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RESEARCH ARTICLE

E-scape: Consumer-specific landscapes of energetic resources derived from stable isotope analysis and remote sensing

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Abstract

1. Energetic resources and habitat distribution are inherently linked. Energetic resource availability is a major driver of the distribution of consumers, but estimating how much specific habitats contribute to the energetic resource needs of a consumer can be problematic.
2. We present a new approach that combines remote sensing information and stable isotope ecology to produce maps of energetic resources (*E*-scapes). *E*-scapes project species-specific resource use information onto the landscape to classify areas based on energetic importance.
3. Using our *E*-scapes, we investigated the relationship between energetic resource distribution and white shrimp distribution and how the scale used to generate the *E*-scape mediated this relationship.
4. *E*-scapes successfully predicted the size, abundance, biomass, and total energy of a consumer in salt marsh habitats in coastal Louisiana, USA at scales relevant to the movement of the consumer.
5. Our *E*-scape maps can be used alone or in combination with existing models to improve habitat management and restoration practices and have potential to be used to test fundamental movement theory.

KEYWORDS

E-scape, habitat cover, remote sensing, species distribution, stable isotopes

1 | INTRODUCTION

The availability of energetic resources and habitat distribution are inherently linked. Habitats produce specific resources that are available to consumers, and energetic resource availability is a major driver of consumer production, movement, and distribution (Pyke, 2019; Wallace et al., 1999; Ware & Thomson, 2005). The distribution of habitats, and therefore energetic resources, is heterogeneous, and there is a substantial body of theoretical and empirical work that demonstrates how organisms respond to patterns of habitat and energetic resources across landscapes (Brown et al., 2004; Currie, 1991; Guégan et al., 1998; Pyke, 2019; Stein et al., 2014; Wright, 1983). This framework provides a link for how consumers are influenced by the distribution of energetic resources and, coupled with technological advances in remote sensing and geographical information systems (GIS), provide an exciting opportunity to answer critical questions in spatial ecology and influence how we manage and restore rapidly changing ecosystems (Fryxell et al., 2020; Merkle et al., 2015).

An accurate species-specific representation of resource availability at the landscape scale is required to test theories linking energetic resource availability and species foraging or distribution. Spatial primary production estimates (e.g. normalized difference vegetation index [NDVI], chlorophyll-a concentration) and prey habitat suitability models are some of the approaches used to map resource availability for consumers across landscape and regional spatial scales (i.e. from 10s to 100s of kilometres; Abrahms et al., 2019; Geary et al., 2020; Mosser et al., 2014). For example, a habitat suitability model of the dominant prey of brown pelicans (which included chlorophyll-a concentration as a model parameter) was used to test how foraging behaviour changed during the breeding season (Geary et al., 2020). Landscape energetic resource maps have typically focused on a single energetic resource or prey species, which is accurate when a consumer specializes on that resource (Abrahms et al., 2019). However, in many cases, a consumer is integrating multiple energetic resources from different habitat types across the landscape. When a consumer is using multiple resources, mapping energetic resource distribution is more difficult because resources are not produced evenly among habitats and consumers typically do not use all resources equally. Thus, to accurately represent energetic resource distribution, information is needed on where resources are being produced across the landscape and the proportion of each resource used by the consumer.

Remote sensing has long been used to produce landscape-level imagery of habitats, and digital platforms provide access and availability of satellite and aerial imagery more than ever before (Harris et al., 2020; Santos et al., 2018; Xie et al., 2008). Satellite programmes like Landsat and Sentinel provide free multispectral imagery of the globe, and commercial satellites and unmanned aircraft systems (UAS) are becoming more affordable for providing high-resolution imagery (Harris et al., 2019; Irons et al., 2012; Tucker et al., 2004). GIS software can easily convert remotely sensed imagery into habitat cover maps, and remote sensing has helped in the mapping of different systems across multiple spatiotemporal scales. These new remote sensing products/maps can be combined with other spatially explicit data such as biogeochemical tracers, population information, or physical parameters to generate novel data products that can answer a wide array of ecological, management, and conservation questions (Abrahms et al., 2019; Effati et al., 2012; West et al., 2007).

Stable isotope ratios, typically of $^{13}C/^{12}C$, $^{15}N/^{14}N$ and $^{34}S/^{32}S$, have been used for decades to determine the relative contributions of primary production sources in food webs (Fry, 2007; Nelson et al., 2015; Peterson & Fry, 1987). The general principle hinges literally upon the age-old adage 'you are what you eat'. Organisms assimilate material from dietary items as they are transferred in the food web (Fry, 2007; Layman et al., 2012). The stable isotope values, typically defined in del notation (δ) and expressed in per mil (‰), of primary producers are controlled by a number of physical and biological processes that impart characteristic isotope values (Chanton et al., 1987; Farquhar et al., 1989). These characteristic values can then be traced as they are assimilated in the food web using Bayesian stable isotope mixing models (Stock et al., 2018). All plants fix carbon from the same atmospheric reservoir of CO_2, currently −8‰ $\delta^{13}C$. For example, in coastal ecosystems, carbon stable isotope values can be most useful in differentiating between C3 plants, such as mangroves, which fix carbon with a net fractionation of about −20‰ relative to the atmosphere and C4 plants, such as tropical and temperate salt-tolerant grasses, which have a net fractionation of about −5‰ (Fry, 2007). In the same systems, sulphate reduction in sediments has a large fractionation factor (30–70‰) and can be used as a strong indicator of pelagic versus benthic primary production (Chanton et al., 1987; Nelson et al., 2012).

