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Trophic niche size and overlap decreases with increasing ecosystem productivity

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The production and transfer of biomass through trophic relationships is a core ecosystem function. The movement of energy through the food web is mediated by organisms operating in their niche space. For generalists, the size of this niche space is inherently plastic and changes in response to available food sources. Therefore, this relationship between ecosystem productivity and niche size is an important determinant of ecosystem function. Competing theories about the nature of this relationship predict that as productivity increases niche size will either increase as species capitalize on a general increase in resource availability or decrease as it becomes viable to focus on preferred production channels. Here, we test these two competing theoretical frameworks using a novel approach to determine trophic niche size using stable isotope analysis and hypervolume metrics. Resource use is quantified in two generalist fish species at three productivity levels in a seagrass ecosystem. Niche size of both species was inversely related to seagrass productivity, consistent with the hypothesis that increasing productivity allows species to focus on a narrower diet. This pattern describes the relationship between ecosystem production and niche size and provides an empirical ecological explanation for the resource maximization behaviors commonly observed in nature.

Keywords: ecosystem productivity, food web theory, hypervolumes, niche theory, stable isotopes, trophic niche

Introduction

Hutchinson's original conceptualization of the 'fundamental niche' was of an n-dimensional abstract space, defined by all of the potential parameters that would afford a species the ability to exist indefinitely in their habitat (Hutchinson 1957). The comprehensiveness of this definition, though purposeful, can make it difficult to quantify this type of niche, since identifying all of the factors important for an organism's persistence remains an arduous task. Earlier characterizations of the 'niche' are more specific in their scope, yet still inherently abstract. Grinnell's niche used a combination of specific habitat characteristics and species traits to represent a species' niche (Grinnell 1917, Soberón 2007). Elton constructed the niche around the way an organism interacts with and affects its environment, via resource use or predator avoidance

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(Elton 1927, Soberón 2007). Though distinct, both of these concepts outline a version of the 'realized niche,' the part of that fundamental niche that is actually occupied by a species. Quantifying at least parts of the realized niche has allowed scientists to test major theories in ecology including how functional traits vary with community assembly and how productivity influences diversity (Soberón and Nakamura 2009, Lamanna et al. 2014, McClain et al. 2016).

Primary productivity is known to be a critical driver of ecosystem structure, composition and function. Generally, an increase in system productivity will lead to a more trophically complex ecosystem (Smith et al. 2008, Scherber et al. 2010) and an increase in the amount of higher order processing of organic matter in that ecosystem (Wallace et al. 1999). Because of this, the size of an omnivorous species' trophic niche should vary along gradients associated with the primary productivity of an ecosystem (MacArthur and Pianka 1966, O'Farrell et al. 2014). Species that can use many types of resources should change the resource channels they use based on their availability and quality. In general, energy transfer in food webs is mediated by a small number of strong trophic interactions between food web nodes, while weak interactions stabilize food web dynamics and dampen oscillations (McCann et al. 1998). The number and strength of these trophic links will vary as a function of ecosystem production (Menge et al. 2004), and therefore consumers must adapt their foraging strategy to meet their metabolic demand as productivity changes.

Consumers deal with variable ecosystem productivity either by increasing their reliance on the stabilizing, weak interactions, thus increasing niche size (Van Valen 1965, Pool et al. 2017), or by strengthening their reliance on few strong links, to forage optimally on a few, energetically-favorable channels, thus narrowing the size of their niche (MacArthur and Pianka 1966, Pyke et al. 1977). Theories detailing the productivity–diversity relationship can be applied to understand the productivity–niche relationship. For our purposes here we are referring to diversity in general terms rather than any specific type of diversity. For example, the niche-width hypothesis proposes that resource availibility makes it difficult for rare species to exist at low productivites, and at higher productivity, more species can persist (Evans et al. 2005b). Empirical quantification of the productivity–niche relationship affords the ability to understand and predict the environmental controls on efficent transfer of biomass through trophic steps in food webs, a key driver of ecosystem function.

Several techniques have been developed to quantify a version of the niche including species occurrence and abiotic factors (Broennimann et al. 2012), habitat metrics (Rödder and Engler 2011) and phylogenetic methods (Prinzing 2001). Recently, ecologists have begun to develop niche metrics with stable isotope analysis (Bearhop et al. 2004, Layman and Post 2007, Jackson et al. 2011, Cucherousset and Villéger 2015). Stable isotope values can provide information on the material assimilated by an organism and thus reveal the production resources on which a species depends (Peterson and Fry 1987, Newsome et al. 2007, 2012, Inger 2008). Attempts have been made to directly translate isotope values to a multidimensional representation of a niche, both in theory and as analytical tools. For example, variance in isotope values has been used to improve calculation of trophic niche widths (Bearhop et al. 2004, Curtis et al. 2017). Layman and Post (2007) described metrics using the geometry of isotope values in space (i.e. convex hulls) to determine changes in niche space. Isotopic variation was incorporated into the calculation of the standard ellipse area (SEA) (Jackson et al. 2011), and Cucherousset and Villéger (2015) used existing metrics developed by functional ecologists to define parameters for quantifying new metrics of niche divergence, dispersion, evenness and uniqueness, as well similarity and turnover between two species. Under certain circumstances these tools provide potential niche representations, which can be quite useful for understanding resource use variability. However, making inferences directly from isotope values themselves can be problematic, as both source variation, as well as variation in both ontogenetic and geographic consumer resource use can alter the resulting niche calculated directly from isotope space (Hoeinghaus and Zeug 2008, Newsome et al. 2012, Gorokhova 2017, Hette-Tronquart 2019). The incorporation of source contribution information into isotope niche metrics can account for variability introduced in this way (Newsome et al. 2007, 2012). Isotope mixing models function as a tool for both the incorporation of source variation into the determination of the percent contributions of sources to consumer mixes (Moore and Semmens 2008, Parnell 2008, Phillips et al. 2014, Stock et al. 2018) and to set the framework for the quantification of a trophic niche in terms of the sources availible to consumers in an environment (Flaherty and Ben-David 2010, Cummings et al. 2012, Newsome et al. 2012, Hopkins III and Kurle 2016, Manlick et al. 2019). Newsome et al. (2012) developed 'DietSpace' metrics that linked information about the spatial arrangment of isotope values in bivariate space with Bayesian mixing model results to quantify diet specialization.

