

Dietary shifts across biogeographic scales alter spatial subsidy dynamics

SHELBY L. ZIEGLER^{1,†} KENNETH W. ABLE,² AND F. JOEL FODRIE¹

¹*Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557 USA*

²*Rutgers University Marine Field Station, Rutgers University, Tuckerton, New Jersey 08087 USA*

Citation: Ziegler, S. L., K. W. Able, and F. J. Fodrie. 2019. Dietary shifts across biogeographic scales alter spatial subsidy dynamics. *Ecosphere* 10(12):e02980. 10.1002/ecs2.2980

Abstract. Over heterogeneous landscapes, organisms and energy move across ecological boundaries and this can have profound effects on overall ecosystem functioning. Both abiotic and biotic factors along habitat boundaries may facilitate or impede key species interactions that drive these energy flows—especially along the land–sea interface. We synthesized the literature detailing estuarine fish diets and habitat characteristics of salt marshes from U.S. East and Gulf coasts to determine patterns and drivers of cross-boundary trophic transfers at the land–sea interface. Notably, marsh-platform species (i.e., killifishes, fiddler crabs) appear virtually absent in the diets of transient estuarine fishes in the Gulf of Mexico, while along the South Atlantic and Mid-Atlantic Bights, marsh-platform species appear regularly in the diets of many transient estuarine fishes. Tidal amplitude varied across these three biogeographic regions and likely regulates the availability of marsh-platform species to transient estuarine fishes via both access to the marsh surface for marine predators and emergence of marsh-resident prey into the adjacent estuary (i.e., higher tidal amplitude increases predator–prey encounter rates). Surprisingly, marsh shoot density was positively correlated with the presence of marsh-platform species in the diet, but this pattern appears to be mediated by increased tidal amplitude, suggesting the mode and periodicity of abiotic cycles drive diet structure of transient estuarine fishes more so than local habitat structural complexity. Subsequently, these processes likely influence the degree to which “trophic relay” moves energy from the marsh toward the open estuary. Understanding the dynamics that determine energy flows, spatial subsidies, and ultimately, ecosystem-level productivity, is essential for implementation of holistic ecosystem-based approaches to conserve and manage complex landscape mosaics.

Key words: energy subsidies; estuary; fish; nekton diets; outwelling; salt marsh; tide.

Received 1 July 2019; revised 24 October 2019; accepted 24 October 2019. Corresponding Editor: Sean P. Powers.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** sziegler@live.unc.edu

INTRODUCTION

Complex landscapes are comprised of diverse habitats connected by the movement of fauna over diel, seasonal, and ontogenetic (and additional) cycles. These faunal movements facilitate the flow of energy between systems, often via trophic interactions, playing a key role in ecosystem productivity. The concept of energy

movement across systems has influenced many ecological disciplines, and there is a trove of terminology encompassing this fundamental dynamic: energy flow, fluxes, spatial subsidies, outwelling, trophic relay, connectivity, f-ratio, allochthonous input, cross-habitat foraging, edge predation, etc. (Eppley and Peterson 1979, Polis and Hurd 1996, Kneib 2002). Concepts of spatial energy flow date back to Lindeman’s seminal

work on aquatic ecosystems (1942), which considered changes in food webs through time and external sources that influenced the availability of nutrients in lake habitats. More formally, Teal (1962) introduced the concept of energy flows across spatial boundaries when he elucidated how detritus moved energy out of salt marsh systems to increase productivity throughout estuarine and coastal ocean habitats. Vannote et al. (1980) proposed the River Continuum Hypothesis suggesting that, along the course of a river, inefficiency of upstream communities to utilize energy provides increased energy resources downstream. More recently, stable isotope analyses have been used to better understand how energy from one ecosystem enhances another. For example, stable isotopes uncovered that salmon-based marine-derived energy allows marten communities to maintain body condition and population levels when traditional prey items are scarce (Ben-David et al. 1997). Additionally, isotopic analysis has shown that energy from inshore seagrass meadows is transferred to offshore waters by migratory coastal fishes (Nelson et al. 2012).

Cross-boundary energy flows occurring at the land-water interface are of particular interest since they can greatly influence overall ecosystem functioning (production and transfer of energy) and dynamics of seemingly disparate systems. Organisms and energy can flow bi-directionally across the land-sea interface (Polis and Hurd 1996), and movement of both predators and prey across these distinct ecological boundaries has been shown to enhance secondary production in adjacent ecosystems (Nakano and Murakami 2001). For example, Brant geese (*Branta bernicla*) forage directly on seagrass and then move to upland areas transferring marine-derived energy toward terrestrial habitats subsidizing upland regions (Heck et al. 2008).

Energy flows that occur across the land-sea interface can extend well beyond neighboring habitats, across large spatial scales, and multiple ecosystems. Pacific salmon gain about 90% of their biomass in marine systems before returning to freshwater systems to spawn (Gende et al. 2002). This migration has been observed to enhance production in aquatic systems upstream and also transfer energy from marine to

terrestrial systems via scavenging insects, raptors, and bears foraging upon salmon enhancing overall secondary production (Hansen 1987, Reimchen 2000).

Tidal salt marshes are situated at the interface between land and sea and have been vigorously debated as sources or sinks of energy in coastal estuaries (inwelling vs. outwelling hypothesis; Ibañez et al. 2000). Originally, it was proposed that marshes outwelled energy through detrital pathways toward the open estuary (Teal 1962, Odum 1980); however, more recent studies suggest that these energy pathways are more varied (Deegan 1993, Peterson and Turner 1994, Kneib 1997). One pathway for energy to move from the marsh to estuarine or offshore habitats is through food webs via a series of predator-prey interactions (e.g., trophic transfer or trophic relay; Kneib 2002). Energy flow across the marsh ecotone by predator-prey interactions is regulated by the ability of transient marine consumers to access prey items that are typically residents of the marsh platform. This access may be mediated by the ability of predators to move onto the marsh platform during high-water-level periods or by discharge of prey items from the marsh surface into adjacent estuarine habitats during low-water-level periods (prey emergence), which may be arbitrated by both abiotic factors (i.e., tidal regime) and biotic factors (i.e., plant density).

