Received: 10 September 2021 | Accepted: 13 October 2021

DOI: 10.1002/ecs2.3944

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Influence of seascape spatial pattern on the trophic niche of an omnivorous fish

Rolando O. Santos[1,2] | **W. Ryan James**[1,2,3] | **James A. Nelson**[4] |
Jennifer S. Rehage[1,3] | **Joseph Serafy**[5,7] | **Simon J. Pittman**[6] | **Diego Lirman**[7]

[1]Institute of Environment, Florida International University, Miami, Florida, USA

[2]Department of Biological Sciences, Florida International University, Miami, Florida, USA

[3]Department of Earth and Environment, Florida International University, Miami, Florida, USA

[4]Department of Biology, University of Louisiana, Lafayette, Louisiana, USA

[5]NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida, USA

[6]Oxford Seascape Ecology Lab, School of Geography and the Environment, University of Oxford, Oxford, UK

[7]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA

Correspondence
Rolando O. Santos
Email: rsantosc@fiu.edu

Funding information
Florida Education Fund; NOAA; RECOVER Monitoring and Assessment Program; U.S. Army Corps of Engineers; Living Marine Resources Cooperative Science Center

Handling Editor: Thomas C. Adam

Abstract

Habitat fragmentation of submerged aquatic vegetation (SAV) transforms the spatial pattern of seascapes by changing both the total area and spatial configuration of the habitat patches. The ecological effects of SAV seascapes are most often assessed using metrics of biological community composition (e.g., species and assemblage changes). We know considerably less about the effects of seascape structure on ecological processes such as food web function and energy flow. Here, we assess the difference in the trophic niche of Pinfish (*Lagodon rhomboides*, a generalist omnivore) across a spatial gradient of SAV from continuous to highly fragmented seascapes in Biscayne Bay (Miami, Florida, USA). The Bay seascapes are influenced by freshwater management practices that alter the distribution of SAV habitat and fish species abundance, diversity, and community assemblage. We combined SAV seascape maps with stable isotope and hypervolume analyses to determine how trophic niche size and overlap varied with changes in the seascape. We observed similar resource use across the seascape, but trophic niche size increased in more fragmented SAV seascapes, suggesting diversification of trophic roles and energy flow pathways. Pinfish collected from more continuous SAV habitats had smaller trophic niche size and higher trophic levels. Both trophic response metrics manifested a threshold response that depended on distinct SAV spatial characteristics (amount vs. spatial configuration) and environmental conditions. Our results suggest that habitat fragmentation of SAV seascape structure has ecological implications that could affect energy flow with cascading consequences for food web stability and ecosystem functioning.

KEYWORDS
habitat fragmentation, hypervolumes, mixing models, seagrass, seascape ecology, stable isotopes

---

Ecosphere. 2022;13:e3944.
https://doi.org/10.1002/ecs2.3944

INTRODUCTION

The process of habitat fragmentation involves both the decline in total habitat amount (i.e., area) and changes to the spatial configuration of habitat patches (e.g., patch size, density, connectivity) (Fahrig, 2003; Yeager et al., 2016). Changes to the amount and spatial configuration of habitat patches can have significant ecological consequences (Didham et al., 2012; Smith et al., 2009). For instance, both patterns of habitat amount and spatial configuration within landscapes/seascapes (i.e., spatially heterogenous area or mosaic of patches within a "inhospitable" matrix) can influence the distribution and abundance of associated species, and the biodiversity and species assemblages of animal communities (Boström et al., 2011, 2017; Fahrig, 2003, 2019; Santos et al., 2017; Yeager et al., 2016). These ecological consequences of fragmentation can affect species interactions (e.g., competition, predation, facilitation) and trophic linkages (Araújo et al., 2014; Layman et al., 2007; Santos, 2014; Smith, Hindell, et al., 2011), which control food web stability and nutrient flow within ecosystems (Buelow et al., 2018; Valladares et al., 2012).

In landscape and seascape ecology studies, there is a theoretical and empirical debate on the relative importance of habitat amount versus spatial configuration of patches in influencing population and community metrics such as abundance, coexistence, and biodiversity (Fahrig, 2003; Ryall & Fahrig, 2006; Trzcinski et al., 1999; Yeager et al., 2016). Various studies have documented negative impacts from declines (losses) of habitat amount on species richness and abundance (Fahrig, 2003; Schmiegelow & Mönkkönen, 2002; Smith, Fahrig, & Francis, 2011). However, the effects of changes in habitat spatial configuration on associated species are more variable and, in some cases, even positive (Debinski & Holt, 2000; Fahrig, 2003). Habitat loss causes negative impacts by eliminating key resources that influence reproduction, recruitment, and survival (Fahrig, 2003; Ryall & Fahrig, 2006). While habitat losses are a required first step of habitat fragmentation (Didham et al., 2012), changes in the spatial configuration of habitat patches may have a positive outcome through the expansion and diversification of microhabitat types (Horinouchi, 2009; Horinouchi et al., 2009). Changes to spatial configuration may also alter animal movement and patch interception (Awade & Metzger, 2008; Connolly & Hindell, 2006), reduced competition for resources, and modified dynamics of predator–prey systems (Hovel & Regan, 2008; Magioli et al., 2019). Still, studies that have explored impacts of fragmentation on associated fauna have reported mixed findings (Boström et al., 2011; Connolly & Hindell, 2006; Fahrig, 2003), and there are knowledge gaps, especially about fragmentation effects on trophic dynamics and food webs (Boström et al., 2017; Ryall & Fahrig, 2006).

A version of the trophic niche can be defined as the resources a species uses in *n*-dimensional space (Elton, 1927; Layman et al., 2007). Thus, this definition of niche represents the overall trophic role of a species given a set of resources. The availability and access to resources can be controlled by both the habitat amount and spatial configuration (Boström et al., 2011, 2017; Santos et al., 2017; Yeager et al., 2016). Under the optimal foraging theory (OFT), the size of the niche (or niche width/volume) is expected to expand as competition becomes stronger and preferred resources become scarce, especially under conditions of habitat loss and fragmentation (Araújo et al., 2011; MacArthur & Pianka, 1966). The trophic niche is often assessed using dietary diversity (e.g., abundance and diversity of prey items in gut contents) (Araújo et al., 2011; Jackson et al., 2011; Layman et al., 2007). Stable isotope analysis (SIA) has become one of the most commonly used tools to depict dietary diversity and the dynamics of trophic niche size, and is useful to compare energy flows and assess dietary diversity changes due to disturbances and habitat conditions (James, Lesser, et al., 2020; Layman et al., 2012; Nelson, Johnson, et al., 2019). Several metrics and statistical tools based on stable isotope data developed over recent years could be useful for assessing and testing shifts in communities' trophic niche position and niche, and intraspecific diet variability under different habitat conditions (Bearhop et al., 2004; Jackson et al., 2011; Layman et al., 2007; Post, 2002b). For instance, metrics that capture the range and variability of isotopic values in $\delta^{13}C$–$\delta^{15}N$ two-dimensional space are widely used to determine changes in niche space and trophic levels among communities (Jackson et al., 2011; Layman et al., 2007). However, making inferences directly from isotope values themselves can be problematic, as both source variation and variation in both ontogenetic and geographic consumer resource uses can alter the resulting niche calculated directly from isotope space (Fry, 2013; Gorokhova, 2018; Hoeinghaus & Zeug, 2008). To account for the variability in isotope values of primary producers or other sources, Bayesian mixing models have become a popular tool for ecologists to estimate resource use of consumers (Stock et al., 2018). Recent approaches have combined Bayesian mixing model estimates of resource use with a new tool for hypervolume analysis (Blonder, 2018; Blonder et al., 2014) to quantify and assess the trophic niche of consumers (James, Lesser, et al., 2020; Lesser et al., 2020).

Our goal was to understand how the trophic niche and trophic level of an important generalist marine consumer, pinfish (*Lagodon rhomboides*), varied in response to the habitat amount and spatial configuration of submerged aquatic vegetation (SAV) seascapes. We concentrated our study in Biscayne Bay (Miami, Florida, USA), where SAV seascapes are influenced by freshwater management and where seascape properties can influence species abundance, diversity, and community assemblages (Santos et al., 2018). Pinfish were collected from two salinity zones of varying levels of anthropogenic influence in both continuous and fragmented seascapes. Hypervolumes were generated using resource use calculated from Bayesian stable isotope mixing models and trophic level as axes. Following OFT, we hypothesized a larger trophic niche in fragmented SAV in comparison with continuous seascapes via increased interindividual diet variation (i.e., incorporating diet sources with a wider range of preference) (Lesser et al., 2020). We hypothesized a higher trophic level of the omnivore fish species in continuous seascapes, considering that seagrass habitats could support more complex food webs than less productive habitat patches (e.g., barren or low-canopy patches), characteristic of highly fragmented seascapes. Also, few seascape studies have separated the effects of habitat amount and spatial configuration on ecological responses (Bonin et al., 2011; Caley et al., 2001; Healey & Hovel, 2004), and even fewer studies have identified critical thresholds where small changes in habitat spatial properties may lead to large changes in population responses (Pittman et al., 2004; Salita et al., 2003; Thistle et al., 2010).

METHODS

Study site and focal species

Our study concentrated on the nearshore habitats of the central-western section of Biscayne Bay, Miami, Florida, USA (Figure 1a), a shallow subtropical lagoon adjacent to the city of Miami (county population 2.5 million) and downstream of the Florida Everglades. We used preserved samples obtained by Santos et al. (2018), a study that sampled marine fishes and crustaceans on nearshore SAV seascapes (<500 m from shore) in western Biscayne Bay, where seagrasses are the dominant benthic macrophyte (Lirman et al., 2008, 2014). SAV patches are mostly composed of the seagrass *Thalassia testudinum*, with some patches mixed with *Halodule wrightii* (seagrass), rhizophytic macroalgae, and drift macroalgae (Lirman et al., 2014). There are distinct SAV seascape structures (i.e., different mosaics and arrangements of SAV patches) along nearshore habitats of Biscayne Bay, which are the result of disturbances associated with freshwater management activities, macroalgae harmful blooms, and other structuring processes (e.g., hydrodynamics, sediment depth, storms) (Santos et al., 2011, 2015, 2020; Stipek et al., 2020).

SAV seascapes, as well as the fringing mangroves, provide habitat for a large number of commercially and recreationally valuable species (e.g., *Farfantepenaeus duorarum*, *Lutjanus griseus*, *Lachnolaimus maximus*; Diaz et al., 2001; Faunce & Serafy, 2008; Serafy et al., 1997, 2003), including the focal species of this study—pinfish *Lagodon rhomboides* (Santos et al., 2018). Pinfish are an omnivorous species, which depends on seagrass seascapes (Jordan et al., 1997; Levin et al., 1997). Pinfish are also an important forage species for SAV predators and prey subsidy for offshore food webs (Nelson et al., 2013; Reynolds & Bruno, 2013). Pinfish are a good candidate for this type of work because their foraging varies in response to seascape and seagrass characteristics (Froeschke & Stunz, 2012; Irlandi & Crawford, 1997; Jordan et al., 1997; Levin et al., 1997), and they exhibit high site fidelity (40–100 m, Potthoff & Allen, 2003).

