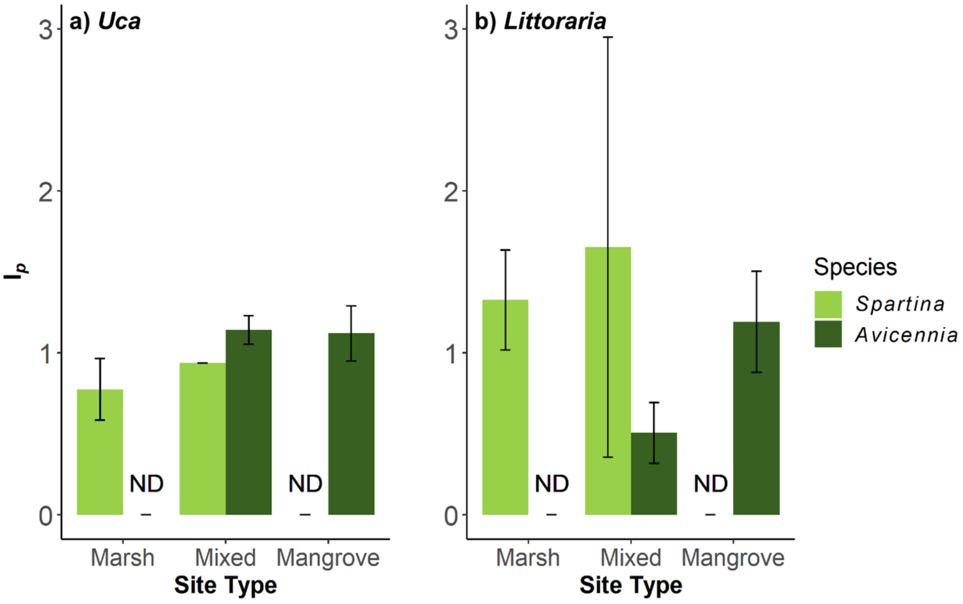

Fig. 3 Plant use index (I_p) of *Spartina* and *Avicennia* at different site types by **a** *Uca* and **b** *Littoraria*. Bars represent site type means ± SD

Table 1 Results of planned contrasts for *Uca* use of different plants and at different site types

Plant use comparison	Estimate	Standard error	*Z*-value	*p*-value
Marsh *Spartina* vs. Mixed *Spartina*	− 0.163	0.191	− 0.856	0.392
Mixed *Avicennia* vs. Mangrove *Avicennia*	0.021	0.156	0.137	0.891
Marsh *Spartina* vs. Mangrove *Avicennia*	− 0.345	0.156	− 2.217	0.027
Mixed *Spartina* vs. Mixed *Avicennia*	− 0.203	0.191	− 1.066	0.287

appropriateness of TDFs and the inclusion of all necessary end members was confirmed through mixing polygon simulation, and all consumers fell within the 95% mixing polygon (Smith et al. 2013). As the goal of this study was to assess general patterns of resource use, we did not perform post hoc pairwise comparisons to statistically evaluate changes in source contributions between sites of different types. This is a potential future direction for a more focused study investigating the magnitude of dietary shifts associated with mangrove encroachment. All analyses were performed in R version 3.6.0 (R Development Core Team 2022).

Results

Physical Associations of Consumers with Plants

Uca physically associated with *Spartina* and *Avicennia* wherever the plants were present and did not show a strong affinity for or avoidance of either plant, as indicated by plant use index (I_p) values ranging from 0.78 to 1.15 (Fig. 3a). When both plants were present at mixed sites, *Uca* did not associate differently with the two plant species (Fig. 3a and Table 1). Their association with *Spartina* did not differ between marsh and mixed sites, nor did their associations with *Avicennia* differ between mixed and mangrove sites (Fig. 3a and Table 1). *Uca* I_p values were slightly higher for *Avicennia* in mangrove sites than for *Spartina* in marsh sites (Table 1), but all I_p values were very close to one, indicating that there was likely no substantial physical preference for either foundation plant species over the other.

Plant use by *Littoraria* was much more variable than by *Uca*, with I_p values ranging from 0.50 to 1.75 (Fig. 3b). *Littoraria* associated with both *Spartina* and *Avicennia* wherever the plants were present, but at the mixed sites where the two species co-occurred, the *Littoraria* I_p was substantially higher for *Spartina* than for *Avicennia*, indicating a preference for *Spartina* (Fig. 3b and Table 2). *Spartina* use by *Littoraria* did not differ between marsh and mixed sites, nor did *Avicennia* use differ between mixed and mangrove sites (Fig. 3b and Table 2). Additionally, there was no difference in *Littoraria* use of the two foundation plant species when they occurred separately in marsh and mangrove sites (Table 2).

Trophic Associations of Consumers with Plants

We were able to collect and isotopically analyze relatively few individuals of each taxa at each site (Table S2), so our estimated dietary contributions generally have some remaining uncertainty and very large 95% confidence intervals. Here, we report on general resource use patterns based on median dietary contributions and the overlap between source contributions, but we acknowledge that there are instances where we were unable to fully resolve diets and address these instances below.