The magnitude and duration of marsh flooding is dictated by astronomical and/or meteorological forces, and the significance of this hydrology in regulating functional roles of intertidal marsh habitats for juvenile fishes and crustaceans is recognized (Rozas 1995, Kneib 1997, Connolly 1999). Specifically, at least 5 cm of water must cover the marsh platform for shrimps, crabs, and small fishes to access the marsh platform (Minello and Rozas 2002, Minello et al. 2012). Small marsh-associated fishes such as a mummichogs, *Fundulus heteroclitus*, and California killifish, *Fundulus parvipinnis*, move onto the marsh platform during flood tide and retreat to shallow subtidal marsh creeks or marsh-enclosed pools at low tide (Talley 2000, Teo and Able 2003). Likely in response to tidally driven prey behaviors, predatory juvenile striped bass *Morone saxatilis* have been shown during ebb tide to move upstream to marsh creeks to

forage upon prey items that emerge from the marsh as the tide falls (Tupper and Able 2000). Beyond this valuable, yet cursory model of predator-prey dynamics along the marsh ecotone, few studies have explicitly examined relationships between hydrodynamics and mobile predatory fish diets, and implications for overall food web dynamics vis-à-vis trophic relay.

Abiotic forces (e.g., fire, tidal cycles, and wind) along ecotones may also influence habitat structure, and how organisms move into/out of and across habitat boundaries. For instance, higher wind speeds have been shown to disturb habitat structure along the edge of habitats decreasing the efficiency of predators, jostling tree branches decreasing prey visibility, and altering olfactory cues (Cherry and Barton 2017). Within salt marsh habitats, the regular inundation by saltwater due to tides can alter plant characteristics and the presence of certain types of plant species. For instance, in salt marshes with semi-diurnal tides (>0.75 m range) primary production has been observed to increase as tidal amplitude increases (Steever et al. 1976). Yet, little is known about how other basic marsh habitat characteristics such as plant shoot density vary with tidal amplitude and duration and its influence on nekton access and habitat use across a broader range of tidal regimes.

To better understand the mode and rate by which marsh-derived production can be exported to marine systems, we synthesized over 50 yr of research on the trophic ecology of fishes along the U.S. Atlantic and Gulf of Mexico coasts. In particular, we evaluated the strength of evidence for trophic relay across systems by quantifying how often and in what amounts marsh-platform residents occur in diets of transient estuarine predators known to forage directly upon the marsh platform and along the seaward edge of marsh habitat. Our literature synthesis explored whether marshes across biogeographic regions, representing a range of tidal and marsh characteristics, exhibited the same or different trophic connections that mediate flows of energy across the land-sea boundary. In particular, we hypothesized that the presence and quantity of marsh-associated prey in diets of transient fish predators would be positively correlated with tidal height and inversely correlated with marsh plant density.

MATERIALS AND METHODS

Database assembly for fish diets

To quantify the diets of transient estuarine predators, we conducted a literature search using ISI Web of Science between January 2017 and October 2017 adopting the following keyword searches: “marsh” AND “[geographic region]” AND “[trophic data]” AND “[predator species].” Geographic regions included (1) Gulf of Mexico (GoM), (2) South Atlantic (SA), and (3) Mid-Atlantic (MA). For our analyses, we designated the GoM as Texas to southwest Florida, the SA as southeast Florida to North Carolina, and the MA region as Virginia to southern New York (south of Long Island Sound). Our trophic data search parameters included (1) diet, (2) gut content, or (3) food webs. Predator species included (1) red drum, *Sciaenops ocellatus*, (2) spotted seatrout, *Cynoscion nebulosus*, (3) bluefish, *Pomatomus saltatrix*, (4) striped bass, *M. saxatilis*, and (5) flounders, *Paralichthys* spp. Predatory species were selected due to known utilization of marsh habitat for foraging during the estuarine portion of their life cycle (Dance and Rooker 2015). Predators had to be present within and have diet information for at least two of three regions of interest. We found data for red drum (stomach $N = 1814$) and spotted seatrout (stomach $N = 670$) in the GoM and SA; we found striped bass (stomach $N = 3699$) data in the SA and MA; finally, we collected flounders (stomach $N = 557$) and bluefish (stomach $N = 3493$) data for all three regions.

We collected data on all prey species consumed by predatory species; however, for the majority of analyses, we focused on two main prey types in diets of transient predators to evaluate key trophic links along the marsh boundary: marsh-platform fishes (i.e., killifishes: Gulf killifish *Fundulus grandis*, Mummichog *F. heteroclitus*, Striped killifish *Fundulus majalis*, Longnose killifish *Fundulus similis*, Rainwater killifish *Lucania parva*, Sheepshead minnow *Cyprinodon variegatus*, and Sailfin molly *Poecilia latipinna*) and fiddler crabs (Red-jointed fiddler crab, *Uca minax*; Sand fiddler crab, *Uca pugilator*; and Atlantic marsh fiddler crab, *Uca pugnax*). Both killifishes and fiddler crabs (marsh-platform species) are numerically dominant, closely associated with the marsh platform and adjacent tidal creeks,

typically share similar trophic levels, and therefore were grouped for analyses. Additionally, these species obtain a large amount (up to 80%) of their energy resources directly from *Spartina alterniflora* primary production (Baker et al. 2013) and marsh-platform benthic microalgae (Currin et al. 2003). In comparison, species such as grass shrimps (*Palaemonetes* sp.), penaeid shrimps, (*Farfantepenaeus* sp.), and blue crabs (*Callinectes sapidus*) utilize the marsh platform; however, they are also found across many estuarine habitats and cannot be reliably identified as marsh-platform residents. Simply, predatory species must either directly access the marsh platform to forage on marsh-platform residents, or these prey species must be flushed off the marsh platform at low tide (prey emergence) to be present in predator diets, and therefore represent key proxies of energy transfer from the marsh to the estuary (i.e., trophic transfer).