The trophic niche should describe how an organism acquires energy from the production channels available to them in their environment. While previous methods focused on the resource use of the population or the individual, our method defines the niche of a population by quantifying the variability by which individuals acquire energy from those available. This is a more accurate representation of a population's trophic niche; a population is made up of individuals, and the differences in how those individuals act from each other defines how energy is moved into and through that population to other species, and therefore, how energy is moved through the system as a whole. Our approach builds upon the previous work by modelling the niche within a multidimensional space, in accordance with Hutchinson's original n-dimensional abstraction, and creating hypervolumes that quantify species' niches in terms of their resource use as determined by Bayesian mixing models, thus calculating a version of their Eltonian niche. In the present study, stable isotope analysis and Bayesian mixing models (Parnell et al. 2013) were used to determine the relative contributions of primary production sources to two omnivorous fish species. The results of the mixing model represent the ecological variability of resources used by a consumer (Newsome et al. 2012, Parnell et al. 2013). Using these source contribution estimates, we define a multidimensional resource use space, and the trophic niche is quantified within that space. This method defines a consumer species' resource use niche as the sum total of the variation in individual reliance on particular blends of the channels of primary production found in their ecosystem, free of the constraints associated with prior niche metrics derived from isotopic space alone, such as baseline variability and spatial and temporal variation in resource use. Metrics of hypervolume change provide insight into the resource-use niche dynamics within a natural productivity regime. These metrics are used to test predictions of ecosystem production and niche dynamics and link ecological processes to observed patterns of foraging behaviors.

Material and methods

The organisms and habitat characteristic metrics for this study were collected from the seagrass meadows of the Big Bend region of Florida, USA (Fig. 1). The region is a vast sub-tidal seagrass ecosystem, dominated by continuous meadows of *Thalassia testudinum* and *Syringodium filiforme*,

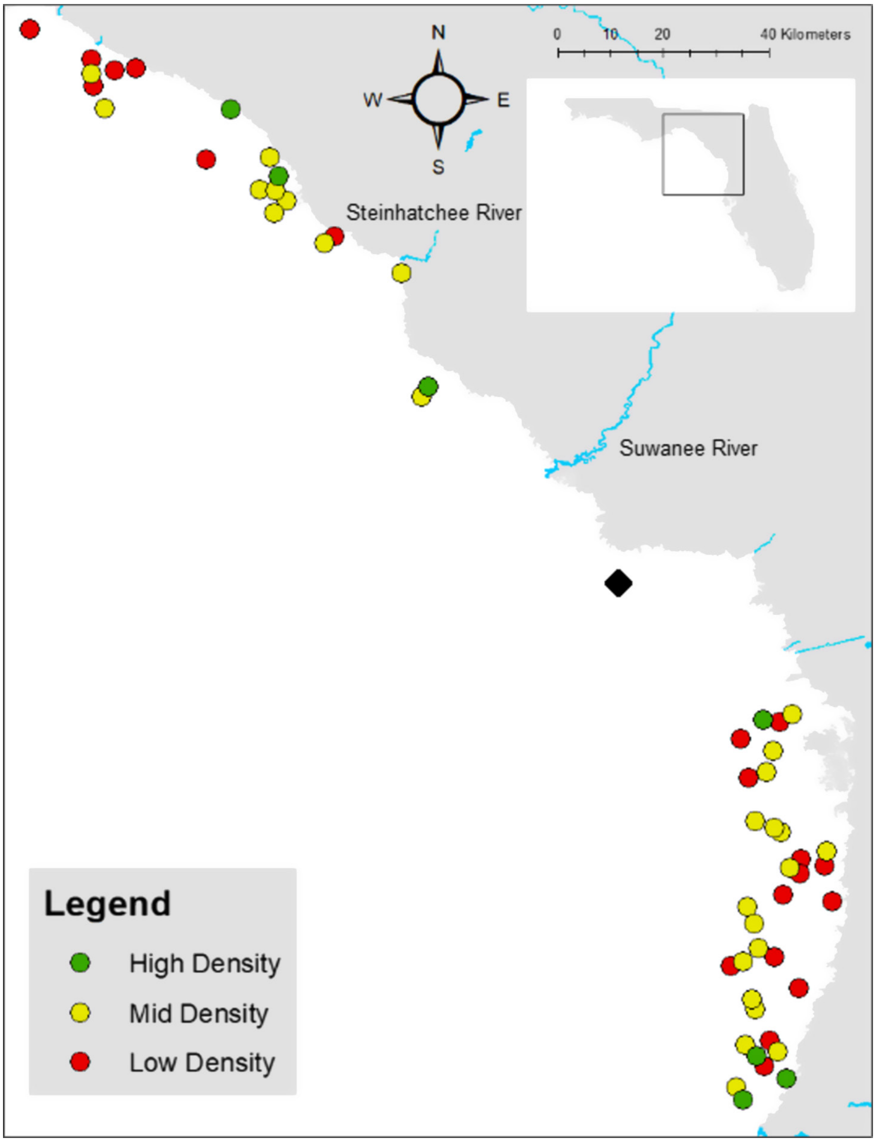

Figure 1. Map of collection sites used in this study. Collections occurred in the Big Bend region of Florida, USA. This area (30°09′16″N to 82°70′16′W) is characterized by extensive, continuous seagrass beds dominated by *Thalassia testudinum* and *Syringodium filiforme*, with a small amount of *Halodule wrightii*. Areas of high seagrass density (productivity) are labeled in green, mid density in yellow and low density in red. Black diamond is Cedar Key, FL, USA.

