



How Does Mangrove Expansion Affect Structure and Function of Adjacent Seagrass Meadows?

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Abstract

Temperatures are increasing globally and causing species-specific geographic range expansions. In the Gulf of Mexico, mangroves are encroaching regions historically dominated by temperate salt marshes, changing animal communities and nutrient cycling in the intertidal zone. Marine systems are highly connected; therefore, we expect that changes in the intertidal will alter functions of adjacent subtidal seagrass meadows. We surveyed seagrass meadows adjacent to mangroves, salt marshes, and a mixture of the two and asked, do changes in intertidal plant composition influence (1) environmental conditions (subtidal water and sediment characteristics); (2) biogeochemical cycling (net oxygen and nitrogen gas fluxes); (3) seagrass meadow cover, biomass, and productivity; and (4) invertebrate community assemblage? There are clear differences in sediment organic matter and net nitrogen gas (N₂) fluxes between adjacent intertidal habitats, but the magnitude or direction of change differs seasonally. We hypothesize that this seasonal pattern is due to outwelling from the intertidal, as mangroves senesce in fall, and marshes senesce later in winter. Therefore, changes in adjacent intertidal habitat can impact the timing of organic matter delivery. This also has implications for seagrass biomass. *Thalassia testudinum* belowground biomass adjacent to mangroves substantially decreased over the winter, suggesting vulnerability to stressors as the intertidal plant community shifts from marsh to mangrove dominance. Epifauna density and diversity did not vary among seagrass meadows based on adjacent intertidal habitats, but subtle differences in community assemblages associated with shifts in intertidal plant community were detected. This work demonstrates that impacts of species range expansions are far-reaching due to connectivity in marine systems.

Keywords *Thalassia testudinum* · Salt marshes · Habitat connectivity · Outwelling · Tropicalization · Denitrification

Introduction

Global temperature increases impact ecosystems through both small-scale shifts in reproductive biology and phenology, and larger scale changes in geographic ranges, community composition, and ecosystem functions (McCarty 2002). In marine

systems, greater habitat connectivity and increased rates of temperature changes facilitate relatively rapid range shifts (Burrows et al. 2011). Based on the understanding that connectivity is greater in marine habitats relative to terrestrial habitats (Burrows et al. 2011), changes in species distribution in marine systems may result in impacts on a larger spatial scale. For example, tropical grazers moving into temperate seagrass meadows alter seagrass canopy structure (Vergés et al. 2014; Heck et al. 2015). Increased grazing can directly and indirectly cause alterations in highly valuable seagrass functions and services, such as carbon sequestration, nursery habitat, nutrient uptake, and sediment trapping, which likely impact nearby systems (Scott et al. 2018).

A common example of tropical species' range expansion is the poleward migration of mangroves into salt marshes (Saintilan et al. 2014; Cavanaugh et al. 2019). Although mangroves and salt marshes provide similar functions (e.g., habitat provision, erosion control, and nutrient cycling), their notable phenological and structural differences result in shifts to these

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highly valuable processes (Kelleway et al. 2017). Salt marsh grasses are herbaceous and die back in the winter, while mangroves have a persistent woody structure. Mangroves tend to have larger aboveground carbon storage, and because their larger structure results in more sediment accretion, sediment carbon storage is elevated (Bianchi et al. 2013; Doughty et al. 2016; Simpson et al. 2017). The fine root structure of salt marsh grasses, compared to mangroves, increases soil water content and decreases soil redox potentials (Perry and Mendelssohn 2009; Comeaux et al. 2012), impacting microbial community structure and rates of nitrogen fixation and denitrification (Barreto et al. 2018; Gao et al. 2019). While these processes result in larger pools of nitrogen in salt marsh soils, mangrove litter tends to be more labile, higher in nitrogen, and decomposes faster, resulting in faster mineralization rates and higher rates of primary production (Lee 1995; Lewis et al. 2014; Simpson et al. 2020).

While both mangroves and marshes share common faunal species and nursery functions, animal communities may differ slightly (Bloomfield and Gillanders 2005). For example, grass shrimp and infauna, such as polychaetes and crustaceans, tend to dominate salt marsh faunal communities, while crabs and fish are more abundant in mangroves (Snee et al. 2017). These invertebrates are prey for commercially important fish species, and therefore could significantly affect higher trophic levels (Glazner et al. 2020). However, there is some redundancy, as recent studies have shown no effects on predator-prey interactions in recently established mangroves compared to salt marshes (Walker et al. 2019); but this may change as mangroves become more mature and established (Scheffel et al. 2018).

Coastal ecosystems are highly interconnected through the coastal ecosystem mosaic (Sheaves 2009). In this mosaic, the intertidal and adjacent subtidal can directly and indirectly influence each other (Huxham et al. 2018). Intertidal plants (e.g., mangroves or salt marshes) can alter water, energy, and nutrient flow into the subtidal by acting either as a source or sink for nutrients (Odum 1968; Valiela and Cole 2002; Taillardat et al. 2019). In India, seagrass meadows adjacent to mangroves had higher density, biomass, and productivity compared to meadows adjacent to shorelines without mangroves (Mishra and Apte 2020). Faunal communities also link the intertidal and subtidal. Salt marsh fish communities depend on adjacent subtidal habitat—the abundance of pinfish in marshes increased with presence of seagrass (Irlandi and Crawford 1997); and richness of nursery species (e.g., *Ocyurus chrysurus* and *Scarus iserti*) in seagrasses was greater in meadows adjacent to mangroves (Nagelkerken et al. 2001).

In the northern Gulf of Mexico, seagrasses, an important ecosystem engineer, are impacted directly by tropicalization (e.g., increased direct consumption by a tropical fish, Heck et al. 2015), and may also be indirectly impacted through intertidal plant species changes. Because seagrasses are highly

connected to adjacent intertidal systems, alterations in habitat function and biogeochemical pools and cycles associated with tropical mangrove expansion into salt marshes will likely spill over into seagrass meadows. Changes in intertidal nutrient and organic matter processing associated with mangrove expansion may alter rates of mineralization and assimilation in adjacent seagrasses through intertidal sequestration or outwelling of terrestrial-derived material (Fulweiler et al. 2013), possibly resulting in changes to plant productivity, radial oxygen loss, and sediment nitrification rates (Eyre et al. 2013a, b). Substantial changes in nutrient loading may also indirectly impact faunal communities. Nutrient loads can impact seagrass productivity, density, and species assemblage, all of which can change the habitat function (Terrados et al. 1999; Pérez et al. 2007; Ruiz-Halpern et al. 2008; Han et al. 2017). Furthermore, high nutrient loads are associated with high epiphyte cover, which is an important food source for many small invertebrates (Gil et al. 2006). Additionally, while seagrasses support a higher density and diversity of fishes and invertebrates than mangroves and salt marshes (approximately 5 and 108× higher densities, respectively; Bloomfield and Gillanders 2005), many of those fish species use both intertidal and subtidal habitats depending on the tide. Thus, changes in intertidal fish communities could alter faunal density or community composition of seagrass meadows. Large faunal community differences could alter grazing rates, with the potential to affect seagrass species composition, as *Syringodium filiforme* and *Halodule wrightii* are more palatable than *T. testudinum* (Armitage and Fourqurean 2006; Prado and Heck 2011).

In this study, we investigate differences in seagrass meadows adjacent to salt marshes, mangroves, and a mixture of the two. Previous studies exploring implications associated with the formation of the mangrove-salt marsh ecotone focus on the intertidal zone (Stevens et al. 2006; Perry and Mendelssohn 2009; Cavanaugh et al. 2013; Yando et al. 2016; Simpson et al. 2017). However, to our knowledge, the impact of these changes on adjacent subtidal seagrass meadows remains unclear. We use seasonal surveys and sediment flux incubations to document differences in seagrass meadow form and function as related to adjacent intertidal plant community and hypothesize that (1) environmental conditions; (2) biogeochemical cycling; (3) cover, biomass, and productivity; and (4) invertebrate community assemblage will vary in seagrass meadows adjacent to mangroves, salt marshes, and a mixture of the two.