For all papers, we extracted metadata such as site, geographic region, latitude, longitude, year, month/season, and broad habitat type (e.g., shallow bay and tidal creek, if available). To describe diet composition, we observed multiple metrics across papers: total number (N), frequency of occurrence (FO), percent volume (V), and percent weight (W) of prey items. We directly extracted all diet data (predator, prey, diet metric) directly from graphs (using Datathief III, Tummers 2006) or tables within each paper. For our analyses below, we utilized the FO diet metric based on the need to have commonality across studies. Frequency of occurrence was the most prominent metric used across papers among the three geographic regions (25 of 56 papers inspected, 10,233 stomachs analyzed; see Dance and Rooker 2015). Based on interrogation of N , FO, V , and W data, we note that our primary conclusions were robust across metrics (Appendix S1: Table S1). A map of fish collection sites and a list of data sources used in the study are provided in the data sources section of the supporting information (Appendix S1: Fig. S1).

Literature search for environmental characteristics

To understand how marsh environmental characteristics differed across geographic regions, we conducted a literature search in ISI Web of Science using the following keyword searches: “marsh” AND “[geographic region]”

AND “[“marsh characteristic”].” Geographic regions included (1) GoM, (2) SA, and (3) MA. Marsh habitat characteristics included (1) shoot density, (2) shoot height, and (3) biomass. Additionally, we gathered marsh characteristic data using habitat monitoring programs from the National Estuarine Research Reserves (NERRs), which was able to provide data from Florida, Maryland, New Jersey, and North Carolina. We considered shoot density, shoot height, and total biomass as biotic characteristics of the marsh that may alter nekton access, prey refuge, and food availability for transient predators and were averaged across geographic region. We aggregated data over multiple sites and dates to best characterize marshes within a given region and time period.

Tidal data acquisition

Sixty-three National Oceanic and Atmospheric Administration (NOAA) tide and current station buoys collected tidal data between January 1983 and December 2001. We chose the nearest tidal buoy to individual fish sampling sites (from literature) or marsh characteristic sites (from literature and NERRs) for data extraction. Tidal data from NOAA buoys provide real data which considers both the astronomical and meteorological influences on tide and is the best proxy for tidal amplitude across large-scale gradients. We used the mean tidal range value for each site as a proxy for the average tidal amplitude and the periodicity of marsh flooding. According to Minello et al. (2012), marshes along the East Coast of the USA with high tidal amplitude had the highest flooding frequency and the lowest flooding duration, while GoM marshes had comparatively low amplitude, low flooding frequency, and the longest flooding durations.

Statistical analyses

To test how predator–prey interactions across the land–sea interface varied among geographic regions, we pooled diet data for the five estuarine predators because we were primarily interested in community level patterns. To compare how predatory fish diets, tidal range, and marsh characteristics varied across geographic regions, we used Kruskal–Wallis tests on how the FO of marsh-platform species (i.e., killifish and fiddler crabs) in the diets of transient predatory fishes,

tidal range, or marsh characteristics, respectively, differed broadly across geographic region. We proceeded with this non-parametric test for our univariate significance testing among regions as diet, tidal range, and marsh characteristic data were non-normally distributed even after transformations. We also investigated the relationship between tidal range (as a proxy for amplitude), which may alter nekton marsh access or prey emergence from the marsh, and the FO of marsh-platform species in the diets of transient estuarine predators. We paired diet data with tidal data from the nearest tidal gauge. Following exploratory analyses with these data pairs, we then transformed FO data to presence-absence data and used binomial logistic regression to determine a threshold in tidal range (amplitude) at which marsh-platform species begin to predictably occur in the diets of transient predatory fishes.

To elucidate differences in biogenic habitat structure broadly across geographic regions, we serially employed a Kruskal–Wallis test for shoot density, shoot height, and combined above- and below-ground biomass. For more in depth habitat analyses, we focused on the parameter of shoot density. Shoot height and total plant biomass (above- and below-ground) may not be as relevant to predator–prey interactions as density, which may have a greater influence on both predator access and/or movement and prey refuge. Several studies in seagrass habitats show that beyond a certain threshold of shoot density, predation success is significantly diminished due to increased structure for prey to hide among (reviewed by Heck and Orth 2007). We assessed the relationships between marsh plant shoot density and tidal amplitude, and marsh plant shoot density and the FO of marsh-platform species in predatory fish diets using linear regression.

To assess the differences in diet composition of transient estuarine predators among regions (including all prey species; e.g., blue crabs *C. sapidus*, brown shrimp *Farfantepenaeus aztecus*, other fishes), we employed a PERMANOVA. We used non-metric multidimensional scaling (NMDS) ordination to assess how diet composition (all prey species consumed) of all five transient predators varied across three geographic regions. We chose to include all predators into

one analysis to determine whether predator species or geographic region was more influential in determining diet composition, and in this context, each species in each publication was considered a separate entry (overall $N = 40$). Using the Vegan package in R (Oksanen et al. 2019), we conducted PERMANOVA and NMDS analyses; we ran the NMDS ordination with Bray–Curtis dissimilarity measures. For all analyses, we used R 3.5.2 (R Development Core Team 2018).

RESULTS

The FO of marsh-platform species in the diets of estuarine predators was greatly affected by geographic region ($H = 8.67$, $P = 0.01$). Marsh-platform species were rarely present in the diets of estuarine predators in the GoM ($0.10 \text{ FO} \pm 0.10$) but marsh-platform fishes and fiddler crabs appear regularly (an order of magnitude greater than the GoM) in predatory fish diets in the SA ($1.35 \text{ FO} \pm 0.83$) and MA regions ($3.55 \text{ FO} \pm 1.23$; Fig. 1). For each region, the maximum FO for marsh-platform species in the diets of transient fishes was 2.9 in the GoM, 8.91 in the SA, and 16.0 in the MA. The maximum FO observed across all predator/studies for all prey items in each region was 57.0 (striped mullet *Mugil cephalus*) in the GoM, 51.8 (menhaden *Brevoortia* spp.) in the SA, and 43.7 (sand shrimp *Crangon* spp.) in the MA.

