

## COASTAL AND MARINE ECOLOGY

# Individual consumer movement mediates food web coupling across a coastal ecosystem

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**Abstract.** The movement and foraging patterns of consumers are a major driver of nutrient and energy distribution in ecosystems. However, relatively little is known about how intraspecific variation in consumer movement behavior might affect food web coupling and ecosystem processes across landscapes and seascapes. Here we use long-term acoustic telemetry and stable isotope niche metrics to understand how differences in predatory fish movement patterns control food web coupling and resource subsidies across the Florida Coastal Everglades (USA). We found common snook (*Centropomus undecimalis*) that spent most of their time in freshwater riverine areas of the Shark River Estuary primarily foraged on prey subsidies originating from adjacent marsh habitats, serving as an important vector of nutrient subsidies to downstream habitats. Snook that spent the majority of their time in downstream estuarine habitats displayed a diversity of resource usage across wide spatial scales, occupied a much larger trophic niche, and serve as a multidirectional vector of trophic coupling among marine, estuarine, and freshwater riverine habitats. These results demonstrate how individual variations in predator movement behavior can mediate the direction and scale of food web subsidies across coastal seascapes.

**Key words:** acoustic telemetry; common snook; Everglades; mixing models; movement; stable isotopes; trophic niche.

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## INTRODUCTION

Consumer foraging and movement behavior are inherently linked and critical to the stability of ecosystems. Consumer movement couples energy channels across landscapes and smooth fluctuations in resource availability by responding to changes in productivity (McCann et al. 2005, Rooney et al. 2006, 2008). These types of trophic connections are known as spatial food

web subsidies, as consumers use resources generated across a large spatial gradient and subsidize the production of local food webs (Ben-David et al. 1997, Polis et al. 1997, Nelson et al. 2013). These subsidies are concentrated in consumer biomass and transported to other food webs through excreta, gamete release, predation mortality, or carcasses (Flecker et al. 2010). Spatial subsidies exert important controls on trophic dynamics across systems; prey subsidies can

drive predator abundance beyond what donor habitats can support, and consumer subsidies can augment top-down effects by exploiting local resources (Polis et al. 1997).

Understanding the role of animals in the transfer of trophic subsidies across coastal seascapes requires information on the patterns of faunal space use over time (Pittman 2018). Consumer-mediated nutrient subsidies differ from physically mediated nutrient subsidies (e.g., current, wind) in that they can transport nutrients counter to abiotic gradients, respond to self-generated patterns of nutrient distribution, and be modified by interactions with other consumers (McInturf et al. 2019). These features can generate feedback loops and form patterns in the distribution of nutrients across seascapes that influence ecological function (McInturf et al. 2019). The movement and foraging patterns that mediate food web coupling can vary widely within species due to the diverse array of behavioral traits that underlie intraspecific differences within populations (e.g., personality-dependent dispersal; Cote et al. 2010). Trophic niche variation among individuals of a species is widespread (Bolnick et al. 2003), and research has shown that accounting for behavioral diversity can be essential for evaluating food web subsidies across coastal systems (Allgeier et al. 2020).

Common snook (*Centropomus undecimalis*) is a tropical euryhaline fish species distributed from Florida to Brazil (Taylor et al. 1998). Snook are obligate marine spawners that typically spend 40–70 d during April–September in coastal environments before migrating to inland estuarine or freshwater habitats, although these movement behaviors vary substantially among individuals, with many snook remaining in coastal or inland habitats at annual scales (Lowerre-Barbieri et al. 2014, Blewett et al. 2017, Boucek et al. 2017). In the Florida Coastal Everglades, snook are known to forage on a seasonal prey subsidy (e.g., *Lepomis* spp.) that moves from the shallow freshwater marshes to deeper oligohaline headwater riverine channels as marshes dry down during seasonal low water levels (Rehage and Loftus 2007, Boucek and Rehage 2013, Boucek et al. 2016). Previous research on snook movement has shown that many individuals migrate from areas lower in the estuary into the upstream headwaters of the system where the prey subsidy occurs,

although there is a substantial amount of variation in snook movement patterns during these periods (Matich et al. 2017, Boucek et al. 2017).