with a small amount of *Halodule wrightii* (Mattson 1999). The area is characterized by its low wave energy, few barrier islands and uniformly shallow bathymetry. Regional variability in seagrass distribution is largely driven by environmental influences, as the area is well established as one of little anthropogenic disturbance or influence (Livingston 1984, Zieman et al. 1989, Mattson 1999). The area is also critical fish habitat for a variety of recreationally and commercially important fisheries (Mattson et al. 2007).

Sampling sites were chosen in a spatially-balanced manner (Stevens and Olsen 2004) that mimicked the distribution of seagrass, with the constraint that each site had a seagrass density >10% (Stallings et al. 2015a). Detailed information on sampling protocols can be found in the published dataset (Stallings et al. 2015a). Nekton at each site was sampled during the summer of 2009 using a beam trawl (mouth opening: 1.87 × 0.40 m, bag dimensions: 19 mm mesh with 3 mm mesh liner) towed on both sides of a 6.1 m research vessel for 2.5 min at a standard speed of 1.8–2.0 $\mathrm{km\,h^{-1}}$ (~85 m tow length). All captured animals were identified, counted and measured in size classes; a subset was frozen for stable isotope analysis. In addition, seagrass and algae density, blade length and species were recorded via a single snorkel belt transect of 8 m wide (4 m on either side of the vessel's track), and environmental data such as depth (via transom-mounted bottom sounder), temperature, salinity, conductivity and dissolved oxygen was recorded (via YSI-85). Seagrass ecosystem productivity at each site was estimated by multiplying the percent cover of seagrass per site (per 85 m trawl) by the mean seagrass height per site. While we acknowledge that this is, at best, a rough measure of seagrass ecosystem productivity, as there are a host of other factors that contribute to productivity, we are confident that this measure of three-dimensional seagrass complexity is an adequate proxy, as seagrass standing crop has been shown to positively correlate with overall areal productivity (Zieman et al. 1989), as well as epiphytic algae abundance (Frankovich and Fourqurean 1997). From this proxy, productivity was defined as 'low' for values below 20, 'mid' for those that were 20–44 and 'high' for those above 44. These categories were necessary to ensure sufficient sample size for the hypervolume analysis and were chosen to reflect the natural breaks in the seagrass ecosystem production data (Supplementary material Appendix 1 Fig. A1).

Orthopristis chrysoptera (pigfish) and *Lagodon rhomboides* (pinfish) individuals, as well as representative samples of all available primary production channels, were collected via the beam trawl protocol described above and subjected to stable isotope analysis. *Orthopristis chrysoptera* and *L. rhomboides* represent two omnivorous, ubiquitous species native to this ecosystem (Stallings et al. 2015a, Faletti et al. 2019), that undergo ontogenetic shifts in their diet (Stoner 1980, Darcy 1983), and use resources over similar, small home ranges (Potthoff and Allen 2003). Epiphytes, seagrass detrius and benthic microalgae are known to make up a large portion of the diet of both species (Hansen 1969, Adams 1976, Stoner and Livingston 1984), both via direct consumption and via the consumption of benthic invertebrates relying on those production channels (Carr and Adams 1973, Stoner 1980). Direct consumption of plankton by pigfish and pinfish is minimal (Carr and Adams 1973, Stoner and Livingston 1984), and reliance on this productivity channel is likely mediated via consumption of deposit feeding epifauna and small planktivorous organisms (Peterson 1999). Pigfish and pinfish captured in the trawl were pooled in groups of five individuals, with each group of five being considered an individual sample. Due to different numbers of the two species captured, a total of 88 *O. chrysoptera* samples and 186 *L. rhomboides* were used to understand how each species' niche varied over the seagrass productivity regime. All fish were young-of-year (meaning they had recruited to the seagrass system in the winter through spring of the year, Chacin et al. 2016, Faletti et al. 2019) and were between 5 and 7 cm total length. Samples of primary production sources (algae, seagrass and epiphytes) were collected haphazardly throughout sampling and averaged over the entire study area. Seagrass (*Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*) blades and red and green drift algae (*Gracilaria* spp. and *Ulva* spp., respectively) pulled in with beam trawl were used for seagrass and algae sources; POM was not specifically sampled as part of this study, but has similar isotope values as algae in this region (Wilson et al 2009, Nelson et al. 2015). Importantly, POM and algae use the same photosynthetic pathway and source nutrients from the water column. The epiphytes on seagrass blades in the Gulf of Mexico are typically composed of coralline algae (*Melobesia membranacea*, *Fosliella farinosa*), red algae (*Ceramium* spp., *Spyridia* spp., *Hypnea* spp., *Laurencia* spp.) and green algae (*Amphiroa fragilissima* spp.) (Frankovich and Fourqurean 1997). Epiphytes were carefully scraped off of seagrass blades similar to the methods in (Wilson et al. 2010). Trophically-corrected sand dollars, *Mellita quinquiesperforata*, were used as a proxy for the microphytobenthos by subtracting the trophic transfer fractionation (Δ = 3.4‰, Post 2002) from the values of each sand dollar sample (Moncreiff and Sullivan 2001, Wilson et al. 2017). Source and fish samples were taken back to the laboratory and frozen at −20°C until they could be processed for isotope analysis (Stallings et al. 2015b). In the laboratory, fish and source samples were thawed and vigorously rinsed in DI water and acid washed to remove carbonates and sulfates. Samples were then dried at 50°C for 48 h, ground to a fine powder using a mortar and pestle and a ball mill grinder, and analyzed individually via a continuous flow stable isotope mass spectrometer coupled to a CHNS analyzer at the National High Magnetic Field Laboratory at Florida State University. Carbon, nitrogen and sulfur isotope values were calculated using the standard formula