SAV seascape characterization

Categorical characterization of seascapes

We quantified the influence of seascape spatial structures on *L. rhomboides* trophic niche across twelve 500 × 500 m (0.25 km^2) seascape sample units (SSUs) (Figure 1a,b). The SSUs were the same as in Santos et al. (2018), and we sampled six fragmented (FS) and six continuous (CS) SAV seascapes across two salinity zones (three of each seascape type in each salinity zone described below; Figure 1b). The 500 m × 500 m SSU classified as CS had a higher proportion of the benthos covered by larger SAV patches with lower shape complexity. In contrast, FS SSU had a higher density of smaller SAV patches with complex shapes and a lower proportion of the substrate cover by SAV patches. For more details on the mapping and SSU classification procedures, see Santos et al. (2018).

To compare the trophic response to habitat amount and spatial configuration independently, we used percentage of the seascape occupied by SAV patches (PLAND) to quantify habitat cover and a fragmentation index (Santos et al., 2015) integrating four measures of configuration to quantify habitat fragmentation: patch density (PD, number of patches per sampling area), landscape division (LD, probability two randomly sampled cells are not in the same patch), area-weighted mean perimeter-to-area ratio (AWMPAR, mean perimeter-to-area ratio of a class

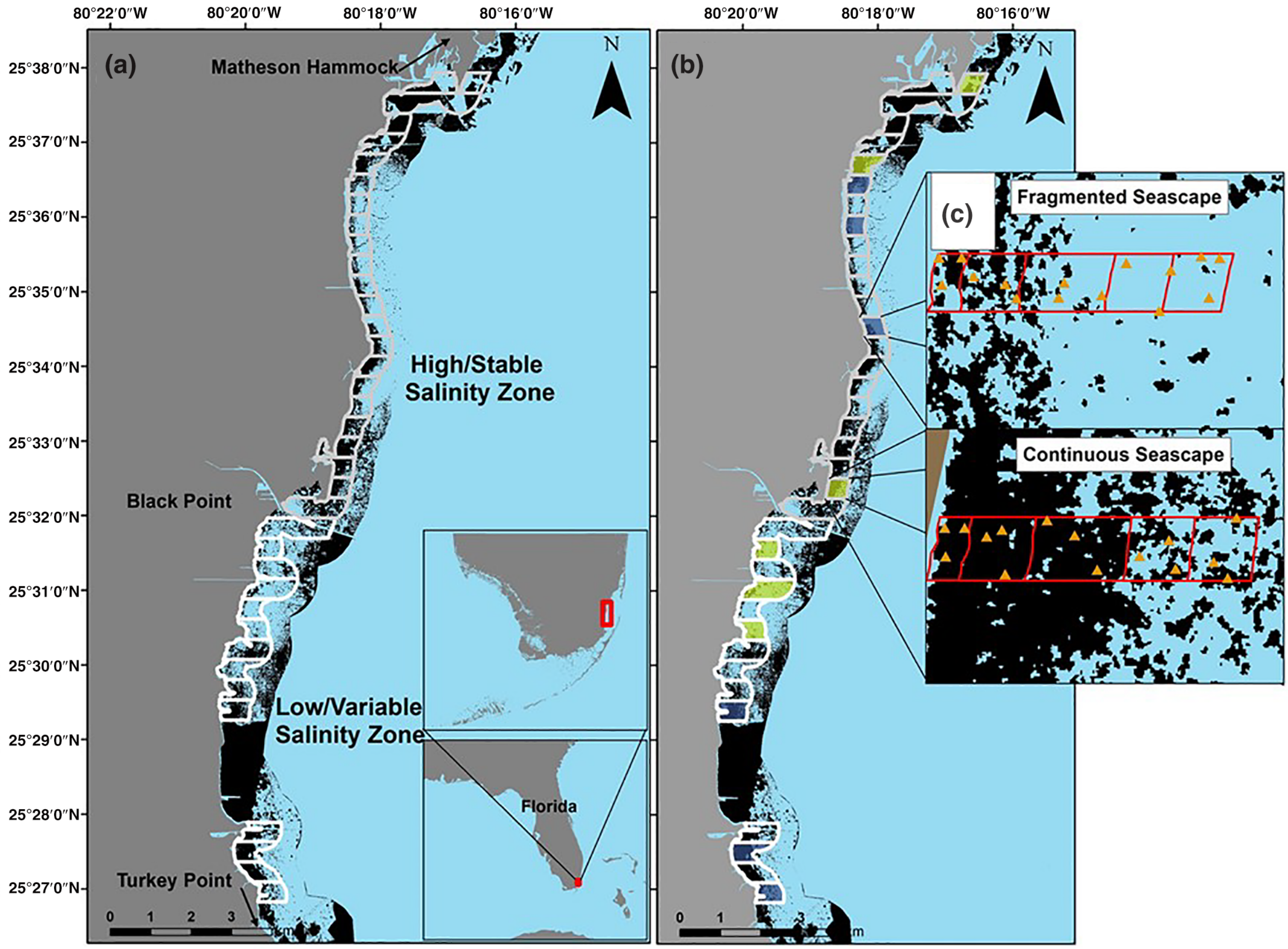

FIGURE 1 (a) Map of the study area and sampling design. The study area was divided into two zones based on salinity regimes: high and stable salinity zone (north, gray grid) and low and variable salinity zone (south, white grid). (b) SAV seascape map with superimposed 500 × 500 m grid cells (i.e., seascape sampling unit) (some grid cells in the south were excluded due to cloud cover interference with the image classification process); seascapes within grids were classified and selected as continuous (dark blue) and fragmented (green) SAV seascapes. (c) Within each selected grid cell, a 100 m × 500 plot was centered. Each plot was divided into five 100 m × 100 m distance-to-shore strata where pinfish samples were obtained across randomly placed sampling replicates (orange triangles)

weighted by the size of the patch relative to the total area of that class), and mean radius of gyration (GYRATE_MN, mean distance from each cell in a patch to the patch centroid). The fragmentation index (FragIndex) was as follows:

$$\mathrm{FragIndex} = \sqrt[4]{(\mathrm{PD} \times \mathrm{LD} \times \mathrm{AWMPAR} \times 1/\mathrm{Gyrate\_MN})}.$$

All metrics were standardized to produce a FragIndex ranging from 0 (low fragmentation) to 1 (high fragmentation). The spatial pattern metrics used in the FragIndex are the most appropriate to assess habitat fragmentation across different levels of habitat cover (Hovel & Lipcius, 2002; Salita et al., 2003; Sleeman et al., 2005).

Sampling stratification

Nutrients and freshwater pulses can influence the prey composition and availability, and the isotopic content of primary producers and trophic linkages within estuarine systems (Nelson et al., 2015; Post, 2002a; Swart et al., 2013). Thus, the sampling in this study was replicated within two zones that have distinct salinity-nutrient regimes, as described by previous studies (high and stable salinity zone and low and variable salinity zone, Figure 1a; Lirman et al., 2008, 2014, Swart et al., 2013). This sampling stratification was performed by randomly selecting three 500 × 500 m SSU replicates for each seascape type (CS and FS) within each salinity zone (Figure 1a). The high and stable salinity zone, an area with limited input of freshwater from canal structures, was characterized by higher and more stable salinity (wet season mean salinity: 26.6 ppt [±4.6 SD], min–max: 13–36 ppt). In contrast, the low and variable salinity zone is influenced by pulsed freshwater flows from canals that create a nearshore environment with low and variable salinity (wet season mean salinity: 17.1 ppt [±8.2 SD], min–max: 2–33 ppt) (Lirman et al., 2008, 2014), and high nutrient concentrations (Swart et al., 2013). This sampling design allowed us to assess the influence of seascape spatial patterns on fish trophic niche under different salinity-nutrient regimes.

Fish sampling and processing

The collection of pinfish was performed via seine nets within a 100 m × 500 m plot starting at the shore that was randomly placed within each SSU (average depth = 1.1 m, average depth range = 0.8 m; Figure 1c). The SSU sampling plots were divided into five distance-to-shore strata (100 m × 100 m), where three seine sampling locations were randomly positioned (i.e., $n = 15$ points per plot—three deployment sites per distance-to-shore stratum) (Figure 1c). At each sampling location, a center bag seine net (21.3 m long, 1.8 m deep, 3 mm mesh) swept a bottom area of approximately 210 m^2 to collect fish samples. The sampling was conducted in 2012, during the wet season (July–October). All fish samples were taken back to the laboratory and frozen at −20°C until they could be processed for isotope analysis.

Ten pinfish were randomly selected across the distance-to-shore strata for isotope analysis ($N = 10$ individuals × 12 sites = 120 samples). All pinfish selected were >90 mm (high and stable salinity zone: fragmented 114.0 mm (90–135) mean (min–max), continuous 122.5 mm (100–170); low and variable salinity zone: fragmented 132.3 mm (95–175), continuous 115 mm (90–155); Appendix S1: Figure S1). Dorsal muscle tissue was obtained for each fish sample, dried at 50°C for 48 h, and ground for stable isotope analysis. Samples were analyzed for carbon and nitrogen isotopic content using a CN analyzer (Euro-EA-Elemental Analyser, Eurovector, Milan, Italy) connected to a mass spectrometer (Elementar, Germany). Additionally, basal resources were also collected for C and N stable isotopes at each of the SSUs. The basal resource collection concentrated on the dominant macrophyte species that constitute most of Biscayne Bay SAV seascapes (*Thalassia testudinum*, *Halodule wrightii*, *Batophora* sp., *Halimeda* sp., red algae drift complex). The basal resource samples were rinsed with deionized water and spin dried to facilitate tissue isolation (i.e., spin out undesired material such as sand and mud particles, carbonate epiphytes). Also, epiphytes were removed either with a small soft brush or using a razor blade. Similar to the muscle tissue, samples were dried and ground for stable isotope analysis.

Generating trophic response metrics

Bayesian mixing models

The basal resource contributions, derived from the stable isotope values, were used to derive trophic response metrics (trophic level and trophic niche volume) of pinfish individuals. The relative contribution of the basal resources was estimated with Bayesian mixing models. The basal resources were grouped into seagrass (*Thalassia testudinum*, *Halodule wrightii*), benthic macroalgae (*Penicillus* sp., *Halimeda* sp.), and drift algae (*Laurencia* sp. and *Hypnea* sp. drifting algae complex), based on isotopic similarity among the macrophyte groups, and to help with resolution of the mixing models (Phillips et al., 2014). Epiphytic algae were not collected for stable isotope analysis in this study, but have been shown to be an important basal resource in seagrass food webs (Chasar et al., 2005; Kitting et al., 1984). Therefore, epiphyte stable isotope values from Chasar et al. (2005) collected from Biscayne Bay were also included as a potential basal resource in the mixing models. Using published literature values of potential sources collected in the same study location is a common way to account for important sources for the mixing model (e.g., Baker et al., 2021; Plumlee et al., 2020).

Bayesian mixing models were run in R version 3.5.2 (R Core Team, 2017) using the package MixSIAR (v 3.1.10; Stock et al., 2018) to determine the relative contribution of seagrass, benthic macroalgae, drift algae, and epiphyte-derived organic matter sources to pinfish individuals. As part of the models, corrections were made for the elemental concentration in each source, and the trophic enrichment for each element was C = 1.0 ± 0.63 (mean ± SD) and N = 3.0 ± 0.74 (Nelson et al., 2015; Phillips et al., 2014; Post, 2002b). Each model was run with a Markov chain Monte Carlo algorithm that consisted of three chains, chain length of 1,000,000, burn-in of 500,000, and thinness of 500 to ensure model convergence. The average of the mixing models' posterior mean output was used to represent the contribution distribution among basal resources.