While there may be a number of factors that regulate the effect of this prey subsidy to down-estuary food webs, a critical factor is the movement of snook, how efficiently these consumers access marsh prey, and the implications for spatial food web coupling across the freshwater marsh, estuarine, and marine habitat boundaries. If the variation in snook movement patterns alters the degree to which they access the freshwater marsh prey subsidy, it may have consequences for food webs and ecological processes downstream in the coastal riverine system. The primary objective of this study is to understand how differences in individual snook movement behavior alter spatial food web subsidies between freshwater marshes and the lower estuarine and marine portions of the Everglades using a combination of acoustic telemetry and stable isotope analysis. Specifically, we investigate potential differences in resource use and trophic niche space among snook that exhibit different scales of movement within a coastal riverine system. We hypothesized that variation in movement strategies between individuals will modify the scales of trophic coupling across the seascape.

## MATERIALS AND METHODS

The Shark River Estuary (SRE) is a coastal river system that flows through red mangrove (*Rhizophora mangle*) fringed marshes in the southwestern region of Everglades National Park and is within the study domain of the Florida Coastal Everglades (FCE) Long-term Ecological Research (LTER) site in Southern Florida, USA. The SRE drains approximately 1700 km<sup>2</sup> and is characterized by three ecologically distinct regions (Fry and Smith 2002, Saha et al. 2012, Fig. 1). These regions consist of a freshwater system and two brackish estuarine systems. The upper river (river km >23) is an oligohaline system with 2–50 m wide creek channels that are typically <3 m deep and bordered by mangroves surrounded by freshwater, sawgrass-dominated marsh (*Cladium* sp.). For the snook movement and prey data described below, we refer to sites in this section of the river as