Methods

Site Description

The study sites are located near Cedar Key, Florida, USA (25° 05' 49" N, 83° 03' 58" W); an estuarine system, in the northern

Gulf of Mexico. The system is dominated by mixed siliciclastic-carbonate sediments (Wright et al. 2005) (Fig. 1), and experiences seasonal changes from warm summers (24 to 30 °C) to cooler winters (12 to 22 °C). Cedar Key is representative of the larger region, with high abundances of salt marsh and seagrass habitats, and expanding mangrove distributions. In the 1980s, freezes (i.e., air temperatures below -6.3 and -7.6 °C, Osland et al. 2017) caused mangroves to regularly die-off, allowing the historically dominant intertidal marsh species, *Spartina alterniflora*, to dominate the area. However, the last few decades of mild winters have allowed mangrove survival and expansion—predominantly *Avicennia germinans*, and *Rhizophora mangle* to a lesser extent (Stevens et al. 2006; Purtlebaugh et al. 2020). Seagrass meadows are common in the shallow subtidal. *T. testudinum* is the most common seagrass species; however, *S. filiforme* and *H. wrightii* are also present. The intertidal plant communities experience frequent flooding in this region (Sweet et al. 2018), as the tidal amplitude ranges about 0.86 m (NOAA 2019).

We chose 3 replicate sites in the subtidal *T. testudinum* dominated seagrass beds adjacent to mangroves, salt marshes, or an ecotone—a mixture of the two plant types (referred to as intertidal habitats). Sites were placed within continuous seagrass at least 5 m from the edge. At these sites, mudflat often occurs between the intertidal and the seagrass meadow, and sites had varying distances from the shoreline. To ensure that hydrology did not co-vary with intertidal habitat, we measured distance from shore, water depth, and exposure direction (N, S, E, W), and used an ANOVA to show that these metrics did not vary systematically. We also quantified plant species composition in each intertidal habitat by taking oblique photos at each site approximately 5 m away from the shoreline, and estimated percent cover (%) ($n = 3$) with quadrats randomly drawn on the image.

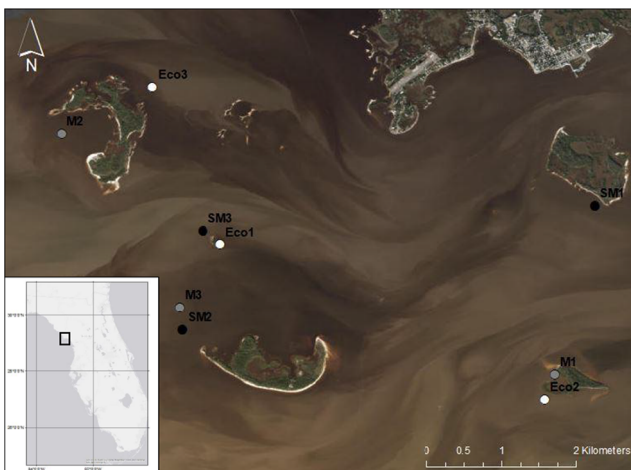


Fig. 1 Map of sampling sites in Cedar Key, FL. There are three sites for each of the adjacent intertidal habitats—ecotone (Eco), mangrove (M), and salt marsh (SM)

Environmental Conditions

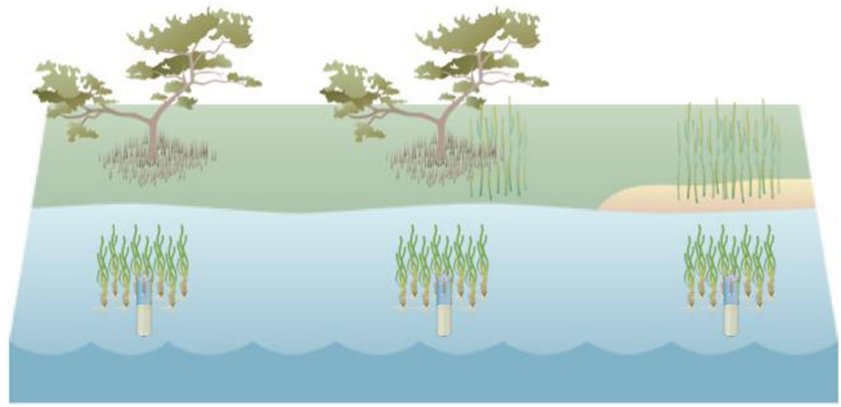
From 2018 to 2019, we collected water chemistry and sediment samples in the adjacent subtidal seagrass meadow of each site a total of 5 times (once in each season, with summer sampled twice). For each sampling event, at each site, 3 replicate samples were collected at each site for a total of 27 samples. We measured water depth (m), dissolved oxygen (DO) (mg L^{-1} and % saturation), salinity (ppt), and temperature (°C) using a YSI Pro DSS data logger and attached probes. On each sampling date, we collected sediment cores—1 cm diameter by 5 cm depth ($n = 3$). Sediments were homogenized and analyzed for organic matter using the loss on ignition method (Heiri et al. 2001). Water and sediment nutrient content were measured 2 times over the sampling year in the summer and spring (to represent the end and beginning of the *T. testudinum* growing season). We collected 50-mL water samples ($n = 3$) to analyze NO_x (nitrate + nitrite) using the automated cadmium reduction method via Bran + Luebbe Auto Analyzer 3 (MDL = 0.010 mg L^{-1}). Sediment samples (bulk, not acidified) were analyzed for carbon (TC) and nitrogen (TN) content using a CE-Elantech Flash EA 1112 Nitrogen and Carbon Analyzer. Separate homogenized cores (1 cm diameter by 5 cm depth) were used to calculate bulk density.

Biogeochemical Cycling

On 2 October 2018 (summer, water temperature 29.6 °C (0.35 SE)) and 5 April 2019 (spring, water temperature 20.6 °C (0.09 SE)), we used sediment core incubations to quantify net oxygen (O_2) and nitrogen (N_2) fluxes across the sediment-water interface (Fig. 2). We extracted one core (9.5 cm diameter by 10 cm depth) from each site ($n = 3$ for each adjacent intertidal habitat). The sampling dates were chosen to represent the end and beginning of *T. testudinum* growing season. All cores contained intact *T. testudinum* above and belowground biomass.

We set up two water baths with five cores in each, containing 95 L of aerated water. Incubations were conducted indoors in dark conditions underneath fluorescent lights. Rotating magnets were placed inside each core, and cores were acclimated for 45 min before they were sealed with a gas tight lid fitted with two ports. One port acted as an outlet and one was connected to the replacement water line. Using a syringe, we removed 15 mL of overlying water from each core at 30-min intervals over 2 h in October, and 45-min intervals over 4.5 h in April. In October, while we measured linear change, the decrease in DO was less than the 2 mg L^{-1} , so we increased the incubation time in April to ensure this recommendation was met (Fulweiler and Nixon 2012). Samples were preserved with 100 μL of saturated zinc chloride and stored in

Fig. 2 Conceptual model demonstrating sampling method within seagrass meadows in relation to their adjacent intertidal habitats—left to right is shown mangrove, ecotone, and salt marsh. Figure created using University of Maryland’s Integration and Application Network images



submerged exetainers below ambient temperature until N_2 , O_2 , and Argon (Ar) analysis.

We analyzed $O_2:Ar$ and $N_2:Ar$ ratios on water samples using a membrane inlet mass spectrometer (MIMS). Coefficients of variation for $O_2:Ar$ and $N_2:Ar$ were 0.10% and 0.06%, respectively. Fluxes were calculated as $\frac{\Delta C}{\Delta t} * \frac{V}{A}$, where $\frac{\Delta C}{\Delta t}$ is the slope of the concentration change in the overlying water over time, V is the volume of the overlying water, and A is the core surface area (flux units = $\mu\text{mol m}^{-2} \text{h}^{-1}$). We only used data from samples where DO concentration was greater than 2 mg L^{-1} (above anoxic conditions). Fluxes were calculated only if the change in time occurs in a linear manner ($R^2 > 0.65$) (Fulweiler et al. 2010).

After the incubation, live plant biomass, invertebrates, and sediment were removed and taken back to the laboratory for further analysis. Total seagrass biomass (g) was dried to a constant weight ($60 \text{ }^\circ\text{C}$ for at least 48 h), and then weighed. We separated and counted all invertebrates in each core (in April only) as potential covariates. A subsample of sediment was also collected from each core and stored frozen at $-20 \text{ }^\circ\text{C}$ for organic matter content analysis as described above.