Trophic response metrics

Two trophic response metrics were developed from the Bayesian mixing model results: trophic level (i.e., position) and size (i.e., volume) of the trophic niche. The trophic level represents the average number of trophic transfers it takes for energy to reach that organism (Lindeman, 1942). The relative trophic level in the food web was calculated for each pinfish individual using the equation:

$$\mathrm{TL} = \frac{\delta^{15}\mathrm{N}_{\mathrm{con}} - \sum\left(\delta^{15}\mathrm{N}_{\mathrm{s}} \times f_{\mathrm{s}}\right)}{\Delta\delta^{15}\mathrm{N}} + 1,$$

where $\Delta\delta^{15}\mathrm{N} = 3$ and represents the trophic enrichment factor (Hussey et al., 2014; Nelson et al., 2015; Post, 2002b), $\delta^{15}\mathrm{N}_{\mathrm{con}}$ represents the consumer nitrogen isotopic value, $\delta^{15}\mathrm{N}_{\mathrm{s}}$ is the nitrogen isotopic value of each basal resource, and f_{s} is the contribution of each basal resource to the consumer diet based on the output of the mixing model (Nelson et al., 2015).

The trophic niche (i.e., niche space) of each SSU pinfish population was estimated with the hypervolume R package (v 2.0.11; Blonder et al., 2014, 2018). Hypervolumes were estimated using the *z*-score for the basal resource contributions predicted by the mixing models and related trophic levels. The *z*-scored basal contribution and trophic level allow for standardized, comparable axes in *n*-dimensional space (Blonder et al., 2014). The *z*-score values were calculated based on the following equation:

$$z = \frac{x_{ij} - \overline{x}_j}{\mathrm{SD}_j},$$

where x_{ij} is the individual value for a given axis, $\overline{x}_j$ is the global mean of that axis, across all the SSUs within each salinity zone, and SD_j is the standard deviation of that axis.

Hypervolumes were created by simulating 5,000,000 points using a Gaussian kernel density estimation for each SSU pinfish population. The bandwidth is a vector that is used to estimate the density of the hypervolume, and the Silverman estimator is used to estimate the bandwidth using a quasi-optimal approach based on the variation of the input data (Blonder et al., 2014). Trophic niche size was calculated by determining the volume of each hypervolume generated. Each hypervolume was remade 100 times using the same parameters as a bootstrapping method to determine the inherent variability in hypervolume size that arises from Gaussian kernel density estimation. A detailed description of the algorithms used to create the hypervolume and calculate hypervolume metrics can be found in Blonder et al. (2014, 2018).

Statistical analyses

Trophic niche overlap

We used the Sorensen overlap to measure and test the overlap between the niche hypervolume estimated in the continuous and fragmented seascapes located in both salinity zones. The Sorensen overlap (SO) was calculated using the following equation:

$$\mathrm{SO}_i = \frac{2V_{\mathrm{int}}}{V_{\mathrm{cont}} + V_{\mathrm{frag}}}.$$

Here, V_{int} is the volume of the intersection of the continuous and fragmented seascape hypervolumes for each respective salinity zone, V_{cont} is the volume of the continuous seascape hypervolume, and V_{frag} is the volume of fragmented seascape hypervolume (Blonder et al., 2018). We created a bootstrap distribution of SO to discern differences between the seascape hypervolume overlap in both salinity zones. Overlap confidence intervals were generated by creating hypervolumes by randomly sampling 2/3 of the data from the fragmented and 2/3 of the data from the continuous habitats and calculating the overlap (Lesser et al., 2020). This process was repeated 100 times for each salinity zone.

Trophic response in continuous and fragmented seascapes and salinity zones

Generalized linear models (GLMs) were used to examine and test for differences in the trophic response metrics among the seascape types and salinity zones (interactive effects were not included in the models). A GLM with a Gaussian error distribution and log link function was used to characterize the differences in trophic niche size among the model factors. A GLM with Gamma error distribution and a log link function was used for trophic level. The full models were simplified further by dropping terms, using the delta-AIC (Akaike information criterion) of less than two units as a selection criterion.

Threshold response of trophic metrics to spatial habitat characteristics

The trophic response metrics (trophic niche size and trophic level) were related to values of habitat amount (PLAND) and spatial configuration (FragIndex) to examine the magnitude and direction of the trophic response, and identify distinct threshold responses to quantities of habitat amount or spatial configuration. The assessment of the relationship between the trophic response metrics and the spatial habitat characteristics was performed with GLMs. All GLMs included a full factorial second-order polynomial structure and salinity zone as a factor. Both response metrics were assessed with a GLM with a Gamma error distribution and log link function. Similar to the factorial analysis, a delta-AIC greater than or equal to two was used as a model simplification and selection criterion.

Residual diagnostics plots were used to assess the assumptions of all GLMs, and D^2 values, which indicate the amount of deviance accounted for by the models (i.e., analogous to R^2), were used to evaluate the goodness of fit of all selected final models. (Barbosa et al., 2013, 2016). All statistical analyses were performed in R v 3.5.2 (R Core Team, 2017). The GLMs, model evaluation, and D^2 calculation were performed respectively with the stats (R Core Team, 2017), MuMIn (Barton, 2013, 2019), and modEvA (Barbosa et al., 2016) R packages.

RESULTS

Trophic niche overlap

The shape and overlap of the pinfish's hypervolumes (i.e., trophic niche space) between continuous and fragmented seascapes differed across salinity zones (Figure 2). In the high and stable salinity zone, pinfish from continuous and fragmented seascapes shared an overlap of 0.44 (Figure 2c). Between the two seascape types in this zone, epiphyte algae showed a higher contribution in fragmented seascapes, and benthic algae, in continuous seascapes (FS: benthic algae = 0.26, epiphytes = 0.62, drift algae = 0.02, seagrass = 0.10; CS: benthic algae = 0.35, epiphytes = 0.53, drift algae = 0.03, seagrass = 0.09; Figures 2a and 3a). In contrast, in the low and variable salinity zone, there was less overlap (0.22) between the continuous and fragmented seascapes (Figure 2b,c). Between the two seascape types in this zone, there was a higher variation in resource contribution in fragmented seascapes, with benthic algae, seagrass, and drift algae showing the higher contribution within this seascape type (FS: benthic algae = 0.06, epiphytes = 0.80, drift algae = 0.09, seagrass = 0.06; CS: benthic algae = 0.04, epiphytes = 0.87, drift algae = 0.06, seagrass = 0.04; Figure 3b). The overlap bootstrap distribution suggested no significant differences in the trophic niche overlap between seascape types in the two salinity zones (Figure 2c); however, the overlap estimates were biased toward lower values in the low and variable salinity zone.

Trophic response in continuous and fragmented seascapes and salinity zones

The trophic response of pinfish in continuous versus in fragmented seascapes varied with the response metric considered (Figure 4). The model selection showed that trophic niche size (as measured through volume of the hypervolume) was best explained by the seascape type, while for trophic level, the best model considered both seascape type and salinity zone. Trophic niche size tended to be larger in fragmented seascapes (mean ± SD, FS = 377 ± 488, CS = 85 ± 102; Figure 4a), with higher variation in basal resource use (Figures 2a and 3a). However, seascape type only explained 31% of the model deviance, and the difference between seascape types was not significant according to the GLM summary table (Table 1a). Trophic-level response was best explained by a combination of seascape type and salinity regime zone. In contrast, the trophic level was significantly higher in continuous seascapes (mean ± SD, FS = 2.8 ± 0.6, CS = 3.1 ± 0.7), and in the low and variable salinity zone (mean ± SD, high and stable = 2.5 ± 0.6, low and variable = 3.4 ± 0.4; Table 1b, Figure 4b).

Threshold response of trophic metrics to spatial habitat characteristics

Trophic niche size and trophic-level response in pinfish to both seascape fragmentation and habitat amount were curvilinear (Figures 5 and 6). The model selection showed that trophic niche size was best explained by just the seascape characteristics (seascape cover and FragIndex). In contrast, for trophic level, the best model considered the seascape characteristics and salinity zones (Table 2). As reflected by the D^2 and fitted values, the fitted response of trophic niche size was more precise with respect to fragmentation (Table 2a,b, Figure 5), showing a stronger response in trophic niche size after intermediate levels of fragmentation (FragIndex < 0.5, Figure 5a). In contrast, trophic niche size showed a weak negative relationship with habitat cover (Table 2b, $D^2 < 0.30$) and notably reflecting a high variance around low-to-intermediate levels of habitat amount (Figure 5b).

Trophic level showed a quadratic, u-shaped relationship with fragmentation and habitat amount (Table 2c,d, Figure 6). Concerning both fragmentation and habitat amount, the trophic level of pinfish was low at intermediate values, with minimum values occurring at 45% for PLAND and 0.66 for FragIndex. However, inversely to the niche volume, higher values of trophic level were observed at lower and higher values of fragmentation and habitat amount, respectively. The trophic-level response type did not vary between salinity regime zone, but it was relatively higher in low and variable salinity zone.

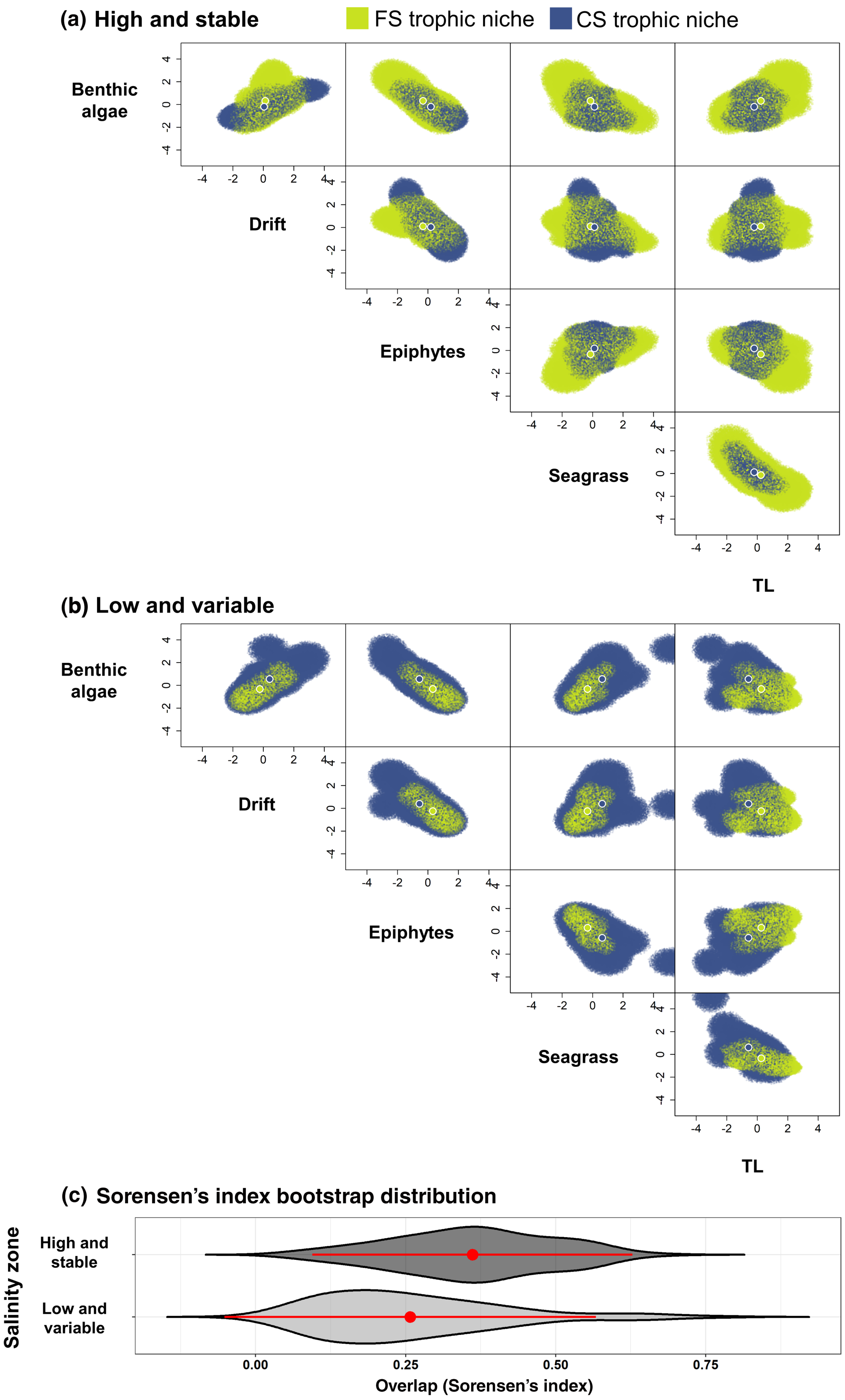

FIGURE 2 Legend on next page.