Mean tidal range was distinct among the three regions ($H = 25.57$, $P < 0.001$). The mean tidal range was greater in both the SA ($1.15 \text{ m} \pm 0.14$) and the MA ($1.02 \text{ m} \pm 0.13$) regions than the GoM ($0.39 \text{ m} \pm 0.02$; Fig. 2A). The presence of marsh-platform species in estuarine fish diets was correlated with mean tidal range ($\chi^2 = 38.03$, $P < 0.001$; Fig. 3A). Notably, there appeared to be a threshold at approximately 1 m in tidal range where the presence of marsh-platform species began to manifest regularly in the diets of transient estuarine predatory fishes.

There was a significant difference in shoot density ($H = 531.97$, $P < 0.001$; Fig. 2B), shoot height ($H = 15.32$, $P = 0.001$), and plant biomass ($H = 44.23$, $P < 0.001$) among geographic regions. The SA region had the highest shoot density ($203.89 \text{ shoots/m}^2 \pm 6.40$), the GoM had

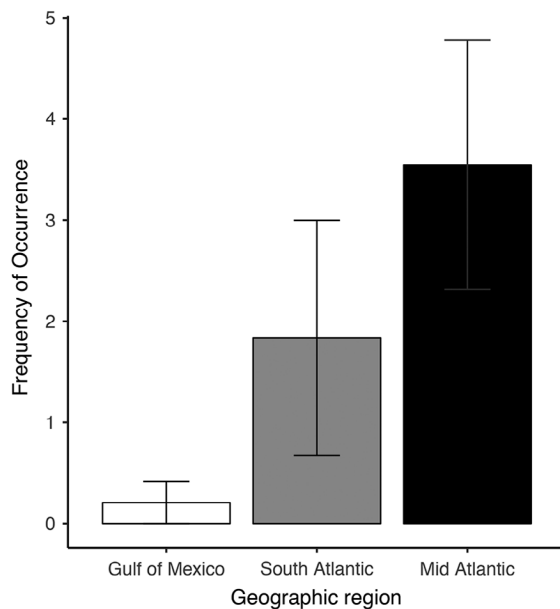


Fig. 1. Frequency of occurrence of marsh-platform species (fiddler crabs and killifish species) in the diets of predatory fish across three geographic regions: Gulf of Mexico, South Atlantic, and Mid-Atlantic. All values are means \pm standard error.

intermediate shoot density ($117.15 \text{ shoots/m}^2 \pm 14.50$), and the MA had the lowest shoot density ($111.33 \text{ shoots/m}^2 \pm 10.20$). Shoot density was positively correlated with both tidal range ($R^2 = 0.185$, $P < 0.001$; Fig. 2C) and the frequency occurrence of marsh-platform species ($R^2 = 0.011$, $P = 0.009$; Fig. 3B).

Geographic region was a significant predictor for differences among estuarine predator diet composition ($F_{2,42} = 1.76$, $R^2 = 0.077$, $P = 0.026$). A two-dimensional axis was utilized for NMDS ordinations with a stress of 0.12. Geographic region was more predictive of diet composition than species identity of estuarine predators (Fig. 4). The differences in diet composition of estuarine predators across regions were driven by the presence or absence of marsh-platform species, indicating that these prey items are significant components in diets of predatory fishes although rating relatively modest FO values. Portunid crabs (e.g., blue crabs), penaeid shrimps (e.g., brown shrimp), and microinvertebrates (e.g., amphipods) were other species that drove differences in diet structure among regions.

DISCUSSION

Our synthesis, encompassing multiple estuarine taxa across three biogeographic providences, demonstrates that numerically dominant marsh-platform fishes and crustaceans (i.e., killifishes and fiddler crabs) rarely appear in diets of estuarine fish in the GoM, while regularly appearing in gut contents in both the SA and MA regions. The presence or absence of these key marsh-platform species in transient predator diets should impact the mode and rate by which energy is moved from terrestrial (i.e., marsh) to marine systems. In these marsh systems, tidal regime and biogenic habitat structure appear to play key roles in regulating the movement of energy across ecological boundaries. Collectively, our synthesis highlights issues with simply presuming that seemingly similar habitats (across all ecosystems) function or transfer energy in the same way. Specifically, our results demystify the idea that fish universally—along all coasts—move into the marsh, obtain terrestrial-derived energy, and link that directly to the estuary or open ocean.

Hot spots for primary productivity, such as areas of upwelling or high plant biomass (e.g., mangroves, salt marshes, rainforests), are generally expected to export energy into adjacent systems (Polis et al. 1997, Heck et al. 2008). Cross-habitat movements by consumers and prey can be a key conduit for this energy flow and thus greatly affect resource dynamics at several spatial scales across terrestrial, aquatic, and marine systems. Few examples, however, document how these movements and energy flows vary across environmental gradients or large geographic scales (Lafage et al. 2019, exception Baker et al. 2013). Our results suggest that patterns of outwelling of energy from marsh habitats via trophic relay are variable across regions, ultimately driven by physical (tidal) gradients. Broadly along ecotones, changes in physical variables such as temperature, wind, or wave action may influence cross-habitat foraging and spatial subsidies. For example, increased riverine discharge (resulting from high precipitation) has been shown to alter food chain length and result in exportation of more aquatic subsidies to downstream communities (Sabo et al. 2010).