Here we present a method that combines stable isotope analysis, Bayesian mixing models, and remote sensing to build a landscape of energetic resources, or *E*-scape, for white shrimp *Litopenaeus setiferus* in Port Fourchon, LA. An *E*-scape combines the spatial locations where energetic resources are being produced (habitat cover map) and how much of each resource the consumer is using (stable isotope analysis) to generate a species-specific map of areas that contain habitats producing the resources being used by that species. Using our *E*-scapes, we investigated the relationship between energetic resource distribution and white shrimp distribution and how the scale used to generate the *E*-scape mediated this relationship.

2 | MATERIALS AND METHODS

Samples of white shrimp *Litopenaeus setiferus* were collected using a 1-m^2 drop sampler at 55 randomly selected sampling locations in Port Fourchon, LA during September 2016 (Figure 1a; Nelson et al., 2019; Zimmerman et al., 1984). We collected all of the white shrimp within the drop sampler to determine the abundance and biomass at each sampling location. Samples for stable isotope analysis and bomb calorimetry were removed, placed on ice and frozen upon returning to the laboratory. White shrimp are omnivores and forage benthically throughout the shallow open-water areas and on the inundated saltmarsh platform, typically on small benthic infauna (Rozas & Reed, 1993). Throughout the study location, we collected *Spartina alterniflora* stems, mangrove leaves and benthic algae (from the water/vegetation edge) by hand, and water samples (for phytoplankton) adjacent to the drop sampler to determine isotope values of primary producers (Nelson et al., 2019). All samples were collected following proper protocols under Louisiana Department of Wildlife and Fisheries Scientific Collection Permit #SCP 149, and no animal ethics approval was required for this study.

Primary production source and animal tissue samples were frozen at −20°C in the laboratory until they could be processed for isotope analysis and bomb calorimetry. For white shrimp at each location, five individuals were pooled to create one composite sample. Samples were dried at 50°C for 48 hr and ground. We determined the energy density (cal/g) of each sample using a Parr 6725 bomb