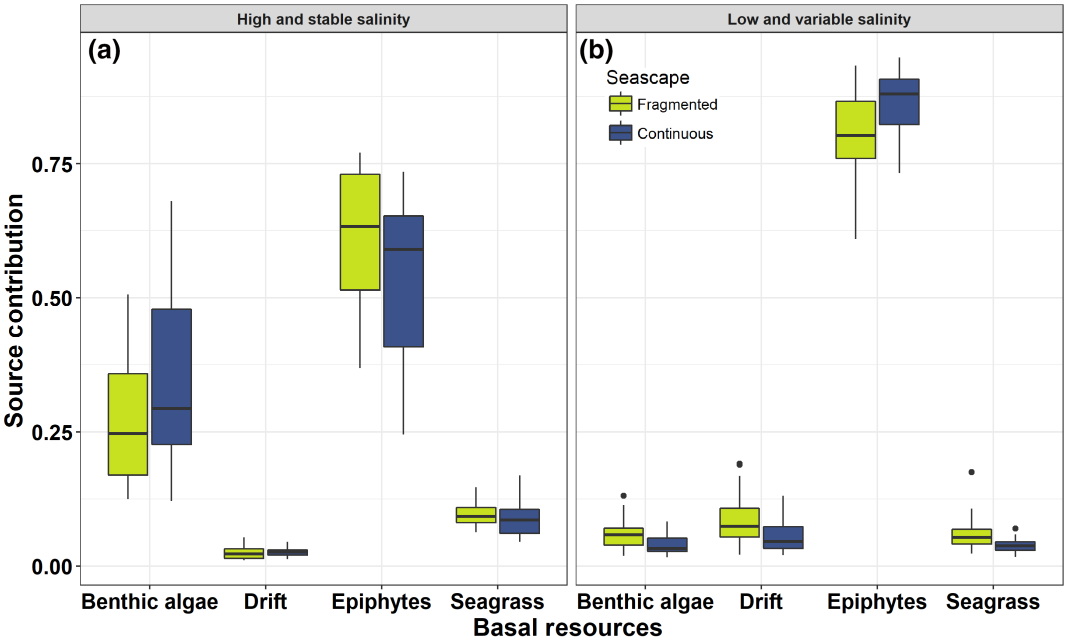

FIGURE 3 Contrast of basal resource contributions for pinfish in continuous (dark blue) and fragmented (light green) seascapes across (panel a) high and stable salinity zone and (panel b) low and variable salinity zone. Basal resource contributions estimated from stable isotope Bayesian mixing models

DISCUSSION

Our study contributes to the limited knowledge of how SAV spatial characteristics influence the realized trophic niche of fish populations by incorporating a seascape ecology approach and stable isotope analysis. The urgency in understanding the ecological consequences of spatial habitat transformation is heightened by the rapid global decline in the extent and quality of coastal SAV seascapes and growing investment in restoration (Boström et al., 2017; Pittman et al., 2011; Santos et al., 2018). Understanding how geographic differences and changes to the amount and spatial configuration of SAV habitats influence ecological processes for species and ecosystem functioning has important implications for conservation, threat management, and restoration design (Boström et al., 2017; Hovel, 2003; Yeager et al., 2016). By combining seascape maps, Bayesian mixing models, and hypervolume analysis, we showed that the trophic niche overlapped between pinfish populations in continuous and fragmented seascapes, but further expanded to distinct regions of the niche in fragmented seascapes. In contrast, the overall trophic level of pinfish populations was higher in continuous seascapes. Nevertheless, both trophic response metrics manifested a threshold response that depended on distinct SAV spatial characteristics (amount vs. spatial configuration) and environmental conditions (salinity zones). Thus, our results suggest that changes to SAV seascape characteristics due to fragmentation processes, as evident in Biscayne Bay and other coastal regions, can have ecological implications that could affect energy flows, food web stability, and ecosystem functioning.

Trophic niche characteristics between continuous and fragmented seascapes

Optimal foraging theory (OFT) (Stephens & Krebs, 1986) and patterns presented by other seascape ecology studies offer a useful framework to explain the larger trophic niche and lower trophic level observed in fragmented

FIGURE 2 Pinfish trophic hypervolumes in the continuous (dark blue) and fragmented (light green) seascapes in (a) high and stable salinity zone and (b) low and variable salinity zone. Note the points in the pair plots are random points generated within the hypervolume. Trophic hypervolumes are depicted as a series of biplots that represent the relationship between the relative contribution of basal resources to consumers and the estimated trophic level. Axes are z-scored measuring standard deviations with being the global mean across seascape sampling units (SSUs). (c) Bootstrap distribution of the degree of overlap between the pinfish continuous and fragmented seascape trophic niche. Overlap estimate based on Sorensen’s similarity index. TL, trophic level

SAV seascapes. Under OFT, the trophic niche can increase as a function of intra- and interspecific competition, low resource abundance, or the diversity of available resources (i.e., ecological opportunity) (Araújo et al., 2011), all conditions favored in fragmented seascapes (Boström et al., 2011, 2017; Horinouchi, 2009; Macreadie, Hindell, et al., 2010). Pinfish individuals could highly concentrate on smaller patches associated with fragmented seascapes (i.e., crowding effect; Debinski & Holt, 2000, Ewers & Didham, 2006, Macreadie, Connolly, et al., 2010) since they rely on dense seagrass patches to increase foraging efficiency and decrease predation risk (Canion & Heck, 2009; Jordan et al., 1997; Levin et al., 1997; Santos, 2014). Thus, crowding effects could increase the trophic niche through pinfish intraspecific competition, which, in theory, reduces preferred resources and increases the consumption of less valuable prey (Araújo et al., 2011, 2014). On the contrary, pinfish manifested smaller trophic niche size in continuous seascape, which suggests optimal foraging on a narrower range of energetically favorable prey resources. Similar results were found in another study where pinfish decreased niche size in response to increased ecosystem productivity (Lesser et al., 2020). Continuous seagrass beds likely have more productivity available to pinfish allowing more individuals to optimally forage than in fragmented habitats, and thus decrease the niche size in these habitats.

Multiple aquatic experimental and field studies support that intraspecific competition among fish species increases foraging specialization (Araújo et al., 2011, 2014; Kobler et al., 2009; Svanbäck et al., 2011); however, very few studies have investigated the mechanisms of trophic niche dynamics under the context of SAV seascape fragmentation. Only three studies, which concentrated on mangrove creek habitats, have recorded changes to trophic niche size of marine fish populations due to hydrologic habitat fragmentation (Araújo et al., 2014; Layman et al., 2007; López-Rasgado et al., 2016). For instance, in the Bahamas, a study showed how the trophic niche of *Gambusia hubbsi* broadened across a gradient of mangrove creek fragmentation due to predation

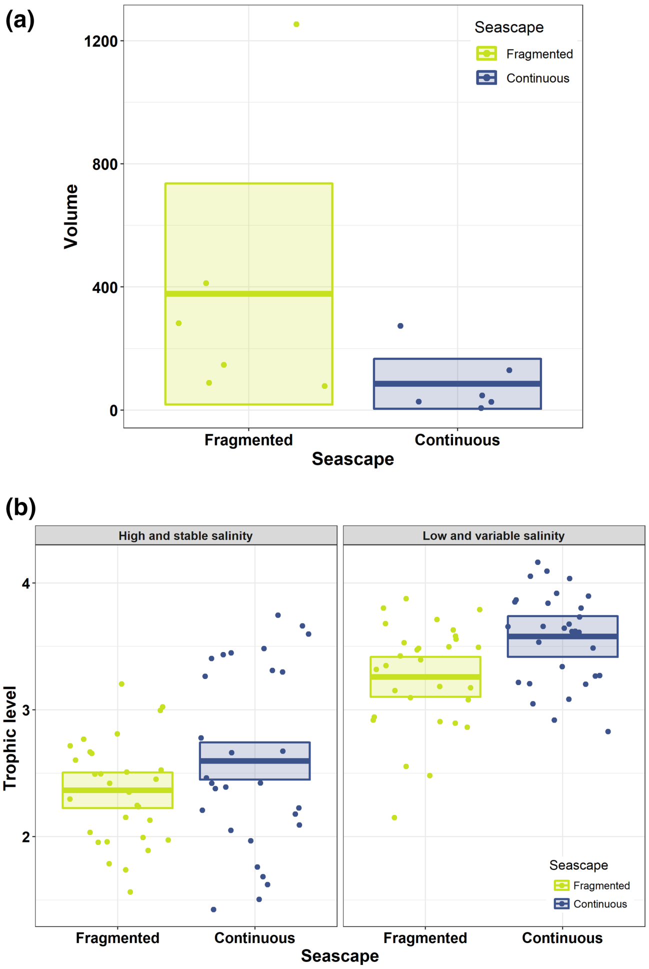

FIGURE 4 Pinfish (a) trophic niche size and (b) trophic level across seascape types and salinity zones. Crossbars show the generalized linear model fitted values (center bolded line) and associated 95% confidence interval (upper/lower extension of bar). Colored points illustrate raw observations in continuous (dark blue) and fragmented (light green) seascapes. Crossbars are based on fitted values from the final selected models presented in Table 1

TABLE 1 Summary table of the generalized linear models (GLMs) used to test the difference of (a) trophic niche size and (b) trophic level across seascape types and salinity zones

Variable	Coefficient	Estimate	SE	t	p	Null deviance	Deviance	D^2
(a) Size	Intercept	5.93	0.49	12.2	2.50E−07	19.59	13.49	0.31
	Seascape: continuous	−1.49	0.69	−2.16	5.60E−02			
(b) Trophic level	Intercept	0.861	0.03	28.41	2.45E−54	56.84	28.08	0.51
	Seascape: continuous	0.093	0.03	3.104	**2.40E−03**			
	Zone: low and variable salinity	0.321	0.031	10.193	**7.61E−18**			

Note: Shown are the coefficient estimates in relation to reference point, standard error of estimates (SE), t statistics, and p values for the null hypothesis of no difference with the reference point. Significant coefficients are bolded. Also included null deviance, deviance, and D^2 to present a quality of fit of the models. Based on final GLMs identified from the model selection procedure.