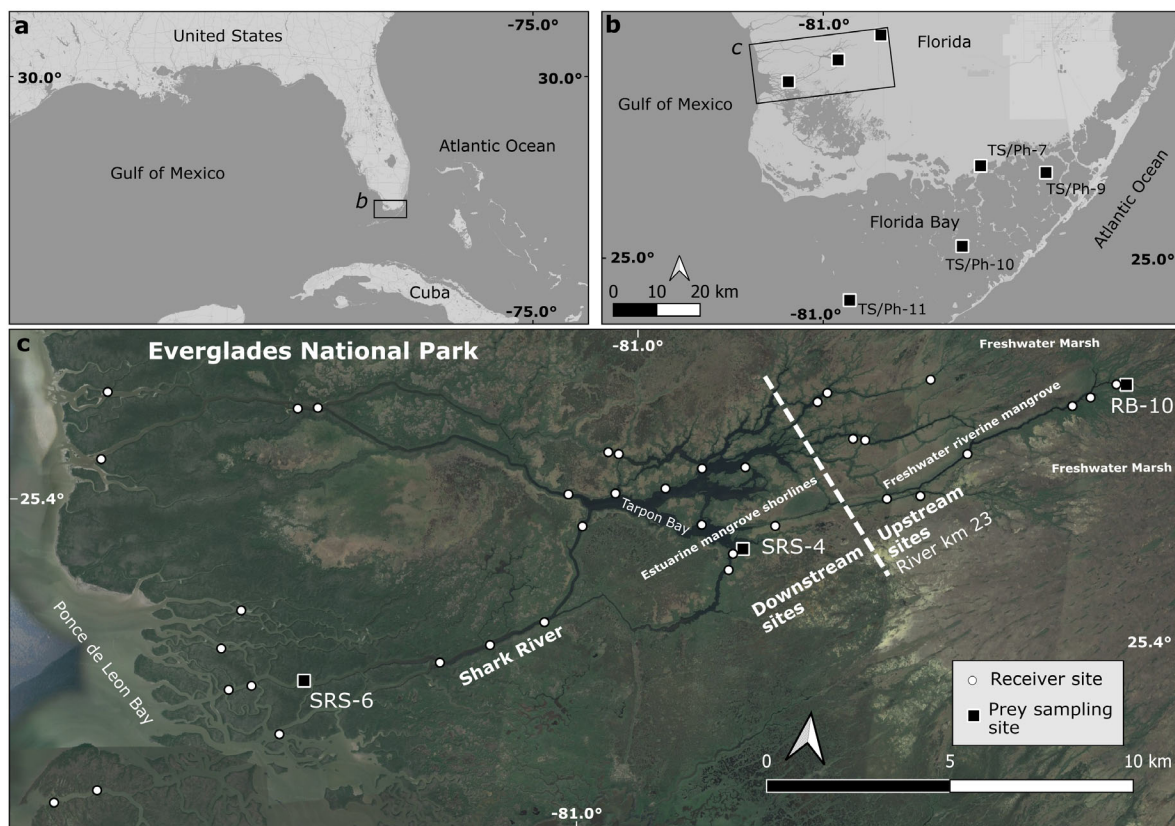


Fig. 1. Map of the study region (a), marine prey sampling sites in Florida Bay (b), and upstream and downstream receiver and prey sampling sites in the Shark River Estuary (c). This figure was created with QGIS v3.1 (qgis.org).

upstream. The Tarpon Bay section of the river (river km 15–23) is 500 m wide with seasonally fluctuating brackish salinities and soft muddy bottoms with some submerged aquatic vegetation. The lower river (river km <15) is typically 3–5 m deep and is heavily influenced by the adjacent marine environment with salinities ranging from 10 to 35 seasonally (Rosenblatt and Heithaus 2011, Boucek and Rehage 2013, Matich et al. 2017, Massie et al. 2019). For snook movement and prey sampling described below, we refer to Tarpon Bay and the lower river areas as downstream sites (Fig. 1c). The Shark River Estuary is north of Florida Bay, a shallow-water marine system of interconnected basins that support expansive seagrass habitat. The SRE and Florida Bay are considered oligotrophic and phosphorus limited, exhibiting a gradient of increased productivity with greater marine influence (Childers 2006).

To examine variation in snook movement patterns, we conducted acoustic telemetry monitoring between 2012 and 2018. All snook were captured and tagged with boat-based electrofishing in Tarpon Bay and the upstream headwaters SRE using the methods outlined in Boucek and Rehage (2013). Each snook was implanted with an acoustic transmitter (69 kHz V13 or V16, Vemco, Halifax, Nova Scotia, Canada) following standard surgical procedures (Lowerre-Barbieri et al. 2014, Massie et al. 2019). The tagged fish positions were monitored using an array of 37 VR2W receivers (Vemco, Halifax, Nova Scotia, Canada) positioned 1–3 km apart using a gated design (Matich et al. 2017, Massie et al. 2019, Fig. 1c). Standard length was measured for all tagged snook, and anal fin clips were taken for stable isotope analysis. The movement patterns of tagged snook were categorized by the proportion of detections (aggregated by hour) occurring

in upstream vs. downstream SRE receiver sites (Fig. 1). We considered the oligohaline upriver reaches of the headwaters 23 km or greater from the river mouth to be upstream sites with 11 receivers, and the mesohaline to marine regions <23 km from the river mouth to be downstream sites with 26 receivers (Fig. 1c). These designations were based on productivity, salinity, fish community, and geomorphological differences between the two zones (Boucek et al. 2017). The movement patterns of individuals with >50% of their detections occurring in upstream sites were classified as upstream snook, and those with more than 50% detections in the downstream estuarine areas were classified as downstream snook. Fish with fewer than 60 d between first and last detection were omitted from the analysis. A total of 74 snook were used for analysis, and the average ( $\pm$  SD) detection timeframe for tagged snook analyzed was  $490 \pm 362$  d. The care of animal subjects was in accordance with institutional guidelines (IACUC-18-002-CR01).

To examine the spatial isotopic variation of the prey base among potential snook foraging habitats, we sampled the coastal prey base between March and April (peak of the dry season) of 2019 at 3 sites along the SRE and 4 sites in Florida Bay encompassing freshwater, estuarine, and marine prey (Fig. 1b, c). Freshwater prey species inhabiting the upper SRE headwaters (RB-10; Fig. 1c) were collected using the same electrofishing methods outline above for snook (Boucek and Rehage 2013). As shown by previous work, these prey originate from the freshwater marsh and pulse into the SRE headwater creeks and mainstem as surrounding marshes dry—driving the movement of euryhaline predators, including snook (Boucek and Rehage 2013, Matich and Heithaus 2014, Boucek et al. 2016). At all other sites, prey species were collected with 5 replicate 1-m<sup>2</sup> throw trap samples in 1–1.5 m water depth, supplemented with hand net collections. Estuarine prey samples were taken along mangrove shorelines in downstream reaches of the SRE (SRS-4 and SRS-6; Fig. 1c), while marine prey samples were collected from Florida Bay (three TS/Ph sites; Fig. 1b) over seagrass beds, which serve as important foraging habitat for snook (Boucek et al. 2017). All small-bodied fish and decapods (<8 cm total length) were retained for stable isotope analysis. Isotope values are