C_3 plants (including *Avicennia*) and succulents contributed very little (median contribution > 10%) to the diets of *Uca* and *Littoraria* at all sites, even those heavily encroached by mangroves (Table 3 and Fig. 5). All consumers had isotopic signatures that were distinct from those of C_3 plants, and much more closely resembled the signatures of graminoid plants and fine organic matter (FOM, the combined particular and benthic organic matter sources) (Fig. 4).

Uca diets in marsh sites were comprised of an estimated 59% graminoid contributions (median, 95% CI: 36–80) and 27% (0–57) FOM contributions. In contrast, in mixed and mangrove sites, graminoid and FOM median contributions to *Uca* diets were relatively similar, with both comprising an estimated 30–50% of the total diet (Table 3). Estimated median contributions from both succulents and C3 plants were < 10% of *Uca* diets in all site types.

The median estimated contribution of graminoids to *Littoraria* diets decreased from 71% (54–82) in marsh sites to

Table 2 Results of planned contrasts for *Littoraria* use of different plants and at different site types

Plant use comparison	Estimate	Standard error	*Z*-value	*p*-value
Marsh *Spartina* vs. Mixed *Spartina*	− 0.556	0.535	− 1.038	0.299
Mixed *Avicennia* vs. Mangrove *Avicennia*	− 0.863	0.535	− 1.611	0.107
Marsh *Spartina* vs. Mangrove *Avicennia*	0.133	0.535	0.249	0.803
Mixed *Spartina* vs. Mixed *Avicennia*	1.552	0.535	2.898	0.004

Table 3 Estimated median dietary contribution percent (95% confidence interval range) of end member groups to *Littoraria* and *Uca* diets at sites with different levels of mangrove encroachment as estimated by MixSIAR models

Consumer	Source	Site Type		
		Marsh	Mixed	Mangrove
Littoraria	% C_3	6 (0–23)	3 (0–40)	3 (0–52)
	% graminoid	71 (54–82)	51 (40–64)	25 (0–57)
	% FOM	14 (0–43)	43 (0–59)	64 (0–100)
	% succulent	3 (0–21)	2 (0–21)	3 (0–43)
Uca	% C_3	7 (0–26)	5 (0–41)	10 (0–36)
	% graminoid	59 (36–80)	41 (12–60)	49 (32–65)
	% FOM	27 (0–57)	49 (3–84)	32 (1–60)
	% succulent	4 (0–24)	3 (0–20)	5 (0–25)

51% (40–64) in mixed sites and 25% (0–57) in mangrove sites. Simultaneously, the median estimated contributions of FOM increased from 14% (0–43) in marsh sites to 43% (0–59) in mixed sites. Median contributions of FOM increased to 64% (0–100) in mangrove sites but the large 95% CI range of FOM contributions to *Littoraria* in mangrove sites (0–100) reflects the bimodal posterior distribution of FOM contributions from the mixing model (Fig. 5). The two modes likely represent the two distinct groups of *Littoraria* that can be seen on the isospace biplot for mangrove sites (Fig. 4c) that both align closely with FOM δ^{13}C values but differ in the extent of δ^{15}N enrichment. The cause of this δ^{15}N enrichment in a subset of *Littoraria* is not known but is not linked to site identity, as both groups contain *Littoraria* from all three mangrove sites. The similar δ^{13}C values of both groups of *Littoraria* indicate their diets likely contains large proportions of FOM, but the differences in δ^{15}N values of the two groups make it difficult for the mixing model to resolve a precise FOM contribution, leading to the large uncertainty. As with *Uca*, both succulents and C3 plants had estimated median dietary contributions of < 10% in all site types.

There was a variation of ~ 4‰ in δ^{13}C between FOM sources at different site types (Fig. 4), but the variation did not follow a consistent pattern with mangrove presence, and so is unlikely to reflect an influence of mangrove carbon on the FOM signature. Any increased consumption of FOM at encroached sites is therefore likely not serving as a pathway for the incorporation of mangrove carbon into the food web.

Discussion

Mangrove encroachment altered consumer-plant associations and consumer diets. Generally, both consumers physically interacted with whatever foundation plant species were present at a site, although *Littoraria* preferred *Spartina* to *Avicennia* when a choice was present in mixed sites. In marsh sites, both *Uca* and *Littoraria* diets contained > 50% median contributions from graminoids, but despite the physical association with mangroves in mixed and mangrove sites, the median dietary contribution of C3 carbon sources did not increase for either *Uca* or *Littoraria*. Instead, both consumers potentially increased reliance on FOM (based on increases in median dietary contributions), although the difficulty in resolving precise FOM contributions means there is remaining uncertainty in the diet. The disconnect between physical and trophic associations indicates that while *Avicennia* is filling a foundational role structurally, it is not serving as a foundation species from a trophic perspective. Differences in functional support between the two species are not wholly surprising, as distinct foundation species typically provide distinct resources and benefits that are utilized by different suites of organisms (Angelini et al. 2011), and the consumers that would normally utilize the benefits provided by *Avicennia* are not yet present in encroached systems. Foundation species disappearance typically results in clear effects on the abundance and diversity of reliant consumers (Ellison et al. 2005; Schöb et al. 2012; Youngquist et al. 2017), but the consequences of foundation species shift typically depend on the phenomenon driving the shift (e.g., woody encroachment, tropicalization, and eutrophication) and if the shift is affecting flora and fauna simultaneously (Scheffer et al. 2001; Angelini et al. 2011; Eldridge et al. 2011; Vergés et al. 2014; Bittick et al. 2019). Our results provide support to the idea that novel foundation species may support only a portion of the functions of the original foundation species for any given consumer (Scheffer et al. 2001; Angelini et al. 2011; Bittick et al. 2019). In the case of mangrove encroachment, the partial functional support by *Avicennia* likely means that while basal consumers will persist in encroached wetlands, some carbon and energy pathways will shift.