$$\delta X = \left(\frac{R\left(X_H / X_L\right)_{\text{sample}} - R\left(X_H / X_L\right)_{\text{standard}}}{R\left(X_H / X_L\right)_{\text{standard}}} \right)$$

where $R(X_H/X_L)$ is the ratio of the heavy to light isotope, respectively, of element X (Nelson et al. 2012). PeeDee Belemnite (PDB), atmospheric nitrogen and Canyon Diablo Troilite (CDT) were used as the reference standards for C, N and S, respectively. No C:N ratio was above 3.5; therefore, no lipid correction was applied (Peterson and Fry 1987, Post et al. 2007, Nelson et al. 2013). Source isotope values are summarized in Supplementary material Appendix 1 Table A1a, mean consumer isotope values are summarized in Supplementary material Appendix 1 Table A1b, and sources used enclosed consumer values in concentration dependent mixing space (Supplementary material Appendix 1 Fig. A2A–C, Phillips and Koch 2002).

The relative contribution of algae, epiphytes, microphytobenthos and seagrass-derived organic matter sources to each species was derived through the use of concentration-dependent Bayesian mixing models (Parnell et al. 2013, Wilson et al. 2010). All stable isotope data were analyzed in R (ver. 3.3.2, <www.r-project.org>) using the package MixSIAR (ver. 3.1.7, Stock et al. 2018). Models were run in three chains with 1 000 000 iterations and a burn-in of 500 000 to allow for adequate model convergence. Fractionation factors of 1.3 (±0.3), 3 (±1) and 0.6 (±0.2) were used for C, N and S, respectively (Vander Zanden and Rasmussen 2001, Hussey et al. 2014a, Nelson et al. 2015, Wilson et al. 2017). Concentration-dependent mean percent contributions of each source were calculated for each individual *O. chrysoptera* and *L. rhomboides* sample. From these source contributions, the relative trophic position of each sample was calculated according to the following formula:

$$\mathrm{TP} = \frac{\delta^{15}\mathrm{N}_{\mathrm{ind}} - \Sigma\left(\delta^{15}\mathrm{N}_{\mathrm{source}} \times \mathrm{mean\,\%\,cont}_{\mathrm{source}}\right)}{\mathrm{TDF}} + 1$$

where TDF = 3‰ (Vander Zanden and Rasmussen 2001, Post 2002, Hussey et al. 2014b), $\delta^{15}\mathrm{N}_{\mathrm{ind}}$ is the nitrogen value of an individual consumer, $\delta^{15}\mathrm{N}_{\mathrm{source}}$ is the nitrogen value of each particular source of primary production, and mean $\%\mathrm{cont}_{\mathrm{source}}$ is the mean proportional contribution of each source to the consumer diet (Post 2002, Wilson et al. 2009, 2010, Nelson et al. 2015). This calculation of relative trophic position accounts for the number of fractionations it took to get from source to consumer and used that to directly determine the relative trophic position of that consumer.

The results of mixing models provide an estimate of the contribution of each resource for each sample of each species in each productivity category as a posterior distribution. Together, these distributions represent the sample's diet as a series of numerically calculated vectors, which incorporates any error present from isotopic measurement or ecological variability (Newsome et al. 2012). The relative trophic position separates consumers in resource-use space by the number of trophic steps taken between production sources and consumers. The mean of these posterior distributions were taken for each resource for each sample and then, along with relative trophic position, z-transformed before analysis to allow for standardized, comparable axes in n-dimensional space (Blonder et al. 2014). z-score values were calculated based on the following equation:

$$z = \frac{x_{ij} - \bar{x}_j}{s_j}$$

where x_{ij} is the individual value for a given axis (resource), $\bar{x}_j$ is the global mean of that axis, across both species and all productivity categories, and s_j is the standard deviation of that axis. So, in addition to each sample having a mean percent contribution of each primary producer and a calculated relative trophic position, each sample has a z-scored percent contribution of each primary producer, and a z-scored relative trophic position, which describes how many standard deviations that individual's percent contribution is from the global mean of that resource. These are then used to seed a Gaussian kernel density estimation, generating a cloud of points based on the distribution of the z-scored values along the five axes (contribution of four sources and relative trophic position) that define the multidimensional trophic niche of the species (per seagrass productivity).