expressed in standard  $\delta$  notation (Peterson and Fry 1987), using PeeDee Belemnite (PDB), atmospheric nitrogen, and Canyon Diablo Troilite (CDT) as reference standards. See Appendix S1 for details on stable isotope analysis methods.

The relative contribution of each spatially distinct prey base (freshwater, estuarine, and marine prey) to snook was derived through Bayesian mixing models (Parnell et al. 2010, Wilson et al. 2010). All stable isotope data were analyzed in R (v 3.6.2; R Development Core Team) using the package MixSIAR (v 3.1.0; Semmens et al. 2013). Models were run in three chains with 1,000,000 iterations and a burn-in of 500,000 to allow for adequate model convergence. Trophic fractionation factors of  $1.3 (\pm 0.3)$ ,  $3.3 (\pm 0.26)$ , and  $0.5 (\pm 0.54)$  were used for C, N, and S, respectively (McCuthchan Jr et al. 2003, Wilson et al. 2017). Using the source contributions determined by the mixing model, we calculated the trophic position of each fish according to the following formula:

$$TP = \frac{\delta^{15}N_{ind} - \sum(\delta^{15}N_{source} \times \text{mean \%Cont}_{source})}{\Delta\delta^{15}N} + 1$$

where  $\Delta\delta^{15}N = 3.3\text{‰}$  (McCuthchan et al. 2003),  $\delta^{15}N_{ind}$  is the nitrogen value of an individual consumer,  $\delta^{15}N_{source}$  is the nitrogen value of each particular food source, and mean %cont<sub>source</sub> is the mean proportional contribution of each source to the consumer diet (Wilson et al. 2010, Nelson et al. 2015). This gives the trophic position relative to the prey base endmembers in the mixing model and not absolute trophic position.

The results of mixing models estimate the contribution of each of the three prey sources to each snook sampled and tracked during the study. Together, these distributions represent the fish's diet as a series of numerically calculated vectors, which incorporates error present from isotopic measurement and/or ecological variability (Newsome et al. 2012). Trophic position separates consumers in resource use space by the number of trophic steps between prey sources and consumers. The means of these posterior distributions from each prey base to each snook along with its calculated trophic position were z-transformed before hypervolume analysis to allow for standardized, comparable axes in n-dimensional space (Blonder et al. 2014). We used the