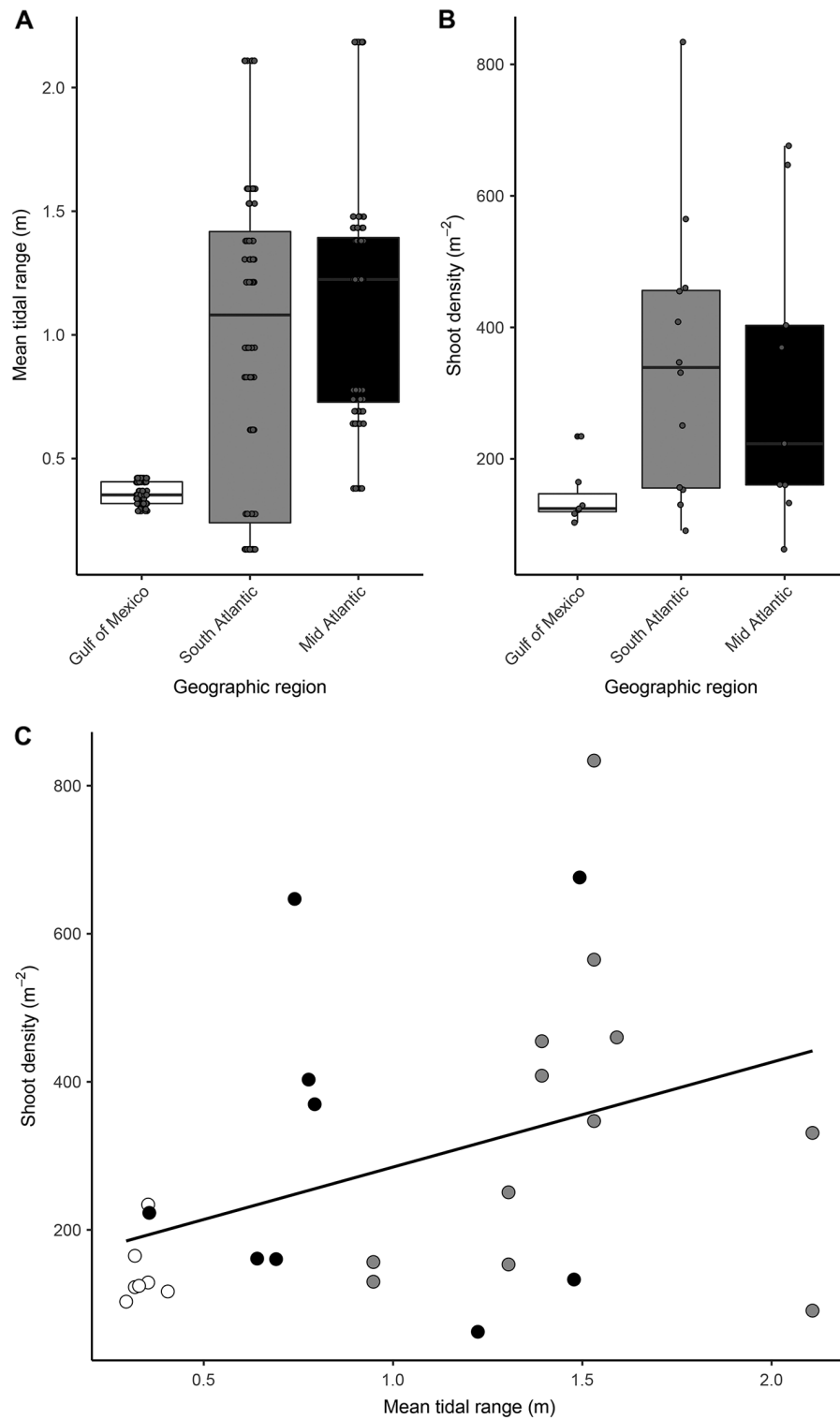


Fig. 2. Marsh habitat characteristics aggregated across three regions of interest: Gulf of Mexico, South Atlantic, and Mid-Atlantic. Habitat variables include (A) tidal range and (B) shoot density. Values are means \pm standard error. *Spartina alterniflora* (C) shoot density as a function of mean tidal range. Values are mean data.

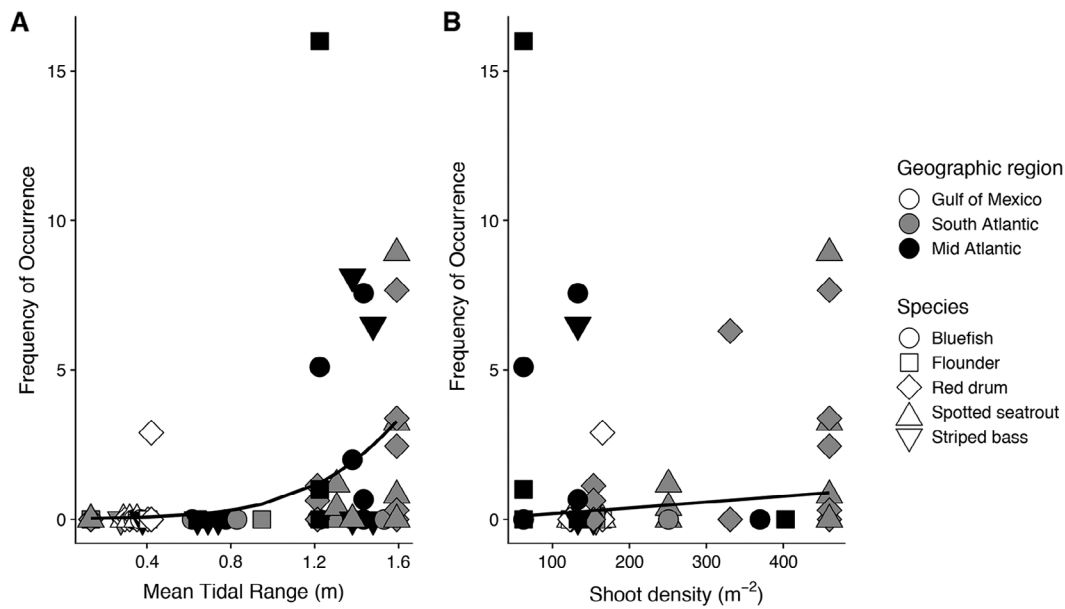


Fig. 3. Frequency of occurrence of marsh-platform species in the diets of predatory fish as a function of marsh habitat characteristics: (A) tidal range and (B) shoot density. Frequency of occurrence data is raw values for each site and predator species. Habitat characteristics are means for a given site per predator species. Solid black lines represent statistical analyses conducted on data (A) binomial regression and (B) linear regression.