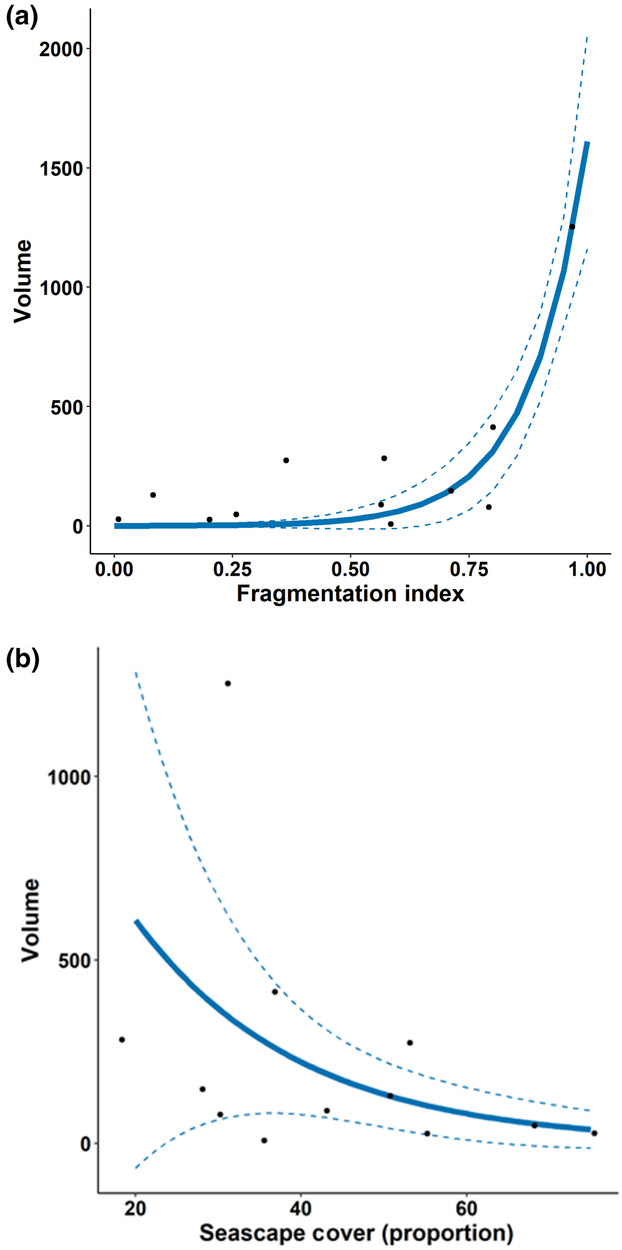

FIGURE 5 Fit of generalized linear models (GLMs) to assess the relationships of trophic niche size (volume) with spatial habitat (a) configuration (fragmentation index) and (b) amount (seascape cover). See Table 2a,b for more details on the GLMs

release and increase in intraspecific competition in highly disturbed, fragmented habitats (Araújo et al., 2014). Despite this limitation of seascape studies on trophic niche, other studies have observed how the intraspecific competition of consumers and the abundance of epibenthic prey are influenced by seascape properties, habitat complexity, and size (Boström et al., 2011; Connolly & Hindell, 2006; Livernois et al., 2019; Santos et al., 2018), all potential drivers of individual specialization and niche expansion. Thus, the prevalence of ecological causes of individual specialization that may arise from spatial habitat characteristics sustains the need for focusing future seascape studies on addressing the trophic niche consequences of seascape fragmentation.

Ecological opportunity (i.e., diversity of available resources) and predation risk (i.e., likelihood of being predated) are also other mechanisms that could drive pinfish trophic intraspecific variability and niche differences between continuous and fragmented SAV seascapes (Araújo et al., 2011). Ecological opportunity could arise from habitat fragmentation due to the increase in the amount and diversity of microhabitats that could be utilized by different pinfish individuals (Horinouchi, 2009; Salita et al., 2003; Santos et al., 2018). For instance, in Biscayne Bay, the abundance of species that are potential prey for pinfish and the diversity of the nektonic community was positively associated with fragmented SAV seascapes (Santos, 2014; Santos et al., 2018). Also, ecological opportunity could arise from edge effects (Ries & Sisk, 2004), which tend to increase from continuous to fragmented seascapes (Macreadie, Connolly, et al., 2010; Santos et al., 2015; Yeager et al., 2012). For instance, several studies have observed more generalist predatory fishes foraging at edges and the accumulation of amphipods, copepods, and isopods (primary consumers in seagrass habitats and essential food sources for pinfish) at seagrass edges (Macreadie, Hindell, et al., 2010; Smith et al., 2010; Smith, Hindell, et al., 2011; Thistle et al., 2010). However, predation risk tends to increase with fragmentation and can affect pinfish foraging behavior by increasing their bias toward large, dense seagrass patches (Froeschke & Stunz, 2012; Jordan et al., 1997; Santos, 2014). Thus, the trophic niche size difference observed between the two SAV seascape types could have been caused by the intravariability of behavioral traits (i.e., risk aversion, boldness, dominance), which control the decision-making process of foraging and diet selection under predation risk (Araújo et al., 2011; Catano et al., 2014, 2015).

The difference in trophic level between the fragmented and continuous SAV seascapes also captured the changes in pinfish trophic interactions across seascape types. As we hypothesized, the higher trophic level was in continuous seascapes, which derived from the other study observations that dense seagrass patches and connected, continuous seascapes support more complex trophic food web and longer food chains (Nelson et al., 2015; Nelson, Johnson, et al., 2019; Nelson, Lesser, et al., 2019; Post, 2002a). Like our study, Layman et al. (2007) found that the trophic level of a generalist fish predator was higher in unfragmented mangrove creeks, which they attributed to an "insertion mechanism" that can affect the relative trophic level of consumers through the extension of intermediate links in a

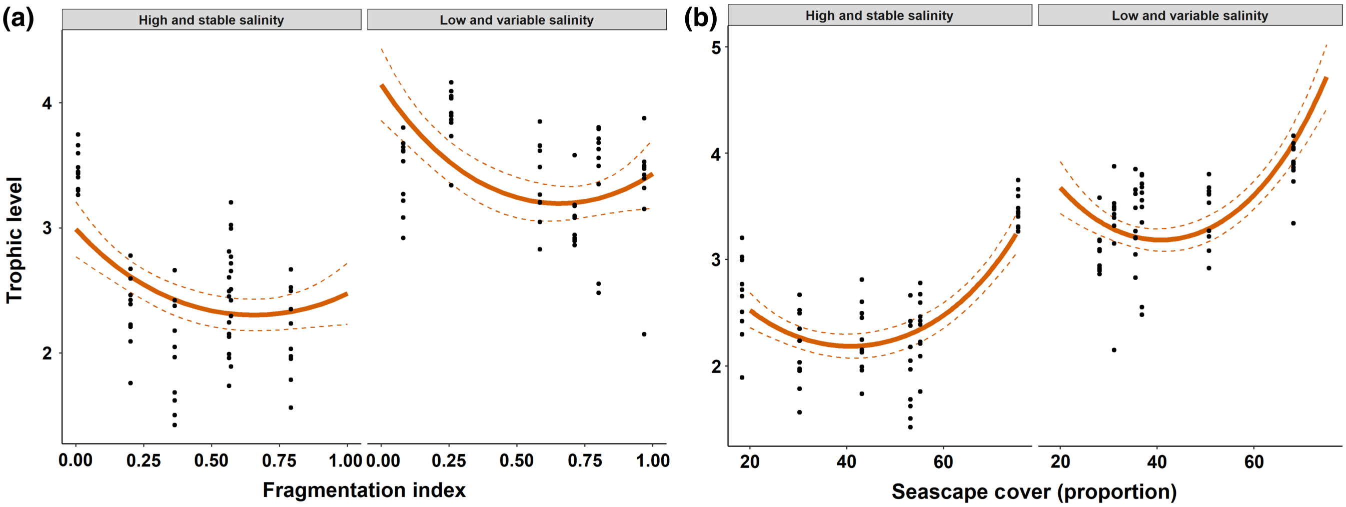

FIGURE 6 Fit of generalized linear models (GLMs) to assess the relationships of trophic level with spatial habitat (a) configuration (fragmentation index) and (b) amount (seascape cover) across the salinity zones. See Table 2c,d for more details on the GLMs

TABLE 2 Summary table of the generalized linear models (GLMs) used to assess the threshold response of (a–b) trophic niche size and (c–d) trophic level as a functional habitat spatial configuration (FragIndex) and amount (seascape cover), respectively

Response variable	Effect	Coefficient	Estimate	SE	t	p	Null deviance	Deviance	D^2
(a) Size	FragIndex	Intercept	−0.8186	1.6055	−0.51	6.21E−01	1.31E+06	2.05E+05	0.84
		Fragmentation	8.2037	1.6954	4.839	6.83E−04			
(b) Size	Seascape cover	Intercept	7.42	0.918	8.083	1.08E−05	19.59	13.91	0.28
		Cover	−0.05	0.02	−2.573	2.77E−02			
(c) Trophic level	FragIndex	Intercept	1.09515	0.0375	29.203	2.71E−55	56.84	23.56	0.59
		Fragmentation	−0.79349	0.17084	−4.645	9.05E−06			
		Fragmentation^2	0.60505	0.17571	3.444	8.00E−04			
		Zone: low and variable salinity	0.32677	0.03004	10.878	2.01E−19			
(d) Trophic level	Seascape cover	Intercept	1.338	0.098	13.643	7.24E−26	56.84	16.51	0.71
		Cover	−0.027	0.005	−5.944	2.99E−08			
		Zone: low and variable salinity	0.376	0.026	1.47E+01	2.52E−28			
		Cover^2	0	0	7.157	8.04E−11			

Note: Shown are the coefficient estimates, standard error of estimates (SE), t statistics, and p values for the null hypothesis of no difference with the reference point. Significant coefficients are bolded. Also included null deviance, deviance, and D^2 to present a quality of fit of the models. Based on GLMs identified from the model selection procedure.

particular food chain. Other studies in estuarine ecosystems in the Gulf of Maine and the Gulf of Mexico have also observed how the trophic level of intermediate aquatic consumers increases with the availability (i.e., through measurements of area and connectivity) of mangrove and marsh habitats that contain higher prey protein (Nelson et al., 2015; Nelson, Lesser, et al., 2019). However, despite not measuring seascape-level metrics directly, another study found that the trophic level of pinfish did not differ as a function of seagrass percent-weighted volume (Lesser et al., 2020). This supports the notion that the trophic interactions and niche of seagrass-dependent species such as pinfish may be influenced by habitat characteristics at multiple spatial scales, mainly operating at or beyond the seascape scale.

Pinfish display ontogenetic shifts throughout life, and pinfish earlier in their life cycle are more carnivorous and have higher trophic levels than mature pinfish (Barbosa & Taylor, 2020; Stoner, 1980). Because pinfish display ontogenetic shifts, it is possible the difference in trophic level across the seascape types is due to differential use of seagrass seascape configuration depending on the life stage. Size-specific shifts in habitat use have been shown in other nekton species depending on the degree of fragmentation (James, Topor, & Santos, 2020). However, in this study pinfish were above the size threshold of when mature pinfish shift to a more herbivorous diet (80 mm; Stoner, 1980), and were similar in size across the different seascape types (Appendix S1: Figure S1). Therefore, the differences observed in trophic level across seascape types were likely not due to ontogenetic shifts based on the size of the pinfish.