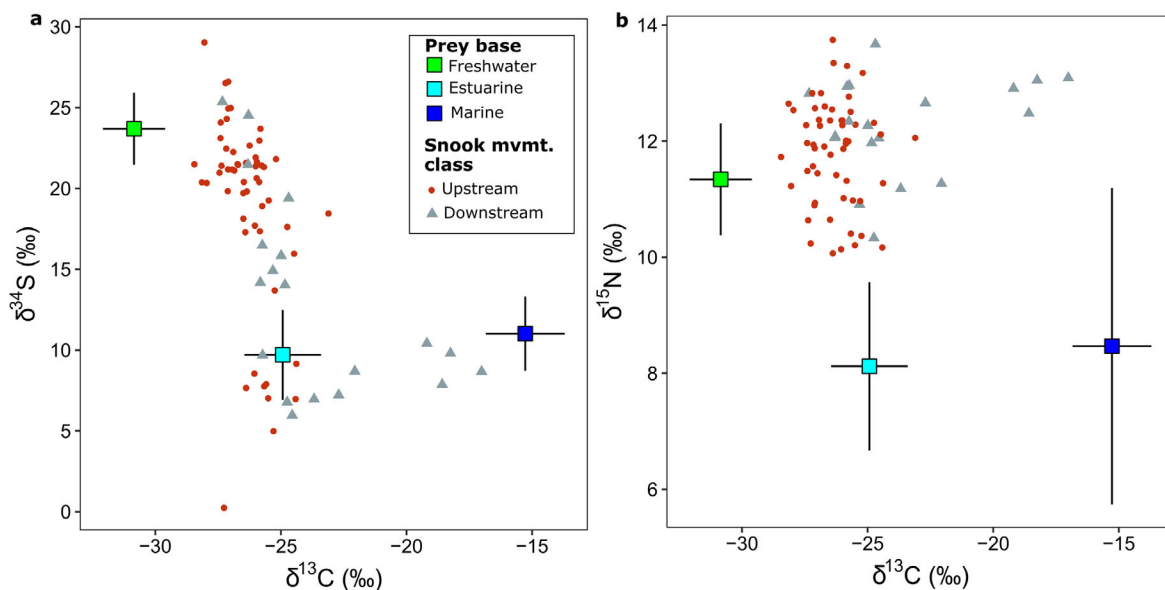


Fig. 2. Carbon/sulfur (a) and carbon/nitrogen (b) stable isotope values of the prey base (mean  $\pm$  SD) from each habitat sampled, and individual snook classified by their movement patterns based on acoustic telemetry data.

Hypervolume R package (v 2.0.12) to seed a Gaussian kernel density estimation, that generated a cloud of points based on the distribution of the z-scored values along the 4 axes that define the multidimensional trophic niche of the species (Blonder et al. 2014, Wilson et al. 2017, James et al. 2019). The quantile threshold used was 0.05, so that each hypervolume included 95% of the total probability density (Blonder et al. 2014). The hypervolumes generated for each snook movement class allow for the comparison of their trophic niche space as a function of their dietary contributions from three spatially distinct prey bases (freshwater, estuarine, and marine) and trophic levels. The fraction of unique hypervolume space for each snook movement class and the percent overlap among group hypervolumes (Sorenson similarity) are reported (Blonder et al. 2014).

## RESULTS

Mean  $\delta^{34}\text{S}$  values of prey taxa ranged from 18.4‰ to 25.8‰ in freshwater ( $n = 8$ ), 7.3–15.4‰ in estuarine ( $n = 7$ ), and 7.5–15.0‰ in marine habitats ( $n = 9$ ; Fig. 2a; Appendix S2: Table S1). Prey  $\delta^{13}\text{C}$  values ranged from  $-32.2\text{‰}$  to  $-27.9\text{‰}$  in freshwater,  $-27.9\text{‰}$  to  $-22.9\text{‰}$  in estuarine, and  $-18.6\text{‰}$  to  $-13.6\text{‰}$  in

marine habitats (Fig. 2a, b). Prey  $\delta^{15}\text{N}$  values ranged from 9.9‰ to 12.8‰ in freshwater, 5.4‰ to 9.7‰ in estuarine, and 4.3‰ to 11.6‰ in marine habitats (Fig. 2b). The  $\delta^{34}\text{S}$ ,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  values of upstream snook ranged from 0.3‰ to 29.1‰,  $-28.4\text{‰}$  to  $-23.1\text{‰}$ , and 10.1‰ to 13.8‰, respectively, and ranged from 6.0‰ to 25.4‰,  $-27.3\text{‰}$  to  $-17.0\text{‰}$ , and 10.3‰ to 13.7‰ for downstream snook, respectively (Fig. 2a, b).

Of 74 individual snook evaluated in this study, 55 (74%) were classified by their movement patterns as upstream snook and 19 (26%) were classified as downstream snook. Individuals classified as upstream snook had a median of 95% of detections occurring in the upstream freshwater portion of the estuary compared with 16% for fish classified as downstream snook (Fig. 3a). The median standard length for upstream snook was 59 and 68 cm for downstream snook at the time of tagging (Fig. 3b). The proportion of detections occurring upstream was negatively correlated with snook standard length (Spearman's  $\rho = -0.48$ ;  $P < 0.001$ ; Appendix S2: Fig. S1). Upstream snook had median dietary contributions of 3% for marine prey, 25% for estuarine prey, and 69% for freshwater prey (Fig. 3c). The median resource contributions for downstream snook were 7% for marine prey,