Physical Support

Understanding the overlap in structural or physical support between original and novel foundation species requires examining similarities between the two species. The similarity in physical support between *Avicennia* and *Spartina* is likely a result of the rigid structures both species possess (pneumatophores and cable roots in *Avicennia*; stems in *Spartina*) and the ability of those structures to ameliorate abiotic and biotic stressors, such as desiccation and predation risk (Vaughn and Fisher 1988; Lim and Heng 2007; Lantz et al. 2011; Iacarella and Helmuth 2012). Consumer identity and preferences also play a role in determining the extent of physical support, as shown by the unwillingness

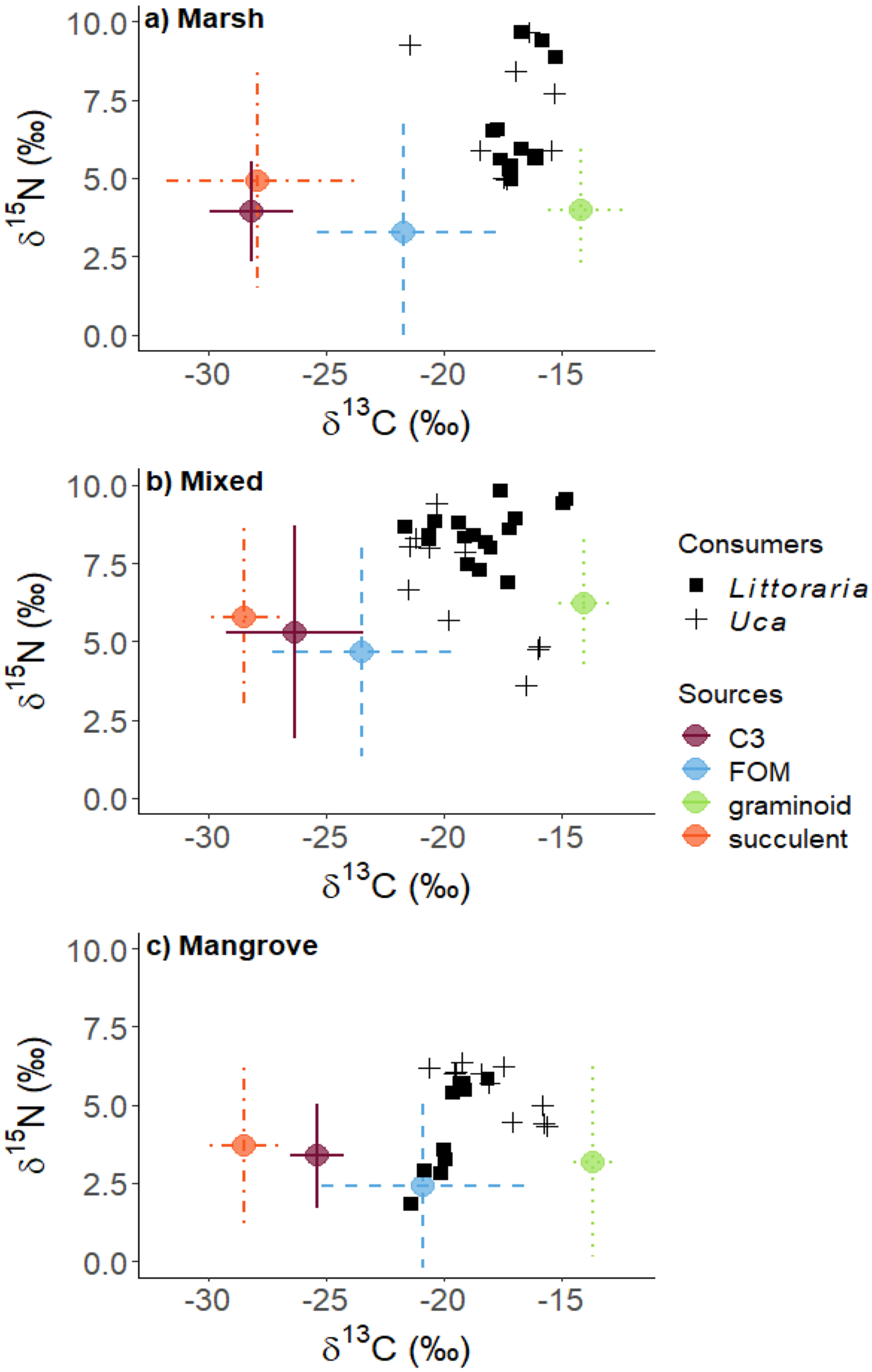

Fig. 4 Stable isotope biplots showing the mean (± SD) carbon and nitrogen isotope ratios for each source group and consumer in **a** *Spartina* dominated marsh sites, **b** sites containing a mix of *Spartina* and *Avicennia*, and **c** *Avicennia* dominated mangrove sites. Plotted consumer isotopic values are not adjusted for trophic discrimination factors