Kernel density estimation is a useful tool to understand the shape of the distribution that underlies a set of data points. This is calculated by weighting the amount of points that are known to exist at a given location in the distribution using a kernel function to look for other known points nearby and draw a smooth curve based on the number of other points it finds near every known data point. The shape of the kernel function can alter the shape of the distribution estimation (here, we use a Gaussian Kernel function), as well as the width the function uses to look for other nearby points, called the bandwidth. We use the Silverman estimator, which is the preferred bandwidth estimator for this particular kernel function, as other bandwidth estimations are sensitive to high (≥4) dimensionality. The quantile threshold used was 0.05, so that each hypervolume included 95% of the total probability density (Blonder et al. 2014, 2017). The hypervolume algorithm computes the multi-dimensional kernel density estimate by overlaying kernels around each z-scored observation in multi-dimensional space. The algorithm then samples from these kernels randomly using a Monte Carlo importance sampling approach and performs range testing using a recursive partitioning tree. It then only retains points that fall within the specified bandwidth. The resulting niche hypervolume objects can then be compared to determine differences in size and overlap. A detailed description of the algorithms used to calculate hypervolume metrics and the hypervolumes themselves can be found in the citation for the hypervolume R package (Blonder et al. 2014, 2017).

The size and overlap of niche hypervolumes were statistically assessed via a bootstrapping protocol (Newsome et al. 2012). Each species/productivity category was bootstrapped by creating 100 hypervolumes derived from randomly sampled sets of a number of individuals equal to two-thirds of the number of individuals within each species/productivity category. In addition, an estimation of the niche size of a ‘random’ individual of each species was created by making 100 hypervolumes, each derived from a randomly sampled set of 50% of the total number of individuals for each species. This allowed us to determine if the differences in niche sizes observed were a result of our productivity bins, rather than a function of randomly grouping individuals from different sites. The number of randomly chosen samples used to create these bootstrapped sets of niche sizes was chosen to ensure that each iteration of the procedure included enough samples to reliably construct niches. These resulting sets of niche volumes were used to create 95% confidence intervals for each species/productivity category and compared using the non-parametric Kruskal–Wallis rank-sum test, with a post hoc Bonferroni-corrected Dunn’s test to compare between all groups. Niche overlap was assessed by calculating 100 hypervolumes that were again derived from randomly sampled sets of two-thirds of the number of individuals within each of the species/productivity categories being compared and obtaining the Sørenson overlap index between them. This afforded a set of overlap index values for each pair of productivities per species, which were used to create 95% confidence intervals and compared using the non-parametric Kruskal–Wallis rank-sum test, with a post hoc Bonferroni-corrected Dunn’s test.

Results

Across all sites, *Orthopristis chrysoptera* relied primarily on the algal production channel, which comprised 56% (±22%) of their diet, followed by the microphytobenthos at 20% (±13%), seagrass at 17% (±12%) and epiphytes at 7% (±6%), and had a mean relative trophic position of 2.11 (±0.13) (Table 1). *Lagodon rhomboides*, relied mostly on the microphytobenthos production channel at 66% (±20%), followed by the algae at 18%. (±16%), epiphytes at 11% (±8%) and seagrass at 5% (±6%), and had a mean relative trophic position of 2.02 (±0.1) (Table 1).

Orthopristis chrysoptera niche hypervolume size significantly increased with decreasing ecosystem productivity (Kruskal–Wallis, $\chi^2 = 3253.34$, df = 3, p-value < 0.05, Table 2A, Fig. 2). Post hoc tests revealed significant differences between niche size at all ecosystem production levels and between each ecosystem production level and the size estimation of a random *O. chrysoptera* individual (Dunn’s test with Bonferroni correction, all $p < 0.05$). Niche size increased by an order of magnitude as seagrass productivity decreased, with volumes of 42.26 (95% CI 2.35–98.30) at high seagrass ecosystem productivities (Fig. 2A), 56.60 (95% CI 27.63–88.46) at mid seagrass ecosystem productivities (Fig. 2B), and 483.31 (95% CI 150.93–951.52) at low seagrass ecosystem productivities (Fig. 2C). *Orthopristis chrysoptera* trophic niche in high productivity regimes had a 91.26% reduction in size compared to those in low productivity regimes.

Lagodon rhomboides niche hypervolume size significantly increased with decreasing ecosystem productivity (Kruskal–Wallis, $\chi^2 = 3079.97$, df = 3, p-value < 0.05, Table 2A, Fig. 3). Post hoc tests revealed significant differences between niche size at all ecosystem production levels, and between each ecosystem production level and the size estimation of a random *L. rhomboides* individual (Dunn’s test with Bonferroni correction, all $p < 0.05$). *Lagodon rhomboides* showed a similar, order-of-magnitude increase in niche size with decreasing seagrass productivity, with volumes of 12.20 (95% CI 2.32–27.11) at high seagrass ecosystem productivities (Fig. 3A), 42.26 (95% CI 15.13–72.59) at mid seagrass ecosystem productivities (Fig. 3B), and 100.58 (95% CI 32.97–219.92) at low seagrass ecosystem productivities (Fig. 3C). *Lagodon rhomboides* in high productivity regimes had an 87.87% reduction in niche size compared to those in low productivity regimes.

Overlap between *O. chrysoptera* and *L. rhomboides* resource use niche significantly increased with decreasing ecosystem productivity (Kruskal–Wallis, $\chi^2 = 2383.23$, df = 2, p-value < 0.05, Supplementary material Appendix 1 Table A3B). Pairwise comparisons between species at each productivity category revealed significantly more niche overlap at lower productivities, and more niche separation at higher productivities (Dunn’s test with Bonferroni correction, all $p < 0.05$). Sorenson overlap index between *O. chrysoptera* and *L. rhomboides* was 0.123 (95% CI 0.02–0.23) at low seagrass productivity, 0.063 (95% CI 0.01–0.09) at mid seagrass productivity, and 0.0008 (95% CI 0–0.005) at high seagrass productivity (Table 2B).

