

1 **Title:** *E*-scape: consumer specific landscapes of energetic resources derived from stable isotope
2 analysis and remote sensing

3
4 **Running Head:** *E*-scapes

5
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22

23 **Abstract**

24 Energy and habitat distribution are inherently linked. Energy is a major driver of the
25 distribution of consumers, but estimating how much specific habitats contribute to the energetic
26 needs of a consumer can be problematic. We present a new approach that combines remote
27 sensing information and stable isotope ecology to produce maps of energetic resources (*E*-
28 scapes). *E*-scapes project species specific resource use information onto the landscape to classify
29 areas based on energetic importance and successfully predict the biomass and energy density of a
30 consumer in salt marsh habitats in coastal Louisiana, USA. Our *E*-scape maps can be used alone
31 or in combination with existing models to improve habitat management and restoration practices
32 and have potential to be used to test fundamental movement theory.

33

34 **Key Words**

35 *E*-scape, Species distribution, Habitat cover, Stable isotopes, Remote sensing

36

37 **Introduction**

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

49 An accurate species specific representation of resource availability at the landscape scale is
50 required to test theories linking energy availability and species foraging or distribution. Spatial
51 primary production estimates (e.g. normalized difference vegetation index (NDVI), chlorophyll-a
52 concentration) and prey habitat suitability models are some of the approaches used to map
53 resource availability for consumers across landscape and regional spatial scales (i.e., from 10s to
54 100s of kilometers) (Mosser *et al.* 2014; Abrahms *et al.* 2019; Geary *et al.* 2020). For example, a
55 habitat suitability model of the dominant prey of brown pelicans (which included chlorophyll-a
56 concentration as a model parameter) was used to test how foraging behavior changed during the
57 breeding season (Geary *et al.* 2020). Landscape resource maps have typically focused on a single
58 resource or prey species, which is accurate when a consumer specializes on that resource.
59 However, in many cases, a consumer is integrating multiple resources from different habitat

60 types across the landscape. When a consumer is using multiple resources, mapping energy
61 distribution is more difficult because resources are not produced evenly amongst habitats and
62 consumers typically do not use all resources equally. Thus, in order to accurately represent
63 energy distribution, information is needed on where resources are being produced across the
64 landscape and the proportion each resource used by the consumer.

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

76 Stable isotope ratios, typically of $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, and $^{34}\text{S}/^{32}\text{S}$, have been used for decades to
77 determine the relative contributions of primary production sources in food webs (Peterson & Fry
78 1987; Fry 2007; Nelson *et al.* 2015). The general principle hinges literally upon the age-old
79 adage “you are what you eat”. Organisms consume food and rearrange the consumed material to
80 create new tissue. The stable isotope values, typically defined in del notation and expressed in
81 per mil, of primary producers are controlled by a number of physical and biological processes
82 that impart characteristic isotope values (Chanton *et al.* 1987; Farquhar *et al.* 1989). These