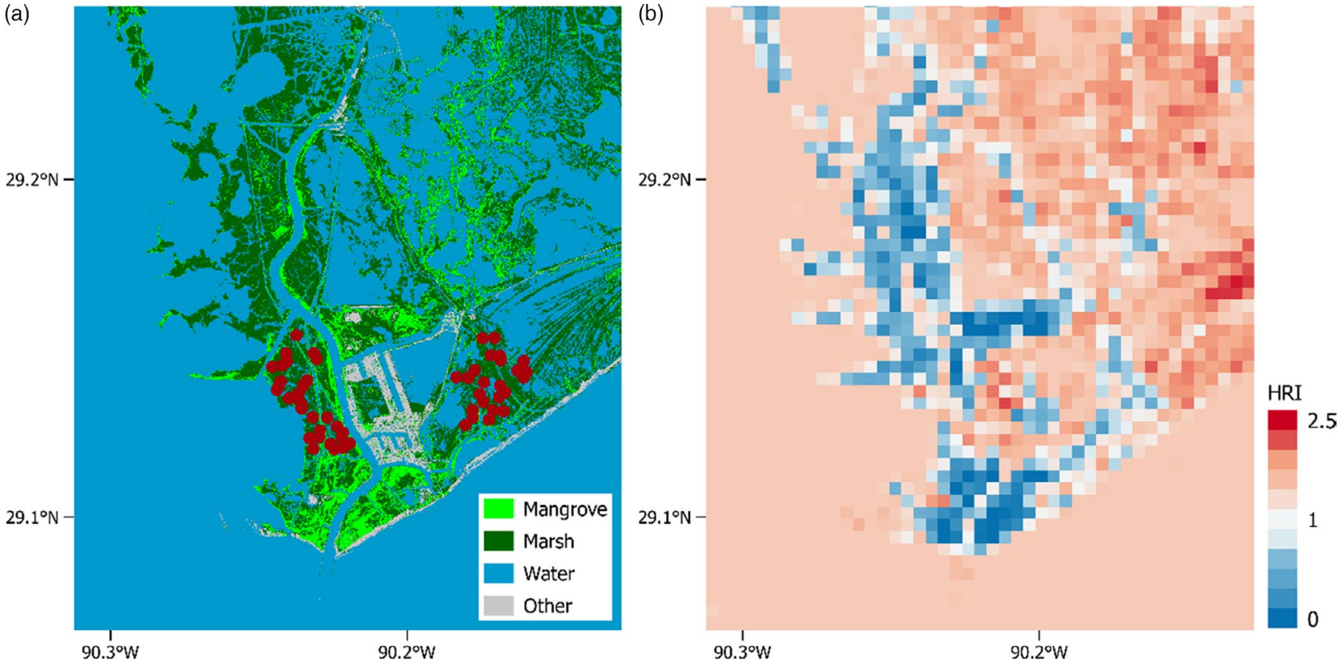

FIGURE 1 The Port Fourchon, LA (a) habitat cover map showing the sampling locations of white shrimp (red points) and (b) the corresponding white shrimp *E*-scape map. Edge habitat was calculated by measuring the linear distance between the water and vegetation (marsh and mangrove) habitat cover classes and multiplying by 2 m to generate an area. Warmer colours (HRI values > 1) contain more area from habitats producing resources being used by white shrimp, and cooler colours (HRI values < 1) contain less amount of these habitats. The *E*-scape was generated at a cell size of 400 m × 400 m (similar area to a 200 m radius circle)

calorimeter (Parr Instrument Company). Total calories of each sample were determined by multiplying the total biomass (g) of shrimp at a site by the energy density (cal/g) at that site. *Spartina* stems, mangrove leaves and benthic algae were rinsed with deionized water, dried at 50°C for 48 hr and ground. Water samples were vacuum filtered with a pre-combusted 0.7 μm glass fibre filter (Nelson et al., 2015). We shipped samples to the Washington State University Stable Isotope Core Facility for C, N, and S content and stable isotope analysis. Carbon, nitrogen and sulphur isotope values are expressed in standard δ notation (Fry, 2007) with PeeDee Belemnite (PDB), atmospheric nitrogen and Canyon Diablo Troilite (CDT) used as the reference standards for C, N, and S, respectively. Analytical error, measured as the standard deviation of replicate samples measured across all runs, was 0.2‰ for δ^{13}C, 0.3‰ for δ^{15}N, and 0.8‰ for δ^{34}S. No C:N ratio was above 3.5; therefore, no lipid correction was applied (Nelson et al., 2011; Post et al., 2007).

Bayesian mixing models were run in R using the package MixSIAR (Stock et al., 2018) to determine the relative basal resource contributions to shrimp at each sampling location. A single isotope mean ± *SD* value was used for each basal resource and calculated by combining source isotope values collected throughout the sampling area (Nelson et al., 2019). Each model was run with a Markov chain Monte Carlo algorithm that consisted of three chains, chain length of 3,000,000, burn-in of 1,500,000, and thin of 500 to ensure model convergence. Corrections were made for the elemental concentration in each source, and the trophic enrichment for each element was $C = 1.0 \pm 0.63$ (mean ± *SD*), $N = 3.0 \pm 0.74$, and $S = 0.5 \pm 0.2$ (Phillips et al., 2014).

The *E*-scape of Port Fourchon, LA for white shrimp was made using the methods outlined in Figure 2. High-resolution aerial imagery from https://atlas.ga.lsu.edu was used to generate a habitat cover map of Port Fourchon, LA using the 'Maximum Likelihood Classification' tool in ArcGIS (v 10.5). This tool uses supervised classification maximum likelihood to assign a habitat class to each pixel of the image based on mean and variances of the habitat classes of the training dataset. Four habitat classes were used: water, marsh, mangrove, and other. The 'marsh' class was comprised mainly of *Spartina alterniflora*, the 'mangrove' class was comprised mainly of *Avicennia germinans* and the 'other' class was comprised mainly of beach area and port facilities. Edge habitat was calculated by measuring the linear distance between the water and vegetation (marsh and mangrove) habitat cover classes and multiplying by 2 m to generate an area. Edge area was calculated this way because benthic algae production is highest at the marsh edge (Litvin et al., 2018; Wainright et al., 2000), and benthic microalgae have recently been shown to have similar biomass at the edge habitat of both marsh and mangrove vegetation (Walker et al., 2019). Relative habitat cover areas were calculated at a range of scales at each of the 55 sampling points. We used buffers with circle radius lengths of 50, 75, 100, 150, 200, 250, 300, 400, 500, 750, 1,000, and 1,500 m around the collection locations to calculate the fraction of each habitat cover type using the LANDSCAPEMETRICS packages in R (Hesselbarth et al., 2019). White shrimp have a home range similar to that of the area of a 200 m radius circle (Nelson et al., 2019; Rozas & Minello, 1997; Webb & Kneib, 2004), but other scales were used to examine the sensitivity of a habitat's