Seagrass Cover, Biomass, and Productivity

To observe potential intertidally driven changes in seagrass structure and function, we conducted seagrass surveys at each established sampling location seasonally, with August and September 2018 representing the summer, November 2018 for the fall, January 2019 for the winter, and April 2019 for the spring. The additional September summer survey was conducted to determine variability within a season. If September was not different from August, then data were considered one sampling event. Data were combined for all parameters except sediment organic matter and infauna. For our sampling events, we sampled on a rising tide and sites were sampled in an order that was not biased towards one adjacent intertidal habitat type.

At each site, we estimated percent cover and species composition in haphazardly placed 1-m^2 quadrats ($n = 3$). We used 15 cm diameter by 15 cm depth cores ($n = 3$) to estimate plant biomass. In the laboratory, live above and belowground tissue for each species present was separated from each core. Tissue was dried to a constant weight ($60 \text{ }^\circ\text{C}$ for at least 48 h), weighed, and ground to analyze TC and TN concentrations using a CE-Elantech Flash EA 1112 Nitrogen and Carbon Analyzer. Biomass per core parameters was converted in units per area (g m^{-2} using the core dimensions).

To quantify leaf growth, on 21 September 2018 and 17 April 2019 (representing the end and beginning of the growing season), every shoot present in a haphazardly selected 10 cm by 20 cm quadrat was marked by punching a hole 1 cm above the bundle sheath with a syringe needle, and collected approximately 1 week after punching to measure growth (Zieman and Wetzel 1980). For each leaf, of each shoot, new and old growth were separated, dried to constant weight ($60 \text{ }^\circ\text{C}$ for at least 48 h), and weighed (g). Productivity was calculated as new growth ($\text{g m}^{-2} \text{d}^{-1}$) and nitrogen assimilation (new growth * TN (%)) ($\text{gN m}^{-2} \text{d}^{-1}$).

Invertebrate Community Assemblage

Seasonally, we quantified epifauna and infauna density, diversity, and community structure. For epifauna, we placed a 0.5-mm mesh bag over the seagrass and harvested all aboveground material into the bag ($n = 3$) (Reynolds et al. 2014). Infauna was separated from the biomass cores described above ($n = 3$). Organisms were separated from harvested material, preserved in scintillation vials with ethanol, and identified to species level. Total individual density (i.e., independent of species) and species richness were calculated in units per area (m^{-2}). We also calculate species diversity as Shannon-Wiener’s Index (Shannon 1948)— $H = -\sum p_i \ln p_i$, where p_i is the proportion of i^{th} species.

Statistical Analysis

Statistical analyses were performed using JMP Pro 14.1.0. To determine differences between seasons, a split plot repeated measures analysis was used ($\alpha = 0.05$) for all response variables. Data were square root transformed when necessary to meet assumptions (split plot comparisons). Significant tests were followed with Tukey's pairwise multiple comparison to further determine differences. For datasets with multiple zeros, the interaction between season and adjacent intertidal habitat was removed ($\alpha = 0.01$), to better meet the assumptions of the model (only for *S. filiforme* biomass parameters). To determine differences within seasons between adjacent intertidal habitats, the non-parametric Wilcoxon test was used. Multiple comparisons were made using the non-parametric Steel-Dwass ($\alpha = 0.05$) to determine differences between adjacent intertidal habitats and within seasons for each of the variables measured. We used non-parametric tests as the data was not normally distributed due to the small sample size in each period. In addition, Spearman rank correlations were used to look for correlations between measured parameters. To quantify community assemblages, compositions (Bray-Curtis similarity, square root transformed) were analyzed using a permutational multivariate analysis of variance (PERMANOVA) ($\alpha = 0.05$). Furthermore, to determine contribution of species to Bray-Curtis index, in respect to adjacent intertidal habitat, a similarity percentage analysis (SIMPER) was performed. Community analyses were conducted in Primer-7 (6.1.5) software (Anderson and Walsh 2013; Clarke and Gorley 2015).

Results

Environmental Conditions

Hydrology is an important factor to consider in this region; however, in our study, water depth ($F_{(2,7)} = 0.088$, $P = 0.92$) and distance to shoreline ($X^2 = 0.27$, $P = 0.88$) did not differ between sites (Supplementary Table 1). Direction of exposure also did not vary by adjacent intertidal habitat (Fig. 1). Additionally, sites did not differ in environmental characteristics with adjacent intertidal habitat—temperature ($F_{(2,33)} = 0.52$, $P = 0.60$), DO (mg L^{-1} : $F_{(2,32)} = 0.0098$, $P = 0.99$; %: $F_{(2,33)} = 0.040$, $P = 0.96$), salinity ($F_{(2,7)} = 0.58$, $P = 0.58$), and water column NO_x ($F_{(2,6)} = 0.83$, $P = 0.48$). As expected, temperature ($F_{(3,33)} = 327$, $P < 0.0001$) and DO ($F_{(3,32)} = 11$, $P < 0.0001$) varied with seasons (Table 1). The highest water temperature was in the summer (30.0 ± 0.33 °C), intermediate in the spring (22.9 ± 0.32 °C), and lowest in the fall (15.9 ± 0.48 °C) and the winter (15.3 ± 0.18 °C). DO was the highest

in the fall (10.8 ± 0.59 mg L^{-1}), intermediate in winter (8.04 ± 0.07 mg L^{-1}) and spring (8.36 ± 0.45 mg L^{-1}), and lowest in the summer (6.72 ± 0.46 mg L^{-1}).

Sediment organic matter (SOM) varied seasonally ($F_{(4,24)} = 7.7$, $P = 0.0004$) and by adjacent intertidal treatment ($X^2 = 7.2$, $P = 0.027$), ranging from 2.67 to 5.48%. SOM was the lowest in August ($3.11 \pm 0.23\%$) and increased over the winter with the highest values in the spring ($4.50 \pm 0.29\%$) (Fig. 3). There was an interaction between sampling event and adjacent intertidal habitat ($F_{(8,24)} = 2.4$, $P = 0.048$). In the spring, meadows adjacent to the ecotone had the highest SOM content ($5.48 \pm 0.50\%$) and meadows adjacent to mangroves had the lowest ($3.38 \pm 0.47\%$) ($X^2 = 7.2$, $P = 0.027$); while in the winter, there were no differences ($X^2 = 0.60$, $P = 0.74$). Sediment C:N did not differ seasonally ($F_{(1,6)} = 1.3$, $P = 0.30$); however, C:N did vary with adjacent intertidal habitat. In the summer, seagrass sediment C:N adjacent to the ecotone (15.7 ± 0.38) was higher compared to adjacent mangroves (14.0 ± 0.40) and salt marshes (14.1 ± 0.51) ($X^2 = 6.4$, $P = 0.042$), while there were no differences between adjacent intertidal habitats in the spring ($X^2 = 3.3$; $P = 0.19$) (Fig. 4a). Bulk sediment TC and TN were tightly, positively correlated with sediment organic matter ($n = 54$; $\rho = 0.82$; $P < 0.0001$ and $n = 54$; $\rho = 0.78$; $P < 0.0001$, respectively) (Supplementary Fig. 1).

Biogeochemical Cycling

As expected, temperature varied between summer and spring incubations. Summer had higher water temperatures ($X^2 = 14$, $P = 0.0002$) (summer = 29.6 ± 0.35 and spring = 20.6 ± 0.09 °C) and higher DO ($X^2 = 3.9$, $P = 0.049$) (summer = 131 ± 10.2 and spring = $98 \pm 1.12\%$) (Supplementary Table 2).

Net O_2 fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) varied by season, but not by adjacent intertidal habitat ($F_{(2,12)} = 0.29$, $P = 0.76$) (Table 2 and Supplementary Table 3). All cores yielded negative net fluxes, indicating an oxygen demand by the sediments (e.g., decomposition of organic matter); but demand was greater in the summer (-5066 ± 313 $\mu\text{mol m}^{-2} \text{h}^{-1}$) than the spring (-2217 ± 244 $\mu\text{mol m}^{-2} \text{h}^{-1}$) ($F_{(1,12)} = 23$, $P = 0.0004$).