of *Littoraria*, but not *Uca*, to associate with *Avicennia* when *Spartina* was present. These findings were not site specific, as *Littoraria* have also been observed associating primarily with *Spartina* in areas undergoing encroachment in Florida (Walker et al. 2019), while *Uca* in those same locations are more evenly distributed and associated with both marsh- and mangrove-dominated locations (Johnston and Gruner 2018; Walker et al. 2019). Although *Uca* and *Littoraria* may be shifting their associations with plants within sites, they are not fully abandoning encroached sites, possibly because they are relatively low mobility organisms whose distributions are largely constrained by larval settlement (Bingham 1972; Christy 2017).

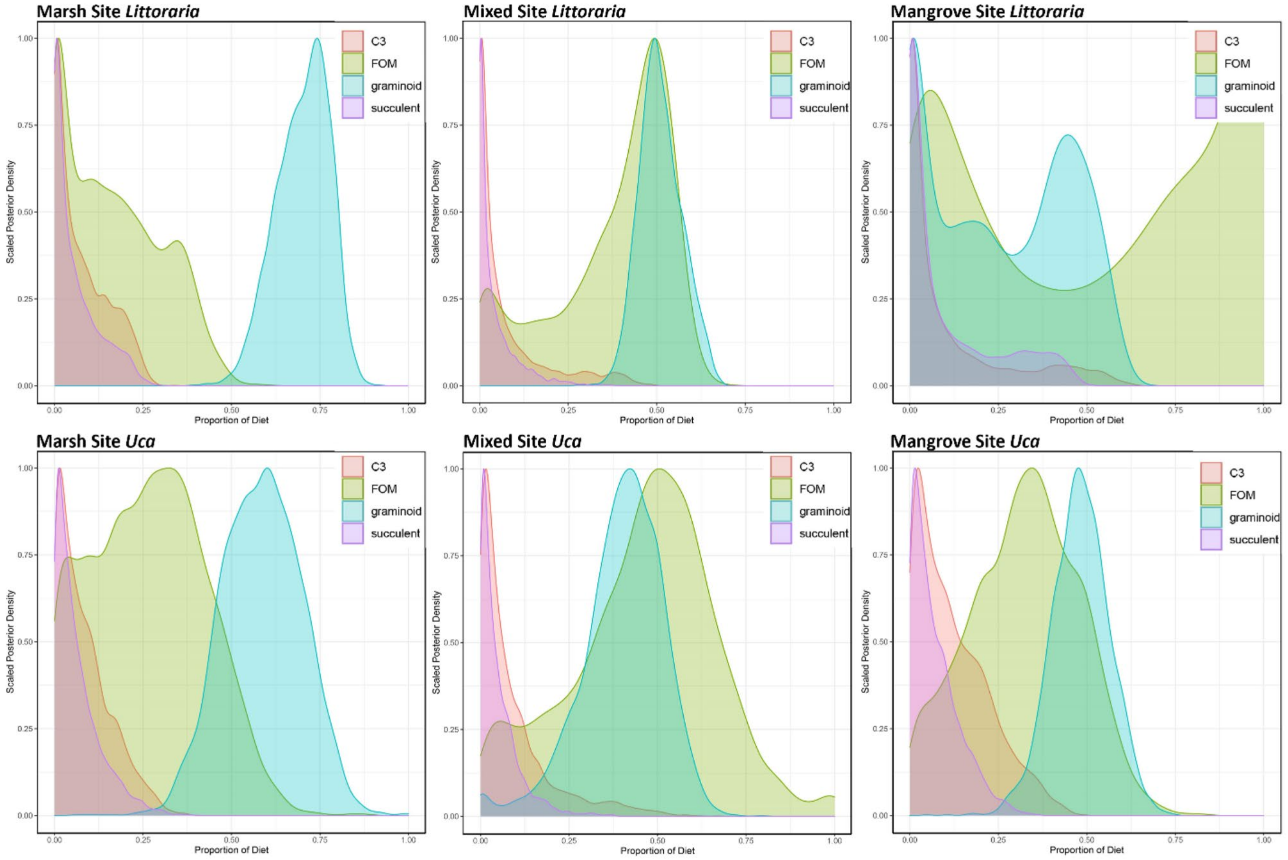

Fig. 5 Scaled posterior density distribution plots for *Littoraria* (top row) and *Uca* (bottom row) showing the predicted dietary proportions from MixSIAR models

