



# OPEN Cause and consequences of Common Snook (*Centropomus undecimalis*) space use specialization in a subtropical riverscape

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Variability in space use among conspecifics can emerge from foraging strategies that track available resources, especially in riverscapes that promote high synchrony between prey pulses and consumers. Projected changes in riverscape hydrological regimes due to water management and climate change accentuate the need to understand the natural variability in animal space use and its implications for population dynamics and ecosystem function. Here, we used long-term tracking of Common Snook (*Centropomus undecimalis*) movement and trophic dynamics in the Shark River, Everglades National Park from 2012 to 2023 to test how specialization in the space use of individuals (i.e.,  $E_{adj}$ ) changes seasonally, how it is influenced by yearly hydrological conditions, and its relationship to the between individual trophic niche. Snook exhibited seasonal variability in space use, with maximum individual specialization (high dissimilarity) in the wet season. The degree of individual specialization increased over the years in association with greater marsh flooding duration, which produced important subsidies. Also, there were threshold responses of individual space use specialization as a function of floodplain conditions. Greater specialization in space use results in a decrease in snook trophic niche size. These results show how hydrological regimes in riverscapes influence individual specialization of resource use (both space and prey), providing insight into how forecasted hydroclimatic scenarios may shape habitat selection processes and the trophic dynamics of mobile consumers.

**Keywords** Acoustic telemetry, Trophic niche, Movement ecology, Habitat use similarity, Everglades

Movement, ranging from frequent small foraging trips to infrequent, extensive migrations, is a primary behavioral adaptation to dynamic resource landscapes<sup>1–3</sup>. For instance, movement allows individuals to respond to the variability of resources (hereafter referred to as resource tracking<sup>4</sup>) at both the landscape and patch scale, as well as to avoid predators and competitors<sup>4–7</sup>. Further, resource landscapes are variable in time, which strongly influences the movement strategies of mobile organisms (e.g., the frequency and length of animal movement steps<sup>8</sup>), and as a consequence, the emergent patterns in species' habitat use and distributions<sup>4,9,10</sup>. Recent work has postulated theoretical frameworks to predict the emergent patterns of animal movement as a function of the spatiotemporal availability, variability, and predictability of resources<sup>4,6,8</sup>. The development of animal tracking technologies has increased our capabilities to test these predictions of spatial distribution and habitat use as a function of the spatiotemporal characteristics of resources<sup>11</sup>. This development is imperative, considering how both the spatiotemporal availability and predictability of resources are changing<sup>12,13</sup> as ecosystems face major alterations to disturbance regimes (i.e., changes in the frequency, magnitude, spatial extent, and legacies of disturbances) associated with climate change and other anthropogenic stressors<sup>14–17</sup>.

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Resource tracking can lead to substantial overlap in habitat use among individuals, away from individual specialization<sup>18–20</sup>. This can occur in environments where resource availability is highly variable and provides opportunities for consumers to concentrate their space use in areas of preferred or dense resources<sup>4</sup>. This is illustrated by the convergence of diverse animal communities on waterholes in the semi-arid savannas of southern Africa during the region's dry season<sup>21</sup>. As water levels decline throughout the landscape, aggregations of consumers seeking water result in a cascade of ecological interactions<sup>22,23</sup>. Likewise, animals track 'resources waves' in which resources increase sequentially through space and time due to phenological shifts in availability<sup>24–26</sup>. Animals, from large-bodied cetaceans to small-bodied pollinators, synchronize their movements in response to these waves, decreasing individual variability or their space use specialization, which is driven by the predictability of resources within heterogeneous landscapes<sup>3,27–29</sup>. Conversely, animals exhibit lower habitat use overlap (i.e., higher specialization in their space use) when navigating landscapes where resources are randomly distributed or less predictable<sup>30–32</sup>.

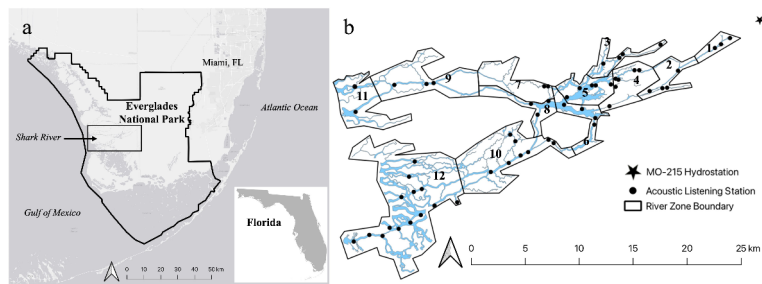
While resource tracking can lead to similarity in space use and lower specialization, high-resolution animal tracking studies also highlight the prevalence of intra-specific variation in movement<sup>33</sup>. These intra-specific differences in movement can be conditioned by both individual behavioral differences and the heterogeneity in the abundance and distribution of diet resources<sup>34–37</sup>. When resources, especially preferred ones, are scarce and distributed randomly throughout the landscape, higher intra-specific variability can develop via the modulation of space use (e.g., home range) and movement traits that minimize competition while satisfying energetic requirements<sup>35,38–40</sup>. For instance, species with collective movement strategies (i.e., emergent patterns formed by the local interactions of group members such as flocks, schools, and packs)<sup>41</sup> can experience spontaneous changes in group formation patterns due to intra-specific variation in how individuals respond to local conditions and to tradeoffs among foraging opportunities, risk, and behavioral types (e.g., dominance, aggression<sup>42</sup>). Also, individuals can switch along an "explorer-resident" movement syndrome gradient (i.e., from low to high specialization in space use) based on the access to high-quality food and distance to areas with preferable environmental conditions<sup>43</sup>, or they can change the intensity of space use, altering traveling and foraging distances according to the predictability, accessibility, and clustering of resources<sup>40,44</sup>.

The degree of space use specialization determined by individual movement variation can have consequences at the individual level, scaling up to affect population, community dynamics and ecosystem functioning<sup>33</sup>. At the population level, it should be expected that the trophic niche and interactions among consumer species will be related to the intra-specific movement and space use variation. Inherently via their movement and space use, consumers alter their foraging strategies in response to changes in habitat profitability and species interactions<sup>9,45–47</sup>. Foraging and niche theory predicts the trophic niche of a population to increase in size in habitats with low availability of preferred food resources and high competition<sup>39,46,48</sup>. Environments with predictable pulses in resources would therefore be expected to support a low specialization in space use due to the quantity of resources available for individuals and consequently decreasing the trophic niche size<sup>12,47,49–51</sup>. Conversely, an expansion in the trophic niche can be expected via foraging on different prey resources, which could result from the increase of intra-specific variance in space use or high specialization<sup>52–54</sup>.

