

1 Comparing shallow seagrass versus fringing marsh habitat use by nekton
2 juvenile recruits with “incomparable” fishing gear in the northern Gulf
3 of Mexico
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18

19 **Abstract**

20 Shallow coastal systems act as nursery habitat for many species of fish and macroinvertebrates.
21 Juveniles of these species may show selective use of certain habitat types over others, but the
22 degree of such selectivity is not well studied for many species. Analysis of habitat selectivity is
23 often hindered by inherently different gear types used in the habitats examined, which may not
24 allow for direct comparison between the habitats. Here we carry out nekton catches in the
25 fringing marsh, using fyke nets, and in the adjacent seagrass habitat, using trawls, in the northern
26 Gulf of Mexico to assess the relative use of the two habitats by the juveniles of six widespread
27 important species. To resolve issues of gear comparability between fyke nets and trawls, we
28 develop a habitat use index (HUI_5). The results reveal a consistent trend where, in relation to
29 pinfish, speckled sea trout shows slightly higher (from 8.4 to 66.9 times); American silver perch
30 and brown shrimp show moderately higher (from 2.3 to 369.4 times); and blue crab and white
31 shrimp show greatly higher (from 90.6 to 2366.4 times) use of marsh over seagrass habitat. Thus,
32 while similar in direction, differences in use of marsh over seagrass habitat in relation to pinfish
33 was more pronounced in some sites. We propose an index that can resolve issues of gear
34 comparability and improve our understanding of coastal habitat selectivity by fish and
35 macroinvertebrates.

36 **1. Introduction**

37 Shallow coastal systems have been long coined “nursery systems” given their importance
38 as recruitment grounds for many species of fish and macroinvertebrates (McDonald et al. 2016,
39 Hollweg et al. 2019). These systems may be very shallow, ranging in depth from 0.2 to 2 meters.
40 Along with species that reside in shallow coastal systems throughout their entire life cycles,
41 many species of fish and macroinvertebrates that live in deeper waters farther from the coastline
42 as adults recruit to shallow coastal systems (Able 2005, Sheaves et al. 2015). Many of such
43 species recruit to structured habitats, such as seagrass beds, oyster reefs, fringing marshes, and
44 mangroves, in shallow coastal systems owing to enhanced refuge and food availability (Heck et
45 al. 2003, Minello et al. 2003, Lefcheck et al. 2019, zu Ermgassen et al. 2021). In these habitats,
46 juveniles find numerous refugia to hide from predators given the habitat’s structural complexity.
47 The leaf canopy and uneven bottom of seagrass beds, complex architecture of oyster reefs,
48 fringing edge and platform of marshes, and intertwined networks of pneumatophores and stems
49 in mangroves provide high levels of shelter and refuge for recruiting juveniles (Castellanos and
50 Rozas 2001, Shervette et al. 2011, Scheffel et al. 2018). Likewise, these habitats, owing to their
51 high levels of primary productivity, nurture prolific resident populations of invertebrates that
52 represent abundant prey for recruiting juveniles (McIvor and Odum 1988, Cebrian 2002).

53 While typically high, the specific nature and magnitude of refuge and food provision
54 varies across seagrass beds, oyster reefs, fringing salt marshes, and mangroves. Some of these
55 habitats may be fully or mostly subtidal, and others intertidal, which may restrict access for some
56 species. The juveniles of some species may find more effective refuge in flexible, soft substrate
57 such as seagrass leaf canopies, whereas the juveniles of other species may find more effective
58 refuge in hard substrate such as oyster reefs (Shervette and Gelwick 2008, Flaherty-Walia et al.

59 2015). The diversity and productivity of epiphytes, a nutritional food source typically preferred
60 by first-order consumers such as crustaceans and gastropods, may vary largely across coastal
61 habitats (Rodriguez and Stoner 1990, Anton et al. 2011), which in turn may generate differences
62 in the types and levels of prey availability for recruiting juveniles across these habitats.

63 Based on differences in the quality and quantity of refuge and food provision among
64 coastal habitats, we can also expect differences in their selectivity by juveniles of species cued
65 for specific types and levels of refuge and food. For instance, recruiting juveniles of speckled sea
66 trout (*Cynoscion nebulosus*) appear to show high preference for seagrass beds in relation to other
67 coastal habitats (McMichael and Peters 1989). In contrast, McDonald et al (2016) found minor
68 differences in the abundance of blue crab (*Callinectes sapidus*) juveniles in the submerged
69 landscape adjacent to the marsh fringe between shallow lagoons with high or little (even none)
70 seagrass cover in the northern Gulf of Mexico, but all of them with much fringing marsh. Based
71 on these results, they suggested the juveniles of this species show little preference for seagrass
72 beds over fringing marshes as habitat grounds.

