Seascape structure likely influences marsh-derived resource use by highly abundant estuarine consumers over a small spatial scale

Shelby L. Ziegler[1,4,*], W. Ryan James[2], Merryl Alber[3], James E. Byers[1]

[1]Odum School of Ecology, University of Georgia, Athens, Georgia 30602, USA
[2]Institute of Environment, Florida International University, Miami, Florida 33199, USA
[3]Department of Marine Sciences, University of Georgia, Athens, Georgia 30602, USA

[4]*Present address:* Department of Biology, Villanova University, Villanova, Pennsylvania 19085, USA

ABSTRACT: Across relatively small spatial scales, differences in seascape structure may influence how species transverse adjacent habitats, with effects on trophic relationships and energy flow dynamics. To understand the effects of seascape structure, we used stable isotope analysis to examine variation in resource use by 2 highly abundant estuarine species, mummichogs *Fundulus heteroclitus* and grass shrimp *Palaemon* spp., both of which are known to forage in intertidal areas. We compared the percent contribution of basal resources, trophic position, and trophic niches of mummichogs and grass shrimp from 2 tidal creeks with differing seascape structure located ~10 km apart on Sapelo Island, Georgia, USA. Belle Marsh creekbank edge elevation was on average 0.5 m lower and channel density was 5 times greater than Dean Creek, potentially influencing marsh platform access. Although we found no difference in the contribution of marsh-derived energy to grass shrimp among sites, the contribution of marsh-derived energy to mummichogs was on average 1.9 times higher at Belle Marsh. In addition, both species had higher trophic positions and larger trophic niches at Dean Creek, suggesting a less efficient route of energy transfer to consumer production. There was also little overlap in trophic niche among sites for either species. Our results suggest that species traits, site characteristics, and their interaction may influence resource use by intertidal estuarine consumers. By examining how marsh resource use by estuarine consumers varies across multiple marshes with differing morphologies, we can better predict and quantify how seascape structure may affect secondary productivity of estuarine systems.

KEY WORDS: Grass shrimp · *Palaemon* spp. · Mummichog · *Fundulus heteroclitus* · Salt marsh · Stable isotopes · Landscapes

1. INTRODUCTION

Faunal distributions and abundance can be closely linked to habitat structure within a landscape across both space and time (Fahrig 1997). Certain habitats may differ in relative importance for an organism based on factors such as the life stage of the organism (Keller et al. 2017), the placement of the habitat within the landscape (Baillie et al. 2015), and how environmental fluctuations influence structural complexity (Keller 2018). Historically, landscape configuration was represented as a habitat matrix of suitable vs. unsuitable patches for species (Fischer & Lindenmayer 2006). However, species use resources from multiple habitat types and can perceive landscapes in a complex manner, leading to a shift toward representing habitats as a continuous, heterogeneous landscape rather than distinct patches (Fahrig et al. 2011).

Across heterogeneous landscapes, organisms and energy move across distinct habitat boundaries or edges (Yarnall et al. 2022). That movement is often controlled by habitat complexity, which is indexed by properties such as the relative amount of edge habitat and shape of the habitat patch. The resulting movement in turn influences species diversity and

resource use by consumers (Dolson et al. 2009). Specifically, edge habitat can alter resource use through changes in predator—prey interactions by altering the detectability or the capture rate of prey (Hebblewhite et al. 2005). For instance, the predation risk of blue crabs is reduced at the edges of seagrass meadows where time to consumption is 2.5 times longer than at the interior of meadows, and survival increases with higher patch-level shoot density (Mahoney et al. 2018). Further, changes in structural complexity along the habitat edge may physically prevent consumers from moving across these ecological boundaries into the adjacent habitat to forage (Fagan et al. 1999, Warfe & Barmuta 2004).

The relative influence of edge habitat on resource use is not consistent for all consumers due to differences in body size, movement behavior, and feeding strategies (Ries et al. 2004, Gross et al. 2018). For instance, ambush predators may have higher foraging success at edges with greater structural complexity, which provide cover that obscures them from potential prey (Říha et al. 2021). In contrast, larger-bodied active hunting predators may prefer to forage along edges with low structural complexity as they provide prey with less refuge to hide (Horinouchi et al. 2009, Klecka & Boukal 2014, Byers et al. 2017). Furthermore, at the land—water interface, edge elevation or geomorphology may affect how consumers with distinct body sizes or life history strategies move across habitat edges to forage and utilize energetic resources (Lesser et al. 2020a).

Within tidal salt marsh ecosystems, habitat edges can alter the movement, foraging behavior, and overall resource use of estuarine consumers through a combination of geomorphologic structure, structural complexity of foundation species, and hydrodynamics (Kneib 2002, Able et al. 2003, Currin et al. 2003, Nelson et al. 2019, Lesser et al. 2021, Ziegler et al. 2021). Regardless of edge structure, previous work has shown that approximately 5 cm of water above the marsh platform is required for estuarine nekton to cross the habitat edge and utilize the vegetated habitat (Minello & Rozas 2002). Therefore, at large spatial scales, the coastal setting and inter-system setting (sensu Yando et al. 2023), specifically the tidal forcing and tidal elevation of a salt marsh, tends to be the key factor influencing resource use by estuarine species (Kneib 1997, Baker et al. 2013). However, at smaller spatial scales, especially in areas where tidal amplitude is high, the intra-system setting (sensu Yando et al. 2023), specifically seascape structure (configuration and habitat edge geomorphologic structure), may be more important in driving ecological pro-

cesses such as consumption and resource use (James et al. 2021).

Previous work has focused on how geomorphological structure has influenced the relative importance of salt marshes for 2 common and highly abundant marsh consumers, mummichogs *Fundulus heteroclitus* and grass shrimp (*Palaemon pugio* and *P. vulgaris*) (Deegan et al. 2007, Lesser et al. 2020a). Combined, these taxa can account for upwards of 98% of the nekton biomass in salt marsh ecosystems (Deegan et al. 2007). Mummichogs are omnivorous species that consume detritus, algae, and macroinfauna in tidal creeks (Allen et al. 1994), and terrestrial invertebrates on the marsh platform during high tides (Kneib 1984). Access to the marsh platform has been shown to correlate with higher growth rates (Able et al. 2006) and trophic levels (Nelson et al. 2015) in mummichogs. Grass shrimp are also omnivorous consumers that forage upon epiphytic and benthic algae, meiofauna, and small macrofauna within salt marsh tidal creeks (Fleeger et al. 1999). These grass shrimp species can move onto the marsh platform but are more often found at the edges of vegetated marsh habitat rather than deep into the marsh platform (Allen et al. 2015). Due to the relative importance of these taxa in salt marsh ecosystems and their distinct foraging and movement strategies, they are ideal model organisms to assess how seascape structure may influence resource use and potentially energy flow dynamics across the salt marsh—tidal creek boundary.

The objective of this research was to determine if seascape structure differentially affects resource use at the tidal creek—marsh platform interface for 2 common estuarine taxa. To evaluate this objective, we conducted bulk stable isotope analysis on 2 highly abundant marsh-associated estuarine consumers, mummichogs and grass shrimp, at 2 salt marshes located approximately 10 km apart with varying seascape configuration, including tidal elevation and differences in cross-cutting channel density. We asked (1) What is the relative contribution of salt marsh-derived vs. aquatic-derived energy resources to mummichogs and grass shrimp across sites? And (2) How do resource use, trophic position, and trophic niche of these 2 taxa vary across distinct marsh seascapes?