Riverscapes (i.e., riverine floodplains) are an ideal system for studying and understanding how resource availability drives the movement patterns, inter-specific variation in space use, and tropho-dynamics of mobile consumers<sup>55–57</sup>. Riverscapes receive subsidies in the form of organic matter and prey resources that are transported from adjacent terrestrial habitats (e.g., floodplain, marshes and, forests) into river channels and, streams, stimulating secondary production via the pulsing of energy sources<sup>58–60</sup>. The overall availability and intensity of food resources is then influenced by these inter-habitat subsidies that are subject to the magnitude, frequency, and timing of freshwater flows, and their press (e.g., sea level rise or land sinking) and pulse dynamics (e.g., high discharge events associated with storms and hurricanes)<sup>57,61,62</sup>. Thus, considering that mobile consumers in riverscapes have developed adaptive responses to track and take advantage of resources pulses via evolved phenologies, and environmental and foraging cues<sup>23,26</sup>, it is expected that both the degree of intraspecific specialization in space use and the trophic niche dynamics are influenced by this hydrological variation that drives the timing and intensity of resource subsidies<sup>63–65</sup>. Climate change, anthropogenic stressors, and water management practices are altering riverscape hydrological regimes and, consequently, the spatiotemporal dynamics of subsidies and prey resources<sup>66,67</sup>. These changes highlight the need to expand our knowledge of how mobile consumers track resources in riverscapes, especially in oligotrophic systems such as the Everglades in which the dynamics of aquatic communities is tightly linked to subsidies' timing and intensity<sup>53,68</sup>.

Most examples of riverscape studies that have assessed the dynamics of intra-specific specialization in space use as a function of environmental conditions and resource availability have concentrated in temperate systems<sup>69,70</sup>. This geographical bias highlights the need for applying new movement and trophic studies in tropical and subtropical riverscape systems (e.g.<sup>71,72</sup>), which are subject to pulsing seasonality and resource subsidies. The Everglades Greater Ecosystem and Everglades National Park contains oligotrophic riverscapes such as the Shark River (SR hereafter) that have altered hydrological regimes through freshwater management, climate change (e.g., droughts, storms), and sea level rise, with major implications to the dynamics of prey pulses (Supplemental Material Fig. 1)<sup>57,73,74</sup>. The SR extends 32 km (Fig. 1) and transitions gradually from expansive freshwater creeks and adjacent graminoid marsh in the upper river to vast mangrove forests near the Gulf of Mexico, resulting in salinity and productivity gradients that vary seasonally based on freshwater flows and the degree of marine influence<sup>75</sup>. Seasonal hydrology is primarily driven by tidal cycles and rainfall patterns, characteristic of the region's subtropical climate, resulting in wet (May–October) and dry (November–April) seasons<sup>76</sup>. Declines in water during the dry season force freshwater taxa to seek refuge from marsh desiccation in the perennially inundated ecotonal creeks of the SR, providing an important prey subsidy for estuarine mesoconsumers<sup>57,77</sup>.

In this study, we took advantage of long-term tracking of animal movement and trophic dynamics of a mesoconsumer fish species (*Centropomus undecimalis* – Common Snook; snook hereafter) in the SR to



**Fig. 1.** Map of Shark River, Everglades National Park (ENP). Panel (a) depicts the boundaries of ENP and the Shark River (solid black lines) in southern Florida. Panel (b) shows the boundaries of each river zone (solid black lines), location of acoustic listening stations (i.e., acoustic receivers; black dots), and location of hydrologic monitoring station immediately upstream of the Shark River’s headwaters (black star). Map was generated using QGIS v3.22.6 (<https://qgis.org/>).

Model	Syntax	AICc	ΔAICc	R <sup>2</sup>	Marginal R <sup>2</sup>
(a) Temporal Trends	Eadj ~ s(Month, bs = “cc”, k = 10) + s(Year)	-257.23	0.00	0.46	NA
	Eadj ~ s(Month, bs = “cc”, k = 10) + Year	-250.78	6.45	0.37	NA
	Eadj ~ Month + Year	-207.97	49.25	NA	0.02
(b) Hydrological Effects	Eadj ~ s(Days Below 30 cm)	-245.88	0.00	0.34	NA
	Eadj ~ Days Below 30 cm	-244.60	1.29	NA	0.06
	Eadj ~ s(Mean Stage)	-243.95	1.94	0.35	NA
	Eadj ~ Mean Stage	-225.42	20.47	NA	0.04
	Eadj ~ s(Lagged Mean Stage)	-217.78	28.10	0.18	NA
	Eadj ~ Lagged Mean stage	-217.49	28.39	NA	0.03

**Table 1.** Candidate generalized additive models (GAMs) and generalized linear models (GLMs) evaluated for temporal trends (a) and hydrological effects (b) on individual space use specialization for common Snook (*Centropomus undecimalis*). GAMs and GLMs were based on a logit link function and beta error distribution, and used month and year as fixed variables for temporal models, as well as mean marsh stage (Mean Stage), the previous months mean marsh stage (Lagged Mean Stage) and the number of days in which stage was below 30 cm (Days Below 30 cm) as fixed variables in models assessing hydrologic effects on  $E_{adj}$ . Shown are the model syntax (Syntax), Akaike’s Information Criterion corrected for small sample sizes (AICc), differences in AICc ( $\Delta AICc$ ; used to assess best-fit models), adjusted  $R^2$  (GAM), and marginal  $R^2$  (GLM). Models with  $\Delta AICc < 4$  were considered equivalent.