Table 1. Relative contribution of primary production and calculated trophic position of *O. chrysoptera* and *L. rhomboides* at categories of seagrass ecosystem productivity. Values are reported as mean (±SD).

Species	Seagrass productivity	Algae	Epiphytes	MPB	Seagrass	Trophic position
Orthopristis chrysoptera	Low	0.54 ± 0.27	0.07 ± 0.09	0.23 ± 0.17	0.15 ± 0.12	2.11 ± 0.15
	Mid	0.56 ± 0.19	0.08 ± 0.04	0.19 ± 0.1	0.18 ± 0.11	2.12 ± 0.11
	High	0.57 ± 0.17	0.06 ± 0.03	0.2 ± 0.07	0.17 ± 0.12	2.09 ± 0.12
	Mean	*0.56 ± 0.22*	*0.07 ± 0.06*	*0.2 ± 0.13*	*0.17 ± 0.12*	*2.11 ± 0.13*
Lagodon rhomboides	Low	0.16 ± 0.18	0.09 ± 0.08	0.7 ± 0.2	0.04 ± 0.08	2.03 ± 0.13
	Mid	0.18 ± 0.15	0.11 ± 0.09	0.65 ± 0.19	0.05 ± 0.04	2.03 ± 0.09
	High	0.22 ± 0.11	0.14 ± 0.07	0.59 ± 0.17	0.05 ± 0.03	1.98 ± 0.05
	Mean	*0.18 ± 0.16*	*0.11 ± 0.08*	*0.66 ± 0.2*	*0.05 ± 0.06*	*2.02 ± 0.1*

Table 2. Comparison of niche size (A) and Sorenson overlap index (B), with 95% confidence intervals, between fish species at each ecosystem production regime. Niche metrics are unitless, as they are defined using the total spread of variability along all axes used in the hypervolume.

Seagrass ecosystem productivity	Niche size (*O. chrysoptera*)	CI 95% (*O. chrysoptera*)	Niche size (*L. rhomboides*)	CI 95% (*L. rhomboides*)
(A)				
Low	483.31	150.93–951.52	100.58	32.97–219.92
Mid	56.60	27.63–88.46	42.26	15.13–72.59
High	42.26	2.35–98.30	12.20	2.32–27.11
Seagrass ecosystem productivity	Sorenson overlap index	CI 95%		
(B)				
Low	0.123	0.02–0.23		
Mid	0.063	0.01–0.09		
High	0.0008	0–0.005		

Discussion

We present a novel method to empirically quantify a consumer species' niche in terms of their use of available resources and quantify changes along a variable productivity regime to test ecological theory regarding the relationship between niche size and productivity. We used a Bayesian mixing model analysis of stable isotope data to produce a multidimensional representation of the resource use niches of two generalist consumers. The resulting niches were defined by the sum of the individual variability in resource use of each species. This approach builds on previous efforts using isotope analysis in isolation to understand niche dynamics by producing niche representations that are free of the caveats associated with niche metrics derived from isotopic space alone, thus producing empirically quantified multidimensional niches that can be useful to test theoretical aspects of ecological and niche theory.

Our results support an ecological extension of the 'niche-width hypothesis', which predicts that at low levels of productivity populations of individuals requiring a specific combination of the resources available to them would face increasing niche overlap and greater potential for resource competition (Evans et al. 2005a, b). At high levels of productivity, one would predict that mean niche size would decline as more individuals with similar, specialized niche ranges can thrive. Increased reliance on fewer resources becomes a viable strategy at high productivity due to greater overall resource abundance; enough energy is available to consumers that individuals can acquire what they need to survive through a specific, similar set of production channels. Conversely, as ecosystem productivity declines, resource production is not sufficient to support strategies focused on few resource channels. Thus, strategies that incorporate resources over a range of channels is favored, and niche sizes tend to increase.

Seagrass ecosystems are notorious for containing complex, reticulated food webs with variability over space and time, making it difficult to draw inferences about trophic niche dynamics using previously described methods. Our method allows for the empirical definition of theoretical relationships in this system, allowing us to test the viability of niche theory, even in a system with large amounts of complexity. By quantifying resource use niches over a variable seagrass ecosystem productivity regime, we demonstrated an inverse relationship between ecosystem productivity and the trophic niche of generalist consumers; niche size decreased as ecosystem productivity increased. Characteristics of the multidimensional niches created, such as their size and overlap, were used to quantitatively describe this relationship. This result underscores the significant applications of this method, as we demonstrated a natural example of this hypothesized relationship in a way that can be applied to models of resource use responses to changes in natural food web systems.

MacArthur and Pianka (1966) theorized that habitat fragmentation should influence the incorporation of prey items into the diet of consumers. Patch size, they proposed, is inversely related to the number of different prey species incorporated into a predator's diet; fragmented, low productivity habitats should force predators to consume a more varied diet over a larger area, while continuous, productive habitats allow for predators to achieve energetic requirements by focusing on specific prey items (MacArthur and Pianka 1966). Very few studies have attempted to empirically demonstrate this hypothesis in a natural setting. However, the few that have generally confirmed the theoretical relationship defined by MacArthur and Pianka (1966). For example, the size and degree to which the isotopic niches of lionfish *Pterois volitans* and Nassau grouper *Epinephelus striatus* overlap is related to the size of habitat these generalist consumers are sampled from; large, continuous reefs had grouper and lionfish with largely separated, small niches, while shallow, unproductive patch reefs held fish that had large, overlapping niches (O'Farrell et al. 2014). The alignment of our results with established theory and the few natural examples in the literature underscores the validity of this novel method and its potential usefulness in the empirical demonstration of theoretical ecological relationships.