More mobile fauna such as fish and nekton are also altering their distributions and associations as a result of mangrove encroachment, but their shifts are much more heterogeneous across sites, seasons, and taxa. For example, Smee et al. (2017) found that fish and blue crabs were most abundant in marshes while mud crabs were most abundant in mangroves, but other studies reported higher fish abundance in mangrove sites (Armitage et al. 2021) and that blue crabs and mud crabs were most common where there is a mix of marsh and mangrove vegetation (Diskin and Smee 2017). The only taxon that shows similar patterns across studies is grass shrimp (*Palaemonetes* spp.), which are consistently more abundant in marsh than mangrove habitats (Diskin and Smee 2017; Smee et al. 2017; Johnston and Gruner 2018; Scheffel et al. 2018; Armitage et al. 2021). Despite the variability in the results, every study found shifts in some of the examined taxa of mobile fauna in response to mangrove encroachment, suggesting mobile fauna may be able to respond to the structural changes resulting from foundation shifts more easily than benthic or sedentary fauna. It is also important to note that many of these studies found other factors including year, season, site, and weather patterns also affected faunal abundances and distributions, and sometimes obscured the effects of *Avicennia* presence (Diskin and Smee 2017; Scheffel et al. 2018; Armitage et al. 2021). These confounding factors and the diversity of responses between benthic and mobile fauna make it challenging to detect patterns in whole faunal assemblages and highlights the need for long-term research that takes species identities and natural history into account in order to detect patterns in responses to foundation shifts.

Trophic Support

Physical support did not serve as a predictor of trophic support. Despite a strong association with *Avicennia* in mangrove sites, both *Uca* and *Littoraria* had low median dietary contributions from mangroves and had the highest median contributions from FOM and graminoids at all site types. The reliance on FOM likely indicates consumption of algae and detritus, based on the similarity of our FOM isotopic values to those of algal and detrital values from other studies (e.g., Sepúlveda-Lozada et al. 2015; Nelson et al. 2019). There appeared to be an almost complete switch between graminoid reliance and FOM reliance in *Littoraria* (median graminoid contributions decreased by 46% between marsh and mangrove sites while median FOM contributions increased by 50%), although there is again some uncertainty due to the challenges producing dietary estimates for FOM. While median graminoid contributions to *Uca* diets were lower in encroached sites, *Uca* appeared to rely approximately equally on both graminoids and FOM (based on median contributions) in both mixed and mangrove sites. This may reflect utilization of different graminoid sources. The graminoid proportion of *Littoraria* diets was likely comprised of *Spartina alterniflora*, which was by far the most abundant graminoid at the low elevations where *Littoraria* were predominantly found (Goeke 2021). *Uca* are more mobile within a site than *Littoraria*, generally feeding over an area of a few meters (Yamaguchi and Tabata 2004; di Virgilio and Ribeiro 2013), and thus the consistent graminoid contributions to *Uca* diets may indicate consumption of both *Spartina* at low elevations and other grasses such as *Distichlis spicata* and *Monanthochloe littoralis* at high elevations. *Avicennia* is relatively uncommon at these higher elevations, but *Uca* burrows were frequently observed across the full elevation range of the wetland. The inability of benthic invertebrates to relocate to new sites means that they necessarily have strong trophic links to the site they inhabit and are likely to have the strongest and most immediate trophic responses to foundational shifts (with the exception of consumers that are fully reliant on allochthonous contributions such as tidally deposited detritus). In contrast, the diets of more mobile, fully aquatic species including blue crabs, multiple species of shrimp, and small fish such as killifish and anchovies appear to be more stable in the face of mangrove encroachment as they are dominated by sources such as POM and benthic and epiphytic algae in both marsh and mangrove areas (Nelson et al. 2019; Baker et al. 2021).

Mangroves, similar to other foundation species, are often valued for their high primary productivity (Nagelkerken et al. 2008), but basal consumers in encroached systems are likely not substantially consuming and/or assimilating mangroves, and therefore are not processing the highly recalcitrant mangrove plant material in ways that make it biologically available to higher level consumers (Cebrian 2004). The FOM diet that we found benthic consumers are relying on in mangrove sites likely includes the same POM and algae sources typically utilized by the previously mentioned mobile consumers. This suggests that mangrove encroachment is shifting the base of the food web to be supported by fewer end members instead of introducing an additional carbon and energy source. Furthermore, studies have found that exposure to *Avicennia* in both the lab and the field has negative physiological effects on *Uca* and *Littoraria* including decreased energy storage, so mangrove presence may be decreasing the fitness of consumers and having detrimental effects on basal consumer populations even in the absence of trophic interactions (Goeke 2021; Goeke and Armitage 2021; Goeke et al. 2023). Taken together, this means that fauna in encroached wetlands may not directly benefit from the high primary productivity typically associated with mangroves.

Conclusion

The results presented here provide one of the first analyses of concurrent trophic and physical associations by selected consumers in response to a foundational shift. This study exemplifies the importance of looking at multiple dimensions of plant-animal interactions, particularly those interactions with foundation species that have a strong potential to influence other ecosystem processes and functions. Co-occurrence cannot be assumed to indicate trophic reliance as shown by the discrepancy between *Uca* and *Littoraria* physical associations and diets (i.e., physical reliance on *Avicennia* structures but lack of consumption of *Avicennia* material), and foundation plant species cannot be assumed to be equivalent as shown by the differences in functional support between *Spartina* and *Avicennia*. Understanding the details of faunal interactions with foundation plant species will help explain the effects foundational shifts are having on ecosystems and may clarify some of the differences based on site, season, and other confounding factors. Detecting patterns in faunal responses to foundation shifts is necessary to form a general idea of what functions are commonly maintained and to predict potential impacts instead of responding as they occur. It is likely that foundation shifts will affect generalists (such as *Uca*) less than specialists (such as *Littoraria*), and more mobile consumers less than benthic or sessile ones (this work, Bartley et al. 2019). In the case of mangrove encroachment, our results support the provision of habitat but not food for *Uca* and *Littoraria* by *Avicennia* (with more extreme responses observed in *Littoraria*). This study has a necessarily broad focus in order to consider both physical and trophic associations. It serves as a starting point for others who may be interested in exploring these topics in more depth to add to our understanding of the complex and multi-faceted ways that coastal wetland fauna are responding to mangrove encroachment.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-024-01389-w.