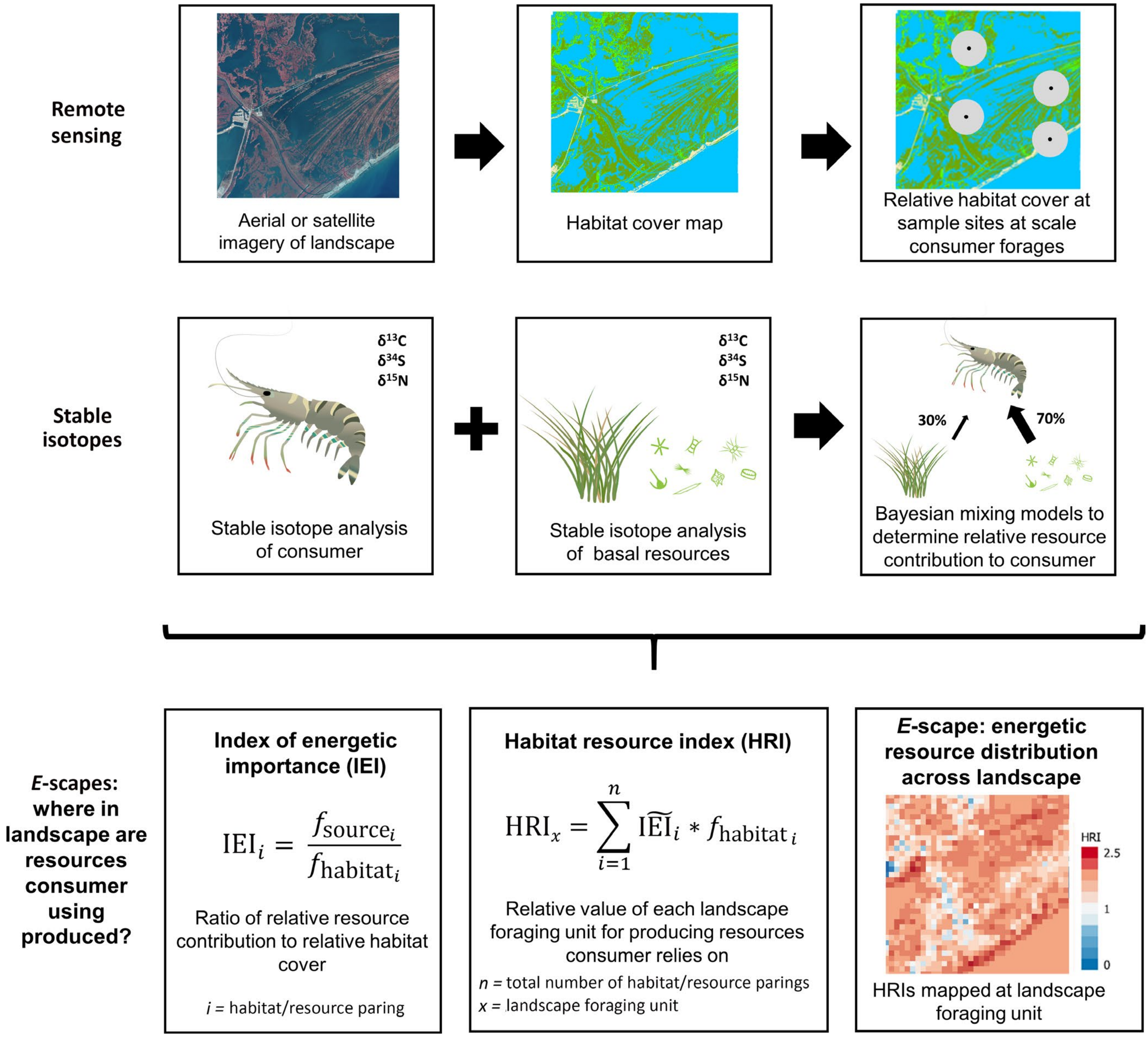

FIGURE 2 General methods for generating an *E*-scape

energetic importance to the scale of measurement. This allowed to explore the role of variation in the scale of consumer movement (either intra or interspecific) into our calculations.

Habitat cover areas were combined with consumer resource use to calculate the index of energetic importance (IEI) for each basal resource and habitat type combination. Each IEI was calculated with the following formula:

$$\mathrm{IEI}_i = \frac{f_{\mathrm{source}_i}}{f_{\mathrm{habitat}_i}}$$

where f_{source_i} is the fraction of the contribution of source *i* to the total source use based on the results of the mixing model and f_{habitat_i} is the fraction of habitat *i* that produces source *i* to the overall area within the movement range of the consumer (i.e. area of the circular buffer around the sampling point). An example of resource/habitat combination is the amount of *Spartina alterniflora* derived production and the cover area of *S. alterniflora* marsh habitat. IEI values were calculated for three distinct source/habitat combinations: phytoplankton/water, *Spartina*/marsh, and benthic algae/edge. The mangrove source/habitat combination was not used in the analysis because resource use of mangrove was <0.01. Each IEI is a measurement of how much a consumer uses an energetic resource relative to the amount of habitat that produces that resource where the consumer is foraging. An IEI around 1 means that the consumer is using a resource (f_{source_i}) around the same amount as the proportion of the habitat (f_{habitat_i}) that produces that resource relative to total area that consumer is foraging over. An IEI greater than one means that the consumer is using that source more than expected based on the proportion of that habitat in the total foraging area, while the opposite is true for an IEI below one.