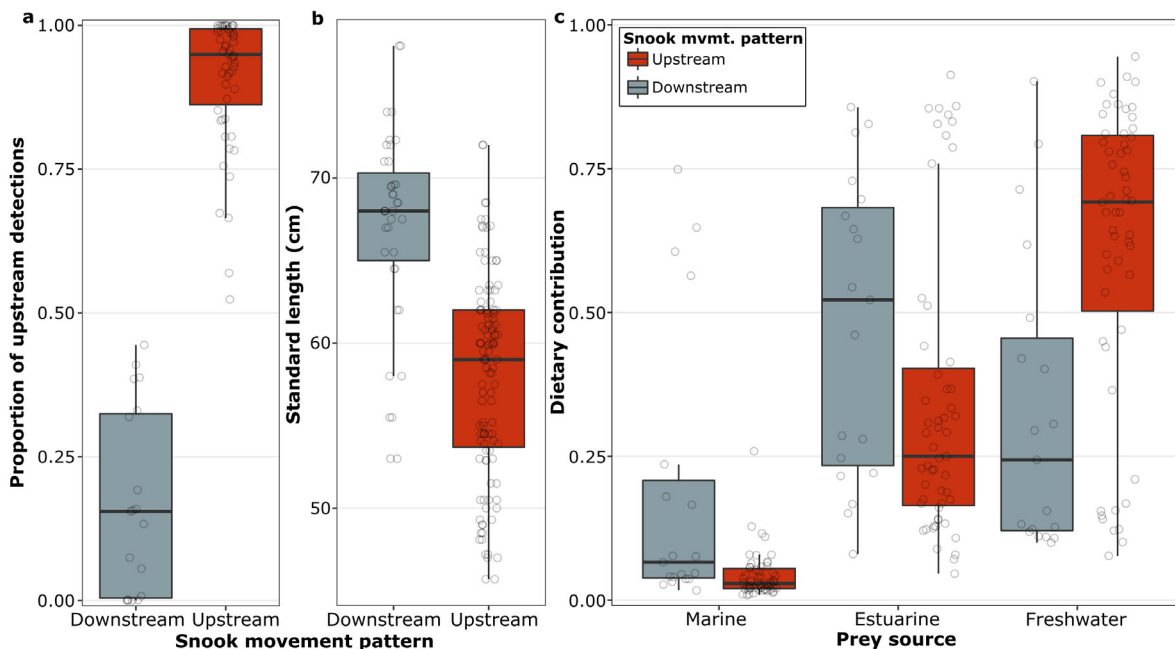


Fig. 3. Boxplots showing the proportion of receiver detections in upstream regions of the Shark River Estuary (a), standard length (b), and estimated prey source dietary contributions (mixing model posterior means) (c) to individuals classified as downstream snook *vs.* upstream snook based on acoustic telemetry data.

52% for estuarine prey, and 24% for freshwater prey (Fig. 3c).

Relative snook trophic positions above the prey baseline ranged from 1.0 to 1.9 (median = 1.5) in upstream snook and 1.4–2.3 (median = 1.9) in downstream snook. Upstream snook had a trophic niche hypervolume size of 25 compared to 307 for downstream snook (Fig. 4). The two calculated trophic niche hypervolumes had a 14% overlap (Sorenson similarity, 0.14), with unique trophic niche space comprising 8% of the upstream snook hypervolume and 92% of the downstream snook hypervolume.

## DISCUSSION

Mobile consumers can have a profound impact on ecological function in habitats they interact with through the food web subsidies they provide, understanding how movement patterns mediate these subsidies is important for the effective monitoring and management of ecosystems (Nelson et al. 2013, Williams et al. 2018, McInturf et al. 2019). Recent research has shown that the relationship between individual movement

patterns and trophic niche variation is a critical, yet understudied, factor determining these subsidies (Williams et al. 2018, Eggenberger et al. 2019, Allgeier et al. 2020).