Acknowledgements We thank Jamie Thompson, Ashley McDonald, and Rachael Glazner for their assistance in field collection of samples and Ashley Hermann and Ryan Glaze for their assistance in the lab.

Funding This research was supported in part by an institutional grant (NA18OAR4170088) to the Texas Sea Grant College Program from the National Oceanic and Atmospheric Administration, U.S. Department of Commerce. Janelle A. Goeke was supported by a Dissertation Fellowship through the Graduate and Professional School at Texas A&M University during a portion of this work.

Data Availability Data are available through the Environmental Data Initiative at edirepository.org or from the corresponding author upon reasonable request.

References

Angelini, C., A.H. Altieri, B.R. Silliman, and M.D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *BioScience* 61: 782–789. https://doi.org/10.1525/bio.2011.61.10.8.

Armitage, A.R., W.E. Highfield, S.D. Brody, and P. Louchouarn. 2015. The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. *PLoS ONE* 10: 1–17. https://doi.org/10.1371/journal.pone.0125404.

Armitage, A.R., C.A. Weaver, J.S. Kominoski, and S.C. Pennings. 2020. Resistance to hurricane effects varies among wetland vegetation types in the marsh–mangrove ecotone. *Estuaries and Coasts* 43: 960–970. https://doi.org/10.1007/s12237-019-00577-3.

Armitage, A.R., C.A. Weaver, A.A. Whitt, and S.C. Pennings. 2021. Effects of mangrove encroachment on tidal wetland plant, nekton, and bird communities in the Western Gulf of Mexico. *Estuarine, Coastal and Shelf Science* 248: 106767. https://doi.org/10.1016/j.ecss.2020.106767.

Baiser, B., N. Whitaker, and A.M. Ellison. 2013. Modeling foundation species in food webs. *Ecosphere* 4: 1–14. https://doi.org/10.1890/ES13-00265.1.

Baker, R., K. Abrantes, and I.C. Feller. 2021. Stable isotopes suggest limited role of wetland macrophyte production supporting aquatic food webs across a mangrove-salt marsh ecotone. *Estuaries and Coasts* 33: 1619–1627. https://doi.org/10.1007/s12237-021-00895-5.

Bartley, T.J., K.S. McCann, C. Bieg, et al. 2019. Food web rewiring in a changing world. *Nat Ecol Evol* 3: 345–354. https://doi.org/10.1038/s41559-018-0772-3.

Bertness, M.D., and T. Miller. 1984. The distribution and dynamics of *Uca pugnax* in a New England Salt Marsh. *J Exp Mar Bio Ecol* 83: 211–237.

Bingham, F.O. 1972. Several aspects of the reproductive biology of *Littorina irrorata* (Gastropoda). *Nautilus (philadelphia)* 86: 8–10. https://doi.org/10.1038/scientificamerican01221846-76b.

Bittick, S.J., R.J. Clausing, C.R. Fong, et al. 2019. A rapidly expanding macroalga acts as a foundational species providing trophic support and habitat in the South Pacific. *Ecosystems* 22: 165–173. https://doi.org/10.1007/s10021-018-0261-1.

Boesch, D.F., and R.E. Turner. 1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7: 460–468. https://doi.org/10.2307/1351627.

Cavanaugh, K.C., J.R. Kellner, A.J. Forde, et al. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences* 111: 723–727. https://doi.org/10.1073/pnas.1315800111.

Cavanaugh, K.C., E.M. Dangremond, C.L. Doughty, et al. 2019. Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proceedings of the National Academy of Sciences* 116: 21602–21608. https://doi.org/10.1073/pnas.1902181116.

Cebrian, J. 2004. Role of first-order consumers in ecosystem carbon flow. *Ecology Letters* 7: 232–240. https://doi.org/10.1111/j.1461-0248.2004.00574.x.

Christy, J.H. 2017. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus Uca): Test of an hypothesis. *Biological Bulletin* 163: 251–263.

Currin, C.A., S.Y. Newell, and H.W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: Considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series* 121: 99–116.

Dayton, P.K. 1972. Toward an understanding of community resilience and the potential effets of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC (ed) Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, pp 81–96.

di Virgilio, A., and P.D. Ribeiro. 2013. Spatial and temporal patterns in the feeding behavior of a fiddler crab. *Marine Biology* 160: 1001–1013. https://doi.org/10.1007/s00227-012-2153-9.