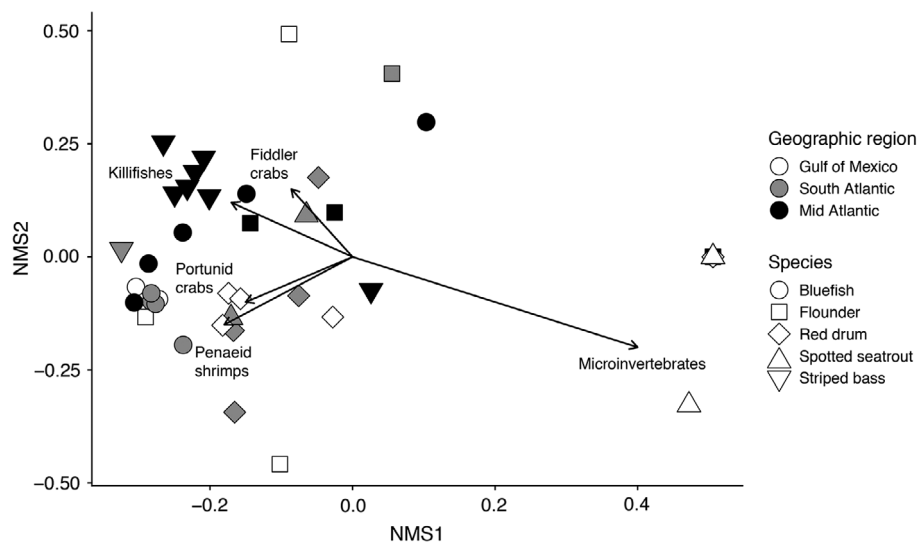


Fig. 4. Non-metric multidimensional scaling ordination of predator species diets was conducted to visualize the dissimilarity between diet composition for a given predator species across the Gulf of Mexico, South Atlantic, and Mid-Atlantic regions. Arrows indicate specific prey taxa driving observed trend.

In SA and MA regions, the traditional marsh outwelling hypothesis via trophic relay appears supported by our findings, while in the GoM,

marsh outwelling through direct trophic interactions involving marsh-platform resident fishes and fiddler crabs does not appear evident. Our

findings do not indicate that transient predators are eating less overall in the GoM, but are not eating resident prey that are most closely linked to the marsh platform. Therefore, in the GoM, we propose that three alternative dynamics are possible: (1) Marsh-derived carbon is not a dominant basal energy source for transient estuarine fish predators; (2) marsh-derived carbon is transferred via transient invertebrate prey (e.g., shrimp and crabs) as opposed to marsh-platform residents, or (3) indirect trophic linkages drive outwelling of marsh energy.

Our results demonstrate that marsh outwelling via direct predator–prey interactions of marsh-platform prey is severely dampened in areas with low tidal amplitude such as the GoM, yet we recognize the GoM is an extremely productive ecosystem. Several factors—beyond energy flow from marsh habitat—may contribute to reconciling this potential contradiction. First, the northern GoM has high nutrient input from riverine sources that support enhanced water-column production of phytoplankton that can serve as another key basal carbon source for transient estuarine fishes (ultimately leading to an extensive hypoxic region south of LA as excess production sinks out of the water column and is metabolized; Turner and Rabalais 1994). Indeed, eutrophication typically shifts coastal food webs toward relative dominance of water-column trophic interactions, and depending on the spatial arrangement, predictability, and persistence of favorable conditions can result in productive coastal fish assemblages (Breitburg 2002; but also see Micheli 1999). Second, marsh erosion currently outpaces marsh accretion in many regions, including the GoM (Kennish 2001), leading to the injection of buried marsh carbon into the open estuary and incorporation into marine food webs (Theuerkauf et al. 2015). In combination with high temperatures allowing for rapid incorporation of labile carbon, these nutrient inputs may subsidize GoM transient estuarine predators and substitute for the role of marsh outwelling. Similarly, Deegan and Garritt (1997) recognized that hydrology might alter the relative importance of phytoplankton vs. macrophytes (e.g., *S. alterniflora*) in serving as the primary source of fixed carbon for estuarine food webs. Conversely, in the GoM, marsh edge-to-area ratio is tightly correlated with the production of penaeid shrimp

(Peterson and Turner 1994). Our analyses confirm that shrimp and portunid crabs do occur regularly in the diets of estuarine predators in the GoM, and these crustaceans (at small sizes; <60 mm) may be key vectors of energy transfer between the marsh platform and transient estuarine predators (Baker et al. 2013). However, we also note that large portunid crabs may forage directly upon marsh-platform fishes and fiddler crabs (McCann et al. 2017) or rely on marsh habitat structure primarily for refuge rather than food acquisition (sensu Boesch and Turner 1984, Heck et al. 2003), emphasizing uncertainty in outwelling dynamics along marsh ecotones.

In the absence of direct trophic linkages between numerically dominant marsh-platform species and transient predators in the GoM, direct consumption of small transient invertebrate prey or indirect trophic pathways may account for marsh carbon export to the open estuary. In the GoM, portunid crabs and penaeid shrimps will aggregate at the marsh-estuarine boundary during extended marsh flooding to forage on marsh production while still accessible to large transient fish predators (Minello et al. 2008). While blue crabs and penaeid shrimp are well documented in diets of transient predators and may directly transfer marsh energy at small sizes, they can also be important predators within marshes and may act as intermediates in marsh energy transfer (Minello et al. 2012). To the degree that intermediates such as large blue crabs and penaeid shrimp are integral energy conduits, an extra link in GoM food chains between marsh-platform residents and transient predatory fishes has important implications regarding net trophic transfer to higher consumers in estuarine systems (even if feeding rates, i.e., average stomach fullness, are equal across regions). In particular, for each additional node added to a food chain, there is approximately a 90% decrease in the amount of biomass accumulated by the next trophic level, due to energy lost as metabolic waste, reducing overall ecosystem productivity (Lindeman 1942, Christensen and Pauly 1992). As noted above, shrimp and blue crabs in the diets of estuarine fishes do not confirm that marsh-derived production is supporting large estuarine fishes, as shrimp and blue crabs are widely distributed throughout estuaries and may exploit other sources of basal

carbon (e.g., seagrass; Hyndes et al. 2014). This point further emphasizes why marsh residents such as killifishes and fiddler crabs may represent key conduits of marsh-derived energy, compared with other prey items common in diets of mobile estuarine predators.