There are clear differences in resource use and trophic niche space between snook exhibiting downstream *vs.* upstream movement patterns along the SRE, indicating a strong link between movement and foraging. The niche volume of upstream snook was an order of magnitude smaller than fish that occupied the lower estuary (Fig. 4). The smaller niche size is indicative of a foraging behavior focused on the subsidy provided by the movement of marsh prey (e.g., *Lepomis* spp.) into the deeper headwaters creeks of the SRE, with estuarine resource use being of secondary importance. These results are consistent with previous gut content-based dietary research on snook in the upper Shark River Estuary, with Boucek and Rehage (2013) finding 59% of sunfish (*Lepomis* spp.) biomass in snook guts compared to 41% in freshwater predator guts. Downstream snook occupied a much broader niche space that encompassed the upstream snook niche, representing a greater dispersion of foraging

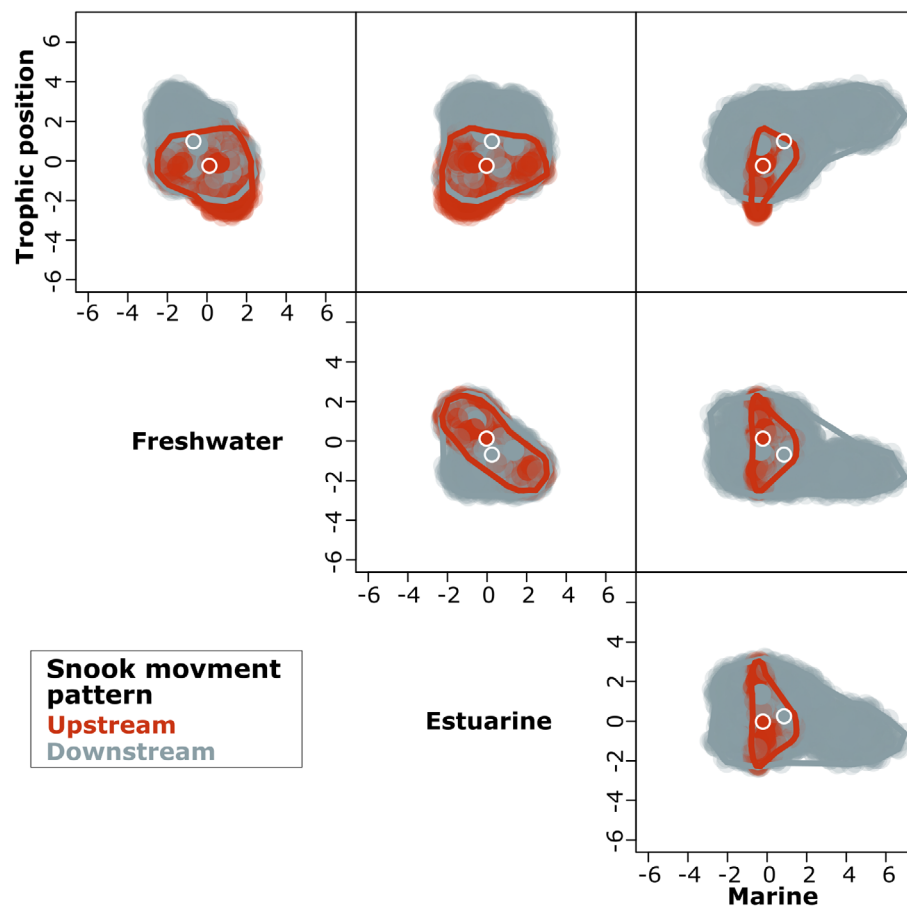


Fig. 4. Trophic niche hypervolumes of individuals classified as downstream snook vs. upstream snook based on acoustic telemetry data. Axes represent z-scores of estimated dietary contributions (mixing model posterior means) or trophic positions, and open points represent hypervolume centroids.

behaviors, with individuals showing significant dietary contributions from prey originating from all habitats evaluated in this study. Movement patterns were moderately correlated with body size, although substantial overlap in standard length was observed between the two movement classes (Fig. 3b). These results are consistent with previous studies that have identified a trend of decreasing freshwater habitat use among larger individuals (Barbour et al. 2014, Lowerre-Barbieri et al. 2014). Our results, demonstrating greater trophic niche volume in downstream snook than upstream snook, along with a high degree of overlap with upstream snook niche space, comport with a trend of habitat use expansion among larger snook as opposed to a clear pattern of ontogenetic habitat partitioning.