73 A number of gear types are used to capture juvenile nekton in shallow coastal systems,
74 including seines, trawls, fyke nets, block nets, drop samplers, cast nets, and benthic traps
75 (Hollweg et al. 2019). These gear types have different nature, characteristics, function, and
76 applications. As a result, some of these types are better suited for specific habitats. For instance,
77 seines and trawls are often used in seagrass beds, fyke nets are used in the marsh platform and
78 fringe, and cast nets are used in small tributaries and creeks hardly accessible with other gear
79 types. Habitat selectivity between two habitats is inferred from values of nekton abundance
80 expressed as number of individuals per unit effort, water volume, or area bottom in the two
81 habitats being compared. If such values are consistently higher in habitat A than habitat B for a

82 given species, the inference can be made that the species prefers the former over the latter
83 habitat.

84 However, it is sometimes not possible to derive abundance values as number of
85 individuals per unit effort, water volume, or bottom area from the catches obtained with the gear.
86 Two pieces of information are needed to derive such abundance values. First, we need to know
87 the total effort, or the water volume or bottom area covered with the capture so we can
88 standardize catches and express them on a per unit effort, water volume or bottom area basis.
89 Second, we need to know the gear efficiency. Gear efficiency consists of two components, i.e.,
90 capture efficiency and recovery efficiency (Hollweg et al. 2019, Cebrian et al. 2020). Capture
91 efficiency corresponds to the fraction of size-apt (i.e., size range that can be captured by the gear
92 given its characteristics) individuals that are actually captured with the gear in the sampled area,
93 and recovery efficiency to the fraction of individuals captured in the gear that are actually
94 recovered and recorded. When these two pieces of information are not known for a given gear,
95 values of individual abundance per unit effort, water volume, or bottom area cannot be derived
96 with the gear (Rozas and Minello 1997, Baker and Minello 2011) and, thus, inferences of habitat
97 selectivity based on such values cannot be carried out with that gear. This is not an uncommon
98 problem, which limits our understanding of nekton use of shallow coastal systems.

99 Here we propose a method to get around the problem of gear incomparability when
100 values of individual abundance per unit effort, water volume, or bottom area cannot be derived
101 for one or both of two gears compared. The method is based on the derivation of a habitat use
102 index (HUI_S), which allows for comparison between habitats from an established benchmark
103 despite not knowing the values of individual abundance per unit effort, water volume, or bottom
104 area. We further apply the index to the examination of fringing marsh over seagrass habitat

105 selectivity by the juveniles of six important species in the northern Gulf of Mexico. The results
106 contribute to our understanding of the nursery role of coastal ecosystems, which is key for the
107 management of fisheries that rely on coastal ecosystems particularly in the face of global
108 anthropogenic stressors and coastal change.

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111 **2. Methods**

112 **2.1 Study Sites**

113 We sampled shallow seagrass and adjacent salt marsh habitats in three sites in Grand
114 Bay, Alabama (USA): Long Island, Marsh Island, and West Point-aux-Pins (Figure 1). Salinity
115 at these study sites oscillates between 5 and 20 ppt (Anton et al. 2011). At each site, subtidal
116 patchworks of bare mud, widgeon grass (*Ruppia maritima*), and shoal grass (*Halodule wrightii*)
117 paralleled adjacent fringing marsh. In the Gulf of Mexico, these seagrass species show a
118 characteristic successional pattern (Dunton 1990, Anton et al. 2009). Widgeon grass biomass
119 typically peaks in spring, with natural senescence occurring in summer after flowering. Shoal
120 grass shows more sustained biomass during the year, typically reaching its peak in late-summer.
121 Leaf density in the study area ranges from ca. 0 to 8,000 leaves/m² for widgeon grass, and from
122 ca. 2,000 to 15,000 leaves/m² for shoal grass (Anton et al. 2009).