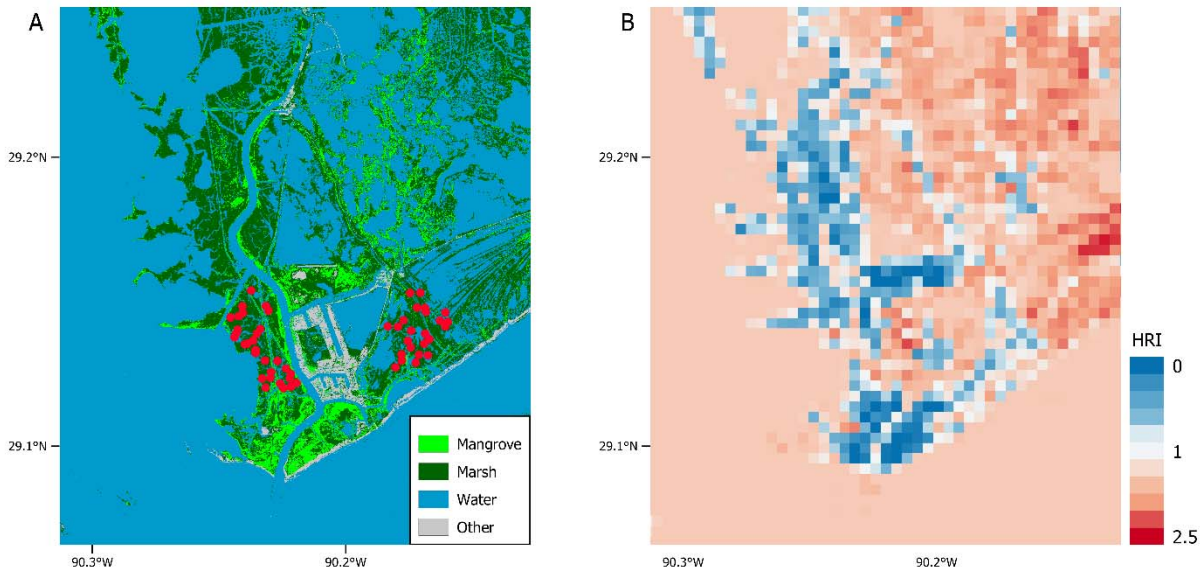
83 characteristic values can then be traced as they are assimilated in the food web using Bayesian
84 stable isotope mixing models (Stock *et al.* 2018). All plants fix carbon from the same
85 atmospheric reservoir of CO₂, currently -8 ‰ δ¹³C. For example, in coastal ecosystems carbon
86 stable isotope values can be most useful in differentiating between C3 plants, such as mangroves,
87 which fix carbon with a net fractionation of about -20 ‰ relative to the atmosphere and C4
88 plants, such as tropical and temperate salt tolerant grasses, which have a net fractionation of
89 about -5 ‰ (Fry 2007). In the same systems sulfate reduction in sediments has large
90 fractionation factor (30-70 ‰) and can be used as a strong indicator of pelagic vs. benthic
91 primary production (Chanton *et al.* 1987; Nelson *et al.* 2012).

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

100 **Methods**

101 Samples of white shrimp (*Litopenaeus setiferus*) were collected using a 1-m² drop sampler at
102 55 randomly selected sampling locations in Port Fourchon, LA (Figure 1A) (Zimmerman *et al.*
103 1984; Nelson *et al.* 2019). We collected all of the white shrimp within the drop sampler to
104 determine the abundance and biomass at each sampling location. Samples for stable isotope

105 analysis and bomb calorimetry were removed, placed on ice, and frozen upon returning to the
106 laboratory.



107
108 Figure 1. The Port Fourchon, LA A) habitat cover map showing the sampling locations of white shrimp (red points)
109 and B) the corresponding white shrimp *E*-scape map. Warmer colors (HRI values > 1) are better energetically for
110 white shrimp, and cooler colors (HRI values < 1) are worse energetically. The *E*-scape was generated at a cell size
111 of 400 m x 400 m (similar area to a 200 m circle)
112

113 Primary production source and animal tissue samples were frozen at - 20°C in the laboratory
114 until they could be processed for isotope analysis and bomb calorimetry. At each location, 5
115 individuals were pooled to create one composite sample. Samples were dried at 50 °C for 48
116 hours and ground. We determined the energy density (calories/g) of each sample using a Parr
117 6725 bomb calorimeter (Parr Instrument Company, Moline, IL, USA). We shipped samples to
118 the Washington State University Stable Isotope Core Facility for C, N, and S content and stable
119 isotope analysis. Carbon, nitrogen, and sulfur isotope values were calculated using the standard
120 formula (Fry 2007). PeeDee Belemnite (PDB), atmospheric nitrogen, and Canyon Diablo Troilite
121 (CDT) were used as the reference standards for C, N, and S, respectively. No C:N ratio was
122 above 3.5; therefore, no lipid correction was applied (Layman *et al.* 2007; Nelson *et al.* 2011).

123 Bayesian mixing models were run in R using the package MixSIAR (Stock *et al.* 2018) to
124 determine the relative basal resource contributions to shrimp at each sampling location. Each
125 model was run with a Markov chain Monte Carlo algorithm that consisted of three chains, chain
126 length of 3,000,000, burn-in of 1,500,000, and thin of 500 to ensure model convergence.
127 Corrections were made for the elemental concentration in each source, and the trophic
128 enrichment for each element was $C = 1.0 \pm 0.63$ (mean \pm sd), $N = 3.0 \pm 0.74$, and $S = 0.5 \pm 0.2$
129 (Phillips *et al.* 2014).