Net N_2 fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) varied by season ($F_{(1,12)} = 10$, $P = 0.0077$) (Fig. 5), but not by adjacent intertidal habitat ($F_{(2,12)} = 2.1$, $P = 0.16$) (Supplementary Table 3). In the summer, on average across all adjacent intertidal habitats, the net N_2 flux was negative (indicating net fixation in excess of denitrification) (-184 ± 101 $\mu\text{mol m}^{-2} \text{h}^{-1}$), while in the spring, the mean net flux across all adjacent intertidal habitats was positive (indicating denitrification in excess of nitrogen fixation) (123 ± 28.8 $\mu\text{mol m}^{-2} \text{h}^{-1}$) (Table 2); however, meadows adjacent to mangroves were always net denitrifying (summer = 170 ± 33.3 and spring = 57.8 ± 28.0 $\mu\text{mol m}^{-2} \text{h}^{-1}$). Net N_2 fluxes interactively varied as a

Table 1 Seasonal water chemistry parameters measured, mean \pm standard error

Season	Salinity (ppt)	Temperature ($^{\circ}$ C)	DO (mg/L)	DO (%)	NO _x (mg L ⁻¹)
Summer	27.06 \pm 0.48	30.04 \pm 0.33	6.72 \pm 0.46	101.37 \pm 7.82	0.008 \pm 0.0002
Fall	25.72 \pm 0.38	15.88 \pm 0.48	10.81 \pm 0.59	128.42 \pm 8.09	–
Winter	27.85 \pm 0.48	15.34 \pm 0.18	8.04 \pm 0.07	95.22 \pm 1.13	–
Spring	27.29 \pm 0.32	22.88 \pm 0.32	8.36 \pm 0.45	113.74 \pm 6.78	0.010 \pm 0.001

function of both season and adjacent intertidal habitat ($F_{(1,12)} = 6.4$, $P = 0.013$) (Fig. 5). Seagrasses adjacent to marshes and the ecotone changed from net fixing to net denitrifying, with a net difference of 857 ($F_{(1,10)} = 15$, $P = 0.003$) and 177 $\mu\text{mol m}^{-2} \text{h}^{-1}$ ($F_{(1,10)} = 17$, $P = 0.002$) respectively, while seagrass sediments adjacent to mangroves were net denitrifying in both seasons and decreased by only 112 $\mu\text{mol m}^{-2} \text{h}^{-1}$ ($F_{(1,10)} = 6.7$, $P = 0.027$).

As expected, total biomass (g) in the cores was higher in the summer (3.04 ± 0.25 g) than the spring (2.01 ± 0.24 g) ($F_{(1,6)} = 9.5$, $P = 0.022$) (Table 2), but biomass per core did not differ between adjacent intertidal habitats ($F_{(2,6)} = 0.59$, $P = 0.58$). Over both seasons, there was a negative relationship between total biomass and net O₂ flux ($n = 18$; $\rho = -0.61$; $P = 0.0077$) (Supplementary Fig. 2); however, there was no relationship between total biomass and net N₂ flux ($n = 18$; $\rho = -0.0093$; $P = 0.97$). Invertebrate total abundance did not differ between adjacent intertidal habitats ($X^2 = 2.8$, $P = 0.25$), and there was a negative correlation between individual abundance and net O₂ flux (only in the spring) ($n = 9$; $\rho = -0.73$; $P = 0.025$) (Supplementary Fig. 3). There was no relationship between invertebrate density and net N₂ flux ($n = 9$; $\rho = 0.45$; $P = 0.22$).

Seagrass Cover, Biomass, and Productivity

Seagrass cover and biomass varied seasonally (Fig. 6). Percent cover ($F_{(3,27)} = 35$, $P < 0.0001$) and aboveground biomass

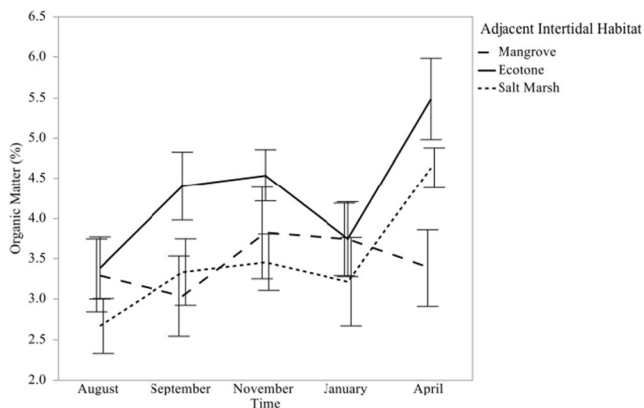


Fig. 3 Percent organic matter (%) for each sampling event, in seagrass meadows adjacent to their respective intertidal habitat, with error bars representing standard error

($F_{(3,27)} = 52$, $P < 0.0001$) were the highest in the summer ($66.8 \pm 3.24\%$ and 15.5 ± 1.07 g m⁻², respectively), intermediate in the fall ($31.5 \pm 2.61\%$ and 6.56 ± 0.40 g m⁻², respectively) and spring ($28.9 \pm 3.15\%$ and 8.68 ± 0.60 g m⁻², respectively), and lowest in the winter ($16.3 \pm 2.40\%$ and 3.85 ± 0.36 g m⁻², respectively). However, belowground biomass (g m⁻²) did not vary by season ($F_{(3,27)} = 0.59$, $P = 0.63$).

Seagrass cover and biomass also varied by adjacent intertidal habitat. *T. testudinum* percent cover was the highest adjacent to the ecotone ($53 \pm 3.85\%$ averaged across seasons), intermediate adjacent to salt marshes ($37.9 \pm 3.47\%$ averaged across seasons), and lowest adjacent to mangroves ($35 \pm 4.66\%$ averaged across seasons) ($F_{(2,7)} = 7.0$, $P = 0.023$) (Fig. 6a). Aboveground and belowground biomass varied with adjacent intertidal habitat, but only in some seasons. In the fall and winter, aboveground biomass was highest adjacent to salt marshes (7.80 ± 0.65 and 4.94 ± 0.65 g m⁻²) ($X^2 = 7.8$, $P = 0.021$ and $X^2 = 6.7$, $P = 0.034$, respectively), while belowground biomass was highest adjacent to the ecotone (41.7 ± 3.89 and 41.1 ± 4.86 g m⁻²) ($X^2 = 9.6$, $P = 0.0084$ and $X^2 = 7.2$, $P = 0.027$, respectively). Biomass was always the lowest adjacent to mangroves (aboveground = 4.90 and 2.59 g m⁻² (Fig. 6b), belowground = 23.1 and 21.6 g m⁻² (Fig. 6c)). Seagrass biomass also correlated with sediment characteristics, as belowground biomass was positively correlated with sediment C:N ($n = 54$; $\rho = 0.39$; $P = 0.0033$) (Supplementary Fig. 4); however, aboveground biomass was not ($n = 54$; $\rho = 0.060$; $P = 0.67$).

Thalassia testudinum primary productivity, estimated as new growth (g m⁻² d⁻¹) ($F_{(1,6)} = 13$, $P = 0.011$) varied seasonally, and was higher in the summer (0.17 ± 0.02 g m⁻² d⁻¹) than in the spring (0.09 ± 0.01 g m⁻² d⁻¹) (Fig. 7). Nitrogen assimilation (gTN m⁻² d⁻¹) was marginally different (summer = 0.004 ± 0.0004 and spring = 0.003 ± 0.0002 gTN m⁻² d⁻¹) ($F_{(1,6)} = 5.4$, $P = 0.061$). Both new growth ($F_{(2,6)} = 0.058$, $P = 0.94$) and nitrogen assimilation ($F_{(2,6)} = 0.042$, $P = 0.96$) did not differ by adjacent intertidal habitat.