IEI values were combined with habitat cover areas within a landscape foraging unit to calculate the habitat resource index (HRI). HRI was calculated with the following formula:

$$\mathrm{HRI}_x = \sum_{i=1}^{n} \widetilde{IEI}_i \times f_{\mathrm{habitat}_i}$$

where $\widetilde{IEI}_i$ is the median of the IEI for the source/habitat combination *i* and f_{habitat_i} is the fraction of habitat *i* to the overall area within landscape foraging unit *x*. HRI is an index that represents a relative measurement of the quality of the habitats for producing the resources used by the consumer based on stable isotope analysis. An HRI value of 1 means that the area is producing the average amount of resources for the consumer. HRI values > 1 mean that the area is better for producing resources (i.e. more energetic resources) being used by the consumer, while HRI values < 1 show that the habitats most important to the production of resources being used by the consumer are underrepresented within the landscape foraging unit (Figure 1). The minimum possible HRI = 0, and the theoretical maximum for HRI is infinity, although it is very unlikely that this value will occur in nature because f_{source_i} and f_{habitat_i} range between 0 and 1. Therefore, a unit of change is not linear for HRI, and log(HRI) should be used for linear modelling purposes so that unit change is similar throughout the possible range of values.

The sampling area was subdivided into a grid of 400 m × 400 m landscape foraging units to generate an *E*-scape for white shrimp (Figure 1b). This size was chosen because it was a similar size to the movement range of white shrimp observed in the field (Nelson et al., 2019; Rozas & Minello, 1997; Webb & Kneib, 2004). The median IEI values for each resource/habitat combination used to generate the HRI in each landscape foraging unit were calculated from the 55 shrimp sampling locations using a 200 m radius (400 m diameter) circular buffer because it was similar in size to the landscape foraging unit.

In addition to generating the *E*-scape map, we calculated one HRI value in a landscape foraging unit around each sampling point to test for the relationship between HRI value and white shrimp population and energetic metrics. HRIs were generated within circular landscape foraging units with a radius length of 200 m based on field movement ranges of white shrimp in the field (Nelson et al., 2019; Rozas & Minello, 1997; Webb & Kneib, 2004). HRI values were also calculated at 50, 75, 100, 150, 250, 300, 400, 500, 750, 1,000, and 1,500 m radius circle landscape foraging units around the sample points to test for the effect of scale. The HRI values were calculated using the median IEIs that were calculated at the same scale (i.e. the IEIs calculated at 100 m were used in the calculation of the HRI at 100 m), and the median IEI was generated from calculating an IEI for each habitat/resource combination at each of the 55 sampling locations (Table 1). A GLM with a Gaussian error was used to test the relationship between log(HRI) and energy density (cal/g). GLMs with a gamma error and log link function were used to test the relationship between log(HRI) and biomass, abundance, total calories (cal/g × biomass) and mean size (biomass/abundance). For each GLM, outliers were removed if the value was outside of 1.5 ± the interquartile range. All analyses were done in R (R Core Team, 2021).

3 | RESULTS

White shrimp used benthic algae more than any other source (mean ± *SD*; 0.49 ± 0.04), followed by phytoplankton (0.38 ± 0.07) and *Spartina* (0.13 ± 0.04; Figure 3). Mangroves had a source contribution of <0.01 of white shrimp (Figure 3).

The IEI values are a representation of how much the white shrimp are using a resource relative to the amount of habitat that produces that resource (Table 1). Benthic algae/edge consistently had the highest IEI across all scales, with much smaller IEI values for both phytoplankton/water and *Spartina*/marsh (Table 1). Edge

TABLE 1 The index of energetic importance (IEI) values and interquartile ranges (IQR) for each source/habitat combination: benthic algae/edge, phytoplankton/water, and *Spartina*/marsh and the habitat resource index (HRI) values (mean ± *SD*) at varying scales of consumer foraging (size circle calculated around sampling location) calculated over the 55 sampling locations. HRI values > 1 are better than average energetically for white shrimp, while the opposite is true for HRI values < 1