130 The *E*-scape of Port Fourchon, LA for white shrimp was made using the methods outlined in
131 Figure 2. High-resolution aerial imagery from <https://atlas.ga.lsu.edu> was used to generate a
132 habitat cover map of Port Fourchon, LA using the ‘Maximum Likelihood Classification’ tool in
133 ArcGIS (v 10.5). This tool uses supervised classification maximum likelihood to assign a habitat
134 class to each pixel of the image based on mean and variances of the habitat classes of the training
135 data set. Four habitat classes were used: water, marsh, mangrove, and other. The ‘marsh’ class
136 was comprised mainly of *Spartina alterniflora*, the ‘mangrove’ class was comprised mainly of
137 *Avicennia germinans*, and the ‘other’ class was comprised mainly beach area and port facilities.
138 Habitat cover areas were calculated using buffers with circle radius lengths of 50, 75, 100, 150,
139 200, 250, 300, 400, 500, 750, 1000, and 1500 m around the collection locations using the
140 ‘landscapemetrics’ packages in R (Hesselbarth *et al.* 2019). White shrimp have a home range
141 similar to that of the area of a 200 m radius circle (Rozas & Minello 1997; Webb & Kneib 2004;
142 Nelson *et al.* 2019). The other size buffers were chosen to test the sensitivity of the *E*-scape at
143 different scales. Edge habitat was calculated by measuring the linear distance between the water
144 and vegetation (marsh and mangrove) habitat cover classes and multiplying by 2 m to generate
145 an area. Edge area was calculated this way because benthic algae production is highest at the

146 marsh edge (Wainright *et al.* 2000; Litvin *et al.* 2018), and benthic microalgae have recently
147 been shown to have similar biomass at the edge habitat of both marsh and mangrove vegetation
148 (Walker *et al.* 2019).