Syringdoium filiforme, another common seagrass species found in the northern Gulf of Mexico, was also identified in biomass cores. Relative contribution was variable and always lower than *T. testudinum*. Mean contribution was 9.2%, and maximum contribution was 47.7% between sites. Results

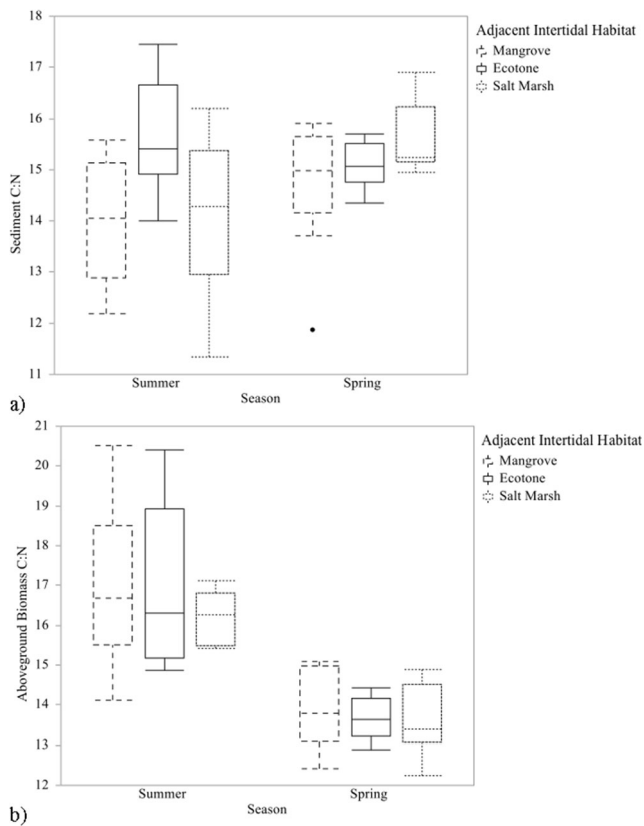


Fig. 4 a Sediment and b *T. testudinum* aboveground biomass C:N ratio in the summer and spring, in seagrass meadows adjacent to their respective intertidal habitat, with error bars representing standard error

show no patterns with season, adjacent intertidal habitat, or interactions (Supplementary Table 4).

Thalassia testudinum aboveground C:N ratio was greater in the summer ($16.7 \pm 0.32 \text{ g m}^{-2}$) than the spring ($13.8 \pm 0.15 \text{ g m}^{-2}$) ($F_{(1,6)} = 39, P = 0.0008$) (Fig. 4b), but did not differ between adjacent intertidal habitats ($F_{(2,6)} = 0.060, P = 0.94$). Additionally, *T. testudinum* aboveground tissue C:N was negatively correlated with SOM (%) and with sediment C:N ($n = 54; \rho = -0.40; P = 0.0025$ and $n = 54; \rho = -0.32; P = 0.021$, respectively) (Supplementary Fig. 5 and 6).

Invertebrate Community Assemblage

Epifauna density, species richness, and species diversity varied seasonally. Total individual density (m^{-2}) ($F_{(3,27)} = 13,$

$P < 0.0001$), richness (m^{-2}) ($F_{(3,27)} = 25, P < 0.0001$), and diversity (H') ($F_{(3,27)} = 3.0, P = 0.049$) were the greatest in the spring ($493 \pm 104 \text{ m}^{-2}, 126 \pm 12.2 \text{ m}^{-2},$ and 2.03 ± 0.07), intermediate in the winter ($360 \pm 57.5 \text{ m}^{-2}, 99.4 \pm 12.1 \text{ m}^{-2},$ and 1.68 ± 0.08) and fall ($265 \pm 61.2 \text{ m}^{-2}, 80.3 \pm 11.1 \text{ m}^{-2},$ and 1.70 ± 0.08), and lowest in the summer ($85.2 \pm 13.3 \text{ m}^{-2}, 30.1 \pm 3.35 \text{ m}^{-2},$ and 1.66 ± 0.07) (Table 3). PERMANOVA analysis indicated that epifauna community assemblage differed by season ($F_{(3,123)} = 10, P = 0.001$). SIMPER analysis showed that *Mitrella lunata*, *Ampithoe longimana*, and *Palaeomonetes pugio* were the primary drivers in each sample, but the relative contribution changed with season (Supplementary Table 5). The largest average dissimilarity was between the summer and winter (76.6%) ($P = 0.001$), and the smallest between the winter and spring (63.7%) ($P = 0.001$).

Adjacent intertidal habitat only explained variation in epifauna density in the summer. Meadows adjacent to the ecotone had the greatest total individual density ($117 \pm 25.5 \text{ m}^{-2}$), adjacent to mangroves were intermediate ($97.8 \pm 27.8 \text{ m}^{-2}$), and adjacent to salt marshes were lowest ($41.2 \pm 6.68 \text{ m}^{-2}$) ($X^2 = 7.5, P = 0.023$) (Supplementary Table 6). PERMANOVA analysis indicated that epifauna community assemblage differed by adjacent intertidal habitat ($F_{(3,123)} = 2.4, P = 0.001$), and there was no interaction between season and adjacent intertidal habitat ($F_{(6,123)} = 1.1, P = 0.20$). SIMPER analysis also showed that epifauna community composition varied by adjacent intertidal habitat driven by *A. longimana*, *M. lunata*, *Clibanarius vittatus*, *P. pugio*, and *Nassarius vibex*, but relative contribution changed (Table 4). The smallest dissimilarity in epifauna assemblage was between meadows adjacent to salt marshes and mangroves (73.5%) ($P = 0.07$), while dissimilarities were greater between the ecotone with marshes ($P = 0.001$) and mangroves ($P = 0.01$).

Infauna total individual density (m^{-2}) ($F_{(4,24)} = 51, P < 0.0001$), species richness (m^{-2}) ($F_{(4,24)} = 37, P < 0.0001$), and species diversity (H') ($F_{(4,24)} = 15, P < 0.0001$) were the greatest in the spring ($296 \pm 23.6 \text{ m}^{-2}, 105 \pm 5.49 \text{ m}^{-2},$ and 1.94 ± 0.06), intermediate in the winter ($133 \pm 6.49 \text{ m}^{-2}, 80.0 \pm 4.10 \text{ m}^{-2},$ and 1.96 ± 0.06), and lowest in the fall ($89.8 \pm 8.49 \text{ m}^{-2}, 56.3 \pm 4.11 \text{ m}^{-2},$ and 1.61 ± 0.09) and summer months (August = $55.2 \pm 6.31 \text{ m}^{-2}, 40.2 \pm 3.58 \text{ m}^{-2},$ and 1.25 ± 0.11 , and September = $79.7 \pm 5.64 \text{ m}^{-2}, 52.4 \pm$

Table 2 Summer and spring total seagrass biomass (g), net oxygen (O_2), and nitrogen (N_2) fluxes measured for sediment flux incubations, mean \pm standard error

Season	Total biomass (g)	DO flux ($\mu\text{mol m}^{-2} \text{ h}^{-1}$)	N_2 flux ($\mu\text{mol m}^{-2} \text{ h}^{-1}$)
Summer	3.04 ± 0.25	-5066.23 ± 313.58	-184.33 ± 101.6
Spring	2.01 ± 0.24	-2217.93 ± 244.64	123.06 ± 28.8

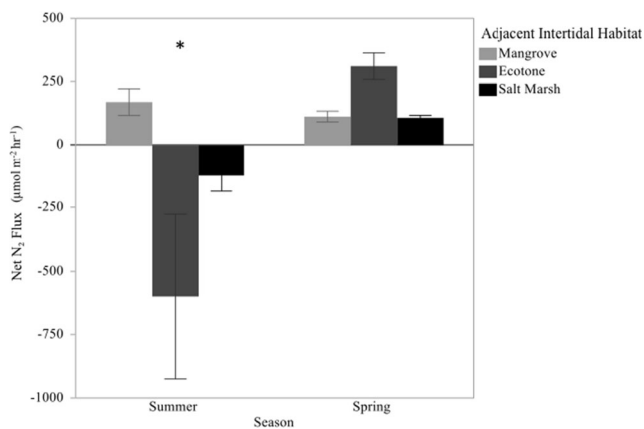


Fig. 5 Net dinitrogen fluxes (N_2) measured in the summer and spring in seagrass meadows adjacent to their respective intertidal habitat, with error bars representing standard error. Asterisk indicates interaction between season and habitat type ($\alpha < 0.05$)

4.01 m^{-2} , and 1.54 ± 0.11) (Table 3). PERMANOVA analysis indicated that there were differences between sampling periods ($F_{(4,120)} = 8.4$, $P = 0.001$). SIMPER analysis shows that infauna community composition varied between the months sampled, except for September and fall, in which differences were driven by the primary contributors *N. vibex*, *Ampelisca abdita*, and *Microphiopholis atra*, but relative contribution changed with season (Supplementary Table 7), with the largest dissimilarity being between August (summer) and the spring (87.9%) ($P = 0.001$), and the smallest being between September (summer) and the fall (67.8%) ($P = 0.26$).