Buffer radius (m)	Edge IEI (IQR)	Water IEI (IQR)	Marsh IEI (IQR)	HRI (mean ± *SD*)
50	11.27 (6.61–28.12)	3.02 (1.03–14.35)	0.18 (0.14–0.25)	1.38 ± 0.90
75	11.00 (6.91–14.13)	1.72 (1.04–4.71)	0.19 (0.15–0.26)	1.16 ± 0.57
100	9.19 (6.54–14.38)	1.48 (1.01–2.72)	0.20 (0.15–0.27)	1.07 ± 0.42
150	8.50 (6.66–12.97)	1.36 (0.89–1.87)	0.21 (0.17–0.27)	1.07 ± 0.36
200	8.19 (6.72–11.26)	1.26 (0.98–1.75)	0.21 (0.18–0.26)	1.04 ± 0.32
250	8.28 (6.48–10.79)	1.29 (0.98–1.69)	0.22 (0.18–0.25)	1.07 ± 0.30
300	8.16 (6.58–10.49)	1.20 (0.92–1.52)	0.21 (0.18–0.26)	1.04 ± 0.26
400	8.38 (6.95–10.36)	1.14 (0.90–1.37)	0.22 (0.19–0.27)	1.03 ± 0.22
500	8.42 (7.02–10.89)	1.10 (0.85–1.34)	0.24 (0.18–0.27)	1.02 ± 0.20
750	9.16 (7.29–11.34)	0.96 (0.78–1.12)	0.25 (0.18–0.30)	1.02 ± 0.14
1,000	9.38 (7.84–11.54)	0.87 (0.74–1.06)	0.27 (0.20–0.34)	0.99 ± 0.11
1,500	9.92 (8.33–11.87)	0.79 (0.69–0.98)	0.31 (0.23–0.38)	0.99 ± 0.11