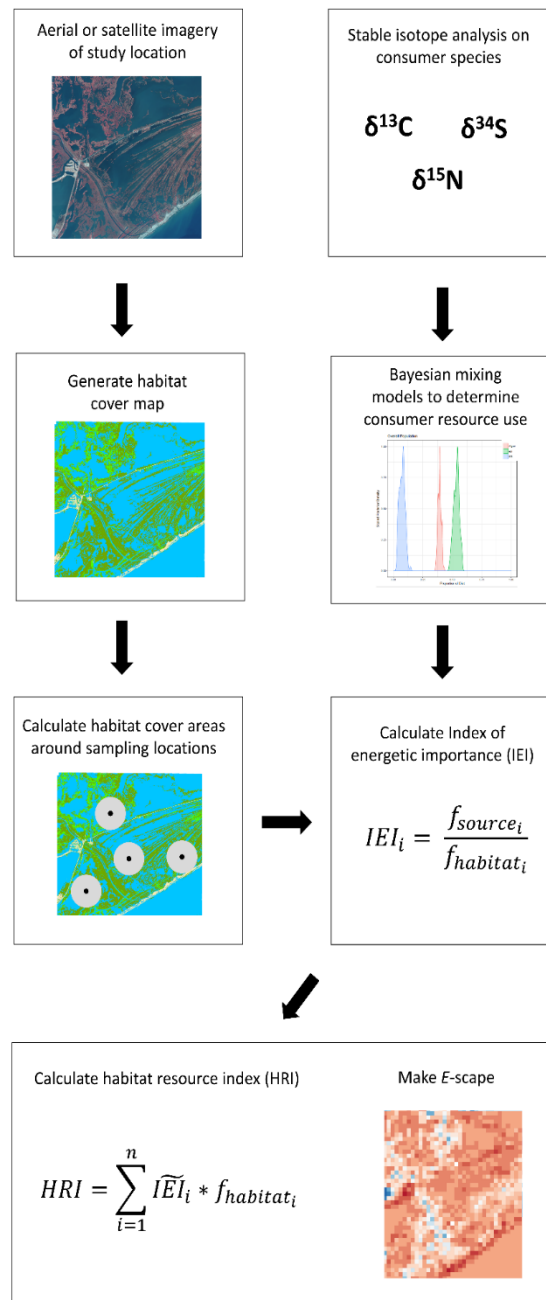


Figure 2. General methods for generating an E-scape

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

$$IEI_i = \frac{f_{source_i}}{f_{habitat_i}}$$

152 where f_{source_i} is the fraction of the contribution of source i to the total source use based on the
153 results of the mixing model and $f_{habitat_i}$ is the fraction of habitat i that produces source i to the
154 overall area within the movement range of the consumer (area of the circle around the sampling
155 point). An example of resource/habitat combination is amount of *Spartina alterniflora* derived
156 production and the cover area of *S. alterniflora* marsh habitat. IEI values were calculated for
157 phytoplankton/water, *Spartina*/marsh, and benthic algae/edge source/habitat combinations. The
158 mangrove habitat source combination was not used in the analysis because resource use of
159 mangrove was < 0.01 . Each IEI is a measurement of how much energy of a resource a consumer
160 is derived from relative to the amount of habitat that produces that resource where the consumer
161 is foraging. An IEI around one means that the consumer is using a resource (f_{source_i}) around the
162 same amount as the proportion of the habitat that produces that resource relative to total area
163 where that consumer is foraging over. An IEI greater than one means that the consumer is using
164 that source more than expected based on the proportion of that habitat in the total foraging area,
165 while the opposite is true for an IEI below one.

166 IEI values were combined with habitat cover areas to calculate the habitat resource index
167 (HRI). HRI was calculated with the following formula:

$$HRI = \sum_{i=1}^n \widetilde{IEI}_i * f_{habitat_i}$$

168 where \widetilde{IEI}_i is the median of the IEI for the source/habitat combination i and $f_{habitat_i}$ is the
169 fraction of habitat i to the overall area within the movement range of the consumer. HRI is an
170 index that represents a relative measurement of the quality of the habitats for producing the
171 resources used by the consumer based on stable isotope analysis. An HRI value of 1 means that
172 the area is producing the average amount of resources for the consumer. HRI values > 1 mean
173 that the area is better for producing resources (i.e. more energy) for the consumer and the
174 opposite is true for HRI values < 1 (Figure 1). The minimum possible HRI = 0, and the
175 theoretical maximum for HRI is infinity, although it is very unlikely that this value will occur in
176 nature because f_{source_i} and $f_{habitat_i}$ range between 0-1. Therefore, a unit of change is not linear
177 for HRI, and $\log(\text{HRI})$ should be used for linear modeling purposes so that unit change is the
178 similar throughout the possible range of values.

179 One HRI value was calculated for each sampling location for the area enclosed within a
180 circular buffer with the equation above. HRIs were calculated within a circular buffer with a
181 radius length of 200 m based on field movement ranges of white shrimp in the field (Rozas &
182 Minello 1997; Webb & Kneib 2004; Nelson *et al.* 2019). HRI values were also calculated at 50,
183 75, 100, 150, 250, 300, 400, 500, 750, 1000, and 1500 m radius circles around the sample points
184 to test for the effect of scale. The HRI values were calculated using the mean IEIs that were
185 calculated at the same scale (i.e. the IEIs calculated at 100 m were used in the calculation of the
186 HRI at 100 m). A GLM with a gaussian error was used to test the relationship between $\log(\text{HRI})$
187 and energy density (cal/g). GLMs with a gamma error and log link function were used to test the
188 relationship between HRI and biomass, abundance, total calories (cal/g * biomass), and mean
189 size (biomass/abundance). For each GLM outliers were removed if the value was outside of 1.5
190 \pm the interquartile range. All analyses were done in R (R Core Team 2020).