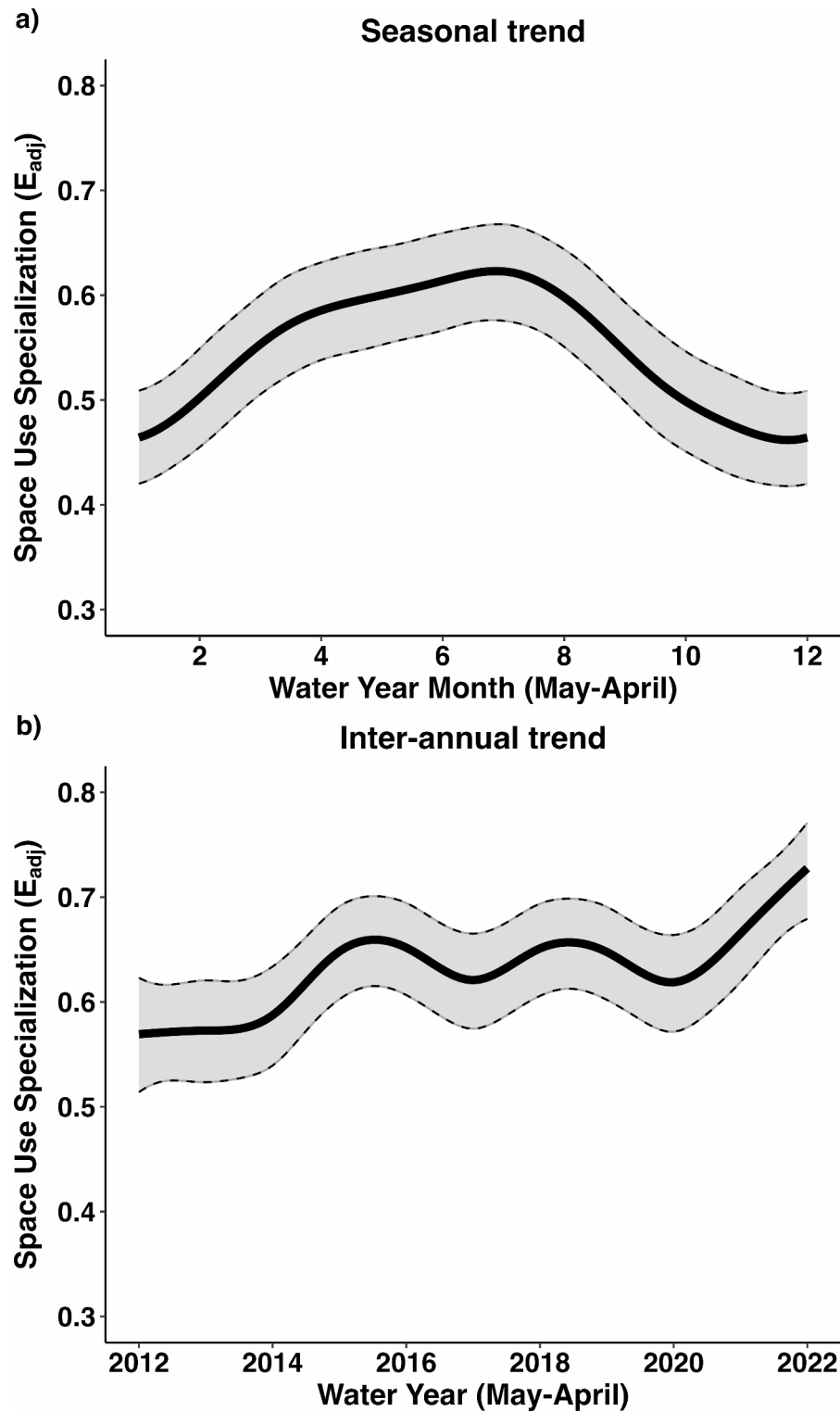
address three research questions: (1) What is the temporal (seasonal and annual) variability in snook space use specialization among individuals?, (2) How do hydrological conditions influence space use specialization?, and (3) Is trophic niche size associated with the degree of specialization in snook space-use? Based on resource tracking and trophic niche dynamics in environments with predictable prey subsidies<sup>78–80</sup>, we hypothesized a seasonal component in space use specialization, with lower specialization in the dry season, interannual variation driven by hydrological conditions known to regulate prey pulses, and a positive correlation between space use specialization and trophic niche size.

Results

After the data processing procedure, we included 227 snook. These selected individuals were detected on average 103.44 days ( $\pm 87.31$  SD) per year and averaged 4.39 zones ( $\pm 2.93$ ) per year. We observed interannual variation in  $E_{adj}$  values (individual space use specialization) over the course of the study (Supplemental Fig. 2). Across the 11 years, snook showed on average an intermediate level of  $E_{adj}$  values ( $\sim 0.55 \pm 0.12$  SD), with individuals ranging from 0.79 (i.e., a high level of space use specialization) to 0.26 (i.e., a low level of space use specialization).

Seasonality & temporal trends in space use specialization (question 1)

In general, snook exhibited lower space use specialization during the dry season (i.e., lower  $E_{adj}$  values), while individual variation increased (i.e., higher  $E_{adj}$  values) in the wet season, but not for all years (Supplemental Fig. 2). Based on AICc scores, the best fitting model was the GAM with a smoother for both the month and hydrologic year (Table 1). The model showed both a significant cycle across the hydrological year months (i.e., from May to April), and an overall incremental trend in  $E_{adj}$  values across the years (Fig. 2; Table 2). This temporal model captured 50% of deviance in the variability of snook individuals’ space use (Table 2a). Monthly  $E_{adj}$  values cycled over the 11 years of snook tracking, with generally higher levels in the wet months (September–October), indicating a higher heterogeneity or spatial specialization in space use across individuals, and lower values in the



**Fig. 2.** Marginal effect plots from generalized additive models (GAMs) for temporal trends in the individual space use specialization ( $E_{adj}$ ) of Common Snook (*Centropomus undecimalis*). Panel (a) depicts the intra-annual (seasonal) cycle of individual space use specialization. Panel (b) depicts the trend across the time series. Solid black lines indicate the estimated mean response, dotted black lines show the 95% confidence intervals, and grey shading illustrates the dispersion around the mean.

Response	Term	edf	red.df	Chi.sq.	p-Value	% Deviance Exp.
(a) E <sub>adj</sub>	Month	3.81	8.00	64.17	2.00 × 10 <sup>-16</sup>	50.1
	Year	6.36	7.52	42.13	2.00 × 10 <sup>-16</sup>	
(b) E <sub>adj</sub>	Mean Stage	5.17	6.29	68.70	2.00 × 10 <sup>-16</sup>	37.6
(c) E <sub>adj</sub>	Days Below 30 cm	2.87	3.49	66.66	2.00 × 10 <sup>-16</sup>	35.7

**Table 2.** Generalized additive models (GAMs) selected for the assessment of temporal trends (a) and hydrological effects (b, c) on individual specialization (E<sub>adj</sub>) of habitat use for common Snook (*Centropomus undecimalis*). Models were based on a logit link function and beta error distribution, and used month and year as fixed variables for temporal models, as well as mean water stage (Mean Stage) and the number of days in which stage was below 30 cm (Days Below 30 cm) as fixed variables in models assessing hydrologic effects on E<sub>adj</sub>. Shown are the smooth term (effective degrees of freedom; edf), the test statistic for assessing the significance of the model smooth terms (Chi.sq.), and approximate p-values for the null-hypotheses that each smooth term is zero (p-value). Percentage deviance explained (% Deviance Exp.) of the GAMs were used as a quality-of-fit statistic.

dryer months (March–April), indicating lower specialization in space use (Fig. 2a). Still, the predicted values in space use specialization tended to be high (> 0.5 E<sub>adj</sub> values) across the hydrologic year seasons.

In contrast, the GAM model captured a significant positive trend in the E<sub>adj</sub> values from 2012 to 2023, signifying increasing specialization in space use in recent years relative to earlier years in the time series (Fig. 2b, Table 2a). Specifically, the interannual smoother demonstrated three periods of changes in the specialization of snook individual’s space use. The E<sub>adj</sub> values during the 2012–2014 hydrologic years were stable until 2015 when values increased and stabilized at higher values until 2020 where values have progressively increased (Fig. 2b).