123 Due to erosion, the seaward (i.e., facing the open Gulf of Mexico) shorelines of Long
124 Island and Marsh Island, oriented approximately east-west, consisted primarily of escarpments
125 ranging from 0.2 to 0.8 m in height with short-form *Spartina alterniflora* on top of the
126 escarpment and its rhizome and roots protruding through the escarpment wall. The leeward (i.e.,
127 facing the sound) shorelines of the islands were less escarped and dominated by black needlerush
128 (*Juncus roemarianus*). In this study we took our samples on the seaward side of the islands. The

129 shoreline at West Point-aux-Pins, oriented approximately south-north, was stable with no net
130 erosion and consisted of a wide band of tall-form *S. alterniflora* gradually transitioning into a
131 narrow band of short-form *S. alterniflora*.

132 Densities of *S. alterniflora* were measured at each site in August, September and October
133 of 2010. Samples at West Point-aux-Pins only included tall-form *S. alterniflora* since it was
134 overwhelmingly the dominant form in that marsh. Plant density did not vary significantly among
135 sampling dates within sites. It did not differ significantly between Long Island and Marsh Island
136 (mean densities \pm SE across dates were 61.7 ± 9.7 plants/m² and 46.9 ± 1.9 plants/m²,
137 respectively), but it was higher at both sites in comparison with West Point-aux-Pins (10.7 ± 1.7
138 plants/m²).

139 **2.2 Nekton Sampling**

140 Sampling was conducted between March 2010 and May 2012 at approximately monthly
141 intervals, except for winter months (December 2010-February 2011; December 2011-January
142 2012).

143 **2.2.a Marsh and seagrass nekton sampling**

144 Tidal fyke nets constructed of seine netting with 0.64-cm mesh were used to sample
145 marsh nekton. Each net enveloped 6 m of fringing marsh and stood 0.75 m tall. The front open
146 mouth of the net was positioned within 0.5 m seaward from the escarpment in Long Island and
147 Marsh Island, and within 0.5 m seaward from the tall-form *S. alterniflora* band in West Point-
148 aux-Pins. The back edge of the net extended 3.25 m seaward and contained a 1m x 1m bag
149 where organisms were trapped. The nets are designed to capture nekton that utilize the marsh
150 edge and platform during flood tide and recede to the adjacent subtidal area on the subsequent

151 falling tide (Hettler 1989, Moody et al. 2013). Three nets were haphazardly positioned along the
152 shoreline at each site on each sampling date (i.e., nine nets per sampling date), keeping a
153 minimum distance of 20 m between nets at the same site. The nets were set up during low tide
154 and left in place for approximately 24 hr.

155 Nekton in the adjacent seagrass beds was sampled with a 5-m otter trawl (2.0 cm body
156 mesh; 0.6 cm bag mesh; 0.3x0.7m doors) towed behind a small research vessel traveling between
157 3-4 km hour⁻¹. Three, 2-minute tows were conducted haphazardly in water depths < 1m at each
158 site on each sampling date (i.e., nine trawls per sampling date).

159 Upon collection with the fyke nets or trawls, organisms were immediately placed on ice
160 and transported to the laboratory where they were frozen. Upon thawing, they were identified to
161 species, enumerated, and re-frozen for individual length measurements at a later date.

162 **2.2.b Sampling pairing**

163 Our initial plan was to pair up the marsh and seagrass samples within the same tidal
164 cycle. That is, we intended to sample marsh nekton over a tidal cycle and seagrass nekton during
165 the high tide period in that cycle (i.e., from ascending mid-tide to descending mid-tide). We
166 purposely intended to sample seagrass nekton during the high tide period since that is a period
167 where nekton has highest accessibility to the marsh, thereby offering a more accurate description
168 of nekton use of marshes in relation to seagrasses than if seagrass nekton is sampled at low tide
169 with limited accessibility to the marsh. However, given the mainly diurnal nature of the tides in
170 the study sites, following such as a sampling design (i.e., setting up the fyke nets at peak low tide
171 and trawling within the high tide period of that cycle) would have required to either set up and
172 retrieve the fyke nets or do the trawling at nighttime on many sampling dates, which we found
173 logistically undoable.

174 Thus, we planned out the study to do both the fyke net deployment/retrieval and trawling
175 during day light. Namely, depending on the specific tidal cycle, we set up the fyke nets at peak
176 low tide in the morning and trawled afterwards during ascending low tide, or we set up the fyke
177 nets at peak low tide in the late afternoon or early evening and trawled the following day before
178 fyke net retrieval during descending low tide. We accomplished this in six out of the total fifteen
179 sampling rounds in the study. Logistic constraints, however, forced us to sample marsh and
180 seagrass nekton on different days (i.e., different tidal cycles) for the rest of sampling rounds.
181 Specifically, in six rounds marsh and seagrass sampling occurred between two and three days of
182 one another, and in three rounds marsh and seagrass sampling occurred between five and eight
183 days of one another, with all three sites being sampled on the same day for each habitat. This
184 time lag between marsh and seagrass samples was definitely not long enough to incur into a
185 change in the tidal diel pattern (i.e., from peak low tide during daytime to peak low tide during
186 nighttime), and thus we always carried out our seagrass sampling during a period equivalent to
187 what we would have done the day of fyke net sampling.