Threshold response as a function of spatial habitat cover and configuration

Robust ecological assessments and effective management practices require an understanding of both the independent and interactive effects of habitat amount and spatial configuration because restoration strategies may differ depending on the primary cause of habitat fragmentation (Lindenmayer & Fischer, 2007). We did not evaluate the interactive effects of these two spatial habitat components due to constraints of our study design; however, we demonstrated how trophic niche size and trophic level related distinctly to habitat amount (seascape cover) and configuration (fragmentation index). More importantly, the analyses evidenced the existence of critical thresholds for both indices of habitat amount and spatial configuration—that is, points of abrupt change in the relationship between trophic interactions and spatial properties of SAV seascapes (Francesco Ficetola & Denoël, 2009). Critical thresholds are valuable information to capture signals of significant ecosystem shifts and provide a better understanding of when and how environmental changes will have considerable consequences on ecological processes and ecosystem dynamics (Francesco Ficetola & Denoël, 2009; Salita et al., 2003; With & Crist, 1995). Here, we observed how the trophic niche size and trophic level of pinfish drastically changed above intermediate values of fragmentation and habitat amount. Thus, the critical thresholds of pinfish's trophic response could help inform how future impacts of restoration and management activities may affect optimal seascape types and determine whether critical ecological thresholds could be exceeded in nearshore habitats of Biscayne Bay.

The critical thresholds identified for trophic niche size and trophic level could be sustained by previous empirical observations and expected outcomes from theoretical models. The fragmentation index more precisely described the trophic niche size threshold response than seascape cover (i.e., highly uncertain response particularly over the lower and intermediate values of seascape cover). Other seascape studies have shown substantial effects of spatial habitat configuration on community patterns (e.g., species abundance, density, diversity; Hovel & Regan, 2008, Bonin et al., 2011, Lirman et al., 2014, Boström et al., 2017) that, in turn, influence trophic niche size through intraspecific competition processes. For example, a study in Biscayne Bay found a stronger nonlinear response of pinfish abundance as a function of a fragmentation index (Santos, 2014), thus supporting the hypothesis of pinfish niche expansion due to non-linear density-dependent effects that influence when consumers decide to add to their diet alternatives or unfavored resources to meet energy requirements.

In contrast to the trophic niche size response, the trophic level threshold was best explained by the relative area of seagrass patches (i.e., habitat amount), findings that may be supported by how prey diversity, resource availability, and consumers' food-chain length interact as a function of SAV habitat size (Post, 2002a). SAV seascape productivity is linked to the seagrass habitat amount (Ricart et al., 2015). Thus, we should expect higher trophic levels in continuous seascapes following hypotheses that predict the expansion of food-chain length as resource availability increases proportionally with habitat size and productivity (e.g., productivity, productive space, and exploitation ecosystem hypothesis; Post, 2002a, 2002b). Although studies suggest a threshold in the resource availability, food-chain length relationship was determined by other factors such as predator–prey interactions (Post, 2002a, 2002b). For instance, the abundance and diversity of prey that elevates pinfish trophic level may be maximized above a connectivity threshold offered by continuous seascapes (i.e., percolation threshold—the level of habitat amount at which the seascape transitions from a connected to a disconnected system) that increase coexistence and availability of intermediate consumers as prey (Caldwell & Gergel, 2013; With & Crist, 1995; Yeager et al., 2016).

Management implications

The results of our study could provide insight on how management and restoration activities can influence ecological processes and ecosystem functioning in coastal environments. For example, our seascape ecology approach integrated with stable isotope analysis demonstrated that Biscayne Bay's water management practices can influence the energy pathways of important consumers by altering both the spatial structure of SAV habitats and nutrient regimes. The results of the overlap analysis suggested that high nutrient regimes can interact with seascape characteristics to increase diversity of food resources, as illustrated by higher niche separation between continuous and fragmented seascapes in the low and variable salinity zone. The interactive effects of nutrient and seascape properties still required further research, but nutrient enrichment is one of the main stressors of urban ecosystems, such as Biscayne Bay, associated with the modification of bottom-up and top-down processes that control food web structure, trophic relationship, and productivity values of coastal ecosystems (Armitage & Fourqurean, 2009; Baeta et al., 2011; Swart et al., 2014; Tewfik et al., 2005). Higher trophic level observed in the low and variable salinity zone, especially in continuous seascapes, corresponded to higher observations of pinfish abundance and biomass by Santos et al. (2018), which suggest a positive effect on pinfish production by nutrients and a larger spatial extension of SAV habitats. However, further field and laboratory experiments in conjunction with mass-balanced models are required to better assess and understand the functional implication of both habitat fragmentation and eutrophication.

By implementing stable isotope analysis and hypervolume metrics, our study captured for the first time how distinct properties of SAV habitat amount and spatial configuration influence the realized trophic niche of a seagrass omnivore fish species. A recent study demonstrated the usefulness of hypervolumes and mixing models to evaluate the functional success of restoration activities (James, Lesser, et al., 2020), and likewise, our results demonstrated that by integrating a seascape approach, managers could evaluate the best spatial attributes of habitat patches that contribute to the restoration of ecological processes and functioning in SAV habitats. In addition, our results highlight the importance of taking into consideration the spatial properties of coastal habitats and the geographic reference (i.e., location relative to distinct spatial attributes) when assessing trophic dynamics that may cause a cascade of unintended ecological and ecosystem-level changes. Landscape ecology studies suggest that the effects of habitat fragmentation are generally much weaker than the impact of habitat loss (Fahrig, 2003); however, critical thresholds for organisms and ecosystem function will vary depending on the system (Andrén, 1994; Pardini et al., 2010). Also, as demonstrated in recent seascape ecology studies, the effect of seagrass habitat configuration on nektonic species diversity and density is only apparent in seascapes with habitat amount levels below or above a certain threshold (i.e., fragmentation threshold hypothesis; Trzcinski et al., 1999) (Santos, 2014; Yeager et al., 2016). Thus, our study should be replicated to depict the interactive effects of habitat amount and spatial configuration on trophic niche dynamics and to identify generalities among trophic guilds and across aquatic systems. Nevertheless, our study approach and results highlight the importance of identifying critical habitat thresholds that could inform management and restoration strategies on the required amount and configuration of habitat necessary to sustain the persistence or recovery of food web functions.

ACKNOWLEDGMENTS

Special thanks to James McCullars, Matthew Dilly, and Amanda Guthrie for help in the field and laboratory. This research was conducted under NPS permit BISC-2011-SCI-0028. Funding was provided by NOAA's Educational Partnership Program and Living Marine Resources Cooperative Science Center, the Army Corps of Engineers, and the RECOVER Monitoring and Assessment Program (MAP). The doctoral studies of R.O.S. were supported by the McKnight Doctoral Fellowship (Florida Education Fund). We thank the anonymous reviewers, and the University of Miami's Stable Isotope Facility and Dr. Leonel Sternberg for providing technical support and mentorship with respect to the stable isotope analysis portion of this study. This is contribution no. 1369 from the Coastlines and Oceans Division of the Institute of Environment at the Florida International University.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (James, 2021) are available from Zenodo: https://doi.org/10.5281/zenodo.5703218.

ORCID

Rolando O. Santos https://orcid.org/0000-0002-3885-9406

W. Ryan James https://orcid.org/0000-0002-4829-7742

REFERENCES

Andrén, H. 1994. "Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat – A Review." *Oikos* 71: 355–66.

Araújo, M.S., D.I. Bolnick, and C.A. Layman. 2011. "The Ecological Causes of Individual Specialisation." *Ecology Letters* 14: 948–58.

Araújo, M.S., R.B. Langerhans, S.T. Giery, and C.A. Layman. 2014. "Ecosystem Fragmentation Drives Increased Diet Variation in an Endemic Livebearing Fish of the Bahamas." *Ecology and Evolution* 4: 3298–308.

Armitage, A.R., and J.W. Fourqurean. 2009. "Stable Isotopes Reveal Complex Changes in Trophic Relationships Following

Nutrient Addition in a Coastal Marine Ecosystem." *Estuaries and Coasts* 32: 1152–64.

Awade, M., and J.P. Metzger. 2008. "Using Gap-Crossing Capacity to Evaluate Functional Connectivity of Two Atlantic Rainforest Birds and their Response to Fragmentation." *Austral Ecology* 33: 863–71.

Baeta, A., N. Niquil, J.C. Marques, and J. Patrício. 2011. "Modelling the Effects of Eutrophication, Mitigation Measures and an Extreme Flood Event on Estuarine Benthic Food Webs." *Ecological Modelling* 222: 1209–21.

Baker, R., K. Abrantes, and I.C. Feller. 2021. "Stable Isotopes Suggest Limited Role of Wetland Macrophyte Production Supporting Aquatic Food Webs Across a Mangrove-Salt Marsh Ecotone." *Estuaries and Coasts* 44: 1619–27.

Barbosa, A.M., J.A. Brown, A. Jimenez-Valverde, and R. Real. 2016. "modEvA: Model Evaluation and Analysis." *R package version 1.3.2.* http://modeva.r-forge.r-project.org/

Barbosa, A.M., R. Real, A.R. Muñoz, and J.A. Brown. 2013. "New Measures for Assessing Model Equilibrium and Prediction Mismatch in Species Distribution Models." *Diversity and Distributions* 19: 1333–8.

Barbosa, M., and C.M. Taylor. 2020. "Spatial and Temporal Trends in Diet for Pinfish (*Lagodon rhomboides*) from Turtle Grass (*Thalassia testudinum*) Beds with Contrasting Environmental Regimes in the Lower Laguna Madre, Texas." *Estuaries and Coasts* 43: 1571–81.

Barton, K. 2019. "MuMIn: Multi-Model Inference." *R package version 1.43.15.* https://cran.r-project.org/package=MuMIn

Bearhop, S., C.E. Adams, S. Waldron, R.A. Fuller, and H. Macleod. 2004. "Determining Trophic Niche Width: A Novel Approach using Stable Isotope Analysis." *Journal of Animal Ecology* 73: 1007–12.

Blonder, B. 2018. "Hypervolume Concepts in Niche- and Trait-Based Ecology." *Ecography* 41: 1441–55.

Blonder, B., C. Lamanna, C. Violle, and B.J. Enquist. 2014. "The *n*-Dimensional Hypervolume." *Global Ecology and Biogeography* 23: 595–609.

Blonder, B., C.B. Morrow, B. Maitner, D.J. Harris, C. Lamanna, C. Violle, B.J. Enquist, and A.J. Kerkhoff. 2018. "New Approaches for Delineating *n*-Dimensional Hypervolumes." *Methods in Ecology and Evolution* 9: 305–19.

Bonin, M.C., G.R. Almany, and G.P. Jones. 2011. "Contrasting Effects of Habitat Loss and Fragmentation on Coral-Associated Reef Fishes." *Ecology* 92: 1503–12.

Boström, C., S.J. Pittman, and C.A. Simenstad. 2017. "Ecological Consequences of Seagrass and Salt-Marsh Seascape Patterning on Marine Fauna." *Seascape Ecology*, 27–56. John Wiley & Sons.