2. MATERIALS AND METHODS

2.1. Study sites and focal species

Our study concentrated on 2 spatially distinct marsh seascapes on Sapelo Island, Georgia, USA,

located within the Georgia Coastal Ecosystems Long Term Ecological Research domain. Dean Creek marsh (31.388°, −81.282°) is located on the southwestern side of the island directly adjacent to Doboy Sound. The creek at Belle Marsh (henceforth Belle Marsh; 31.477°, −81.271°) is located off the Duplin River approximately 8 km north of Doboy Sound. Dean Creek and Belle Marsh are characterized by similar salinities (mean ± SD: 19.6 ± 6.5 and 20.2 ± 3.4, respectively) and water temperatures (23.2 ± 6.4 and 24.1 ± 5.8°C, respectively) (NOAA NERRS 2024). Both sites are dominated by the salt marsh cordgrass *Spartina alterniflora* across the low marsh. Our 2 focal organisms, grass shrimp (*Palaemon vulgaris* and *P. pugio*) and mummichog, are present at both sites and are abundant residents of shallow-water marsh habitats in estuaries along the US Atlantic coast (Kneib 1997, Hagan et al. 2007, Allen et al. 2015). These taxa are both omnivorous, have high site fidelity (radius ~200−300 m), and are important prey taxa in estuarine food webs (Lesser et al. 2020a).

2.2. Marsh seascape characterization

To examine differences in seascape structure between the 2 marsh sites, we collected images of the tidal creeks and their associated channels within each site in June 2022 using a DJI Matrice 210 unmanned aerial vehicle (UAV) carrying a MicaSense Altum camera. Images were collected during morning low tides at solar noon and the UAV was flown at an altitude of 120 m (resulting in a pixel resolution of 5 cm). In ArcGIS Pro 3.0.1 (ESRI 2022), we constructed a 250 m radius buffer at the center of each tidal creek (Fig. 1). Within each buffer, we quantified the channel density, total marsh area (m^2), and total channel area (m^2). We also extracted marsh edge elevation data within 1 m of the tidal creek from the National Elevation Dataset with a 1/9 arc-second resolution (USGS 2012). These variables provide site characterization and insight into influential habitat differences that might underlie differences in resource use but were not included in formal analyses.

2.3. Nekton sampling and processing

We collected adult grass shrimp (mean ± SD length: 22 ± 4.5 cm) and mummichogs (62 ± 12.2 cm) in late July/early August 2023 via a combination of lift nets (1 m × 1 m, 0.1 cm mesh) and Gee-style min-

now traps placed 1 m seaward from the vegetated marsh platform within tidal creek channels or marsh ponds at each site. We placed traps or nets at low tide and collected at the following high tide. Additionally, we collected basal resources at both Dean Creek and Belle Marsh. We focused basal resource collection on the dominant resources in salt marsh ecosystems: suspended particulate organic matter (sPOM), benthic microalgae, and *S. alterniflora*. At each site, for sPOM, we collected 1 l water samples (n = 6) from the mid-channel at ebb tide. For benthic microalgae, we placed 10 cm × 10 cm, 200 µm Nitex mesh (n = 10) onto the mudflat adjacent to the marsh platform at low tide. We left the mesh in place for 20 min to allow benthic algae migration and then placed mesh in individual bags. For *S. alterniflora*, we clipped 5 live (green) leaves from 6 stems randomly dispersed across the marsh platform. We then placed all samples on ice and returned them to the lab for processing for C, N, and S stable isotope analysis.

At the laboratory, we gently rinsed benthic microalgae from mesh and then filtered benthic microalgae (n = 3−6 per site) and sPOM (n = 3−6 per site) samples individually onto 47 mm GF/F filters until saturated. For sPOM, we filtered between 1 and 2 l per sample. Due to differences in the benthic microalgae and sPOM concentrations at each site, final sample sizes varied. We soaked *S. alterniflora* shoots in deionized water to remove additional salts and then scraped each leaf to remove any epibionts. We obtained dorsal muscle tissue for each fish (n = 8 samples per site) and tail muscle tissue for each shrimp. To ensure enough tissue for shrimp sample processing, we homogenized 2−4 individuals per sample (n = 6 shrimp samples per site). All samples were dried at 60°C for at least 48 h, ground into a fine powder, and packed into tins for stable isotope analysis.

The relative abundances of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and sulfur ($^{34}S/^{32}S$) isotopes were measured using an ECS 4010 elemental analyzer (Costech Analytical) interfaced with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan) at the Washington State University Stable Isotope Laboratory. For reference standards, we compared carbon isotope ratios to Vienna PeeDee Belemnite, nitrogen isotope ratios to atmospheric N_2, and sulfur isotope ratios to Vienna Canyon Diablo Troilite. Laboratory internal standards included the internationally distributed reference materials USGS40 and USGS41a (glutamic acids). Stable isotope values are presented using delta notation:

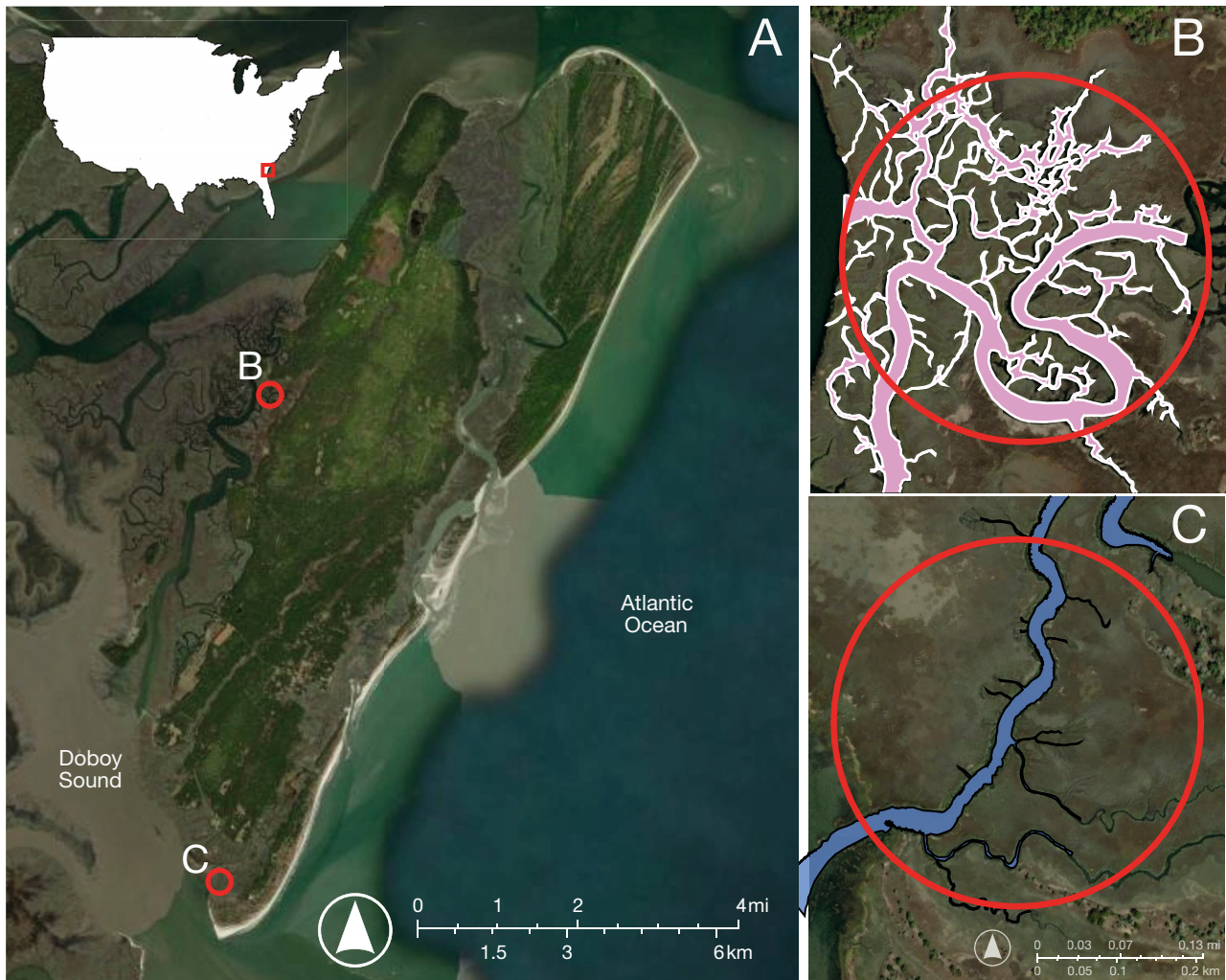$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \qquad (1)$$