The observed pattern of decreasing niche size with increasing productivity can also provide insight into how ecosystem production can drive the establishment of behavior patterns in resident animals. Optimal foraging theory is a collection of models that predicts how a particular animal might acquire resources in a way that maximizes its fitness in a given environment (Pyke et al. 1977). The pattern

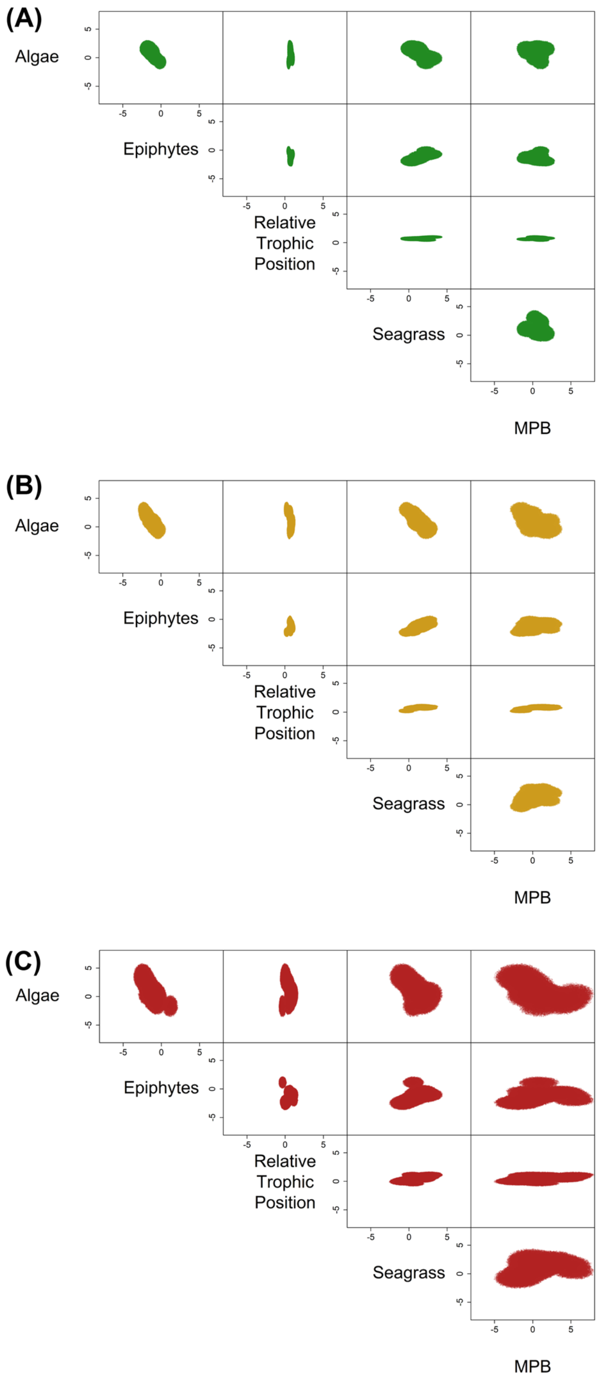

Figure 2. Resource use niches for *O. chrysoptera* in High (A, n = 15), Mid (B, n = 43) and Low (C, n = 30) seagrass productivity regimes. Niches are represented as the colored areas and their size indicates within population variation in resource use. Axes are z-scored source contributions or trophic position; values greater than zero indicate relatively more resource use/greater trophic position than the global mean, and negative values less.

presented here of niche expansion at low productivities, and contraction at high productivities, fits these predictions and, therefore, affords an ecological explanation for the resource maximization behaviors commonly observed in nature.