Infauna differed by adjacent intertidal habitat only in the spring, where species diversity (H') was the greatest in meadows adjacent to salt marshes (2.13 ± 0.08), intermediate to mangroves (1.94 ± 0.10), and lowest to the ecotone (1.76 ± 0.10) ($X^2 = 6.7$, $P = 0.034$) (Supplementary Table 8). PERMANOVA and SIMPER analysis showed no differences in infauna community composition among meadows driven by adjacent intertidal habitats or an interaction ($F_{(2,120)} = 1.5$, $P = 0.06$ and $F_{(8,120)} = 1.0$, $P = 0.37$, respectively).

Discussion

Seagrass meadow environment (SOM); biogeochemical cycling (N_2 and O_2 fluxes); plant cover, standing biomass, and productivity; and invertebrate community (density, diversity, and assemblage) differed with adjacent intertidal habitat (mangroves, salt marshes, or ecotone). Importantly, the magnitude and direction of those differences varied seasonally. Other studies have linked seagrass form and function to impacts from adjacent intertidal habitat (Nagelkerken et al. 2001; Valiela and Cole 2002; Mishra and Apte 2020), and it is logical that a shift in intertidal function with mangrove encroachment could drive these changes. Although we did not directly measure it, the seasonality suggests that outwelling

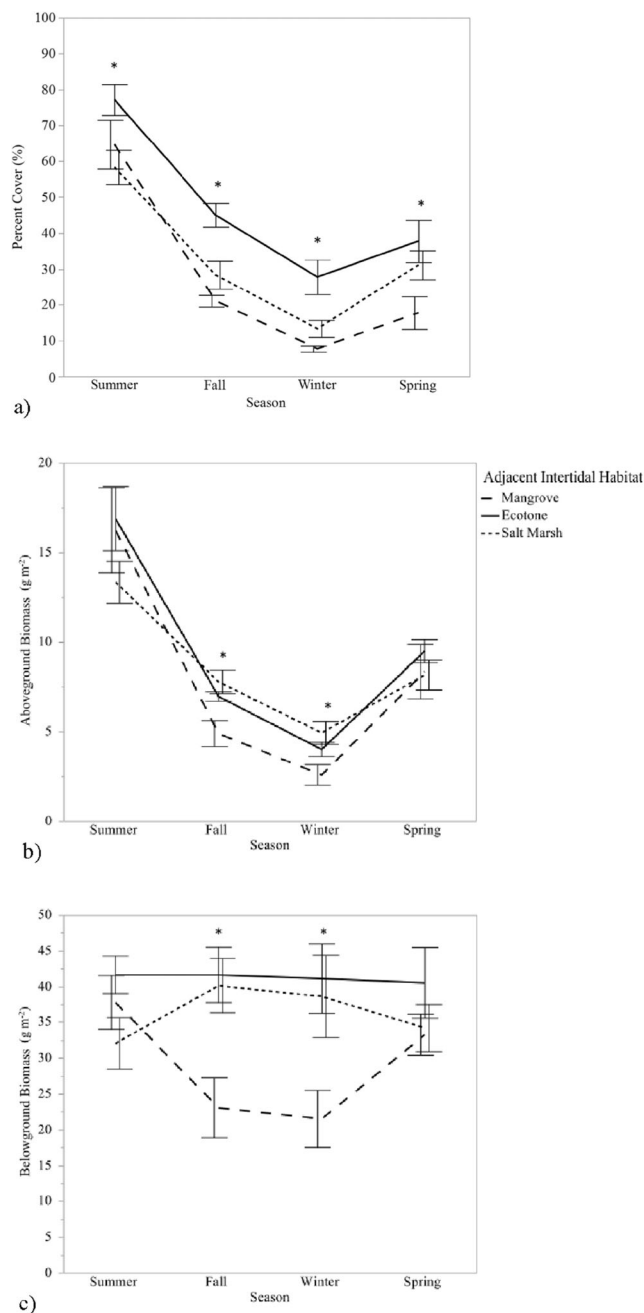


Fig. 6 *Thalassia testudinum* biomass parameters throughout the year. **a** Percent cover (%), **b** aboveground biomass (g m^{-2}), and **c** belowground biomass (g m^{-2}), for their respective adjacent intertidal habitat, with error bars representing standard error. Asterisk indicates differences between intertidal habitat type within seasons (fall and winter) ($\alpha < 0.05$)

differences between mangroves and salt marshes may have driven the changes we observed in seagrass meadows. In the northern Gulf of Mexico, the timing of peak outwelling is expected to differ—mangroves senesce in September (Twilley et al. 1986; Dawes et al. 1999; Aké-Castillo et al. 2006), while salt marsh grass senesce in January (Kirby and Gosselink 1976; Lana et al. 1991; Pezeshki and DeLaune 1991; Darby and Turner 2008). That timing of organic matter

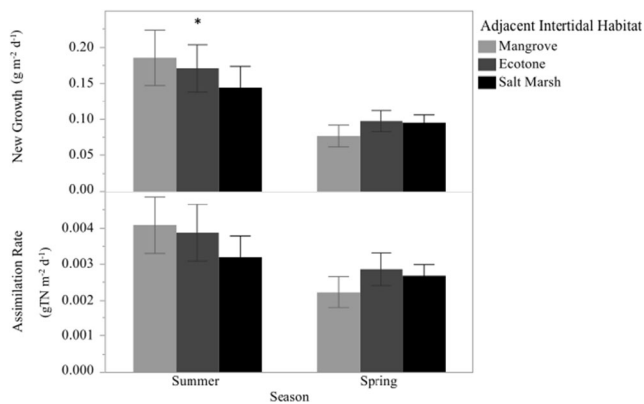


Fig. 7 New growth ($\text{g m}^{-2} \text{d}^{-1}$) and assimilation rate ($\text{gTN m}^{-2} \text{d}^{-1}$) measured for *T. testudinum* in the summer and spring for their respective adjacent intertidal habitat, with error bars representing standard error. Asterisk indicates difference between summer and spring ($\alpha < 0.05$)

delivery would explain our observed differences in SOM and gas fluxes. Meadows adjacent to mangroves and the ecotone had higher net denitrification (positive net N_2 flux) rates, in the summer and spring, respectively, when organic matter delivery was the highest. Seagrass biomass also changed with intertidal plant community, as meadows adjacent to mangroves experienced a dramatic decrease in belowground biomass in the winter, while adjacent to marshes and the ecotone stayed consistent. Additionally, although epifauna density and diversity did not vary among adjacent intertidal habitats, meadows experienced subtle differences in community assemblage that may be correlated with adjacent intertidal habitat. Together these results suggest that shifts in intertidal species assemblage can scale-up and impact key ecosystem functions and services in seagrass meadows.

Environmental Conditions

Water chemistry within seagrass meadows did not vary by adjacent intertidal habitat; however, we observed a strong difference in SOM, which is a potential driver of our observed differences in net N_2 and O_2 fluxes. Mangroves senesce

around September, and we observed an overall increase in SOM in seagrass meadows adjacent to mangroves from September to January, while meadows adjacent to the other two intertidal habitats showed a decrease in SOM (Fig. 3). Conversely, sediments in meadows adjacent to marshes and the ecotone increased in SOM from January to April, after salt marsh senesce. Concomitantly, we observed a decrease in meadows adjacent to mangroves. These results coincide with literature, from the Gulf of Mexico, documenting variability in porewater nutrient concentrations between marshes, mangroves, and the ecotone (Patterson and Mendelssohn 1991). The marshes and ecotone porewater nutrient concentrations peaked in early spring and declined late in the summer, while porewater nutrients in mangroves peaked in late summer and declined in early spring (Patterson and Mendelssohn 1991).

Other environmental factors, for example, hydrodynamic characteristics (e.g., tidal fluctuations and wave exposure), not measured as part of this study, may also explain our observed results. High wave action can impact organic matter delivery, nutrient concentrations and fluxes, the depth of the aerobic-anaerobic interface, and light availability (Koch and Gust 1999). More specifically, high energy can result in mixing, altering water column and sediment dissolved oxygen levels. These influences to organic matter and dissolved oxygen levels can scale-up to affect denitrification rates, biomass, plant growth, and faunal community assemblages, which result in consequences for altering key ecosystem functions observed in this study. However, our sites did not systematically vary in direction of exposure (a proxy for wave exposure) or water depth.