191 **Results**

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

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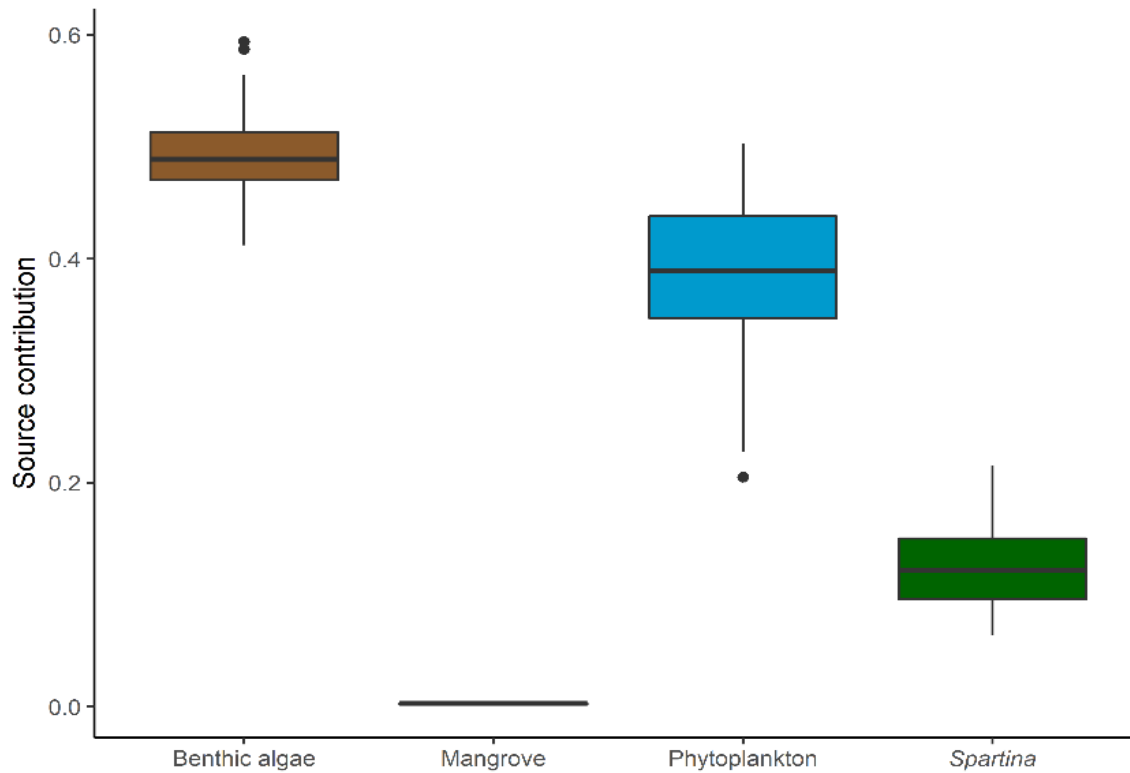


Figure 3. Bayesian mixing model results for white shrimp in Port Fourchon, LA.

196 The index of energetic importance (IEI) values are a representation of how much the white
 197 shrimp are using a resource relative to the amount of habitat that produces that resource (Table
 198 1). Edge had consistently the highest IEI across all scales, with much smaller IEI values for both
 199 water and marsh (Table 1). Edge IEI values were highest at the smallest scale and declined until
 200 the 300 m radius, the lowest IEI value, where it increased as scale increased. Water IEI values
 201 were highest at the smallest scale and decreased as scale increase. Marsh IEI values were lowest
 202 at all scales of the three habitats and increased in value as scale increased.

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

Size	Edge IEI (IQR)	Water IEI (IQR)	Marsh IEI (IQR)	HRI (mean \pm SD)
50	11.27 (6.61-28.12)	3.02 (1.03-14.35)	0.18 (0.14-0.25)	1.38 \pm 0.90
75	11.00 (6.91-14.13)	1.72 (1.04- 4.71)	0.19 (0.15-0.26)	1.16 \pm 0.57
100	9.19 (6.54-14.38)	1.48 (1.01- 2.72)	0.20 (0.15-0.27)	1.07 \pm 0.42
150	8.50 (6.66-12.97)	1.36 (0.89- 1.87)	0.21 (0.17-0.27)	1.07 \pm 0.36
200	8.19 (6.72-11.26)	1.26 (0.98- 1.75)	0.21 (0.18-0.26)	1.04 \pm 0.32
250	8.28 (6.48-10.79)	1.29 (0.98- 1.69)	0.22 (0.18-0.25)	1.07 \pm 0.30
300	8.16 (6.58-10.49)	1.20 (0.92- 1.52)	0.21 (0.18-0.26)	1.04 \pm 0.26
400	8.38 (6.95-10.36)	1.14 (0.90- 1.37)	0.22 (0.19-0.27)	1.03 \pm 0.22
500	8.42 (7.02-10.89)	1.10 (0.85- 1.34)	0.24 (0.18-0.27)	1.02 \pm 0.20
750	9.16 (7.29-11.34)	0.96 (0.78- 1.12)	0.25 (0.18-0.30)	1.02 \pm 0.14
1000	9.38 (7.84-11.54)	0.87 (0.74- 1.06)	0.27 (0.20-0.34)	0.99 \pm 0.11
1500	9.92 (8.33-11.87)	0.79 (0.69- 0.98)	0.31 (0.23-0.38)	0.99 \pm 0.11

208
 209 Habitat resource index (HRI) values at the 200 m scale were 1.04 ± 0.32 (mean \pm SD) around
 210 the sampling locations (Table 1). HRI values are a relative metric of quality of the habitats for
 211 producing resources used by the white shrimp and were highest in areas that contained the most
 212 edge habitat (Figure 1). There was a significant relationship between HRI value and body size (t -
 213 value = 4.8, $p < 0.001$), abundance (t -value = 2.5, $p = 0.018$), biomass (t -value = 5.4, $p < 0.001$),
 214 and total calories (t -value = 5.1, $p < 0.001$) at the 200 m scale (Figure 4, Table S1). The

215 relationship between HRI values and energy density (calories/g) was not significant ($p > 0.05$).