Hydrological influence on space use specialization (question 2)

The variation in snook space use across seasons and years was partially explained by hydrological variables (Table 2b, c, Fig. 3). The two best models were the GAMs that included either marsh stage (water depth in cm above ground elevation) or the period of marsh flooding (number of days below 30 cm marsh stage), which did not differ based on AICc (Table 1). The GAM with marsh stage explained 37.6% of the deviance, and the smoother model captured a non-linear threshold response of E<sub>adj</sub> (Table 2b), in which space use specialization was relatively stable until 20 cm of marsh stage when values increased until 40 cm, after which values plateau at high levels of spatial specialization (Fig. 3a). The GAM with the days with stage below 30 cm explained 35.7% of the deviance (Table 2c), and the smoother model reflected a non-linear decrease in the specialization of snook space use with increases in the number of days below 30 cm, with E<sub>adj</sub> stabilizing at lower values after 20 days of marsh dry conditions (Fig. 3b).

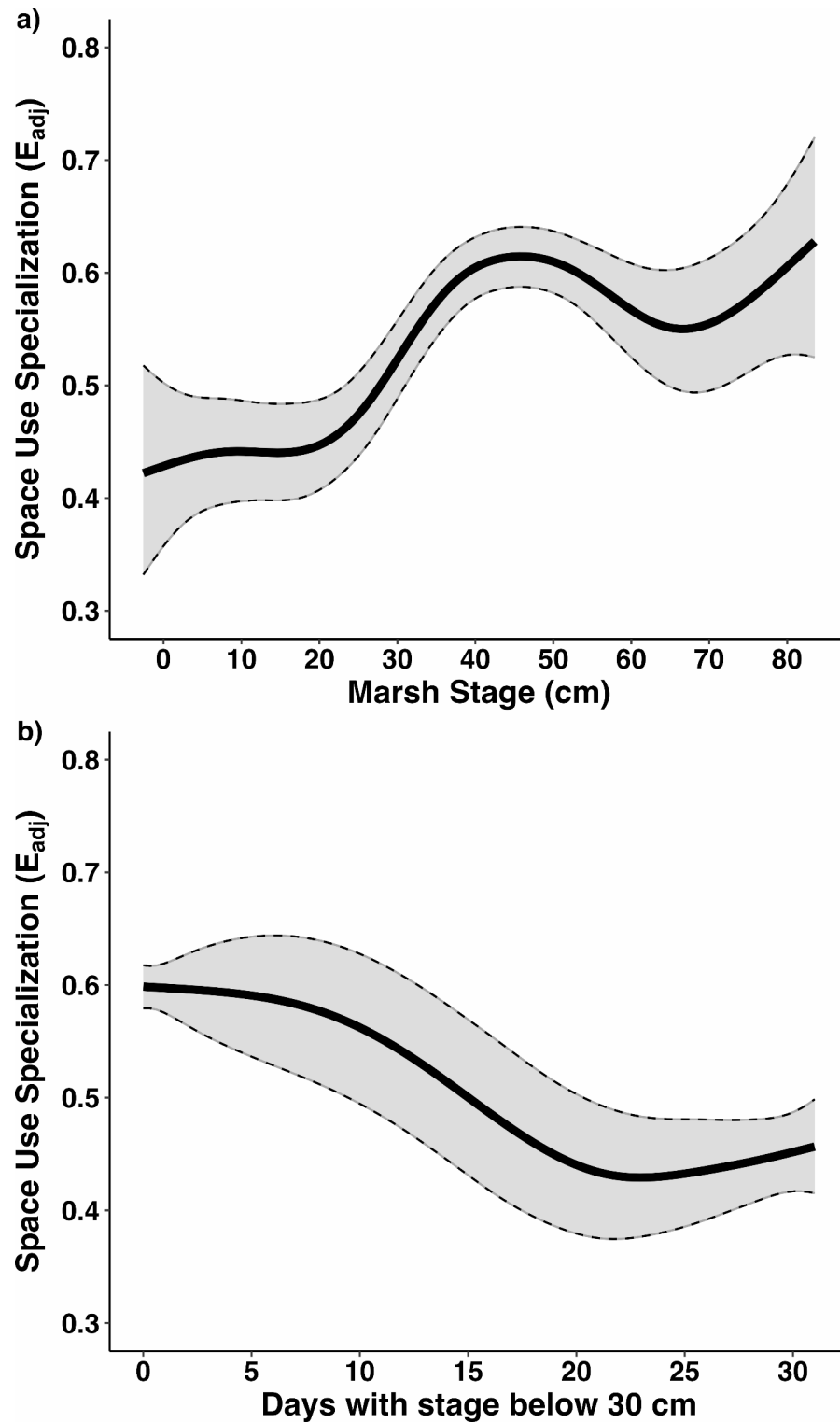
Association of space use specialization and trophic niche (question 3)

There was temporal variation in resource use of snook, but generally, snook relied mainly on prey from freshwater sources followed by estuarine prey. Prey from seagrass were not a common energy source for snook (Table 3). Trophic niche size was variable across years, ranging from 0.02 in 2021 to 175.62 in 2011. Snook trophic niche size exhibited a significant negative correlation ( $r = -0.63$ ,  $p = 0.05$ ) with individual specialization in space use, indicating greater variability in resource use as snook space use becomes less specialized across individuals (Fig. 4).

Discussion

Here, we show how fluctuations in the availability and predictability of resources due to environmental changes can influence the capacity of habitats to support individuals and trophic dynamics. In riverscapes, such as our focal study system, resource subsidies may vary over time in response to altered hydrological regimes that influence connectivity across riverine floodplains and, thus, floodplain prey production and concentration<sup>57,77</sup>. In this study, we used the SR in the Everglades to test how specialization in space use among snook (an estuarine mesopredator) varied seasonally, how it was influenced by hydrological conditions over a decade, and its effect on trophic niche size. Snook space use specialization displayed a seasonal pattern, with a maximum specialization (i.e., high dissimilarity) during the wet season and lower space use specialization during the dry season, indicative of the aggregation of snook in certain regions of the riverscape. The degree of space use specialization displayed three periods of oscillation and an overall increase over the years, suggesting that over time, snook space use is becoming more heterogenous across individuals. As predicted, snook space use specialization was related to the hydrology of surrounding floodplain marshes. The distribution of snook across the riverscape became more dissimilar with wetter hydrological conditions, revealed by higher marsh stages and lower number of days at low stages (Fig. 3). Last and counter our prediction, space use specialization was negatively related to trophic niche size. That is, as snook space use became more dissimilar and specialized across river zones, they relied on less diverse food resources, decreasing trophic niche size. These results highlight how fluctuations in the availability and predictability of resources due to environmental changes can influence the capacity of habitats to support individuals and trophic dynamics, with implications at the population<sup>81</sup>, community<sup>82</sup>, and ecosystem level<sup>83</sup>.