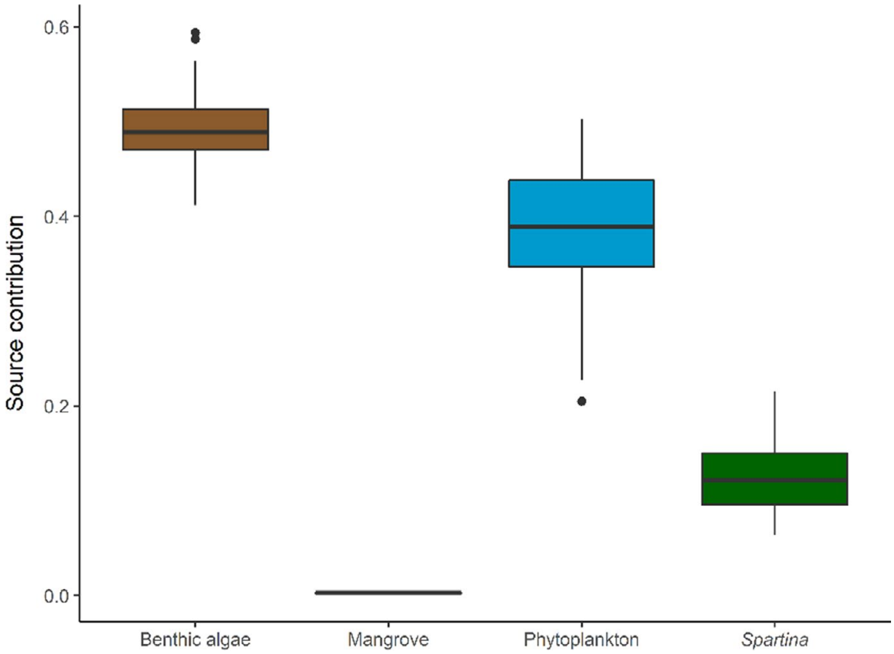

FIGURE 3 Bayesian mixing model results for white shrimp in Port Fourchon, LA

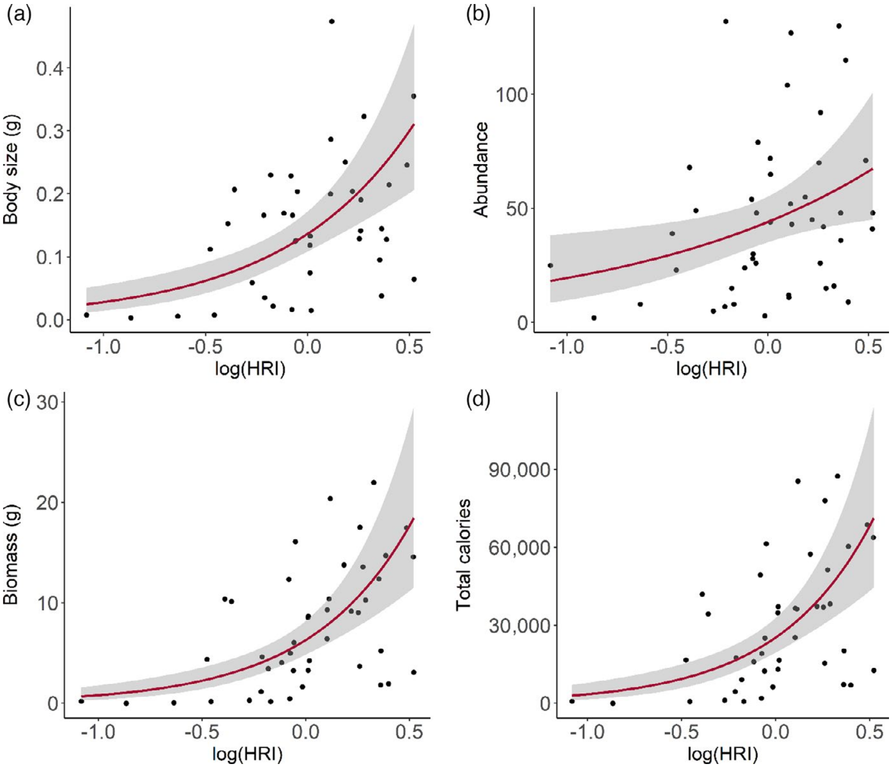

FIGURE 4 The relationship between habitat resource index (HRI) and white shrimp (a) body size, (b) abundance, (c) biomass, and (d) total calories. HRI values were calculated within a 200 m radius circle around sampling locations

IEI values were highest at the smallest scale and declined until the 300 m radius, the lowest IEI value, where it increased as scale increased. Water IEI values were highest at the smallest scale and decreased as scale increased. Marsh IEI values were lowest at all scales of the three habitats and increased in value as scale increased.

Habitat resource index values at the 200 m scale were 1.04 ± 0.32 (mean ± *SD*) around the sampling locations (Table 1). HRI values are a relative metric of quality of the habitats for producing resources used by the white shrimp and were highest in areas that contained the most edge habitat (Figure 1). There was a relationship between HRI value and body size (t-value = 4.8, $p < 0.001$), abundance (t-value = 2.5, $p = 0.018$), biomass (t-value = 5.4, $p < 0.001$) and total calories (t-value = 5.1, $p < 0.001$) at the 200 m scale (Figure 4; Table S1). The relationship between HRI values and energy density (cal/g) was not detectable ($p = 0.555$). For the other scales, the relationship between HRI values and body size was detectable at intermediate scales (100–750 m, Table S1). At the 150–250 m scales, there was a detectable relationship with HRI values and abundance (Table S1). There was a detectable relationship between HRI value and biomass for all but the 1,500 m scale (Table S1). The same was true for total calories (Table S1). There was no detectable relationship between HRI value and energy density at any scale.

4 | DISCUSSION

Our results demonstrate that *E*-scapes can predict the spatial distribution of biomass and total energy of a consumer by combining spatial habitat and resource use data (Figure 4). White shrimp size, abundance, biomass, and total calories increased as the HRI increased across the marsh seascape (Figure 4). White shrimp energy density (cal/g) was not related to energetic resource distribution. These results are supported by previous work that showed white shrimp energy density did not change depending on the habitat type of the shrimp (Nelson et al., 2019).

Habitat resource index values predicted white shrimp distribution within its foraging range (200 m), but not at all scales tested. At scales less than 200 m, the areas sampled failed to include all the habitats and resources used by shrimp, resulting in an oversampling artefact. At the larger scales, the opposite was true, and the forage areas were over aggregated leading to poor representation of foraging habitat. These results demonstrate that choosing the right scale for generating the *E*-scape is critical and should be informed by the foraging range of the consumer. For example, consumers that are foraging over much larger areas than shrimp (e.g. whale or bird) would require a larger *E*-scape landscape foraging unit on the order kilometres instead of meters (Abrahms et al., 2019; Geary et al., 2020). New tracking techniques can be used to inform these scales of foraging movements which were previously poorly understood (Abrahms et al., 2019; Geary et al., 2020).

The IEI represents how much a consumer is using a resource relative to the amount of habitat that is producing that resource. White shrimp are derived from 49% benthic algae and 38% phytoplankton, but since there is much less edge habitat (the habitat where benthic algae are produced), the IEI for edge is almost an order of magnitude larger than the IEI for water (Table 1). Therefore, the areas that contain the most edge habitat are of the highest energetic importance for white shrimp (Figure 1). The IEI for marsh is <1 at all scales indicating that white shrimp use energetic resources from the marsh at a lower rate than their availability in the system (Table 1). Although areas that contain a high amount of marsh habitat are less favourable energetically than the average habitat (HRI < 1), these habitats are still producing resources being used by white shrimp and are more energetically favourable than areas of high mangrove habitat (which white shrimp are not using as an basal resource; Figure 3; Harris et al., 2020; Nelson et al., 2019). Thus, the maps can differentiate between habitats suitable to occupy versus habitats that are producing resources the consumer relies on.