216 For the other scales, the relationship between HRI values and body size was significant ($p <$

217 0.05) at intermediate scales (100 – 750 m, Table S1). At the 150-250 m scales, there was a

218 significant relationship with HRI values and abundance (Table S1). There was a significant

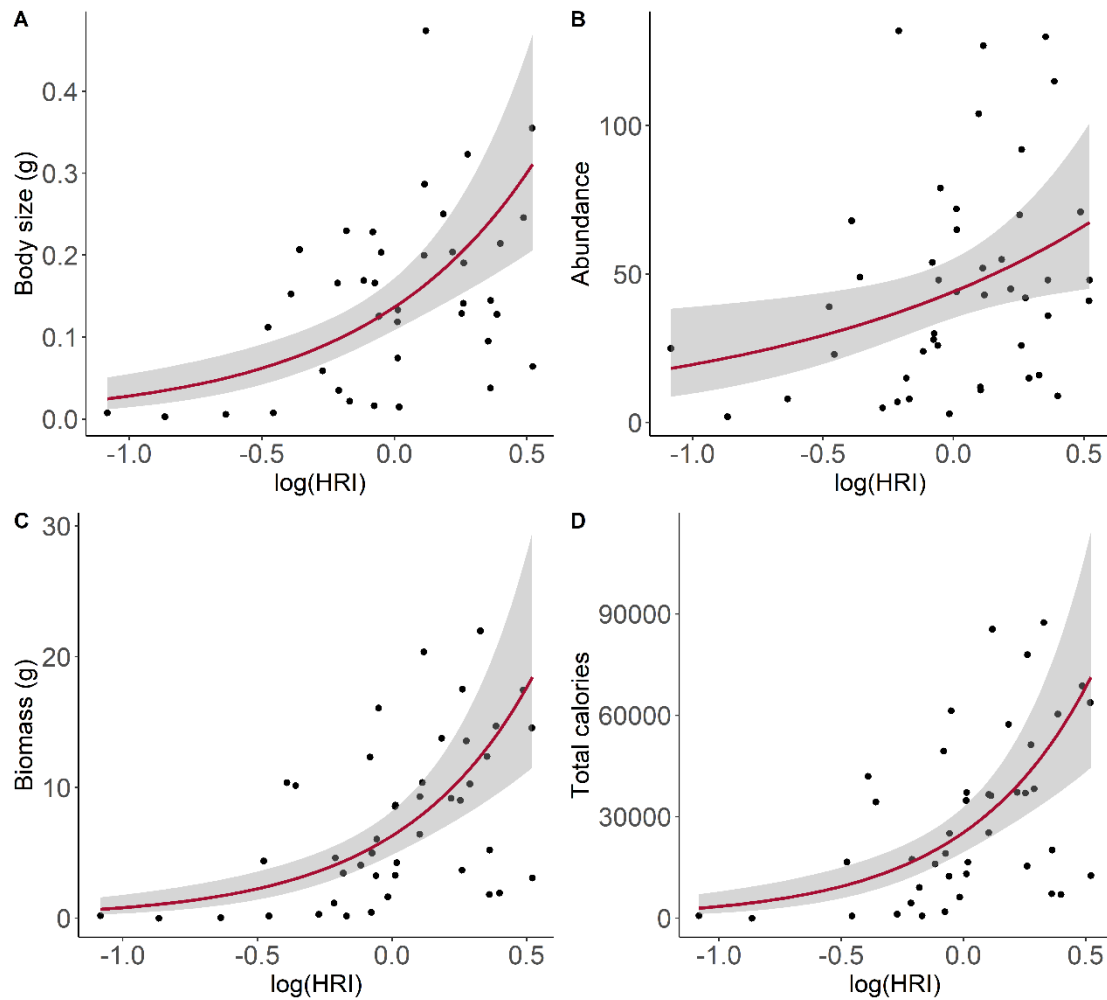
219 relationship ($p < 0.05$) between HRI value and biomass for all but the 1500 m scale. The same

220 was true for total calories (Table S1). There was no significant relationship between HRI value

221 and Calories/g at any scale.