Diskin, M.S., and D.L. Smee. 2017. Effects of black mangrove *Avicennia germinans* expansion on salt marsh nekton assemblages before and after a flood. *Hydrobiologia* 803: 283–294. https://doi.org/10.1007/s10750-017-3179-2.

Eldridge, D.J., M.A. Bowker, F.T. Maestre, et al. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. *Ecology Letters* 14: 709–722. https://doi.org/10.1111/j.1461-0248.2011.01630.x.

Ellison, A.M., M.S. Bank, B.D. Clinton, et al. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3: 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Everitt, J.H., F.W. Judd, D.E. Escobar, and M.R. Davis. 1996. Integration of remote sensing and spatial information technologies for mapping black mangrove on the Texas Gulf Coast. *Journal of Coastal Research* 12: 64–69.

Glazner, R., J. Blennau, and A.R. Armitage. 2020. Mangroves alter predator-prey interactions by enhancing prey refuge value in a mangrove-marsh ecotone. *J Exp Mar Bio Ecol* 526: 151336. https://doi.org/10.1016/j.jembe.2020.151336.

Goeke, J.A., and A.R. Armitage. 2021. Coastal woody encroachment reduces food quality for basal consumers. *Ecosphere* 12: 1–8. https://doi.org/10.1002/ecs2.3511.

Goeke, J.A., E.M. Foster, and A.R. Armitage. 2023. Negative outcomes of novel trophic interactions along mangrove range edges. *Ecology* 1–11. https://doi.org/10.1002/ecy.4051.

Goeke, J.A. 2021. Bottom-up effects of mangrove encroachment on basal consumers in the Gulf of Mexico. PhD dissertation, Ecology and Evolutionary Biology Program, Texas A&M University, College Station, Texas, USA.

Harris, J.M., W.R. James, and J.S. Lesser, et al. 2020. Foundation species shift alters the energetic landscape of marsh nekton. *Estuaries and Coasts* 44: 1671–1680. https://doi.org/10.1007/s12237-020-00852-8.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical J* 50: 346–363.

Iacarella, J.C., and B. Helmuth. 2012. Body temperature and desiccation constrain the activity of *Littoraria irrorata* within the *Spartina alterniflora* canopy. *Journal of Thermal Biology* 37: 15–22. https://doi.org/10.1016/j.jtherbio.2011.10.003.

Johnston, C.A., and D.S. Gruner. 2018. Marine fauna sort at fine resolution in an ecotone of shifting wetland foundation species. *Ecology* 99: 0–2. https://doi.org/10.1002/ecy.2505.

Kelleway, J.J., K. Cavanaugh, K. Rogers, et al. 2017. Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology* 23: 3967–3983. https://doi.org/10.1111/gcb.13727.

Lantz, S.M., D.E. Gawlik, and M.I. Cook. 2011. The effects of water depth and emergent vegetation on foraging success and habitat selection of wading birds in the Everglades. *Waterbirds Int J Waterbird Biol* 34: 439–447.

Leary, M.H.O. 1988. Carbon isotopes in photosynthesis. *BioScience* 38: 328–336.

Levin, L.A., and C. Currin. 2012. Stable isotope protocols: sampling and sample processing. In: UC San Diego Libr. – Scripps Digit. Collect. https://escholarship.org/uc/item/3jw2v1hh.

Lim, S.S.L., and M.M.S. Heng. 2007. Mangrove micro-habitat influence on bioturbative activities and burrow morphology of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) (Decapoda, Ocypodidae). *Crustaceana* 80: 31–45.

Nagelkerken, I., S.J.M. Blaber, S. Bouillon, et al. 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany* 89: 155–185. https://doi.org/10.1016/j.aquabot.2007.12.007.

Nelson, J.A., J. Lesser, W.R. James, et al. 2019. Food web response to foundation species change in a coastal ecosystem. *Food Webs* 21: e00125. https://doi.org/10.1016/j.fooweb.2019.e00125.

O'Brien, J.M., K.A. Krumhansl, R.E. Scheibling, et al. 2013. Invasive bryozoan alters interaction between a native grazer and its algal food. *J Mar Biol Assoc United Kingdom* 93: 1393–1400. https://doi.org/10.1017/S0025315412001683.

Osland, M.J., N. Enwright, R.H. Day, and T.W. Doyle. 2013. Winter climate change and coastal wetland foundation species: Salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology* 19: 1482–1494. https://doi.org/10.1111/gcb.12126.

Osland, M.J., N. Enwright, and C.L. Stagg. 2014. Freshwater availability and coastal wetland foundation species: Ecological transitions along a rainfall gradient. *Ecology* 95: 2778–2788. https://doi.org/10.1890/13-1269.1.

Osland, M.J., N.M. Enwright, R.H. Day, et al. 2016. Beyond just sea-level rise: Considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology* 22: 1–11. https://doi.org/10.1111/gcb.13084.

Osland, M.J., R.H. Day, C.T. Hall, et al. 2020. Temperature thresholds for black mangrove (*Avicennia germinans*) freeze damage, mortality and recovery in North America: Refining tipping points for range expansion in a warming climate. *Journal of Ecology* 108: 654–665. https://doi.org/10.1111/1365-2745.13285.