Our results revealed phenological shifts in snook individual specialization in space use, underscoring the important role of seasonal variability in hydroclimatic conditions mediating the spatial arrangement of

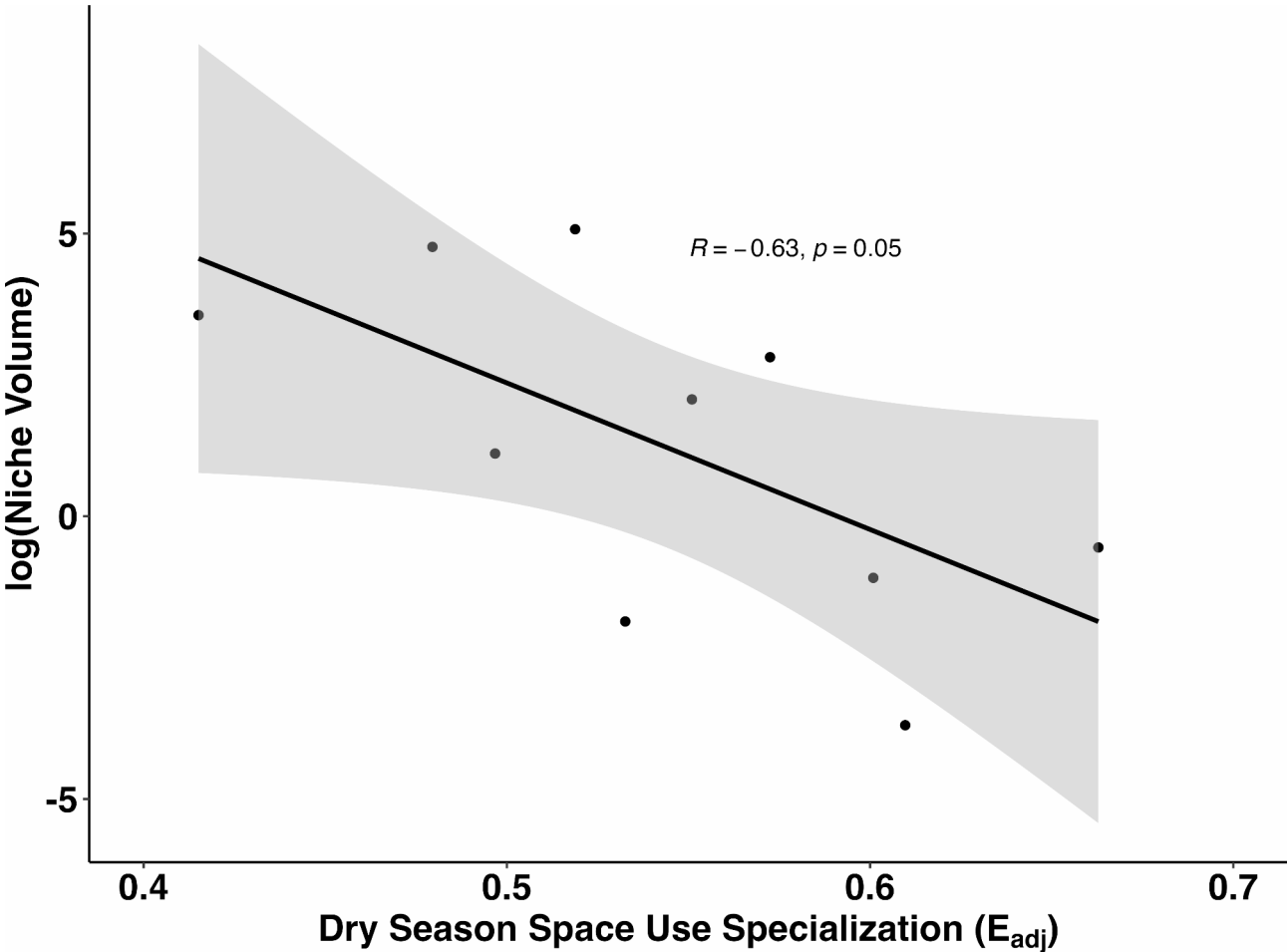


**Fig. 3.** Marginal effect plots from generalized additive models (GAMs) for hydrological effects on individual space use specialization ( $E_{adj}$ ) of Common Snook (*Centropomus undecimalis*). Panel (a) depicts the relationship between mean marsh stage (cm) and individual space use specialization. Panel (b) depicts the relationship between days with mean river stage < 30 cm and individual space use specialization. Solid black lines indicate the estimated mean response, dotted black lines show the 95% confidence intervals, and grey shading illustrates the dispersion around the mean.



Year	Freshwater contribution	Estuarine contribution	Seagrass contribution	Niche volume	Sample size	Total length
2011	0.59 ± 0.42	0.31 ± 0.37	0.1 ± 0.18	175.62	12	70.19 ± 10.53
2012	0.97 ± 0.05	0.02 ± 0.02	0.02 ± 0.04	0.16	7	68.94 ± 8.10
2013	0.59 ± 0.33	0.31 ± 0.31	0.1 ± 0.16	117.18	11	74.81 ± 7.42
2014	0.85 ± 0.26	0.1 ± 0.18	0.06 ± 0.16	35.03	17	74.01 ± 5.46
2016	0.86 ± 0.31	0.13 ± 0.3	0.01 ± 0.01	3.03	8	69.41 ± 7.67
2017	0.77 ± 0.36	0.22 ± 0.34	0.02 ± 0.03	16.65	14	69.61 ± 6.77
2018	0.76 ± 0.27	0.22 ± 0.27	0.02 ± 0.02	7.89	14	68.92 ± 6.46
2019	0.9 ± 0.06	0.07 ± 0.04	0.02 ± 0.02	0.34	4	75.10 ± 9.98
2020	0.6 ± 0.4	0.31 ± 0.35	0.1 ± 0.17	159.99	10	69.25 ± 9.56
2021	0.95 ± 0.02	0.02 ± 0.01	0.02 ± 0.02	0.02	4	71.98 ± 12.8
2022	0.92 ± 0.06	0.03 ± 0.02	0.05 ± 0.06	0.58	4	79.60 ± 8.31

**Table 3.** Annual dry season proportional dietary contribution of spatially distinct forage bases (i.e., Freshwater Contribution, Estuarine Contribution, Seagrass Contribution) expressed as mean ± standard deviation and trophic niche volume. Sample size denotes the number of individual Common Snook (*Centropomus undecimalis*) used in Bayesian mixing models to estimate the proportional dietary contributions. Results of mixing models were used to estimate the trophic niche volume.