Fig. 1. (A) Sapelo Island, within the state of Georgia, USA (inset, in white), showing locations of the Belle Marsh (B) and Dean Creek (C) study sites. (B) Belle Marsh (channels in pink) and (C) Dean Creek (channels in blue) encompassed by a 250 m radius buffer (red circle). Channel networks delineated from digitized unmanned aerial vehicle imagery

where δX denotes the deviation of the heavy isotope in the sample in ‰, R_{sample} is the ratio of heavy to light isotope in the sample, and $R_{standard}$ is the ratio of heavy to light isotope in the reference standard. We obtained $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ ratios for all target taxa.

2.4. Analysis

We used the basal resource contributions, derived from the stable isotope values, to derive trophic response metrics (trophic level and trophic niche volume) of mummichogs and grass shrimp for both Belle Marsh and Dean Creek. We estimated the relative contribution of the basal resources with Bayesian stable isotope mixing models using C, N, and S.

We ran Bayesian mixing models in R version 4.3.1 (R Core Team 2023) using the package 'MixSIAR' (v 3.1.12; Stock et al. 2018) to determine the relative contribution of sPOM, benthic algae, and *S. alterniflora* sources to mummichog and grass shrimp at each site. As part of the models, we made corrections for the elemental concentration in each source, and the trophic enrichment for each element was C = 1.3 ± 0.3 (mean ± SD), N = 3.3 ± 0.36, and S = 0.5 ± 0.54 (McCutchan et al. 2003, Rezek et al. 2020). We ran each with a Markov chain Monte Carlo algorithm that consisted of 3 chains, with chain lengths of 3 000 000 and a burn-in of 1 500 000.

To assess the relative differences in trophic level of mummichogs and grass shrimp within and among the 2 marsh sites, we calculated the concentration-

dependent percent contributions of each source for each taxon at each site and then calculated trophic position (TP) according to the following formula:

$$TP = \frac{\delta^{15}N_{ind} - \sum \left(\delta^{15}N_{source} \times \text{mean } \%cont_{source}\right)}{TDF} + 1 \quad (2)$$

where the trophic discrimination factor (TDF) = 3.3 ± 0.36‰ (McCutchan et al. 2003), $\delta^{15}N_{ind}$ is the nitrogen isotope value of an individual consumer, $\delta^{15}N_{source}$ is the nitrogen isotope value of each basal resource, and mean $\%cont_{source}$ is the proportional contribution of each source to the consumer diet (Post 2002, Wilson et al. 2009, 2010, Nelson et al. 2015). To account for the uncertainty in model variables in trophic position calculations, for each species and site combination, we extracted all runs (n = 9000) from each mixing model posterior distribution and used the source contribution for each run of the model. We then used a random enrichment factor extracted from the normal distribution of the mean ± SD of the TDF (3.3 ± 0.36‰). We then used a Kruskal-Wallis rank-sum test to evaluate differences in the trophic position of mummichog and grass shrimp within and among marsh sites, and a post hoc Bonferroni-corrected Dunn's test was used to examine all pairwise comparisons.

To assess differences in the trophic niches of the same taxa across sites and the different taxa within marsh sites, we constructed *n*-dimensional hypervolumes by simulating 5000 points for each sample using a Gaussian kernel density estimation for each species at each site using the 'hypervolumes' package in R (version 3.1.1; Blonder et al. 2018, 2024). We used a quantile threshold of 0.05, so that each hypervolume included 95% of the probability density. These hypervolumes allowed us to examine differences in trophic niche size and overlap among the trophic niches of each taxon across sites. To examine the differences in the amount of the available resources used by the taxa across sites, we statistically assessed the size and overlap of trophic niche hypervolumes via a bootstrapping protocol (Newsome et al. 2012, Lesser et al. 2020b) and compared the differences in niche size and overlap (Sorensen overlap index) using the nonparametric Kruskal-Wallis rank-sum test and a post hoc Bonferroni-corrected Dunn's test for all pairwise comparisons.

3. RESULTS

3.1. Marsh characteristics

Within the 250 m radius buffer surrounding each tidal creek, there were substantial differences in channel density (n), channel area (m²), marsh area (m²), and marsh edge elevation (m) between the 2 sites (Table 1). Specifically, Dean Creek was characterized by low channel density (n = 13) while Belle Marsh had high channel density (n = 73). Correspondingly, Dean Creek had lower channel area (~21500 m²) and higher relative marsh area (~175000 m²) compared to Belle Marsh, which had a channel area of ~48000 m² and relative marsh area of ~148500 m². This results in a marsh to water ratio of 8.1 for Dean Creek and 3.1 for Belle Marsh. Additionally, marsh creekbank edge elevation at Dean Creek was substantially higher, with an average edge elevation of 0.38 ± 0.39 m (mean ± SD; NADV88), compared to Belle Marsh, with an average edge elevation of −0.19 ± 0.43 m (NADV88) (Table 1).