Osland, M.J., A.R. Hughes, A.R. Armitage, et al. 2022. The impacts of mangrove range expansion on wetland ecosystem services in the southeastern United States: Current understanding, knowledge gaps, and emerging research needs. *Global Change Biology*. https://doi.org/10.1111/gcb.16111.

Pennings, S.C., R.M. Glazner, Z.J. Hughes, et al. 2021. Effects of mangrove cover on coastal erosion during a hurricane in Texas, USA. *Ecology* 102: 1–8. https://doi.org/10.1002/ecy.3309.

Peters, D.P.C., and J. Yao. 2012. Long-term experimental loss of foundation species: Consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere* 3: 27. https://doi.org/10.1890/es11-00273.1.

R Development Core Team. 2022. The R project for statistical computing.https://www.r-project.org/.

Reid, A.M., and C.J. Lortie. 2012. Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere* 3: 96. https://doi.org/10.1890/es12-00106.1.

Saintilan, N., N.C. Wilson, K. Rogers, et al. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* 20: 147–157. https://doi.org/10.1111/gcb.12341.

Saintilan, N., K. Rogers., and K.L. McKee. 2018. The shifting saltmarsh-mangrove ecotone in Australasia and the Americas. In: Coastal wetlands: an integrated ecosystem approach. pp 915–945.

Scheffel, W.A., K.L.J. Heck, and M.W. Johnson. 2018. Tropicalization of the northern Gulf of Mexico: impacts of salt marsh transition to black mangrove dominance on faunal communities. *Estuaries and Coasts* 41: 1193–1205. https://doi.org/10.1007/s12237-017-0334-y.

Scheffer, M., S. Carpenter, J.A. Foley, et al. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596. https://doi.org/10.1038/35098000.

Schlacher, T.A., S. Lucrezi, C.H. Peterson, et al. 2016. Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand. *Journal of Sea Research* 112: 55–64. https://doi.org/10.1016/j.seares.2016.04.001.

Schöb, C., B.J. Butterfield, and F.I. Pugnaire. 2012. Foundation species influence trait-based community assembly. *New Phytologist* 196: 824–834.

Sepúlveda-Lozada, A., M. Mendoza-Carranza, M. Wolff, et al. 2015. Differences in food web structure of mangroves and freshwater marshes: Evidence from stable isotope studies in the Southern Gulf of Mexico. *Wetlands Ecology and Management* 23: 293–314. https://doi.org/10.1007/s11273-014-9382-2.

Silliman, B.R., and J.C. Ziemann. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virgina salt marsh. *Ecology* 82: 2830–2845. https://doi.org/10.1890/0012-9658.

Smee, D.L., J.A. Sanchez, M. Diskin, and C. Trettin. 2017. Mangrove expansion into salt marshes alters associated faunal communities. *Estuarine, Coastal and Shelf Science* 187: 306–313. https://doi.org/10.1016/j.ecss.2017.02.005.

Smith, J.A., D. Mazumder, I.M. Suthers, and M.D. Taylor. 2013. To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. 612–618. https://doi.org/10.1111/2041-210X.12048.

Stock, B.C., A.L. Jackson, E.J. Ward, et al. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 2018: 1–27. https://doi.org/10.7717/peerj.5096.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614–624.

Thompson, J.E. 2022. Abiotic and biotic influences on black mangrove (*Avicennia germinans*) growth and survival along their northern range limit in the Gulf of Mexico. Texas A&M University.

Vander Zanden, M.J., and J.B. Rasmussen. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography* 46: 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061.

Vaughn, C.C., and F.M. Fisher. 1988. Vertical migration as a refuge from predation in intertidal marsh snails: A field test. *J Exp Mar Bio Ecol* 123: 163–176. https://doi.org/10.1016/0022-0981(88)90167-0.

Vaughn, C.C., and F.M. Fisher. 1992. Dispersion of the salt-marsh periwinkle Littoraria irrorata: Effects of water level, size, and season. *Estuaries* 15: 246–250. https://doi.org/10.2307/1352699.

Vergés, A., P.D. Steinberg, M.E. Hay, et al. 2014. The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proc R Soc B Biol Sci* 281: 20140846. https://doi.org/10.1098/rspb.2014.0846.

Walker, J.E., C. Angelini, I. Safak, et al. 2019. Effects of changing vegetation composition on community structure, ecosystem functioning, and predator-prey interactions at the saltmarsh-mangrove ecotone. *Diversity* 11: 1–17. https://doi.org/10.3390/d11110208.

Yamaguchi, T., and S. Tabata. 2004. Territory usage and defence of the fiddler crab, *Uca lactea* (De Haan) (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 77: 1055–1080.

Yando, E.S., M.J. Osland, S.F. Jones, and M.W. Hester. 2019. Jump-starting coastal wetland restoration: A comparison of marsh and mangrove foundation species. *Restoration Ecology* 27: 1145–1154. https://doi.org/10.1111/rec.12963.

Youngquist, M.B., S.L. Eggert, A.W. D'Amato, et al. 2017. Potential effects of foundation species loss on wetland communities: A case study of black ash wetlands threatened by emerald ash borer. *Wetlands* 37: 787–799. https://doi.org/10.1007/s13157-017-0908-2.