In our calculation of HRI and IEI values, the fraction of habitat (f_{habitat_i}) is based on the area of habitat cover. This calculation assumes that all areas of a given habitat type have an equal chance of producing a resource. For example, we make the assumption that all areas of water in our habitat cover map (Figure 1a) have an equal chance of producing phytoplankton. This assumption may not be acceptable in all applications, especially when applying these methods to consumers that have very large foraging ranges (Geary et al., 2020). For these cases, modifications can be made to f_{habitat_i} to incorporate the spatial differences in production such as incorporating chlorophyll-a maps or lidar data to incorporate the three-dimensional structure of the habitats. One limitation to our approach is that phytoplankton is produced in three dimensions, unlike the other sources, and we are presently not able to account for the three-dimensional structure of water across the seascape with the available data. Accounting for water volume will be especially important in systems that are stratified or in which phytoplankton production is integrated over a significant depth (Cole & Cloern, 1984). One way to incorporate volume into f_{habitat_i} is to modify by accounting for the depth of the habitat in relation to the euphotic zone of the system (Cole & Cloern, 1984). Unfortunately, these types of data are not always available and were not available in our study area. Other modifications could include parameters that include temporal differences in access to habitats which can be major drivers of foraging behaviours of consumers (Nelson et al., 2015). Additionally, mixing models assume that the consumer is in equilibrium with the local food webs, and therefore, constrains our approach to consumers that meet this assumption (Phillips et al., 2014). Lastly, special consideration is needed for consumers that rely heavily on fluxes of energetic resources that are not produced locally (e.g. gag grouper on offshore reef habitats relying heavily on pinfish migration from inshore seagrass habitats; Nelson et al., 2012), as these consumers would be using energetic resources from allochthonous sources not present within the spatial extent of the study area.

These *E*-scape maps allow users to identify key areas of the landscape in terms of their importance to the energetic resource use of a consumer. Researchers could apply *E*-scape maps to conservation, management, or restoration questions to identify areas of importance and to take management action. *E*-scape maps could improve habitat suitability models and integrate energetic resource distribution into existing modelling frameworks in combination with other parameters. Similar approaches have been applied to terrestrial ecosystems to investigate population and movement responses of large-bodied herbivores (Fryxell et al., 2020; Merkle et al., 2015). For example, the population viability of caribou was determined by modelling the response to resource distribution as well as other environmental and biological factors (Fryxell et al., 2020). Field observations of diet and grazing amount to quantify digestible energy content and combined with habitat cover maps were used to quantify the distribution of energy (Fryxell et al., 2020). Although effective, this technique requires extensive field work and data and is limited to terrestrial herbivores where the direct measurements of grazing can occur. Our method improves upon previous methods using stable isotope analysis, which provides a representation of the assimilated resources used by a consumer (Layman et al., 2012). With stable isotope analysis and Bayesian mixing models, estimates of consumer resource use are not limited to consumers where direct consumption can be observed (e.g. terrestrial herbivores), expanding the number of ecosystems and types of consumers that can be studied.

Our study links energetic resource distribution to population and energetic distribution of white shrimp, but if paired with tracking data *E*-scapes have the capability to further our understanding of consumer movement and foraging. Optimal foraging theory predicts that consumers will optimize net energy intake per unit time foraging and consumers would be expected to spend more time foraging in areas of greater resources (MacArthur & Pianka, 1966). Therefore, *E*-scape maps describe a 'null model' to test optimal foraging theory for a particular consumer. Tracking data can be used in combination with *E*-scapes to test foraging tactics in the context of energetic resource distribution (e.g. even vs. patchy distribution) or paired with other spatial environmental (e.g. salinity, temperature) or biotic factors (e.g. predation risk) to identify key drivers of movement and test hypotheses on deviations from OFT.

An emerging field in foraging ecology is animal resource tracking, which combines principles from landscape ecology and OFT (Abrahms et al., 2021). Studies in resource tracking have focused on consumers optimizing foraging by tracking temporal resource waves but have been limited to systems with a dominant energetic resource (Abrahms et al., 2019; Mosser et al., 2014). Because our approach quantifies which energetic resources a consumer is using with stable isotope analysis, it is an improvement on mapping energetic resource distribution. *E*-scapes will expand the systems where foraging patterns can be tested in the field, especially when resources do not have discrete waves and spatial and spatiotemporal variation dominate where resources are located, increasing our understanding of consumer foraging. *E*-scapes can be made at multiple time points using habitat maps from different periods or stable isotope analysis from different time points to indicate temporal variation in energetic resource availability. These temporal approaches could improve our understanding of seasonal variation in energetic resource availability and distribution, as well as increase understanding of how consumers will respond to large-scale landscape change by mapping the corresponding change in energetic resource distribution (Harris et al., 2020; Nelson et al., 2020). *E*-scapes can be used alone or in combination with existing models to test fundamental movement theory and improve habitat management and restoration practices.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

W.R.J., R.O.S., J.S.R. and J.A.N. designed the study; W.R.J. and J.C.D. collected and processed the samples; W.R.J. analysed the data; W.R.J. wrote the first draft with input from J.A.N.; All authors contributed substantially to revising the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.n02v6wwzr (James et al., 2021).

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SUPPORTING INFORMATION

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