222

223



224

225 Figure 4. The relationship between habitat resource index and white shrimp A) body size, B) abundance, C)
226 biomass, and D) total calories. HRI values were calculated within a 200 m radius circle around sampling locations.
227

228 Discussion

229 Our results demonstrate that *E*-scapes can predict the spatial distribution of biomass and
230 energetic density of a consumer by combining spatial habitat and resource use data (Figure 4).
231 White shrimp size, abundance, biomass, and total calories increased as the habitat resource index
232 increased across the marsh seascape (Figure 4). Individual white shrimp energy density (cal/g)
233 was not related to energy distribution. These results are supported by previous work that showed

234 white shrimp energy density did not change depending on the habitat type of the shrimp (Nelson
235 *et al.* 2019).

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

246 The index of energetic importance (IEI) represents how much a consumer is using a resource
247 relative to the amount of habitat that is producing that resource. White shrimp are derived of
248 49% benthic algae and 38% phytoplankton, but since there is much less edge habitat (the habitat
249 where benthic algae is produced), the IEI for edge is almost an order of magnitude larger than the
250 IEI for water (Table 1). Therefore, the habitats that contain the most edge habitat are of the
251 highest energetic importance for white shrimp (Figure 1). The IEI for marsh is < 1 at all scales
252 indicating that white shrimp use energetic resources from the marsh at a lower rate than their
253 availability in the system (Table 1). Although areas that contain a high amount of marsh habitat
254 are less favorable energetically than the average habitat ($HRI < 1$), these habitats are still
255 producing energy being used by white shrimp and are more energetically favorable than areas of
256 high mangrove habitat (which white shrimp are not using as an energy source, Figure 3,(Nelson

257 *et al.* 2019). Thus, the maps can differentiate between habitats suitable to occupy vs habitats that
258 are producing energy.

259 In our calculation of HRI and IEI values, the fraction of habitat ($f_{habitat_i}$) is based on the
260 area of habitat cover. This calculation assumes that all areas of a given habitat type have an equal
261 chance of producing a resource. For example, we make the assumption that all areas of water in
262 our habitat cover map (Figure 1A) have an equal chance of producing phytoplankton. This
263 assumption may not be acceptable in all applications, especially when applying these methods to
264 consumers that have very large foraging ranges (Geary *et al.* 2020). For these cases,
265 modifications can be made to $f_{habitat_i}$ to incorporate the spatial differences in production such as
266 incorporating chlorophyll-a maps or lidar data to incorporate the three dimensional structure of
267 the habitats. One limitation to our approach is that phytoplankton is produced in three
268 dimensions, unlike the other sources, and we are presently not able to account for the three-
269 dimensional structure of water across the seascape with the available data. Accounting for water
270 volume will be especially important in systems that are stratified or in which phytoplankton
271 production is integrated over a significant depth (Cole & Cloern 1984). One way to incorporate
272 volume into $f_{habitat_i}$ is to modify by accounting for the depth of the habitat in relation to the
273 euphotic zone of the system (Cole & Cloern 1984). Unfortunately, this type of data is not always
274 available and was not available in our study area. Other modifications could include parameters
275 that include temporal differences in access to habitats which can be major drivers of foraging
276 behaviors of consumers (Nelson *et al.* 2015).

277 These *E*-scape maps allow users to identify key areas of the landscape in terms of their
278 importance to the energetic requirements of a consumer. Researchers could apply *E*-scape maps
279 to conservation, management, or restoration questions to identify areas of importance and to take

280 management action. In combination with other parameters, *E*-scape maps could improve habitat
281 suitability models and integrate energetics into existing modelling frameworks. Similar
282 approaches have been applied to terrestrial ecosystems to investigate population and movement
283 responses of large-bodied herbivores (Merkle *et al.* 2015; Fryxell *et al.* 2020). For example, the
284 population viability of caribou was determined by modeling the response to resource distribution
285 as well as other environmental and biological factors (Fryxell *et al.* 2020). Field observations of
286 diet and grazing amount to determine digestible energy content and combined with habitat cover
287 maps were used quantify the distribution of energy (Fryxell *et al.* 2020). Although effective, this
288 technique requires extensive field work and data, and is limited to terrestrial herbivores where
289 the direct measurements of grazing can occur. Our method improves upon previous methods by
290 using stable isotope analysis, which provides a representation of the assimilated energy for which
291 a consumer is derived (Layman *et al.* 2012). With stable isotope analysis and Bayesian mixing
292 models, estimates of consumer resource use are not limited to consumers where direct
293 consumption can be observed (e.g. terrestrial herbivores), expanding the number of ecosystems
294 and types of consumers that can studied.