Underpinning the food web patterns we observed, tide likely regulates the magnitude of outwelling of primary productivity via trophic transfer as tidal amplitude can dictate the means or functional groups by which energy is transferred off-platform. The conceptual model of energy flow out of marshes relayed by trophic interactions was formalized by Kneib (1997), who examined trophic dynamics in the SA at Sapelo Island, Georgia, USA. Notably, Sapelo Island is an area with large expanses of *S. alterniflora* marsh with high primary productivity, relatively large tidal range (~2 m; Steever et al. 1976), and relatively deep and regular marsh flooding. Based on our synthesis findings, our own long-term observations, and available tracking data (Rountree and Able 1992, Szedlmayer and Able 1993, Fodrie et al. 2015), we speculate that large transient predators such as red drum and bluefish can access the marsh platform only at higher water amplitudes/inundation depths, such as along coastal GA, while smaller taxa, such as shrimps and crabs, are able to use the platform at shallower inundation depths (>5 cm; Minello et al. 2012). Thus, energy flow through trophic interactions of marsh-platform prey may be reduced or impeded due to low habitat connectivity via predator and prey movements in areas of low tidal amplitude (<1 m) or wind-driven systems with erratic flooding (i.e., GoM). Similarly, Byers et al. (2017) examined the ability of bonnethead sharks (*Sphyrna tiburo*) to access intertidal oyster reefs along a tidal gradient and found that in areas of high tidal amplitude (~2 m mean tidal range) these large predators easily accessed the reefs to forage; however, this did not hold true in areas with lower tidal amplitude (<1.5 m mean tidal range).

Tidal amplitude may have both direct effects on predator–prey encounter rates at the land–sea interface and indirect effects via mediation of biogenic habitat structure. Biological features along ecotones such as changing plant structure may act as a physical barrier that alters the ability of large-bodied predators to easily move

through a given habitat, thus inhibiting the flow of energy from one habitat to an adjacent one. For example, spiders foraging along the shore of the Baltic Sea tend to have lower aquatic-based energy subsidies on shorelines with reeds than on shorelines with no plant structure (Hambäck et al. 2016). On bare shoreline, spiders are able to forage upon aquatic larvae (with marine-derived energy) but on reedy shorelines the spiders can no longer access this prey resource, thus shifting its diet to more terrestrial-based prey items. Following this example, we would have expected marsh shoot density to be negatively correlated with FO of marsh residents in the diets of transient fishes due to the typically dampening effect of increased structural complexity on predation (sensu Heck and Crowder 1991). Surprisingly, our results indicate that areas with higher shoot densities display characteristically higher numbers of marsh-associated species in the diets of transient fish, and due to relatively low sample size and high variability among sites, may not be ecologically relevant. Alternatively, a positive relationship between the FO of marsh-platform species and shoot density may be due to the positive correlation between tidal amplitude and shoot density, indicating the primacy of abiotic forcing, such as tidal amplitude and periodicity, relative to biogenic structural complexity, in regulating spatial energy flows in our study system.

Understanding the dynamics of energy flow from marshes to the estuary is vital with continuing landscape change and marsh loss. Marsh habitats are being depleted at high rates globally, with >40% of marshes in the USA already degraded or destroyed (Gedan and Silliman 2009). This depletion is especially important in the GoM with marsh habitats subsidizing while sea levels continue to rise (Alizad et al. 2016). If primary production from marshes is transferred with less efficiency in the GoM in part due to the lack of regular and deep marsh flooding, we may see unique, temporary, and non-intuitive dynamics with regard to marsh-derived secondary production in GoM estuaries in response to continued or accelerated global change. As coastal habitats continue to be degraded and impacted by a variety of anthropogenic activities (e.g., Deepwater Horizon Oil Spill; McCann et al. 2017), it is crucial that we develop a stronger

understanding of food web dynamics and energy flows across regional scales to have increased predictive power regarding the vulnerability or resilience of coastal ecosystems to anticipated future perturbations.

ACKNOWLEDGMENTS

We would like to thank Cori Lopanzanski for assistance with marsh habitat data collection and Danielle, Keller, Lewis Naisbett-Jones, Dr. Pete Peterson, and two anonymous reviewers for valuable comments that improved this manuscript. This study was supported by funding from North Carolina, Division of Marine Fisheries Coastal Recreational Fish License (CRFL) Marine Resources Fund, a grant from NSF Division of Environmental Biology (1926395), and by a grant from the Gulf of Mexico Research Initiative to the Coastal Waters Consortium. Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC; <https://doi.org/10.7266/n7-mw9x-0y68>).

LITERATURE CITED

- Alizad, K., S. C. Hagen, J. T. Morris, S. C. Medeiros, M. V. Bilskie, and J. F. Weishampel. 2016. Coastal wetland response to sea-level rise in a fluvial estuarine system: Wetland response to SLR. *Earth's Future* 4:483–497.
- Baker, R., B. Fry, L. P. Rozas, and T. J. Minello. 2013. Hydrodynamic regulation of salt marsh contributions to aquatic food webs. *Marine Ecology Progress Series* 490:37–52.
- Ben-David, M., R. W. Flynn, and D. M. Schell. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111:280–291.
- Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7:460–468.
- Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25:767–781.
- Byers, J. E., Z. C. Holmes, and J. C. Malek. 2017. Contrasting complexity of adjacent habitats influences the strength of cascading predatory effects. *Oecologia* 185:107–117.
- Cherry, M. J., and B. T. Barton. 2017. Effects of wind on predator-prey interactions. *Food Webs* 13:92–97.
- Christensen, V., and D. Pauly. 1992. ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61:169–185.
- Connolly, R. M. 1999. Saltmarsh as habitat for fish and nektonic crustaceans: challenges in sampling designs and methods. *Australian Journal of Ecology* 24:422–430.
- Curran, C., S. C. Wainright, K. W. Able, M. Weinstein, and C. M. Fuller. 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.
- Dance, M. A., and J. R. Rooker. 2015. Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. *Estuarine, Coastal and Shelf Science* 167:447–457.
- Deegan, L. A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences* 50:74–79.
- Deegan, L., and R. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series* 147:31–47.
- Eppley, R. W., and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282:677.
- Fodrie, F. J., L. A. Yeager, J. H. Grabowski, C. A. Layman, G. D. Sherwood, and M. D. Kenworthy. 2015. Measuring individuality in habitat use across complex landscapes: approaches, constraints, and implications for assessing resource specialization. *Oecologia* 178:75–87.
- Gedan, K. B., and B. R. Silliman. 2009. Patterns of salt marsh loss within coastal regions of North America: presettlement to present. Pages 253–266 in *Human impacts on salt marshes: a global perspective*. University of California Press, Berkeley, California, USA.
- Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific Salmon in Aquatic and Terrestrial Ecosystems: Pacific salmon subsidize freshwater and terrestrial ecosystems through several pathways, which generates unique management and conservation issues but also provides valuable research opportunities. *BioScience* 52:917–928.
- Hambäck, P. A., E. Weingartner, L. Dalén, H. Wirta, and T. Roslin. 2016. Spatial subsidies in spider diets vary with shoreline structure: complementary evidence from molecular diet analysis and stable isotopes. *Ecology and Evolution* 6:8431–8439.
- Hansen, A. J. 1987. Regulation of bald eagle reproductive rates in southeast Alaska. *Ecology* 68:1387–1392.
- Heck, K. L., T. J. B. Carruthers, C. M. Duarte, A. R. Hughes, G. Kendrick, R. J. Orth, and S. W. Williams. 2008. Trophic transfers from seagrass

- meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11:1198–1210.
- Heck, K. L., and L. B. Crowder. 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. Pages 281–299 in S. S. Bell, E. D. McCoy, and H. R. Mushinsky, editors. *Habitat structure: the physical arrangement of objects in space*. Springer, Dordrecht, The Netherlands.
- Heck, K. L., G. Hays, and R. J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123–136.
- Heck Jr., K. L., and R. J. Orth. 2007. Predation in seagrass beds. In *Seagrasses: biology, ecology, and conservation*. Springer, Dordrecht, The Netherlands.
- Hyndes, G. A., I. Nagelkerken, R. J. McLeod, R. M. Connolly, P. S. Lavery, and M. A. Vanderklift. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biological Reviews* 89:232–254.
- Ibañez, C., A. Curco, J. W. Day, and N. Prat. 2000. Structure and productivity of microtidal Mediterranean coastal marshes. Pages 107–136 in M. P. Weinstein and D. A. Kreeger, editors. *Concepts and controversies in tidal marsh ecology*. Springer, Dordrecht, The Netherlands.
- Kennish, M. J. 2001. Coastal salt marsh systems in the U.S.: a review of anthropogenic impacts. *Journal of Coastal Research* 17:731–748.
- Kneib, R. T. 1997. Early life stages of resident nekton in intertidal marshes. *Estuaries* 20:214–230.
- Kneib, R. T. 2002. Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. Pages 267–291 in M. P. Weinstein and D. A. Kreeger, editors. *Concepts and controversies in tidal marsh ecology*. Springer, Dordrecht, The Netherlands.
- Lafage, D., E. Bergman, R. L. Eckstein, E. M. Österling, J. P. Sadler, and J. J. Piccolo. 2019. Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: a worldwide meta-analysis. *Ecosphere* 10:e02697.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–417.
- McCann, M. J., et al. 2017. Key taxa in food web responses to stressors: the Deepwater Horizon oil spill. *Frontiers in Ecology and the Environment* 15:142–149.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285:1396–1398.
- Minello, T. J., G. A. Matthews, P. A. Caldwell, and L. P. Rozas. 2008. Population and production estimates for decapod crustaceans in wetlands of Galveston Bay, Texas. *Transactions of the American Fisheries Society* 137:129–146.
- Minello, T. J., and L. P. Rozas. 2002. Nekton in Gulf Coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12:441–455.
- Minello, T. J., L. P. Rozas, and R. Baker. 2012. Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. *Estuaries and Coasts* 35:501–514.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences USA* 98:166–170.
- Nelson, J., R. Wilson, F. Coleman, C. Koenig, D. Devries, C. Gardner, and J. Chanton. 2012. Flux by Fin: fish-mediated carbon and nutrient flux in the north-eastern Gulf of Mexico. *Marine Biology* 159:365–372.
- Odum, E. P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling, and detritus-based food chains. Pages 485–495 in V. S. Kennedy, editor. *Estuarine perspectives*. Academic Press, Cambridge, Massachusetts, USA.
- Oksanen, J., et al. 2019. *vegan: community ecology package*. R package version 2.5-4. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Peterson, G. W., and R. E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17:235–262.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147:396–423.
- R Core Team. 2018. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reimchen, T. E. 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. *Canadian Journal of Zoology* 78:448–457.
- Rountree, R. A., and K. W. Able. 1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. *Transactions of the American Fisheries Society* 121:765–776.
- Rozas, L. P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18:579–590.

- Sabo, J. L., J. C. Finlay, T. Kennedy, and D. M. Post. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* 330:965–967.
- Steever, E. Z., R. S. Warren, and W. A. Niering. 1976. Tidal energy subsidy and standing crop production of *Spartina alterniflora*. *Estuarine and Coastal Marine Science* 4:473–478.
- Szedlmayer, S. T., and K. W. Able. 1993. Ultrasonic telemetry of age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. *Copeia* 1993:728–736.
- Talley, D. M. 2000. Ichthyofaunal utilization of newly-created versus natural salt marsh creeks in Mission Bay, CA. *Wetlands Ecology and Management* 8:117–132.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624.
- Teo, S. L. H., and K. W. Able. 2003. Habitat use and movement of the mummichog (*Fundulus heteroclitus*) in a restored salt marsh. *Estuaries* 26:720–730.
- Theuerkauf, E. J., J. D. Stephens, J. T. Ridge, F. J. Fodrie, and A. B. Rodriguez. 2015. Carbon export from fringing saltmarsh shoreline erosion overwhelms carbon storage across a critical width threshold. *Estuarine, Coastal and Shelf Science* 164:367–378.
- Tummers, B. 2006. DataThief II. Based on DataThief. <https://datathief.org/>
- Tupper, M., and K. W. Able. 2000. Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. *Marine Biology* 137:1049–1058.
- Turner, R. E., and N. N. Rabalais. 1994. Coastal eutrophication near the Mississippi river delta. *Nature* 368:619–621.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2980/full>