**Fig. 4.** Pearson correlation between log(trophic niche volume) and mean dry season individual space use specialization (E<sub>adj</sub>). The grey shading illustrates 95% confidence intervals.

individuals across the riverscape. For this study, we adopted the E<sub>adj</sub> metric, which was developed to describe the degree of diet specialization, to quantify space use specialization by a coastal mesopredator in SR. The flexibility of the definition of resource (e.g., light, space, nutrients, food) allowed for the adoption of this metric and the theory of niche size and individual specialization supporting it. Similar approaches have been used to quantify the

specialization in space and habitat use by other mesopredators<sup>47,84,85</sup>. However, in contrast to the quantification of specialization based on diet, assessing space-use specialization could be influenced by spatial autocorrelation and the spatial order of observations inherent in movement assessments, which are not accounted for in the calculation of the  $E_{adj}$ . Future studies could develop models that incorporate estimates of spatial autocorrelation to investigate its influence on space use specialization.

Using  $E_{adj}$  we observed pronounced decreases in space use specialization during the dry season, as well as threshold response around 30 cm of marsh stage. These patterns align with several other studies of large estuarine consumers from tropical and subtropical coastal river systems, which highlight resource tracking of small-bodied fishes and invertebrates as they seek refuge in perennial river systems from falling water levels in adjacent floodplains<sup>77,86–88</sup>. This tracking of resource pulses has been shown to subsidize consumer diets, positively affecting population-level fitness and influencing fish abundance, body condition, and reproductive movements. For example, Massie et al.<sup>86</sup> demonstrated that the duration of marsh dry-down was a significant factor in determining the proportion of snook in the SR undergoing spawning migrations annually, and that this phenomenon was likely tied to enhanced foraging opportunities in which individuals were able to increase their energy reserves prior to spawning. The thresholds in marsh stage found in this study could provide valuable targets for water management and Everglades restoration efforts.

Changing hydroclimatic conditions resulting from global change and water management decisions have been shown to disrupt the phenology of individual specialization in space use<sup>68,89,90</sup>. By influencing the timing, intensity, and distribution of resources and subsidies, press (e.g., eutrophication, continuous changes in temperature and precipitation) and pulse (e.g., storms, droughts) disturbances can alter the degree of specialization in space use by consumers and other emergent patterns associated with resource tracking. For instance, Wei et al.<sup>91</sup> showed, using species distribution modeling, a collapse in the migration network of Pacific waterfowl species due to phenological mismatches caused by multiple climate change scenarios. In the Everglades, the space use variability of two mesoconsumers moving along coastal lakes corresponded to unique nutrient and hydrological connectivity regimes caused by hydroclimatic patterns and freshwater management<sup>92</sup>. However, most studies have quantified individual variability in space use in the short term<sup>33,93</sup>, which accentuates the need for studies incorporating long-term movement datasets that uniquely allow for the understanding of the true response of animal movement to environmental and climate variation<sup>94</sup>.

Over a decade, we observed increased levels of individual specialization in snook indicating likely disruptions to phenological patterns. This change in the intra-annual variability in space use could be attributed to various factors, with unique ecological impacts. For instance, changes in seasonal hydrologic conditions, with the timing, magnitude, and duration of dry-down decreasing in recent years (Supplemental Fig. 1)<sup>76,95,96</sup>, potentially negate the need for marsh prey to seek refuge in permanent riverine habitats. Changes to phenological patterns in space use may be attributed to reductions in floodplain biomass as a result of species invasion and associated predation and competition and/or changing thermal regimes<sup>57,97</sup>. These would reduce the total flux of marsh biomass into estuarine habitats, as well as the energetic benefit of tracking resources into the marsh-riverine ecotone<sup>57</sup>. It is likely that both these processes of changing prey production and changing prey concentration<sup>57,98</sup> are interacting to alter marsh subsidies and the response of consumers, in terms of both space and resource use. Future studies should couple field experimental manipulations with long-term data streams to improve our understanding of the ecological implications of mismatch phenologies and of the extent and drivers of temporal variance in both consumer space and resource use.

Several studies have coupled tracking and diet analyses, using telemetry and stable isotope analyses, to understand how foraging and movement strategies are jointly derived from unique environmental conditions and resource availability<sup>53,92,99</sup>. Still, few have directly assessed the association between population trophic niche size and space use<sup>53,100</sup>. Based on the coupling of movement and trophic niche observations in our study, we observed a negative correlation between the trophic niche size and the individual specialization in space use of snook. Snook niches were larger when snook had less specialized space use. This result contradicted our original prediction that higher spatial clustering in space by the consumer (i.e., low space use specialization), due to the concentration of preferable prey resources, would result in smaller trophic niche sizes<sup>50,51,54</sup>. For instance, lower water levels in marshes connected to the SR are associated with a low space use specialization for snook, which rely mostly on freshwater prey subsidies originating from the marshes. These subsidies increase the amount of energy available<sup>7,57,77</sup>, increasing snook body condition and reproductive output<sup>86</sup>. In other systems, increased production has been shown to lead to decreases in the trophic niche size of consumers<sup>54,101</sup>. Higher availability of prey resources with a high potential of contributing energetically to consumers can reduce species' trophic niche size by buffering intra- and inter-specific competition, and allowing individuals to specialize in common sources of energy<sup>39,46,102</sup>. However, an opposite relationship could be expected, as the one observed in this study, if the pulse is not sufficient in size (or biomass), if it is low in quality, asynchronous with consumers, or if the resource is allochthonous and ephemeral<sup>103</sup>.

One potential limitation about our calculation of trophic niche size is that this metric was positively correlated with the sample size of snook used to calculate the trophic niche throughout the time series, suggesting a potential sampling effect that could bias the ecological interpretations of this relationship (Supplemental Material Fig. 3a). Still, there are some patterns in resource use and snook abundance that point out that the variability in trophic niche size observed in the study is not due to a bias in sampling, but due to ecological reasons. First, the years with low sample sizes were due to the difficulty in catching snook in SR, which also corresponded to high levels of space-space use specialization (Supplemental Material Fig. 3b). Second, there was a strong negative relationship between trophic niche size and the reliance on freshwater prey as an energy source (Supplemental Material Fig. 3c), suggesting changes in individual specialization of energy sources through the time series. Also, another possibility explaining the changes in trophic niche size is that when the prey subsidy is strong, the population of snook in the upper SR is comprised of local individuals and individuals immigrating from



other areas where they have been shown to rely on more estuarine and marine prey<sup>53</sup>. Since there is a temporal disconnection between the elemental content of animal tissues and space use<sup>104,105</sup>, these migrant snooks would be partially supported by resources from other areas, which could expand the population trophic niche that does not exist when these individuals are not in the SR. Still, expanding the stable isotope time series as well as adding observations across different seasons will improve and expand our understanding of trophic niche dynamics and its relationship to space use.