295 Our study links energy to population and energetic distribution of white shrimp, but if paired
296 with tracking data *E*-scapes have the capability to further our understanding of consumer
297 movement and foraging. Optimal Foraging Theory predicts that consumers will optimize net
298 energy intake per unit time foraging and consumers would be expected to spend more time
299 foraging in areas of greater resources (MacArthur & Pianka 1966). Therefore, *E*-scape maps
300 describe a “null model” to test Optimal Foraging Theory for a particular consumer. Tracking
301 data can be used in combination of *E*-scapes to test foraging strategies in the context of energy
302 distribution (e.g. even vs patchy distribution) or paired with other spatial environmental (e.g.

303 salinity, temperature) or biotic factors (e.g. predation risk) to identify key drivers of movement
304 and test hypotheses on variations of OFT. Recent studies have focused on consumers optimizing
305 foraging by tracking temporal resource waves but have been limited to systems with discrete
306 waves of a dominant energy source (Mosser *et al.* 2014; Abrahms *et al.* 2019). Because our
307 approach quantifies which energy sources a consumer is using, it is an improvement of mapping
308 energy distribution. *E*-scapes will expand the systems where foraging patterns can be tested in
309 the field, especially when resources do not have discrete waves and spatial and spatiotemporal
310 variation dominate where resources are located, expanding our understanding of consumer
311 foraging. *E*-scapes can be used alone or in combination with existing models to test fundamental
312 movement theory and improve habitat management and restoration practices.

313

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322

323 **Authorship:** WRJ, ROS, JSR and JAN designed the study. WRJ and JD collected and processed
324 samples. WRJ analyzed the data. WRJ wrote the first draft with input from JAN. All authors
325 contributed substantially to revising the manuscript.

326

327 **Data Accessibility:** Data will be archived in an appropriate public repository and the data DOI

328 will be included at the end of the article.

329

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432 **Supporting information.** Model results for GLMs testing the relationship between the log(HRI) and different biomass and energy
 433 measurements of for white shrimp at each scale tested. Significant ($p < 0.05$) model results in bold. T = *t*-vale, AIC = Akaike
 434 information criterion
 435

Size	Size			Abundance			Biomass			Calories/g			Total calories		
	T	P value	AIC	T	P value	AIC	T	P value	AIC	T	P value	AIC	T	P value	AIC
50	1.0	0.317	-68.8	0.3	0.780	436.8	2.7	0.009	265.6	0.3	0.733	698.2	2.6	0.013	951.6
75	1.5	0.132	-69.6	1.2	0.219	435.6	2.6	0.012	265.4	0.6	0.545	697.9	2.3	0.024	951.9
100	1.8	0.078	-70.5	1.4	0.158	435.1	2.2	0.031	266.1	1.1	0.292	697.2	2.0	0.049	952.3
150	4.1	0.000	-76.1	2.4	0.019	432.5	4.5	0.000	260.0	0.5	0.627	698.1	4.3	0.000	946.8
200	4.8	0.000	-78.6	2.5	0.018	432.3	5.4	0.000	256.9	0.6	0.555	698.0	5.1	0.000	943.7
250	4.2	0.000	-76.9	2.0	0.049	433.6	5.0	0.000	258.0	0.8	0.413	697.6	4.9	0.000	944.3
300	3.2	0.003	-73.9	1.6	0.126	434.9	4.1	0.000	261.5	1.0	0.324	697.3	4.0	0.000	947.3
400	2.8	0.007	-72.9	1.2	0.232	435.7	3.8	0.001	262.9	0.8	0.408	697.6	3.7	0.001	948.6
500	3.0	0.005	-72.9	0.9	0.382	436.2	3.8	0.000	262.8	0.9	0.389	697.5	3.8	0.001	948.2
750	2.4	0.020	-71.1	0.0	0.995	436.9	3.0	0.004	265.3	0.8	0.453	697.7	2.9	0.006	950.9
1000	2.0	0.054	-70.0	-0.8	0.416	436.3	2.2	0.037	267.5	1.1	0.267	697.0	2.1	0.046	953.2
1500	1.2	0.225	-68.9	-1.1	0.277	435.9	1.0	0.302	269.0	1.4	0.154	696.2	1.0	0.303	954.6

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