The stable isotope values found among prey were well separated between habitats, permitting the evaluation of snook dietary contributions and foraging behavior across large spatial scales with considerable resolution. There was no overlap in taxa mean  $\delta^{34}\text{S}$  values between freshwater and estuarine/marine resident consumers, or in  $\delta^{13}\text{C}$  values between marine and freshwater/estuarine resident consumers. The variations in consumer  $\delta^{34}\text{S}$  values found across the SRE are consistent with previous research demonstrating  $^{34}\text{S}$  enriched values among suspension feeders in freshwater reaches (23.2‰) of the SRE and relatively depleted values in brackish estuarine habitats (1.8–14.7‰; Fry and Smith 2002). The high  $\delta^{34}\text{S}$  values among freshwater consumers reflect those of oligotrophic surface waters of the

southern Everglades marshes (15–35‰; Orem et al. 2011). The range of marine prey  $\delta^{13}\text{C}$  values was similar to those found by Chasar et al. (2005) in Florida Bay consumers (–15.0‰ to –12.5‰), reflecting the values of seagrass and their associated epiphytes (–17.4‰ to –8.5‰). The consistency in the spatial gradient of resident prey isotope values among this and previous studies across the system demonstrates that it is a temporally stable feature of the coastal Everglades isotopic landscape, with promising implications for the utility of C/S/N stable isotope analysis for investigating trophodynamics and energy flux patterns across the system.

Consumer movement-based nutrient subsidies are a particularly important driver of ecological processes in oligotrophic systems (Flecker et al. 2010), such as those of the FCE (Childers 2006). The differences in snook niche space between upstream and downstream movement classes indicate they reflect functionally distinct vectors of spatial food web subsidies, with important implications for nutrient redistribution across the Everglades seascape. Upstream snook accumulate biomass derived primarily from marsh production and eventually transport it to nutrient-limited downstream estuarine and marine habitats when spawning or emigrating, whereas downstream snook forage across a wide range of habitats, with individual-level movement behavior playing an important role in mediating multi-directional trophic coupling across food webs within the seascape.

Hydrological characteristics related to the duration of flooding and the timing/extent of dry downs strongly influence the functional interactions between floodplain and river systems (Bayley 1995). The rising and falling of water control the extent of habitat and production that can be accessed by prey during flooding periods and the transfer of this production to larger river-dwelling predators as receding waters drive prey into deeper refuges (Winemiller and Jepsen 1998, Jardine et al. 2012, Farly et al. 2019). The Florida Coastal Everglades is currently undergoing system-wide hydrological alterations due to increasing saltwater intrusion associated with sea level rise and increased freshwater deliveries related to the ongoing implementation of the Comprehensive Everglades Restoration Plan (Childers 2006). Snook are known to modify their

movement and foraging behavior in response to environmental conditions and disturbance events (Boucek et al. 2016, Blewett et al. 2017, Eggenberger et al. 2019, Massie et al. 2019). Large-scale environmental perturbations could lead to a reorganization of movement behavior and resource availability, effecting nutrient redistribution patterns and ecological processes across the system (Tunney et al. 2012, Bartley et al. 2019).

Spatial trophic subsidies from marsh to downstream habitats in the SRE have the potential to be disrupted under several hydrological scenarios. Prolonged drought conditions decrease prey production in marsh habitats (DeAngelis et al. 1997) which can decouple freshwater resources from the estuarine/marine food webs (Boucek et al. 2016, Blewett et al. 2017). If freshwater riverine mangrove habitats experience increased salinity due to sea level rise (Saha et al. 2012, Dessu et al. 2018), their suitability as a refuge for freshwater marsh prey during seasonal dry periods may be substantially reduced (Rehage and Loftus 2007)—preventing snook from accessing this subsidy. Excessively high water levels during seasonal dry periods could also decouple this trophic link if the prey concentrating effect of marsh drying is not realized (DeAngelis et al. 1997). Future research aimed at quantifying the effects of environmental alterations on the foraging and movement behavior of mobile consumers will be critical for developing a predictive understanding of how the structure and functioning of the Coastal Everglades will change. Maintaining hydrological regimes that sustain spatial trophic links in a changing environment will be a principle challenge for water resource management in the future.

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