Nitrogen Cycling

In estuarine systems, habitat connectivity has been shown to be an influential driver in denitrification rates through organic matter subsidies (Smyth et al. 2015). Subsidies, in the form of senesced biomass, can stimulate denitrification by providing a source of nitrogen and labile carbon, in the form of organic matter, to denitrifying microbes in sediment (McMillan et al.

Table 3 Seasonal epifaunal and infaunal assemblage parameters in seagrass meadows, mean \pm standard error

Faunal group	Season	Individual density (m^{-2})	Species richness (m^{-2})	Species diversity (H')
Epifauna	Summer	85.21 \pm 13.28	30.10 \pm 3.35	1.66 \pm 0.07
	Fall	264.99 \pm 61.21	80.29 \pm 11.07	1.70 \pm 0.08
	Winter	359.97 \pm 57.53	99.41 \pm 12.09	1.68 \pm 0.08
	Spring	492.63 \pm 103.82	125.63 \pm 12.18	2.03 \pm 0.07
Infauna	August	55.21 \pm 6.31	40.18 \pm 3.58	1.25 \pm 0.11
	September	79.66 \pm 5.64	52.41 \pm 4.01	1.54 \pm 0.11
	Fall	89.80 \pm 8.49	56.25 \pm 4.11	1.61 \pm 0.09
	Winter	133.47 \pm 6.49	80.01 \pm 4.10	1.96 \pm 0.06
	Spring	295.60 \pm 23.60	104.47 \pm 5.49	1.94 \pm 0.06

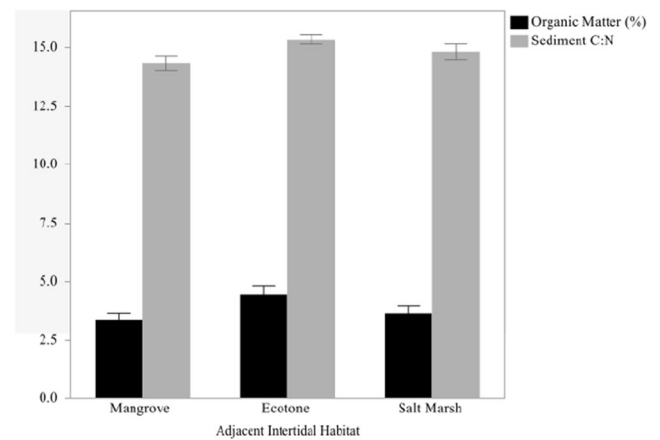
Table 4 Top epifaunal species drivers in seagrass meadows adjacent to their respective intertidal habitat, with contribution (%)

Adjacent intertidal habitat	Species	Contribution (%)
Mangrove	<i>Ampithoe longimana</i>	34.12
	<i>Mitrella lunata</i>	18.04
	<i>Clibanarius vittatus</i>	8.13
	<i>Palaeomonetes pugio</i>	7.60
	<i>Pagurus longicarpus</i>	5.18
Ecotone	<i>Ampithoe longimana</i>	25.99
	<i>Mitrella lunata</i>	22.11
	<i>Palaeomonetes pugio</i>	11.32
	<i>Clibanarius vittatus</i>	7.03
	<i>Nassarius vibex</i>	6.07
Salt Marsh	<i>Ampithoe longimana</i>	36.17
	<i>Mitrella lunata</i>	17.84
	<i>Nassarius vibex</i>	9.38
	<i>Clibanarius vittatus</i>	5.94
	<i>Palaeomonetes pugio</i>	4.97

2010; Smyth et al. 2015). Likewise, the timing of senescence and subsequent outwelling of nutrients and organic matter can be a controlling factor in net N_2 fluxes (Fulweiler et al. 2013).

Net N_2 fluxes in the seagrass meadows studied here varied between summer and spring, and outwelling from the adjacent intertidal habitat may explain these seasonal differences. In October, just a month after expected mangrove senescence (Twilley et al. 1986; Dawes et al. 1999; Aké-Castillo et al. 2006), positive net N_2 flux and increases in oxygen demand were observed adjacent to mangroves (Supplementary Table 3). In April, a few months after *Spartina* senescence (Kirby and Gosselink 1976; Lana et al. 1991; Pezeshki and DeLaune 1991; Darby and Turner 2008), positive net N_2 flux and oxygen demands were greatest in meadows adjacent to the ecotone (Supplementary Table 3). The increase in oxygen demand suggests active organic matter mineralization and increased organic quality (Piehler and Smyth 2011; Eyre et al. 2013a, likely supported by senesced biomass from the adjacent intertidal habitat.

Our seagrass sediment data show differences in organic matter quantity and quality between adjacent intertidal habitats. Meadows adjacent to marshes and ecotones had higher SOM quantity, overall, but had lower quality (evidenced by higher sediment C:N), while meadows adjacent to mangroves had lower SOM quantity, but higher quality (evidenced by lower sediment C:N) (Fig. 8). The quality (C:N ratio, mixture of C:N ratios, and structure of the organic matter) can be more important than quantity in driving denitrification rates, and higher organic matter quality is typically observed in mangroves compared to marshes (Lee 1995; Eyre et al. 2013a; Lewis et al. 2014; Simpson et al. 2020).

**Fig. 8** Relationship between sediment organic matter (%) quantity and quality, in the form of sediment C:N in seagrass meadows adjacent to their respective intertidal habitat

Differences in organic matter delivery, both in terms of quantity (higher SOM) and quality (lower sediment C:N), may be greater than differences observed in this study and are likely to become more dramatic over time. The standing stock of SOM does not accurately represent the recent delivery, since organic matter in these systems can come from a variety of internal and external sources and may have long residence times. We integrated the top 5 cm in our samples, which may include contributions from several years ago, and mangrove encroachment into this region is relatively both recent and incomplete—mangroves have historically been small and patchy along the landscape. In future studies, measuring sediment properties in smaller vertical segments may increase understanding. Furthermore, as mangroves get larger and older, they become more different compared to salt marsh grasses, in terms of biomass and structure (C:N and % woody) (Osland et al. 2012; Kelleway et al. 2016), and therefore seasonal differences in organic matter delivery are likely to increase in magnitude. Applying a chronosequence approach would fill the knowledge gap of long-term impacts of mangrove encroachment on seagrass meadows. While we have anecdotal evidence that over the last few decades in Cedar Key mangroves have expanded and retracted multiple times, there are not enough frequent aerial images to efficiently study this in this region.

In the spring, net N_2 fluxes adjacent to marshes were somewhat unexpected as they did not differ from zero, while seagrass sediments adjacent to ecotones had a positive net flux (Fig. 5). Our results show that meadows adjacent to marshes and the ecotone have the same seasonal fluctuations in SOM; however, we did not observe these patterns in gas fluxes. Marsh grass species can make a difference in retention and nutrient quality as low marsh species tend to decompose faster and are of higher organic matter quality than high marsh species, resulting in differences in leaching of soluble materials related to tidal elevation (Valiela et al. 1985). In the ecotone,

mangrove species are more likely to colonize in the upper intertidal zone and outcompete high marsh species for space and nutrients (Alleman and Hester 2011; Peterson and Bell 2018). We measured fringing marsh species composition and biomass but not upper marsh species. Variation in high marsh species may also influence the quality and quantity of outwelled organic matter.

Although net N_2 fluxes differed between summer and spring (Table 2), we observed the largest variation in meadows adjacent to salt marshes and the ecotone. Meadows adjacent to marshes and the ecotone shifted from net fixing to net denitrifying, from summer to spring, while meadows adjacent to mangroves were always net denitrifying (Fig. 5). Because these systems tend to be connected, a shift in meadows adjacent to marshes and the ecotone may be explained by intertidal outwelling, where marsh biomass senescence in the winter provided labile carbon to meadows, and increased denitrification rates. On the other hand, mangroves senesce in September, which explains net denitrification in the summer, but not in the spring. In the fall and winter, belowground biomass adjacent to mangroves experienced a dramatic decrease (Fig. 6c), while adjacent to marshes and the ecotone stayed consistent, which could explain why net fluxes adjacent to mangroves did not change. There was another nutrient source—internal (decomposing seagrass belowground biomass) rather than external. It is also possible these increased denitrification rates could have been driven by nitrate (Smyth et al. 2015). Although we did not measure it directly or extensively, organic matter availability is mineralized into ammonium, which will then undergo nitrification and increase nitrate concentrations. Through tight nitrification and denitrification coupling, N_2 removal may be maximized (Piehler and Smyth 2011). Furthermore, this study only focused on the beginning and end of the growing season, and therefore it is possible that mangroves are net N_2 fixing in another season not sampled here.