Boström, C., S.J. Pittman, C. Simenstad, and R.T. Kneib. 2011. "Seascape Ecology of Coastal Biogenic Habitats: Advances, Gaps, and Challenges." *Marine Ecology Progress Series* 427: 191–217.

Buelow, C.A., A.E. Reside, R. Baker, and M. Sheaves. 2018. "Stable Isotopes Reveal Opportunistic Foraging in a Spatiotemporally Heterogeneous Environment: Bird Assemblages in Mangrove Forests." *PLoS One* 13: e0206145.

Caldwell, I.R., and S.E. Gergel. 2013. "Thresholds in Seascape Connectivity: Influence of Mobility, Habitat Distribution, and Current Strength on Fish Movement." *Landscape Ecology* 28: 1937–48.

Caley, M.J., K.A. Buckley, and G.P. Jones. 2001. "Separating Ecological Effects of Habitat Fragmentation, Degradation, and Loss on Coral Commensals." *Ecology* 82: 3435–48.

Canion, C.R., and K.L. Heck. 2009. "Effect of Habitat Complexity on Predation Success: Re-Evaluating the Current Paradigm in Seagrass Beds." *Marine Ecology Progress Series* 393: 37–46.

Catano, L.B., M.C. Rojas, R.J. Malossi, J.R. Peters, M.R. Heithaus, J. W. Fourqurean, and D.E. Burkepile. 2015. "Reefscapes of Fear: Predation Risk and Reef Heterogeneity Interact to Shape Herbivore Foraging Behaviour." *Journal of Animal Ecology* 85: 146–56.

Catano, L.B., A.A. Shantz, and D.E. Burkepile. 2014. "Predation Risk, Competition, and Territorial Damselfishes as Drivers of Herbivore Foraging on Caribbean Coral Reefs." *Marine Ecology Progress Series* 511: 193–207.

Chasar, L.C., J.P. Chanton, C.C. Koenig, and F.C. Coleman. 2005. "Evaluating the Effect of Environmental Disturbance on the Trophic Structure of Florida Bay, U.S.A.: Multiple Stable Isotope Analyses of Contemporary and Historical Specimens." *Limnology and Oceanography* 50: 1059–72.

Connolly, R.M., and J.S. Hindell. 2006. "Review of Nekton Patterns and Ecological Processes in Seagrass Landscapes." *Estuarine, Coastal and Shelf Science* 68: 433–44.

Debinski, D.M., and R.D. Holt. 2000. "A Survey and Overview of Habitat Fragmentation Experiments." *Conservation Biology* 14: 342–55.

Diaz, G.A., S.G. Smith, J.E. Serafy, and J.S. Ault. 2001. "Allometry of the Growth of Pink Shrimp *Farfantepenaeus duorarum* in a Subtropical Bay." *Transactions of the American Fisheries Society* 130: 328–35.

Didham, R.K., V. Kapos, and R.M. Ewers. 2012. "Rethinking the Conceptual Foundations of Habitat Fragmentation Research." *Oikos* 121: 161–70.

Elton, C. 1927. *Animal Ecology*. New York: Macmillan Co.

Ewers, R., and R. Didham. 2006. "Confounding Factors in the Detection of Species Responses to Habitat Fragmentation." *Biological Reviews of the Cambridge Philosophical Society* 81: 117–42.

Fahrig, L. 2003. "Effects of Habitat Fragmentation on Biodiversity." *Annual Review of Ecological and Environmental Systems* 34: 487–515.

Fahrig, L. 2019. "Habitat Fragmentation: A Long and Tangled Tale." *Global Ecology and Biogeography* 28: 33–41.

Faunce, C.H., and J.E. Serafy. 2008. "Selective Use of Mangrove Shorelines by Snappers, Grunts, and Great Barracuda." *Marine Ecology Progress Series* 356: 153–62.

Francesco Ficetola, G., and M. Denoël. 2009. "Ecological Thresholds: An Assessment of Methods to Identify Abrupt Changes in Species-Habitat Relationships." *Ecography* 32: 1075–84.

Froeschke, J.T., and G.W. Stunz. 2012. "Hierarchical and Interactive Habitat Selection in Response to Abiotic and Biotic Factors: The Effect of Hypoxia on Habitat Selection of Juvenile Estuarine Fishes." *Environmental Biology of Fishes* 93: 31–41.

Fry, B. 2013. "Alternative Approaches for Solving Underdetermined Isotope Mixing Problems." *Marine Ecology Progress Series* 472: 1–13.

Gorokhova, E. 2018. "Individual Growth as a Non-Dietary Determinant of the Isotopic Niche Metrics." *Methods in Ecology and Evolution* 9: 269–77.

Healey, D., and K.A. Hovel. 2004. "Seagrass Bed Patchiness: Effects on Epifaunal Communities in San Diego Bay, USA." *Journal of Experimental Marine Biology and Ecology* 313: 155–74.

Hoeinghaus, D.J., and S.C. Zeug. 2008. “Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure? Comment.” *Ecology* 89: 2353–7.

Horinouchi, M. 2009. “Horizontal Gradient in Fish Assemblage Structures in and around a Seagrass Habitat: Some Implications for Seagrass Habitat Conservation.” *Ichthyological Research* 56: 109–25.

Horinouchi, M., P. Tongnunui, K. Nanjyo, Y. Nakamura, M. Sano, and H. Ogawa. 2009. “Differences in Fish Assemblage Structures between Fragmented and Continuous Seagrass Beds in Trang, Southern Thailand.” *Fisheries Science* 75: 1409–16.

Hovel, K.A. 2003. “Habitat Fragmentation in Marine Landscapes: Relative Effects of Habitat Cover and Configuration on Juvenile Crab Survival in California and North Carolina Seagrass Beds.” *Biological Conservation* 110: 401–12.

Hovel, K.A., and R.N. Lipcius. 2002. “Effects of Seagrass Habitat Fragmentation on Juvenile Blue Crab Survival and Abundance.” *Journal of Experimental Marine Biology and Ecology* 271: 75–98.

Hovel, K.A., and H.M. Regan. 2008. “Using an Individual-Based Model to Examine the Roles of Habitat Fragmentation and Behavior on Predator–Prey Relationships in Seagrass Landscapes.” *Landscape Ecology* 23: 75–89.

Hussey, N.E., M.A. MacNeil, B.C. McMeans, J.A. Olin, S.F.J. Dudley, G. Cliff, S.P. Wintner, S.T. Fennessy, and A.T. Fisk. 2014. “Rescaling the Trophic Structure of Marine Food Webs.” *Ecology Letters* 17: 239–50.

Irlandi, E.A., and M.K. Crawford. 1997. “Habitat Linkages: The Effect of Intertidal Saltmarshes and Adjacent Subtidal Habitats on Abundance, Movement, and Growth of an Estuarine Fish.” *Oecologia* 110: 222–30.

Jackson, A.L., R. Inger, A.C. Parnell, and S. Bearhop. 2011. “Comparing Isotopic Niche Widths among and within Communities: SIBER – Stable Isotope Bayesian Ellipses in R.” *Journal of Animal Ecology* 80: 595–602.

James, W.R., 2021. “*wryanjames/Santos_etal_Ecosphere*.” Data set. Zenodo. https://doi.org/10.5281/zenodo.5703218.

James, W.R., J.S. Lesser, S.Y. Litvin, and J.A. Nelson. 2020. “Assessment of Food Web Recovery Following Restoration Using Resource Niche Metrics.” *Science of the Total Environment* 711: 134801.

James, W.R., Z.M. Topor, and R.O. Santos. 2020. “Seascape Configuration Influences the Community Structure of Marsh Nekton.” *Estuaries and Coasts* 44: 1521–33.

Jordan, F., M. Bartolini, C. Nelson, P.E. Patterson, and H.L. Soulen. 1997. “Risk of Predation Affects Habitat Selection by the Pinfish *Lagodon rhomboides* (Linnaeus).” *Journal of Experimental Marine Biology and Ecology* 208: 45–56.

Kitting, C.L., B. Fry, and M.D. Morgan. 1984. “Detection of Inconspicuous Epiphytic Algae Supporting Food Webs in Seagrass Meadows.” *Oecologia* 62: 145–9.

Kobler, A., T. Klefoth, T. Mehner, and R. Arlinghaus. 2009. “Coexistence of Behavioural Types in an Aquatic Top Predator: A Response to Resource Limitation?” *Oecologia* 161: 837–47.

Layman, C.A., M.S. Araujo, R. Boucek, C.M. Hammerschlag-Peyer, E. Harrison, Z.R. Jud, P. Matich, et al. 2012. “Applying Stable Isotopes to Examine Food-Web Structure: An Overview of Analytical Tools.” *Biological Reviews* 87: 545–62.

Layman, C.A., J.P. Quattrochi, C.M. Peyer, and J.E. Allgeier. 2007. “Niche Width Collapse in a Resilient Top Predator Following Ecosystem Fragmentation.” *Ecology Letters* 10: 937–44.

Lesser, J.S., W.R. James, C.D. Stallings, R.M. Wilson, and J.A. Nelson. 2020. “Trophic Niche Size and Overlap Decreases with Increasing Ecosystem Productivity.” *Oikos* 129: 1303–13.

Levin, P., R. Petrik, and J. Malone. 1997. “Interactive Effects of Habitat Selection, Food Supply and Predation on Recruitment of an Estuarine Fish.” *Oecologia* 112: 55–63.

Lindeman, R.L. 1942. “The Trophic-Dynamic Aspect of Ecology.” *Ecology* 23: 399–417.

Lindenmayer, D.B., and J. Fischer. 2007. “Tackling the Habitat Fragmentation Panchreston.” *Trends in Ecology and Evolution* 22: 127–32.

Lirman, D., G. Deangelo, J. Serafy, A. Hazra, D. Smith Hazra, J. Herlan, J. Luo, S. Bellmund, J. Wang, and R. Clausing. 2008. “Seasonal Changes in the Abundance and Distribution of Submerged Aquatic Vegetation in a Highly Managed Coastal Lagoon.” *Hydrobiologia* 596: 105–20.

Lirman, D., T. Thyberg, R. Santos, S. Schopmeyer, C. Drury, L. Collado-Vides, S. Bellmund, and J. Serafy. 2014. “SAV Communities of Western Biscayne Bay, Miami, Florida, USA: Human and Natural Drivers of Seagrass and Macroalgae Abundance and Distribution Along a Continuous Shoreline.” *Estuaries and Coasts* 37: 1243–55.

Livernois, M.C., F.J. Fodrie, K.L. Heck, and S.P. Powers. 2019. “Emergent Intraspecific Multiple Predator Effects Shape Estuarine Trophic Dynamics across a Gradient of Habitat Complexity.” *Journal of Experimental Marine Biology and Ecology* 511: 120–8.

López-Rasgado, F.J., S.E. Lluch-Cota, E.F. Balart, and S.Z. Herzka. 2016. “Variation in Isotopic Trophic Structure and Fish Diversity in Mangrove Systems Subject to Different Levels of Habitat Modification in the Gulf of California, Mexico.” *Bulletin of Marine Science* 92: 399–422.

MacArthur, R.H., and E.R. Pianka. 1966. “On Optimal Use of a Patchy Environment.” *The American Naturalist* 100: 603–9.

Macreadie, P.I., R.M. Connolly, M.J. Keough, G.P. Jenkins, and J.S. Hindell. 2010. “Short-Term Differences in Animal Assemblages in Patches Formed by Loss and Growth of Habitat.” *Austral Ecology* 35: 515–21.