3.2. Stable isotope values across marsh sites

Basal resources (*Spartina alterniflora*, sPOM, and benthic microalgae) encompassed similar isotopic space, but the 2 marshes had distinct $\delta^{13}C$ and $\delta^{34}S$ values (Table 2). *S. alterniflora* $\delta^{13}C$ values were the most similar across sites with mean $\delta^{13}C$ of −14.3 ± 0.4‰ at Dean Creek and −14.8 ± 0.2‰ at Belle Marsh. sPOM and benthic algae had more distinct $\delta^{13}C$ values across sites with −21.1 ± 0.4‰ for sPOM and −18.3 ± 1.0‰ for benthic algae at Dean Creek and −23.4 ± 0.4‰ for sPOM and at −16.9 ± 0.5‰ for benthic algae at Belle Marsh. There were also large variations in sulfur isotopic values among basal resources across the 2 marsh sites. Mean $\delta^{34}S$ values for *S. alterniflora* varied the most and were −14.0 ±

Table 1. Marsh seascape characteristics measured in ArcGIS Pro (v. 3.0.1), including channel density (number of channels within 250 m radius buffer), average marsh edge elevation (NADV88) (±SD), total area within the buffer comprised of tidal creek channels, total area within the buffer comprised of salt marsh platform (vegetation), and ratio of marsh platform to tidal creek channel within the buffer

	Dean Creek	Belle Marsh
Channel density (n)	13	73
Main channels	1	2
Secondary channels	12	71
Elevation (m)	0.38 (0.39)	−0.19 (0.43)
Channel area (m²)	21532	47814
Marsh area (m²)	174818	148535
Marsh to water ratio	8.12	3.11

Table 2. Bulk stable isotope values (mean ± SD) and sample size for all basal resources (benthic algae, suspended particulate organic matter [sPOM], and cordgrass *Spartina alterniflora*) and consumers (mummichogs *Fundulus heteroclitus* and grass shrimp *Palaemon* spp.) at Dean Creek and Belle Marsh, Georgia, USA; n: number of samples processed for stable isotope analysis

Site	Taxon	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	n
Dean Creek	Benthic algae	−18.3 ± 1.0	3.6 ± 1.2	−16.7 ± 0.6	3
	sPOM	−21.1 ± 0.4	4.6 ± 0.2	13.2 ± 15.5	3
	S. alterniflora	−14.3 ± 0.4	5.4 ± 0.8	−14.0 ± 11.6	6
	F. heteroclitus	−17.0 ± 0.6	10.8 ± 0.6	12.6 ± 0.9	8
	Palaemon spp.	−17.0 ± 0.4	9.2 ± 0.3	13.6 ± 0.5	6
Belle Marsh	Benthic algae	−16.9 ± 0.5	4.0 ± 1.4	−13.9 ± 2.0	6
	sPOM	−23.4 ± 0.4	4.5 ± 0.6	8.0 ± 4.6	3
	S. alterniflora	−14.8 ± 0.2	5.0 ± 0.9	−0.6 ± 6.8	6
	F. heteroclitus	−16.7 ± 0.6	7.5 ± 0.3	6.0 ± 0.8	8
	Palaemon spp.	−18.7 ± 0.9	8.5 ± 0.3	11.4 ± 0.6	6

11.6‰ at Dean Creek and −0.6 ± 6.8‰ at Belle Marsh. sPOM $\delta^{34}S$ was 13.2 ± 15.5‰ at Dean Creek and 8.04 ± 4.6‰ at Belle Marsh, and benthic algae was −16.7 ± 0.6‰ at Dean Creek and −13.9 ± 2.0‰ at Belle Marsh. $\delta^{15}N$ values were similar across both sites for all basal resources (mean difference in $\delta^{15}N$ = 0.3‰; Table 2).

Across marsh sites, grass shrimp had $\delta^{13}C$ values of 17.0 ± 0.4‰ at Dean Creek and 18.7 ± 0.9‰ at Belle Marsh (Table 2). At Dean Creek, $\delta^{15}N$ values were greater for grass shrimp (9.2 ± 0.3‰) compared to at

Belle Marsh (8.5 ± 0.3‰). $\delta^{34}S$ values for grass shrimp were similar across the 2 sites: 13.6 ± 0.5‰ at Dean Creek and 11.4 ± 0.7‰ at Belle Marsh.

Like grass shrimp, $\delta^{13}C$ values for mummichogs were similar across the 2 sites, with $\delta^{13}C$ values of −17.0 ± 0.6‰ at Dean Creek and −16.7 ± 0.6‰ at Belle Marsh (Table 2). There were large differences in $\delta^{15}N$ for mummichog at the 2 sites: 10.8 ± 0.9‰ at Dean Creek and 7.5 ± 0.6‰ at Belle Marsh. Interestingly, there was also a large difference in $\delta^{34}S$ values for mummichogs across the 2 marsh sites, with 12.6 ± 0.9‰ at Dean Creek and 6.0 ± 0.8‰ at Belle Marsh.

3.3. Mixing model results

Across both marsh sites, the patterns in resource use by grass shrimp were similar (Fig. 2). sPOM-derived energy made the greatest contribution to grass shrimp production, contributing approximately 52.5 ± 5.3% at Dean Creek and 62.8 ± 3.5% at Belle Marsh. *S. alterniflora*-derived energy contributed the second most to grass shrimp production, ranging between 33.0 ± 7.7 and 33.7 ± 5.6%, and benthic algae-derived energy contributed the least at both sites. Interestingly, the source contribution of benthic algae was higher and had greater variation in values (i.e. high SD) at Dean Creek (14.6 ± 10.5%) compared to Belle Marsh, where benthic algae had minimal contribution to grass shrimp production (3.5 ± 2.7%).

Mummichog resource use differed among the 2 marsh sites (Fig. 2). At Dean Creek, resource use mirrored that of grass shrimp, with sPOM-derived energy making the greatest contribution to mummichog production (~48%). Benthic algae and *S. alterniflora* resource contributions were approximately the same for mummichogs at Dean Creek (24.8 ± 11.7 and 26.9 ± 8.9%, respectively). In contrast, at Belle Marsh, *S. alterniflora*-derived energy made the greatest contribution to mummichog production (50.4 ± 6.3%) followed by sPOM (35.9 ± 3.0%) and then benthic algae (13.8 ± 6.9%).
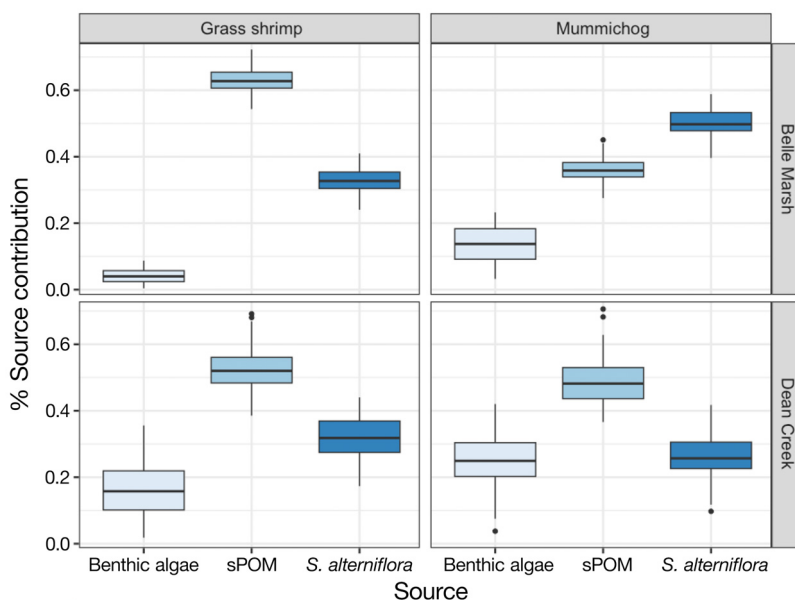