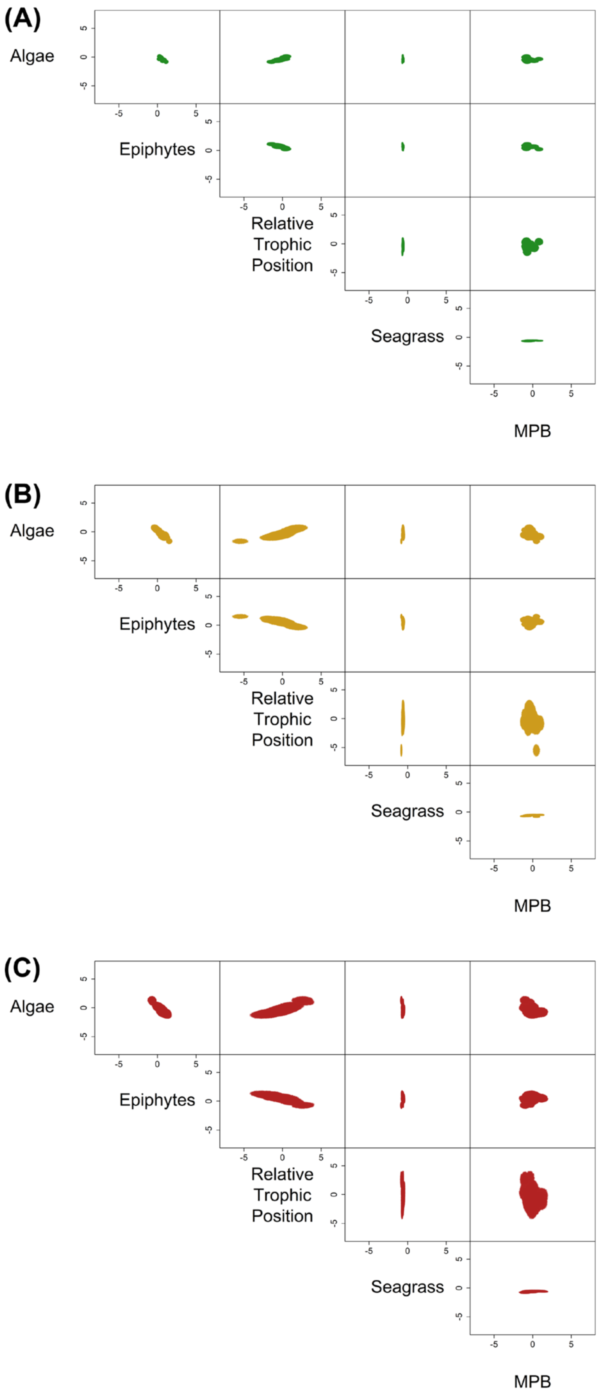

Figure 3. Resource use niches for *L. rhomboides* in High (A, n = 27), Mid (B, n = 82) and Low (C, n = 77) seagrass productivity regimes. Niches are represented as the colored areas and their size indicates within population variation in resource use. Axes are z-scored source contributions or trophic position; values greater than zero indicate relatively more resource use/greater trophic position than the global mean, and negative values less.

At low productivities, energetically favorable resources become scarce. To meet metabolic demands, species must increase the breadth of their niche to include other, less favorable sources. Therefore, large niches that result from generalist strategies which can incorporate these less favorable resources are optimal and increase that species' fitness. A shift in the optimal feeding strategy can occur when energetic demands require a switch, such as when faced with a decline in available prey sizes (Werner and Hall 1974) or the onset of rapid habitat degradation (Karkarey et al. 2017). In this way, the maximization of an individual's fitness across a variable productivity regime within a single ecosystem type requires the ability to alter feeding strategy, thus leading to a change in resource use niche.

Our results afford empirical evidence of the adaptive foraging strategies theorized to stabilize food web dynamics. Despite its widespread prevalence, omnivory is thought to be a destabilizing force in structuring food webs, as the incorporation of multiple food web nodes makes stable coexistence difficult to achieve in simple models (Pimm and Lawton 1978). However, omnivores adapting their foraging strategy to exploit less energetically profitable sources only when preferred sources become rare affords simple food web models the ability to persist more regularly in theoretical settings (Křivan and Diehl 2005). Here, this concept was demonstrated empirically, as both generalist species began to incorporate more varied suites of resource channels only as resources became rare with decreasing ecosystem productivity. *Othopristis chrysoptera* and *Lagodon rhomboides* responded to uneven ecosystem production by expanding or contracting their niche allowing for the maintenance of a stable food web. The expansion of the niche of the two generalist species examined here provides real-world evidence in support of this theoretical solution to the problem of stable, persistent omnivory in marine food webs.

The idea to use stable isotope analysis to define a species' trophic niche is not new, and has spawned a host of metrics and tools designed to quanify a niche object within the space they provide (Layman and Post 2007, Jackson et al. 2011, Cucherousset and Villéger 2015). However, while these tools quickly became widely used and accepted, many have documented the issues with inferences about trophic niche dynamics directly from isotope values themselves. Consumer isotope values are directly related to the isotopic baselines of the sources they incorporate. Therefore, the niche metrics calculated from isotope space alone can be greatly influenced by these values alone, instead of by meaningful shifts in feeding pattern (Hette-Tronquart 2019). Other factors such as variation in both ontogenetic and geographic consumer resource use can directly influence niche metric results and obscure any definitive conclusions that can be made about them (Hoeinghaus and Zeug 2008, Newsome et al. 2012, Gorokhova 2017, Marshall et al. 2019). Part of the solution to these issues with stable isotope space is to use mixing models, which determine the percent contributions of sources to consumer which are considered mixtures of those sources (Moore and Semmens 2008, Parnell 2008, Phillips et al. 2014, Stock et al. 2018). Converting isotope data into contributions of source channels to consumers allows for direct comparison of isotope data to more traditional ecological information, (Newsome et al. 2007, 2012, Hopkins III and Kurle 2016, Manlick et al. 2019). Newsome's DietSpace incorporates source information to create metrics that assess dietary specialization and similarity of individuals within populations, demonstraing how source contribution information can break free of the limitations of isotope space itself and generate meaningful insight into the dynamics of the trophic niche. However, these methods focus on the individual or the population, when individual variability in resource use is in fact population tophic niche. For this reason, our method is the best for quantifying a population's trophic niche, as it represents how energy is moving to and through individuals in a population, and thus quantifies how energy is flowing through a food web.

This work combined Bayesian mixing models and n-dimensional hypervolume metrics to construct and quantify versions of the Eltonian niche. This approach builds upon previous studies which have moved stable isotope analysis from inferring trophic connections using bi-plots to delineating food webs using Bayesian mixing models and testing ecological theory using isotopic niche metrics (Layman and Post 2007, Jackson et al. 2011, Newsome et al. 2012). This study improves these analyses to quantify trophic niches that conform to well-understood paradigms and are free of many of the problems associated with previous methods. The method outlined by this study provides a powerful tool for the empirical testing of ecological theories related to resource use, food web dynamics, competition and species assemblages.

Data accessibility

Data are also available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.xwdbrv1b3> (Lesser et al. 2020).

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Permits – Data were collected under NMFS General Authorization no. 1055-1732. All work involving animals was conducted under the Florida State University Animal Care and Use Committee (Protocol no. 9408).

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Supplementary material (available online as Appendix oik-07026 at <www.oikosjournal.org/appendix/oik-07026>). Appendix 1.

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