Even though the dry season marsh prey subsidy is a major driver of ecosystem processes in the SR<sup>73,77</sup>, there is a large amount of temporal variation in the amount, composition and quality of the subsidy<sup>57,68</sup>. This temporal variation can cause periods of asynchrony between prey and snook (i.e., a phenological mismatch)<sup>106</sup>, resulting in a higher resource use variance between and within individuals due to smaller subsidies and potentially greater intraspecific competition<sup>101,107</sup>. This would support the negative relationship between trophic niche size and space use specialization found in this study. Also, other consumers depend on these SR marsh prey subsidies<sup>47,77</sup>, which could reduce resources available to snook, allowing only highly competitive individuals to specialize, forcing others to incorporate other food sources to meet energetic demands. These mechanisms are plausible under certain conditions, but should not be the prevalent ones, considering the high reliance of snook on marsh prey subsidies<sup>53,77</sup>, and the habitat partitioning observed among the multiple consumers of the SR<sup>47</sup>.

The correlation coefficient between space use specialization and trophic niche size was high and different from zero, but there was high variability around this linear association, which may suggest different mechanisms driving the trophic niche size besides the ones influenced by the specialization in space use. Further investigation is needed to discern the mechanisms that drive trophic niche size in snook, especially in relation to individual foraging and movement patterns. The variability in space use of conspecifics can have major consequences across different levels of ecological organization – e.g., from population dynamics up to ecosystem functioning<sup>33</sup>. Several studies in SR and other subtropical systems have investigated movement responses of snook at the population level using a “mean” approach (i.e., quantification of averaged responses); however, this is the first study demonstrating how the variability in space use at the individual level is also responsive to hydrological conditions, and how this variability can potentially influence population-level trophic dynamics. Evidence points toward changes in the level of synchrony between snook space use and prey subsidies (i.e., a phenology mismatch), with unknown consequences to snook population dynamics and resilience.

Resource tracking, via the movement of animals, supports several ecological processes operating at multiple scales (e.g., foraging, mating, species interactions) that influence the fitness of individuals and, as a result, species population dynamics<sup>108</sup>. Specifically, resource tracking in landscapes with predictable and clustered prey subsidies can sustain the aggregation of individuals. This can result in decreased space use specialization across conspecifics, consequently influencing the between individual trophic niche size at multiple scales of biological organization via the foraging specialization on abundant prey pulses. At the same time, anthropogenic effects on climate and landscape connectivity can alter the heterogeneity, predictability, and phenology of resource landscapes with consequences for the animals tracking resource landscapes<sup>13</sup>. Our findings argue for the need for long-term data sets tracking individual specialization in order to understand its dependency on environmental conditions and climate change.

## Methods

### Acoustic telemetry to measure snook movement and spatial use

The monitoring of snook movements with passive acoustic telemetry in the SR began in February 2012 in coordination with the Florida Coastal Everglades Long Term Ecological Research program (<https://fclter.fiu.edu/>). Individuals were sampled monthly across 15 sites along the upper SR during the dry season using boat-based electrofishing<sup>47,86</sup>. Immediately upon capture, snook individuals were placed in an aerated live well, promptly measured (total and standard length; cm), weighed (wet weight; kg), and then transferred to an onboard tagging station. Individuals underwent a minor surgical procedure following Lowerre-Barbieri<sup>109</sup> and Young et al.<sup>110</sup>. Implantation of acoustic tags (Vemco 69 kHz V13 or V16, Innovasea, Halifax, NS, Canada) consisted of a small (~3 cm) incision in the lower abdominal cavity for tag insertion followed by a single Vicryl™ suture to close the incision. Post-tagging, fish were fin-clipped for stable isotope analysis and acclimatized before release at the point of capture, with tags expected to last 3.7 to 6.7 years for V13 and V16 model tags, respectively.

From 2012 to 2023, the spatiotemporal distribution and upstream-downstream SR migrations of tagged snook were monitored via 37–41 Vemco VR2W acoustic receivers (Vemco, Halifax, NS, Canada) spaced 1–3 km apart and partitioned amongst twelve river zones (Fig. 1). River zones were defined as areas of unique physiochemical (e.g., salinity and geomorphology) features of the river following methods outlined by Matich et al.<sup>47</sup> and informed by similar studies of animal movement in the SR<sup>53,111,112</sup>. The gated configuration of the array (i.e., paired acoustic receivers at choke points such as creek mouths or the convergence of braided river channels) permitted the determination of snook movements among unique river zones. As tagged individuals swam near acoustic receivers (approximately 500 m<sup>111</sup>), their unique tag number and associated date, time, and location (i.e., latitude and longitude) information were recorded. Previous research has demonstrated this longitudinal array along 32 km of the SR to be effective at quantifying the directional movements, life history migrations, and space use of fishes and crocodilians under varying hydrologic conditions, including high flow events<sup>47,86,111,113</sup>.

### Calculating spatial similarity

Interspecific variability in space use by snook was calculated each month between February 2012 and July 2023 using acoustic detections of individual snook detected within the SR, representing 10 complete hydrologic years (2011–2022). A hydrologic year was defined from May to April, capturing the start of the wet season in May to the end of the dry season in April of the following year. Telemetry data were filtered before analysis to retain only those individuals with ≥ 100 unique detections and detection period of ≥ 90 days within record. Screening

of the data enabled the exclusion of unreliable observations, ensuring only fish with comprehensive records were analyzed to infer space use patterns within the SR, allowed only for the inclusion of snook that moved throughout the system, and is common in datasets with a large number of detections<sup>110,114,115</sup>. Space use was quantified by counting the number of days each tagged snook was detected within each river zone during each month and year. This analysis provided a frequency value for each zone, individual ID, and time, serving as a metric of individual space use at a monthly time step.

To determine the similarity in space use among SR snook over the 10 hydrologic years of movement tracking, we calculated the E-index, as described by Araujo et al.<sup>116</sup>, adjusted for small sample size ( $E_{adj}$ ) using the RInSp package in R<sup>117</sup>

$$E_{adj} = 1 - \frac{\sum_{j=1}^n p_j^2}{\frac{1}{N} \sum_{i=1}^N \left( \sum_{j=1}^n p_{ij}^2 \right)}$$

where  $p_j$  is the proportion of total river zone<sub>*j*</sub> used by the entire population,  $n$  is the number of river zones,  $p_{ij}$  is the proportion of river zone<sub>*j*</sub> used by an individual<sub>*i*</sub>, and  $N$  is the total number of individuals. Monte Carlo resampling ( $n=999$ ) was employed to account for potential biases arising from uneven sampling sizes (i.e., number of individuals tracked within the system monthly) using the *average* method as described by Zaccarelli et al.<sup>117</sup> to permit comparison across the time series.