Fig. 2. Percent contribution of 3 basal resources to grass shrimp and mummichogs across 2 marshes with distinct seascape configuration. Boxplots display the entire distribution of bootstrapped source contributions for 100 individuals. Bars indicate median values, boxes encompass the 25−75% quartile range, whiskers indicate 95% confidence intervals and points indicate outliers
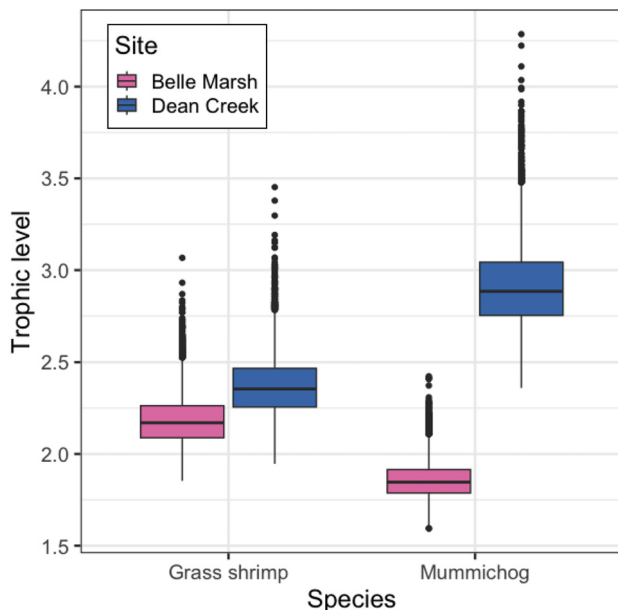
Fig. 3. Trophic level of mummichogs and grass shrimp across 2 marshes with distinct seascape configuration. Boxplots display the distribution of trophic levels for 9000 individuals (extracted from the posterior distributions of each run of the mixing model with a random trophic discrimination factor). Boxplot parameters as in Fig. 2

3.4. Trophic position and resource niche

Trophic positions of both mummichog and grass shrimp were higher at Dean Creek compared to Belle Marsh (Kruskal-Wallis, χ^2 = 13499, df = 1, p < 0.001, χ^2 = 5536.8, df =1, p < 0.001, respectively) (Fig. 3). Notably, mummichogs were approximately 1 trophic level higher (2.91 ± 0.22) at Dean Creek compared to Belle Marsh (1.86 ± 0.10). Grass shrimp trophic levels, while closer, were still higher at Dean Creek (2.37 ± 0.16) compared to Belle Marsh (2.18 ± 0.13).

Trophic niche size varied greatly for the same taxa across the 2 sites (Kruskal-Wallis, χ^2 = 149.3, df = 1, p < 0.001). Both mummichogs and grass shrimp had larger trophic niches at Dean Creek (mummichog: 37.1 ± 4.4; grass shrimp: 29.0 ± 2.8) compared to Belle Marsh (mummichog: 4.7 ± 0.5; grass shrimp: 2.5 ± 0.3) (Fig. 4; Fig. A1 in the Appendix).

Even though there were similarities in resource use patterns (% contributions), there was only about a 20% overlap in trophic niche for grass shrimp between the 2 sites (Sorensen overlap index = 0.21, 95% CI = 0.20, 0.21) (Table 3, Fig. 4B), and no statistical overlap in trophic niche of mummichog (Sorensen overlap index = 0.0, 95% CI = 0, 0) (Fig. 4A). Within sites, there was no overlap in trophic niche between

mummichogs and grass shrimp at Belle Marsh (Sorensen overlap index = 0.0, 95% CI = 0, 0) (Fig. 4D) as compared to Dean Creek (Sorensen overlap index = 0.34, 95% CI = 0.33, 0.35) (Table 3, Fig. 4C).

4. DISCUSSION

Determining how landscape or seascape structure influences resource use by taxa across distinct habitat boundaries is a key step to understanding spatial subsidy and food web dynamics and how they might respond to habitat loss and degradation (Polis & Hurd 1996). Our results suggest than even over relatively small spatial scales (~10 km), differences in seascape structure, specifically edge habitat, can drive differences in overall resource use. In general, we found that sPOM was the dominant basal resource contributing to shrimp and mummichog, both of which are abundant estuarine taxa. However, the magnitude of sPOM contribution varied between sites and between the 2 taxa. The relatively high contributions of sPOM to these estuarine taxa is to be expected, as it is the most prominent and readily accessible basal resource in these ecosystems (Lebreton et al. 2016). More interestingly, we found high variation in the relative importance of marsh-derived (*Spartina alterniflora*) resources across sites and taxa, most likely driven by differences in landscape structure affecting cross-boundary energy flow.

Specifically, we found that mummichogs utilized 1.9 times more marsh-derived energy resources (*S. alterniflora*) at Belle Marsh compared to Dean Creek. Belle Marsh is characterized by low edge elevation and high channel density, which increases both the overall habitat edge amount and the edge to area ratio. The combination of these factors may facilitate the movement of mummichogs, which conduct daily tidal migrations onto the marsh platform and into interior sub-habitats (ponds, pools, etc.; Able et al. 2012) to forage on marsh-associated prey items such as terrestrial insects (Nelson et al. 2019, Lesser et al. 2021), thereby increasing the utilization of marsh-derived energy resources. In contrast, Dean Creek is characterized by higher marsh edge elevation (~0.5 m higher than Belle Marsh) and low channel density resulting in greater marsh platform area compared to channel edge. Even in an area with high tidal amplitude such as in Georgia, USA (2−3 m), the higher edge elevation at Dean Creek may reduce seascape connectivity and impede nekton such as mummichogs from accessing the marsh platform, thereby reducing the use of marsh-derived energy resources.
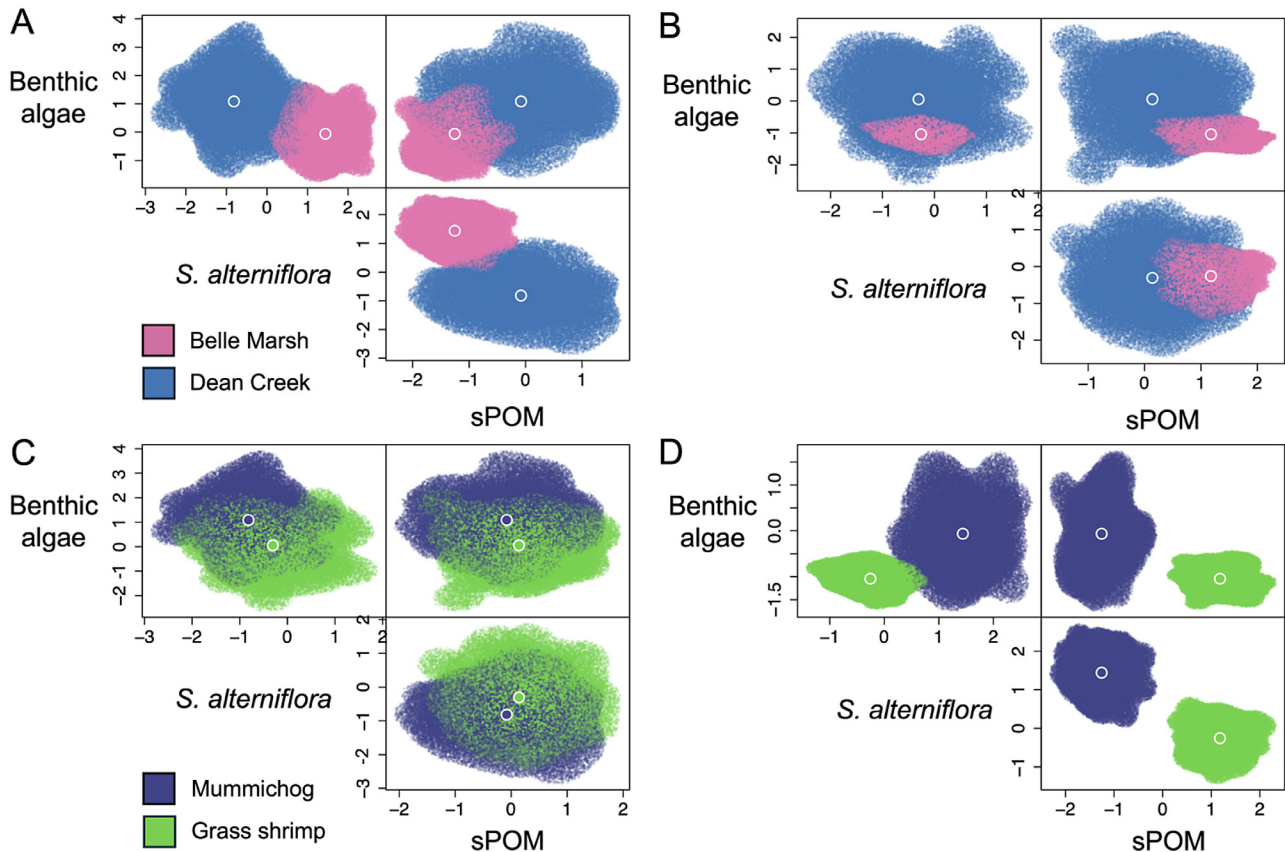
Fig. 4. Visual comparison of the trophic niche (hypervolume) between (A) mummichogs at Belle Marsh (pink) and Dean Creek (blue), (B) grass shrimp at Belle Marsh (pink) and Dean Creek (blue), (C) Mummichog (purple) and grass shrimp (green) at Dean Creek, and (D) mummichog (purple) and grass shrimp (green) at Belle Marsh. Axes represent the z-score for the basal resource contributions predicted by the mixing models to mummichogs or grass shrimp at each site. White circles represent the centroids of the trophic niches