Seagrass Cover, Biomass, and Productivity

Seagrass cover and biomass varied by adjacent intertidal habitat and, like SOM and gas fluxes, the magnitude of the difference varied with season. Seagrass belowground biomass in meadows adjacent to mangroves was reduced in colder months, while roots and rhizome biomass was consistent over seasons adjacent to marshes and the ecotone. In these colder months, *T. testudinum* nitrogen uptake is dominated by the roots and rhizomes, while in the summer and fall, uptake is greater in the leaves (Lee and Dunton 1999). Furthermore, in the early growing season (when salt marsh grasses senesce, and mangroves do not), plants require high nutrient levels and use their belowground storage, which has been depleted over the winter (Lee and Dunton 1999). This may explain the decline in belowground biomass adjacent to mangroves in the

winter since there is a reduction in outwelling of material to the seagrass meadow, while in the late summer and early fall, plants are under less nutrient stress as growth rates are declining; therefore, organic matter delivery from mangrove senescence has less impact on plant growth.

The influence of adjacent intertidal habitat on seagrass biomass was driven by differential shifts in belowground biomass. As expected, aboveground biomass was generally more responsive to seasonal change, while belowground biomass was generally more stable (Kaldy and Dunton 2000), except when seagrass meadows were adjacent to mangroves. The belowground biomass of seagrass meadows adjacent to mangroves decreased by almost half (42.9%) from summer to winter, while an order of magnitude less adjacent to the ecotone (1.4%), and marshes increased by less than half (20.2%) (Fig. 6c). Belowground material contains carbohydrate reserves and loss of these reserves may make seagrasses more vulnerable to stressors in general. Tropical systems with large, mature mangroves have a positive influence on seagrass density, biomass, and productivity through connectivity (Mishra and Apte 2020); however, our system is historically more temperate and mangroves here are patchy both spatially and temporally. The variability caused by colder temperatures, and possible winter freezes, hinders mangrove maturity, and therefore may drive instability in the system.

In this oligotrophic environment, organic matter and nutrient delivery of adjacent intertidal habitats to seagrasses potentially drives seagrass nutrient assimilation and primary productivity. Aboveground biomass C:N and production rates were greater in the summer than the spring, however did not vary among adjacent intertidal habitats (Fig. 4b and 7). Temperatures were much greater in the summer, compared to the spring (Table 1), and therefore seagrasses are assimilating nitrogen at greater rates to sustain higher rates of productivity (Fig. 7). Correlations between SOM, nutrients, and biomass indicate that, with increased organic matter, there will be higher mineralization and nitrification rates, which results in higher assimilation rates to sustain high growth rates (Supplementary Fig. 4–6). In this system, we expect seagrass meadows to respond to nutrient shifts that are potentially influenced by mangrove encroachment.

Invertebrate Community Assemblage

Our results suggest that, although seagrass epifauna community assemblage responded to adjacent intertidal habitat type, seasonality may be a more influential driver of faunal density and diversity. Both epifaunal and infaunal densities, diversities, and assemblage responded to seasonal changes, with the highest densities and diversities observed in the spring (Table 3). These findings are consistent with previous work in Gulf of Mexico *H. wrightii* beds, with invertebrate densities increased from the fall to the spring, peaking in April, and

decreased gradually throughout the summer (Sheridan and Livingston 1983). Here, only epifaunal community assemblage differed by adjacent intertidal habitat.

Our results do show small but distinct differences in epifaunal species assemblage potentially related to indirect effects of adjacent intertidal habitat (Table 4). Previous work in intertidal communities show similar patterns, in which epifaunal community assemblages were driven by intertidal habitat (i.e., mangroves vs. marshes) (Smee et al. 2017; Scheffel et al. 2018). Although literature indicates that intertidal infauna vary between salt marshes and mangroves, those differences may not directly affect subtidal seagrass, because infauna tend to be less mobile than epifauna. Habitat connectivity can drive differences in species composition through migration between habitats (Sheaves 2009). We did not measure larger, more mobile organisms (e.g., fishes), but we expect changes in these organisms may regulate the invertebrate organisms we did measure through predation, as the presence of mangroves in marsh systems alter associated fish biomass and community structure (Caudill 2005; Smee et al. 2017; Scheffel et al. 2018).

Epifauna is more responsive to changes in standing seagrass biomass, while infauna are more dependent on the roots and rhizomes which are not as subjected to change with seasonal and environmental shifts (Tanner 2005). In our study, *T. testudinum* aboveground biomass differed by both adjacent intertidal habitat and seasons, while overall belowground biomass was typically more stable (Fig. 6b, c), as from summer to winter, aboveground biomass (g m^{-2}) experienced an overall decrease by 75.2%, while belowground biomass (g m^{-2}) only decreased by 9.14%. The water column is more dynamic than the sediment as it experiences greater seasonal variability, and therefore has a greater impact on their associated fauna. The variability of the aboveground biomass and water column, possibly influenced by adjacent intertidal habitat, indirectly influenced epifaunal community assemblage. Importantly, adjacent to mangroves, belowground biomass did significantly decline in winter but we did not see equal reductions in infauna density or biomass, maybe because that reduction was short in duration and during a time when predation was low.

Conclusion

Species range expansions, induced by warming temperatures, have a wide range of ecological implications, and those changes may spill over into adjacent, connected habitats. Our results show that seagrass meadows differed with adjacent intertidal plant communities (mangroves, salt marshes, and the ecotone—a mixture of the two habitats), suggesting that mangrove encroachment may drive changes to seagrass meadows. Mangroves are becoming more dominant along

northern Gulf of Mexico shorelines (Osland et al. 2012; Saintilan et al. 2014; Cavanaugh et al. 2019) and are not only changing intertidal characteristics, but, as demonstrated here, also impacting subtidal habitats. Connectivity, specifically through the outwelling influence from the intertidal zone, is a critical component that is often overlooked. We observed changes in subtidal environmental conditions, gas fluxes, seagrass standing biomass, and epifaunal community assemblage that correlate with delivery of organic matter possibly through the outwelling of senesced biomass. Differences in SOM within the seagrass meadows suggest that timing of outwelling, from intertidal senesced biomass, influenced functions provided by meadows. Our results demonstrate that net N_2 fluxes differed between adjacent intertidal habitats, but the magnitude and direction of these fluxes depended on seasonality. Peak denitrification rates (net positive N_2 flux) within meadows coincided with when their respective adjacent intertidal habitat's biomass senesced. Additionally, shifts from net fixing to denitrifying induces changes in nutrient regimes, which influenced seagrass biomass and their associated epifaunal communities.

Our study focused on seagrass meadows adjacent to different intertidal habitats, which meant that our spatial scale was relatively small. Despite this, our results showed differences in seagrasses form and function correlating with adjacent habitat, suggesting the importance of connectivity between the intertidal and subtidal. It is important to note that these differences may amplify on a larger spatial and temporal scale (Valiela and Cole 2002). Conversely, these impacts may be smaller in systems with a lower tidal amplitude, which occur in the northern Gulf of Mexico, where connectivity may be reduced. Likewise, small changes in nutrient availability result in observable changes in this oligotrophic environment. Impacts to system with a different nutrient history may differ in magnitude and direction. Importantly, the shifts we observed impact key ecosystem services—nitrogen cycling (Costanza et al. 1997; Waycott et al. 2009), blue carbon (Pendleton et al. 2012; Lavery et al. 2013), and food and recreation (McArthur and Boland 2006), that have further implications to other nearby habitats and even to coastal residents who rely on these services. Tropicalization, urbanization, and restoration are all changing intertidal habitats (Kennish 2001; Románach et al. 2018; Kelleway et al. 2017; Scheffel et al. 2018), and connectivity can facilitate broad impacts on adjacent systems in these cases, as well.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-020-00879-x>.

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