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189 **2.3 Analyses of relative habitat use**

190 In our study, we used fyke nets to capture nekton that access the flooded marsh and
191 trawls to capture nekton in the adjacent seagrass beds. However, the mechanisms through which
192 these gear types capture nekton are very different, i.e., tidal water movement in fyke nets and
193 active pulling in trawls. For trawls, we can calculate the water volume or bottom area covered,
194 and gear efficiency values also exist for this gear (Hollweg et al. 2019, Baker and Minello 2011).
195 Thus, for trawls we can calculate nekton abundance on a per unit effort, water volume, or bottom
196 area basis. However, this is not the case for fyke nets. First, it is utterly difficult to derive

197 realistic estimates of the water volume drained through the fyke net during ebbing tide, or the
 198 marsh bottom area covered by the water that drains through the fyke net (Moody et al. 2013,
 199 Sharma et al 2016). Second, gear efficiency is not known for fyke nets (Hollweg et al. 2019,
 200 Cebrian et al. 2020). Thus, unlike trawls, we cannot calculate nekton abundance on a per unit
 201 effort, water volume, or bottom area basis for fyke nets. As a result, direct comparisons of nekton
 202 abundance per unit effort, water volume or bottom area between these two gears as a proxy for
 203 habitat selectivity between marshes and seagrasses are not possible.

204 To find a way around this problem, we propose a habitat use index (HUI_S) as a means to
 205 infer habitat selectivity from the catch numbers. The index is calculated as:

$$206 \quad HUI_S = \frac{\left(TC_{marsh} / TC_{seagrass} \right)_S}{\left(TC_{marsh} / TC_{seagrass} \right)_{S \text{ lowest ratio}}}$$

207 Equation 1

208 where $\left(TC_{marsh} / TC_{seagrass} \right)_S$ is the ratio of total capture (i.e., total number of individuals
 209 captured) in the marsh to total capture in the seagrass over the study period for the given species;
 210 and $\left(TC_{marsh} / TC_{seagrass} \right)_{S \text{ lowest ratio}}$ is the ratio of total capture in the marsh to total capture in
 211 the seagrass over the study period for the species with the lowest ratio.

212 Here we apply the index to a situation with different gear in each of two habitats where
 213 we know the water volume or the bottom area covered, and the efficiency, for one of the gears
 214 but we do not know any of this information for the other gear. The index can also be applied
 215 when we know the water volume or the bottom area covered, and the efficiency, for one of the
 216 gears, and the water volume or the bottom area covered, but not the efficiency for the other gear;

217 we know the water volume or the bottom area covered for both gears, but not the efficiency for
218 any of the gears; we know the water volume or the bottom area covered by one gear, but no other
219 information; or we have no information about the water volume or the bottom area covered by
220 the gear, or efficiency, for none of the gears. The index can also be applied to situations where
221 we have the same gear in the two habitats, and we do not know the water volume or bottom area
222 covered by the gear; or we know the water volume or bottom area covered, but not the
223 efficiency, for the gear. This is because the terms corresponding to water volume or bottom area
224 covered, as well as gear efficiency, cancel each other out, resulting in Equation 1.

225 The index is a ratio of ratios, signifying how many more times a species is captured in the
226 marsh over the seagrass in relation to the species that is captured the least in the marsh over the
227 seagrass. This is equivalent to gauging the use of marsh over seagrass habitat by the given
228 species in relation to the species with the least use of marsh over seagrass habitat. For instance, a
229 value of 5 denotes the species in question uses marsh over seagrass habitat to a five-fold larger
230 extent than does the species with the least use. We calculated the index separately for each of
231 the three sites to examine how habitat selectivity by the juveniles of the species studied varied
232 across sites.