Table 3. Comparisons of n-dimensional hypervolumes (HV) for mummichog and grass shrimp within and across sites (DC: Dean Creek; BM: Belle Marsh). Sorensen overlap index indicates the proportion of the overlap between the 2 niches, and the fraction unique indicates the proportion of the niche that is unique. Values are means (lower, upper 95% CI). These statistics correspond to the visual representations of trophic niche in Fig. 4

HV 1	HV 2	Sorensen overlap index	Fraction unique HV1	Fraction unique HV2
DC mummichog	BM mummichog	0.00 (0, 0)	1.00 (1, 1)	1.00 (1, 1)
DC grass shrimp	BM grass shrimp	0.21 (0.20, 0.21)	0.88 (0.87, 0.88)	0.31 (0.30, 0.33)
DC mummichog	DC grass shrimp	0.34 (0.33, 0.35)	0.72 (0.71, 0.74)	0.51 (0.49, 0.52)
BM mummichog	BM grass shrimp	0.00 (0, 0)	1.00 (1, 1)	1.00 (1, 1)

In contrast to mummichogs, we found little difference in the utilization of marsh- or aquatic-derived energy resources for grass shrimp at either site. While seascape structure is one important factor modulating consumer movement and foraging behavior, species life history can also play an important role in resource use (van Noordwijk & de Jong 1986). Although grass shrimp and mummichogs are both highly abundant and integral players in the salt marsh ecosystem,

differences in their movement behavior may dictate differences in their resource use. Mummichogs move throughout a tidal creek system and have been recaptured 300 m from their initial tagging locations (Able et al. 2006). Mummichogs actively move onto the marsh platform with changes in the tidal height and have been shown to move across 15 ha of vegetated marsh during a single tide cycle (Teo & Able 2003). In contrast, grass shrimp captured in intertidal creeks

have extremely high site fidelity, with 82−100% being recaptured in the same area of a creek (Allen et al. 2015). In fact, Allen et al. (2007) found that grass shrimp tend to reside in the same area within a creek for weeks or months at a time without migrating onto the marsh platform to forage. We captured grass shrimp within the intertidal creek channels at both marsh sites, suggesting little or no recent movement onto the marsh platform. It is therefore not surprising there was high similarity in resource use regardless of the marsh seascape structure. This finding was further supported by higher overlap in trophic niche of grass shrimp among sites, indicating more similar use of the available resources compared to mummichogs, which had little overlap in trophic niche.

Although resource use was similar between grass shrimp among sites, both grass shrimp and mummichogs had higher trophic levels at Dean Creek compared to their conspecifics at Belle Marsh. Trophic position can assist in the characterization of organisms within a food web and provide information to track energy flow through ecological communities (Peterson & Fry 1987, Post 2002). The higher trophic level of both grass shrimp and mummichog indicates that the route of energy transfer to the consumer is less efficient and requires more primary production to support the same amount of biomass at Dean Creek compared to Belle Marsh (Mehner et al. 2022). Reduced seascape connectivity at Dean Creek may require shifts in foraging behavior of these small marsh-associated nekton, altering not only resource use but trophic position. Klaus et al. (2024) suggested that trophic position may shift with the amount of habitat area and habitat diversity within a landscape or seascape and is dependent on how different species perceive the environment. The increased channel density and lower edge elevation increasing connectivity and facilitating access to the marsh platform at Belle Marsh may have increased the overall perceived habitat availability and diversity for both estuarine species and resulted in the lower trophic positions at this site compared to Dean Creek.

In addition to differences in trophic position among sites, we found that the trophic niche of both taxa was larger at Dean Creek compared to Belle Marsh and there was high overlap in the trophic niches of the 2 taxa at Dean Creek. A larger trophic niche (greater trophic niche width) has been found to correlate with decreased ecosystem productivity (Lesser et al. 2020b). Lower habitat connectivity has also been shown to decrease the conversion of primary production into consumer biomass, lowering overall ecosystem productivity (Cloern 2007). In seagrass sys-

tems, pinfish *Lagodon rhomboides* tend to have larger trophic niches in areas with low seagrass cover (lower productivity) and increased fragmentation, which decrease connectivity between habitat patches (Santos et al. 2022). Thus, decreased seascape connectivity at Dean Creek, resulting from higher marsh edge elevation and lower channel density, could be indicative of lower ecosystem productivity and correspond to larger trophic niches of taxa observed at this site. Further, previous work has shown that in landscapes or seascapes with lower productivity there is higher overlap in the trophic niche of distinct species (Lesser et al. 2020b). For instance, the trophic niches of lionfish *Pterois volitans* and Nassau grouper *Epinephelus striatus* tend to have higher overlap at shallow, less productive patch reefs than at large continuous reef habitats (O'Farrell et al. 2014). In areas with high connectivity (e.g. Belle Marsh) there could be a higher diversity of resources available, reducing interspecific competition and decreasing overlap in trophic niches (Matich et al. 2021), whereas with low habitat connectivity (e.g. Dean Creek) there may be higher competition for the available resources, thereby increasing overlap in trophic niche (Bolnick et al. 2010).