Macreadie, P.I., J.S. Hindell, M.J. Keough, G.P. Jenkins, and R.M. Connolly. 2010. “Resource Distribution Influences Positive Edge Effects in in a Seagrass Fish.” *Ecology* 91: 2013–21.

Magioli, M., M.Z. Moreira, R.C.B. Fonseca, M.C. Ribeiro, M.G. Rodrigues, and K.M.P.M. de B. Ferraz. 2019. “Human-Modified Landscapes Alter Mammal Resource and Habitat Use and Trophic Structure.” *Proceedings of the National Academy of Sciences* 116: 18466–72.

Nelson, J., L. Deegan, and R. Garritt. 2015. “Drivers of Spatial and Temporal Variability in Estuarine Food Webs.” *Marine Ecology Progress Series* 533: 67–77.

Nelson, J.A., D.S. Johnson, L.A. Deegan, A.C. Spivak, and N.R. Sommer. 2019. “Feedbacks Between Nutrient Enrichment and Geomorphology Alter Bottom-Up Control on Food Webs.” *Ecosystems* 22: 229–42.

Nelson, J.A., J. Lesser, W.R. James, D.P. Behringer, V. Furka, and J. C. Doerr. 2019. “Food Web Response to Foundation Species Change in a Coastal Ecosystem.” *Food Webs* 21: e00125.

Nelson, J.A., C.D. Stallings, W.M. Landing, and J. Chanton. 2013. "Biomass Transfer Subsidizes Nitrogen to Offshore Food Webs." *Ecosystems* 16: 1130–8.

Pardini, R., A.A. de Bueno, T.A. Gardner, P.I. Prado, and J.P. Metzger. 2010. "Beyond the Fragmentation Threshold Hypothesis: Regime Shifts in Biodiversity across Fragmented Landscapes." *PLoS ONE* 5: e13666.

Phillips, D.L., R. Inger, S. Bearhop, A.L. Jackson, J.W. Moore, A.C. Parnell, B.X. Semmens, and E.J. Ward. 2014. "Best Practices for Use of Stable Isotope Mixing Models in Food-Web Studies." *Canadian Journal of Zoology* 92: 823–35.

Pittman, S.J., R.T. Kneib, and C.A. Simenstad. 2011. "Practicing Coastal Seascape Ecology." *Marine Ecology Progress Series* 427: 187–90.

Pittman, S.J., C.A. McAlpine, and K.M. Pittman. 2004. "Linking Fish and Prawns to their Environment: A Hierarchical Landscape Approach." *Marine Ecology Progress Series* 283: 233–54.

Plumlee, J.D., L.A. Yeager, and F.J. Fodrie. 2020. "Role of Saltmarsh Production in Subsidizing Adjacent Seagrass Food Webs: Implications for Landscape-Scale Restoration." *Food Webs* 24: e00158.

Post, D. 2002a. "The Long and Short of Food-Chain Length." *Trends in Ecology & Evolution* 17: 269–77.

Post, D.M. 2002b. "Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions." *Ecology* 83: 703–18.

Potthoff, M.T., and D.M. Allen. 2003. "Site Fidelity, Home Range, and Tidal Migrations of Juvenile Pinfish, *Lagodon rhomboides*, in Salt Marsh Creeks." *Environmental Biology of Fishes* 67: 231–40.

R Core Team. 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reynolds, P.L., and J.F. Bruno. 2013. "Multiple Predator Species Alter Prey Behavior, Population Growth, and a Trophic Cascade in a Model Estuarine Food Web." *Ecological Monographs* 83: 119–32.

Ricart, A.M., A. Dalmau, M. Pérez, and J. Romero. 2015. "Effects of Landscape Configuration on the Exchange of Materials in Seagrass Ecosystems." *Marine Ecology Progress Series* 532: 89–100.

Ries, L., and T.D. Sisk. 2004. "A Predictive Model of Edge Effects." *Ecology* 85: 2917–26.

Ryall, K.L., and L. Fahrig. 2006. "Response of Predators to Loss and Fragmentation of Prey Habitat: A Review of Theory." *Ecology* 87: 1086–93.

Salita, J.T., W. Ekau, and U. Saint-Paul. 2003. "Field Evidence on the Influence of Seagrass Landscapes on Fish Abundance in Bolinao, Northern Philippines." *Marine Ecology Progress Series* 247: 183–95.

Santos, R.O. 2014. "*Spatial Dynamics of Vegetated Seascapes and the Influence on Fish and Crustaceans*." Open Access Dissertations: 11200.

Santos, R.O., D. Lirman, and S.J. Pittman. 2015. "Long-Term Spatial Dynamics in Vegetated Seascapes: Fragmentation and Habitat Loss in a Human-Impacted Subtropical Lagoon." *Marine Ecology* 37: 200–14.

Santos, R.O., D. Lirman, S.J. Pittman, and J.E. Serafy. 2018. "Spatial Patterns of Seagrasses and Salinity Regimes Interact to Structure Marine Faunal Assemblages in a Subtropical Bay." *Marine Ecology Progress Series* 594: 21–38.

Santos, R.O., D. Lirman, and J.E. Serafy. 2011. "Quantifying Freshwater-Induced Fragmentation of Submerged Aquatic Vegetation Communities Using a Multi-Scale Landscape Ecology Approach." *Marine Ecology Progress Series* 427: 233–46.

Santos, R.O., J.S. Rehage, A.J. Adams, B.D. Black, J. Osborne, and E.K.N.N. Kroloff. 2017. "Quantitative Assessment of a Data-Limited Recreational Bonefish Fishery Using a Time-Series of Fishing Guides Reports." *PLoS One* 12: e0184776.

Santos, R.O., G. Varona, C.L. Avila, D. Lirman, and L. Collado-Vides. 2020. "Implications of Macroalgae Blooms to the Spatial Structure of Seagrass Seascapes: The Case of the *Anadyomene* spp. (Chlorophyta) Bloom in Biscayne Bay, Florida." *Marine Pollution Bulletin* 150: 110742.

Schmiegelow, F., and M. Mönkkönen. 2002. "Habitat Loss and Fragmentation in Dynamic Landscape: Avian Perspectives from the Boreal Forest." *Ecological Applications* 12: 375–89.

Serafy, J.E., C.H. Faunce, and J.J. Lorenz. 2003. "Mangrove Shoreline Fishes of Biscayne Bay, Florida." *Bulletin of Marine Science* 72: 161–80.

Serafy, J.E., K.C. Linderman, T.E. Hopkins, and J.S. Ault. 1997. "Effects of Freshwater Canal Discharges on Subtropical Marine Fish Assemblages: Field and Laboratory Observations." *Marine Ecology Progress Series* 160: 161–72.

Sleeman, J.C., G.S. Boggs, B.C. Radford, and G.A. Kendrick. 2005. "Using Agent-Based Models to Aid Reef Restoration: Enhancing Coral Cover and Topographic Complexity through the Spatial Arrangement of Coral Transplants." *Restoration Ecology* 13: 685–94.

Smith, A.C., L. Fahrig, and C.M. Francis. 2011. "Landscape Size Affects the Relative Importance of Habitat Amount, Habitat Fragmentation, and Matrix Quality on Forest Birds." *Ecography* 34: 103–13.

Smith, T.M., J.S. Hindell, G.P. Jenkins, and R.M. Connolly. 2010. "Seagrass Patch Size Affects Fish Responses to Edges." *Journal of Animal Ecology* 79: 275–81.

Smith, T.M., J.S. Hindell, G.P. Jenkins, R.M. Connolly, and M.J. Keough. 2011. "Edge Effects in Patchy Seagrass Landscapes: The Role of Predation in Determining Fish Distribution." *Journal of Experimental Marine Biology and Ecology* 399: 8–16.

Smith, A.C., N. Koper, C.M. Francis, and L. Fahrig. 2009. "Confronting Collinearity: Comparing Methods for Disentangling the Effects of Habitat Loss and Fragmentation." *Landscape Ecology* 24: 1271.

Stephens, D.W., and J.R. Krebs. 1986. *Foraging Theory: Foraging Theory*. Princeton, NJ: Princeton University Press.

Stipek, C., R. Santos, E. Babcock, and D. Lirman. 2020. "Modelling the Resilience of Seagrass Communities Exposed to Pulsed Freshwater Discharges: A Seascape Approach." *PLoS One* 15: e0229147.

Stock, B.C., A.L. Jackson, E.J. Ward, A.C. Parnell, D.L. Phillips, and B.X. Semmens. 2018. "Analyzing Mixing Systems Using a New Generation of Bayesian Tracer Mixing Models." *PeerJ* 6: e5096.

Stoner, A.W. 1980. "Feeding Ecology of *Lagodon rhomboides* (Pisces, Sparidae): Variation and Functional Responses." *Fishery Bulletin* 78: 337–52.

Svanbäck, R., C. Rydberg, K. Leonardsson, and G. Englund. 2011. "Diet Specialization in a Fluctuating Population of Saduria Entomon: A Consequence of Resource or Forager Densities?" *Oikos* 120: 848–54.

Swart, P.K., W.T. Anderson, M.A. Altabet, C. Drayer, and S. Bellmund. 2013. "Sources of Dissolved Inorganic Nitrogen in a Coastal Lagoon Adjacent to a Major Metropolitan Area, Miami Florida (USA)." *Applied Geochemistry* 38: 134–46.

Swart, P.K., S. Evans, T. Capo, and M.A. Altabet. 2014. "The Fractionation of Nitrogen and Oxygen Isotopes in Macroalgae during the Assimilation of Nitrate." *Biogeosciences* 11: 6147–57.

Tewfik, A., J.B. Rasmussen, and K.S. McCann. 2005. "Anthropogenic Enrichment Alters a Marine Benthic Food Web." *Ecology* 86: 2726–36.

Thistle, M.E., D.C. Schneider, R.S. Gregory, and N.J. Wells. 2010. "Fractal Measures of Habitat Structure: Maximum Densities of Juvenile Cod Occur at Intermediate Eelgrass Complexity." *Marine Ecology Progress Series* 405: 39–56.

Trzcinski, M.K., L. Fahrig, and G. Merriam. 1999. "Independent Effects of Forest Cover and Fragmentation on the Distribution of Forest Breeding Birds." *Ecological Applications* 9: 586–93.

Valladares, G., L. Cagnolo, and A. Salvo. 2012. "Forest Fragmentation Leads to Food Web Contraction." *Oikos* 121: 299–305.

With, K.A., and T.O. Crist. 1995. "Critical Thresholds in Species Responses to Landscape Structure." *Ecology* 76: 2446–59.

Yeager, L.A., C. Acevedo, and C.A. Layman. 2012. "Effects of Seascape Context on Condition, Abundance, and Secondary Production of a Coral Reef Fish, *Haemulon plumierii*." *Marine Ecology Progress Series* 462: 231–40.

Yeager, L.A., D.A. Keller, T.R. Burns, A.S. Pool, and F.J. Fodrie. 2016. "Threshold Effects of Habitat Fragmentation Per Se on Fish Diversity at Landscapes Scales." *Ecology* 97: 2157–66.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Santos, Rolando O., W. Ryan James, James A. Nelson, Jennifer S. Rehage, Joseph Serafy, Simon J. Pittman, and Diego Lirman. 2022. "Influence of Seascape Spatial Pattern on the Trophic Niche of an Omnivorous Fish." *Ecosphere* 13(2): e3944. https://doi.org/10.1002/ecs2.3944