The RInSp's  $E$  and  $E_{adj}$  indices were originally defined and designed for the purposes of quantifying individual diet specialization contextualized around the definition of the total niche width by Roughgarden<sup>118</sup>. In this study, we adapted this index to quantify the level of specialization in space use among SR snook over the study period. We chose  $E_{adj}$  to reduce potential biases in detection frequency, and space use similarity estimates resulting from variable sample sizes across time (Supplemental Material Table 1). The  $E_{adj}$  calculation was performed 999 times via Monte Carlo simulation to estimate an unbiased metric of spatial similarity at the population-level each month ( $n=138$ ) across the time series. Although this metric uses each individual to calculate space use similarity across the population for each month, the individuals ID is not taken into consideration in the calculation. However, because the mix of individuals change each month due to tagging period and snook entering and leaving the system, there is a unique combination of snook individuals across the sampling period which likely reduces the bias of specific individuals on the calculation of the metric. Similar approaches incorporating acoustic telemetry data have been used to quantify intra-specific space use patterns and specialization<sup>47,84,85</sup>.

## Statistical analyses

### *Seasonality & temporal trends in space use specialization (question 1)*

We used a combination of Generalized Additive Models (GAMs) and Generalized Linear Models (GLMs) to evaluate temporal trends in snook space use specialization (i.e.,  $E_{adj}$ ). Models were constructed to assess intra-annual seasonality and temporal trends in snook space use similarity. Models were fit using the *mgcv*<sup>119</sup> and *glmmTMB*<sup>120</sup> packages and compared their performance in R (v 4.4.0<sup>123</sup>). For GAMs, seasonality was captured using a cyclic cubic spline, while inter-annual trends were modeled with a smoother spline for the hydrologic year. Both GAMs and GLMs were run with beta distribution and logit link function due to the bounded nature of  $E_{adj}$  (i.e., 0–1). We used Akaike's Information Criterion corrected for small sample sizes (AICc) values to compare three candidate models: (1) GAM with a smoother for both month and hydrologic year, (2) GAM with a smoother for month and a linear term for the hydrologic year, and (3) GLM with linear terms for month and hydrologic year (Table 1).

### *Hydrological influence on space use specialization (question 2)*

We characterized the relationship between the  $E_{adj}$  describing the specialization among snook's space use and floodplain hydrologic variables using GAMs and GLMs. Marsh stage in the context of our study refers to the water depth in marshes surrounding the upstream SR. As predictors, we selected the mean stage of the month, the mean stage of the previous month, and the number of days that the stage was below 30 cm. Daily stage data were obtained from the Everglades Depth Estimation Network for hydrologic monitoring station MO-215 immediately upstream of SR headwaters (Fig. 1). These variables have been linked by previous research to the timing and quantity of the marsh prey pulse during the dry season<sup>57,68,77</sup>, and to snook abundance and spawning migration patterns out of the SR<sup>7,86,122</sup>. Models were fitted using the *mgcv* and *glmmTMB* packages in R; however, due to high collinearity among these 3 hydrological variables only single variable models were performed and compared (Supplemental Material Fig. 4). Similarly, the best type of model (GAM vs. GLM) for each of the three hydrological variables was selected using AICc.

### *Association of space use specialization and trophic niche (question 3)*

Stable isotope analysis was used to generate trophic niche of snook to compare to intra-specific space use of snook in the SR. Bayesian mixing models were utilized to determine the proportional contribution of each spatially distinct forage base (i.e., freshwater, estuarine, and marine) to the diet of individual snook annually during the dry season across the time series<sup>53</sup>. Snook fin clips were collected for stable isotope analysis during the dry season, and therefore, we constrained our analysis between snook trophic niche and space use specialization to the dry season. More specifically, isotope values were collected from January to June, integrating a two-month lag period to account for tissue turnover rates (~1–2 months) of carbon (C), nitrogen (N), and sulfur (S) isotopes<sup>92,123</sup>. Bayesian mixing models were run in three chains with 300,000 iterations and a burn-in of 50,000

to allow for model convergence. Trophic fractionation factors of 1.3 (0.3), 3.3 (1.0), and 0.5 (0.5) were used for C, N, and S, respectively<sup>53,124</sup>. Mixing models were conducted using the MixSIAR package in R<sup>125</sup>.

Mixing model results were used as axes to delineate and measure the trophic niche space of snook using the hypervolume package in R<sup>53,101,126</sup>. Mixing model results were z-scored across all individuals and years prior to generating hypervolumes to facilitate standardized, comparable axes within n-dimensional space<sup>126,127</sup> (Table 3). Hypervolumes were generated for each year using Gaussian kernel density estimation with 1000 random points per sample and a 95% probability density. The relationship between the trophic niche size (i.e., volume of hypervolume) and the average dry season  $E_{adj}$  values for the corresponding year was calculated using a Pearson correlation. Values for trophic niche size were log-transformed before conducting the correlation.

## Data availability

Data will be accessible through the Environmental Data Initiative (EDI) upon reasonable request by contacting corresponding authors: Rehage, J. 2023. Movements of aquatic mesopredators within the Shark River estuary (FCE LTER), Everglades National Park, South Florida, USA, February 2012 - ongoing ver 6. Environmental-Data Initiative. <https://doi.org/10.6073/pasta/dc3a992e2eb71472a89e70f837d3010f>, and Rezek, R. 2024. Stable isotope values of consumers, producers, and organic matter in the Shark River Slough and Taylor Slough, Everglades National Park (FCE LTER), Florida, USA, 2019 – ongoing ver 4. Environmental Data Initiative. <https://doi.org/10.6073/pasta/da36c97eccd5461ba32eecc23a53892>. R scripts used for models, as well as main text and supplemental figures/analyses are available at <https://github.com/CoastalFishScience/spatsim>.

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## Author contributions

R.O.S. and J.S.R. conceptualized and designed the study in collaboration with R.B., J.M., R.B., N.V., M.W., and J.S.R. contributed to the acquisition of data. R.O.S., M.W. and W.R.J. performed data analyses, and all contributed to the interpretation of data. R.O.S., J.S.R., M.W. and W.R.J. wrote and revised the manuscript.

## Declarations

## Competing interests

The authors declare no competing interests.

## Ethical approval

The Florida International University Institution Animal Care and Use Committee (IACUC-18-002-CR01) approved the project's sampling and animal handling protocol. Project activities were conducted under the Everglades National Park research permit EVER-2022-SCI-0056. This study is reported following ARRIVE guidelines.

## Additional information

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-82158-4>.

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