Across distinct ecosystem boundaries such as those within estuaries, habitat connectivity can be dictated by a variety of mechanisms including tidal dynamics and seascape structure (Green et al. 2012, Yando et al. 2023). This study focuses on examining differences in the trophic dynamics of 2 important and abundant estuarine taxa at only 2 distinct marsh seascapes across a relatively small spatial scale. It is important to highlight that differences in resource use by grass shrimp and mummichogs across sites may be due to seascape structure and species life histories but could also be due to differences in prey composition, availability, or accessibility. Moreover, isotopic signatures can fluctuate over time due to changes in prey availability or environmental conditions, and these data provide a single snapshot in time. Further, the turnover rate of isotopic signatures in muscle tissue provides a relatively long-term integration for fauna while sPOM and benthic algae signatures may change at a much more rapid rate (Layman et al. 2012). Therefore, future efforts will benefit from examining the trophic dynamics of taxa from a greater diversity of marsh seascapes with similar tidal dynamics over both space and time to provide further insight into estuarine food web structure and function. As landscapes and seascapes become more fragmented, reducing habitat connectivity, there may be shifts in how different species utilize adjacent habitats as both refuge and for energetic resources.

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Understanding the relative importance of landscape or seascape structure and species traits is key to determining how food webs will shift in response to environmental change, even across relatively small spatial scales.

LITERATURE CITED

Able KW, Rowe P, Burlas M, Byrne D (2003) Use of ocean and estuarine habitats by young-of-year bluefish (*Pomatomus saltatrix*) in the New York Bight. Fish Bull 101:201—214

Able KW, Hagan SM, Brown SA (2006) Habitat use, movement, and growth of young-of-the-year *Fundulus* spp. in southern New Jersey salt marshes: comparisons based on tag/recapture. J Exp Mar Biol Ecol 335:177—187

Able KW, Vivian DN, Petruzzelli G, Hagan SM (2012) Connectivity among salt marsh subhabitats: residency and movements of the mummichog (*Fundulus heteroclitus*). Estuaries Coasts 35:743—753

Allen EA, Fell PE, Peck MA, Gieg JA, Guthke CR, Newkirk MD (1994) Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural reference marshes. Estuaries 17:462—471

Allen DM, Haertel-Borer SS, Milan BJ, Bushek D, Dame RF (2007) Geomorphological determinants of nekton use of intertidal salt marsh creeks. Mar Ecol Prog Ser 329:57—71

Allen DM, Harding JM, Stroud KB, Yozzo KL (2015) Movements and site fidelity of grass shrimp (*Palaemonetes pugio* and *P. vulgaris*) in salt marsh intertidal creeks. Mar Biol 162:1275—1285

Baillie CJ, Fear JM, Fodrie FJ (2015) Ecotone effects on seagrass and saltmarsh habitat use by juvenile nekton in a temperate estuary. Estuaries Coasts 38:1414—1430

Baker R, Fry B, Rozas LP, Minello TJ (2013) Hydrodynamic regulation of salt marsh contributions to aquatic food webs. Mar Ecol Prog Ser 490:37—52

Blonder B, Morrow CB, Maitner B, Harris DJ and others (2018) New approaches for delineating *n*-dimensional hypervolumes. Methods Ecol Evol 9:305—319

Blonder B, Morrow CB, Brown S, Butruille G, Chen D, Laini A, Harris DJ (2024) hypervolume: high dimensional geometry, set operations, projection, and inference using kernel density estimation, support vector machines, and convex hulls. R package version 3.1.4. https://CRAN.R-project.org/package=hypervolume

Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proc R Soc B 277:1789—1797

Byers JE, Holmes ZC, Malek JC (2017) Contrasting complexity of adjacent habitats influences the strength of cascading predatory effects. Oecologia 185:107—117

Cloern JE, Grover AEJP, DeAngelis EDL (2007) Habitat connectivity and ecosystem productivity: implications from a simple model. Am Nat 169:E21—E33

Currin CA, Wainright SC, Able KW, Weinstein MP, Fuller CM (2003) Determination of food web support and trophic position of the mummichog, *Fundulus heteroclitus*, in New Jersey smooth cordgrass (*Spartina alterniflora*), common reed (*Phragmites australis*), and restored salt marshes. Estuaries 26:495—510

Deegan LA, Bowen JL, Drake D, Fleeger JW and others (2007) Susceptibility of salt marshes to nutrient enrichment and predator removal. Ecol Appl 17:S42—S63

Dolson R, McCann K, Rooney N, Ridgway M (2009) Lake morphometry predicts the degree of habitat coupling by a mobile predator. Oikos 118:1230—1238

ESRI (2022) ArcGIS Pro: release 3.0.1. Esri, Redlands, CA. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview

Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. Am Nat 153:165—182

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wildl Manag 61:603—610

Fahrig L, Baudry J, Brotons L, Burel FG and others (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14:101—112

Fischer JB, Lindenmayer D (2006) Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. Oikos 112:473—480

Fleeger JW, Carman KR, Webb S, Hilbun N, Pace MC (1999) Consumption of microalgae by the grass shrimp *Palaemonetes pugio*. J Crustac Biol 19:324—336

Green BC, Smith DJ, Underwood GJC (2012) Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. Mar Ecol Prog Ser 466:177—192

Gross C, Donoghue C, Pruitt C, Ruesink JL (2018) Habitat use patterns and edge effects across a seagrass—unvegetated ecotone depend on species-specific behaviors and sampling methods. Mar Ecol Prog Ser 598:21—33

Hagan SM, Brown SA, Able KW (2007) Production of mummichog (*Fundulus heteroclitus*): response in marshes treated for common reed (*Phragmites australis*) removal. Wetlands 27:54—67

Hebblewhite M, Merrill EH, McDonald TL (2005) Spatial decomposition of predation risk using resource selection functions: an example in a wolf—elk predator—prey system. Oikos 111:101—111

Horinouchi M, Mizuno N, Jo Y, Fujita M, Sano M, Suzuki Y (2009) Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. Mar Ecol Prog Ser 377:43—49

James WR, Topor ZM, Santos RO (2021) Seascape configuration influences the community structure of marsh nekton. Estuaries Coasts 44:1521—1533

Keller DA (2018) How the structure and spatial components of habitat affect estuarine communities. PhD dissertation, The University of North Carolina at Chapel Hill, NC

Keller DA, Gittman RK, Bouchillon RK, Fodrie FJ (2017) Life stage and species identity affect whether habitat subsidies enhance or simply redistribute consumer biomass. J Anim Ecol 86:1394—1403

Klaus F, Tscharntke T, Grass I (2024) Trophic level and specialization moderate effects of habitat loss and landscape diversity on cavity-nesting bees, wasps and their parasitoids. Insect Conserv Divers 17:65—76

Klecka J, Boukal DS (2014) The effect of habitat structure on prey mortality depends on predator and prey microhabitat use. Oecologia 176:183−191

Kneib RT (1984) Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). J Exp Mar Biol Ecol 83:41−51

Kneib RT (1997) Early life stages of resident nekton in intertidal marshes. Estuaries 20:214−230

Kneib RT (2002) Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Springer Netherlands, Dordrecht, p 267−291

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM and others (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol Rev Camb Philos Soc 87:545−562

Lebreton B, Beseres Pollack J, Blomberg B, Palmer TA, Adams L, Guillou G, Montagna PA (2016) Origin, composition and quality of suspended particulate organic matter in relation to freshwater inflow in a South Texas estuary. Estuar Coast Shelf Sci 170:70−82

Lesser JS, Bechtold CA, Deegan LA, Nelson JA (2020a) Habitat decoupling via saltmarsh creek geomorphology alters connection between spatially-coupled food webs. Estuar Coast Shelf Sci 241:106825

Lesser JS, James WR, Stallings CD, Wilson RM, Nelson JA (2020b) Trophic niche size and overlap decreases with increasing ecosystem productivity. Oikos 129:1303−1313

Lesser JS, Floyd O, Fedors K, Deegan LA, Johnson DS, Nelson JA (2021) Cross-habitat access modifies the 'trophic relay' in New England saltmarsh ecosystems. Food Webs 29: e00206

Mahoney RD, Kenworthy MD, Geyer JK, Hovel KA, Joel Fodrie F (2018) Distribution and relative predation risk of nekton reveal complex edge effects within temperate seagrass habitat. J Exp Mar Biol Ecol 503:52−59

Matich P, Bizzarro JJ, Shipley ON (2021) Are stable isotope ratios suitable for describing niche partitioning and individual specialization? Ecol Appl 31:e02392

McCutchan JH Jr, Lewis WM Jr, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378−390

Mehner T, Attermeyer K, Brauns M, Brothers S and others (2022) Trophic transfer efficiency in lakes. Ecosystems 25:1628−1652

Minello TJ, Rozas LP (2002) Nekton in Gulf Coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. Ecol Appl 12:441−455

Nelson JA, Deegan L, Garritt R (2015) Drivers of spatial and temporal variability in estuarine food webs. Mar Ecol Prog Ser 533:67−77

Nelson JA, Lesser J, James WR, Behringer DP, Furka V, Doerr JC (2019) Food web response to foundation species change in a coastal ecosystem. Food Webs 21:e00125

Newsome SD, Yeakel JD, Wheatley PV, Tinker MT (2012) Tools for quantifying isotopic niche space and dietary variation at the individual and population level. J Mammal 93:329−341

NOAA NERRS (National Estuarine Research Reserve System) (2024) System-wide monitoring program. Centralized Data Management Office. www.nerrsdata.org (accessed 19 February 2024)

O'Farrell S, Bearhop S, McGill RAR, Dahlgren CP, Brum-baugh DR, Mumby PJ (2014) Habitat and body size effects on the isotopic niche space of invasive lionfish and endangered Nassau grouper. Ecosphere 5:123

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Evol Syst 18:293−320

Polis GA, Hurd SD (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am Nat 147:396−423

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703−718

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rezek RJ, Massie JA, Nelson JA, Santos RO, Viadero NM, Boucek RE, Rehage JS (2020) Individual consumer movement mediates food web coupling across a coastal ecosystem. Ecosphere 11:e03305

Ries L, Jr RJF, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491−522

Říha M, Gjelland KØ, Děd V, Eloranta AP and others (2021) Contrasting structural complexity differentiate [sic] hunting strategy in an ambush apex predator. Sci Rep 11:17472

Santos RO, James WR, Nelson JA, Rehage JS, Serafy J, Pittman SJ, Lirman D (2022) Influence of seascape spatial pattern on the trophic niche of an omnivorous fish. Ecosphere 13:e3944

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096

Teo SLH, Able KW (2003) Habitat use and movement of the mummichog (*Fundulus heteroclitus*) in a restored salt marsh. Estuaries 26:720−730

USGS (US Geological Survey) (2012) USGS NED ned19_ n31x50_w081x50_ga_17counties_lot3_2011. 1/9 arc-second 2012 15 × 15 minute IMG. US Geological Survey. https://www.sciencebase.gov/catalog/item/581d26eae4 b08da350d5cf08

van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137−142

Warfe DM, Barmuta LA (2004) Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141:171−178

Wilson RM, Chanton J, Lewis G, Nowacek D (2009) Isotopic variation (δ^{15}N, δ^{13}C, and δ^{34}S) with body size in post-larval estuarine consumers. Estuar Coast Shelf Sci 83:307−312

Wilson RM, Chanton J, Lewis FG, Nowacek D (2010) Concentration-dependent stable isotope analysis of consumers in the upper reaches of a freshwater-dominated estuary: Apalachicola Bay, FL, USA. Estuaries Coasts 33: 1406−1419

Yando ES, Jones SF, James WR, Colombano DD and others (2023) An integrative salt marsh conceptual framework for global comparisons. Limnol Oceanogr Lett 8:830−849

Yarnall AH, Byers JE, Yeager LA, Fodrie FJ (2022) Comparing edge and fragmentation effects within seagrass communities: a meta-analysis. Ecology 103:e3603

Ziegler SL, Miller MD, Smith CS, Fodrie FJ (2021) Abiotic cycles mediate the strength of cross-boundary consumption within coastal food webs. Estuaries Coasts 44: 1147−1156
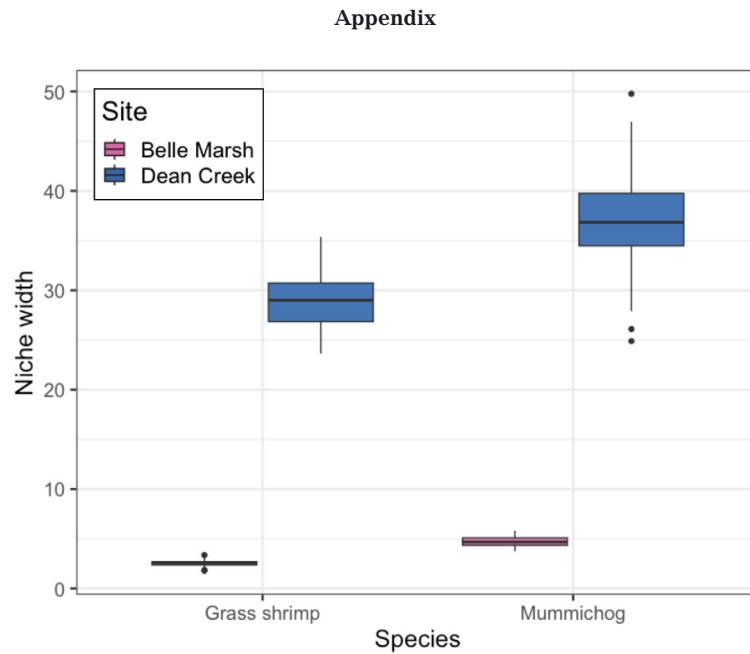
Appendix

Fig. A1. Niche width of mummichogs and grass shrimp calculated from n-dimensional hypervolumes across 2 marshes with distinct seascape configuration. Boxplots display the entire distribution of bootstrapped trophic niche widths for 100 individuals. Boxplot parameters as in Fig. 2