233

234

235 **3. Results**

236 **3.1 Species captured and examined**

237 We captured a total of 71,570 individuals encompassing 80 taxa for the entire project
238 (Table S1). Given the aim of this paper, we restricted our analysis to species that (1) recruit to

239 shallow coastal systems, and then large juveniles and small adults move to deeper waters; (2)
240 whose juveniles are cued for structure and, thus, recruit to structured habitats; and (3) were
241 abundant enough in our samples, for one or both habitats, to allow for robust habitat use
242 comparisons (i.e., habitat selectivity). Based on these criteria, the species examined here are blue
243 crab (*Callinectes sapidus*), brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus*
244 *setiferus*), American silver perch (*Bairdiella chrysoura*), pinfish (*Lagodon rhomboides*), and
245 spotted sea trout (*Cynoscion nebulosus*).

246 Individual length ranged from 1.6 to 130 mm for blue crab (carapace width); 8.1 to 98
247 mm for brown shrimp; 3.6 to 101.2 mm for white shrimp; 2.5 to 165 mm for American silver
248 perch; 17.4 to 180 mm for pinfish; and 14.3 to 93.2 mm for spotted sea trout (Table 2S). Indeed,
249 all the individual length measurements taken for brown shrimp, white shrimp, pinfish, and
250 spotted sea trout were within their juvenile size range, although those measurements varied
251 widely and included from very small juveniles to large juveniles. For blue crab and silver perch
252 only a tiny fraction of the individual length measurements may have corresponded to small
253 adults

254

255 **3.2 Temporal variation in catch**

256 Catches remained elevated throughout spring, summer, and fall for blue crab (Figure 2);
257 were highest in late spring and summer for brown shrimp (Figure 3); highest in summer for
258 white shrimp (Figure 4); highest again in late spring and summer for American silver perch
259 (Figure 5) and pinfish (Figure 6); and highest in late summer and early fall for spotted sea trout
260 (Figure 7).

261 3.3 Seagrass vs. fringing marsh HUI_S

262 Values of HUI_S varied widely within and across sites (Table 1). Namely, HUI_S ranged
263 from 1 to 2,366.4 in Long Island; from 1 to 94.8 in Marsh Island; and from 1 to 693 in West
264 Point-aux-Pins. Pinfish featured a HUI_S value of 1 in all three sites. In Long Island, HUI_S
265 increased from pinfish to spotted sea trout to American silver perch to brown shrimp to blue crab
266 to white shrimp. In Marsh Island, HUI_S increased from pinfish to spotted sea trout to brown
267 shrimp to American silver perch to blue crab to white shrimp. In West Point-aux-Pins HUI_S
268 increased from pinfish to American silver perch to spotted sea trout to brown shrimp to blue crab
269 to white shrimp. Thus, all other species examined featured larger use of fringing marsh over
270 adjacent seagrass habitat in relation to pinfish, with spotted sea trout, American silver perch and
271 brown shrimp varying slightly in their relative rankings across sites but with blue crab and white
272 shrimp maintaining the highest relative rankings. In addition, HUI_S varied largely across sites
273 within the same species, indicating large site-dependent differences in the extent of use of
274 fringing marsh over adjacent seagrass habitat by the species in relation to pinfish despite the
275 species' identical or similar ranking in the three sites.

276

277 4. Discussion

278 In this study we sought to assess the use of fringing marsh and adjacent seagrass beds by
279 recruiting juveniles of fish and macroinvertebrate species whose large juveniles and small adults
280 move to deeper waters away from those shallow systems. This is an important topic, yet
281 understudied, to understand the life cycle of such species, evaluate their dependence on different
282 kinds of shallow coastal habitats, and manage the species in view of global anthropogenic

283 change. We focus on three sites in the northern Gulf of Mexico and six species captured in
284 sufficient numbers to allow for sound comparison of fringing marsh over adjacent seagrass
285 habitat use, i.e., blue crab, brown shrimp, white shrimp, American silver perch, pinfish, and
286 spotted sea trout. All (or nearly all) the individuals captured for these species in our study were
287 juveniles (references for juvenile size are VanderKooy 2013 and Lycett et al. 2020 for blue crab;
288 Renfro and Brusher 1982 for brown and white shrimp; Grammer et al. 2009 for American silver
289 perch; Nelson 2002 for pinfish; and Brown-Peterson and Warren 2001 for spotted sea trout).
290 These species are wide-spread, play salient ecological roles as prey and predators, and, with the
291 exception of pinfish, constitute important commercial or recreational fisheries (Shipp 2012).

292 Our two years of monitoring reveal different recruitment periods for the juveniles of
293 these species, ranging from sustained recruitment through spring, summer and fall (blue crab) to
294 more restricted recruitment in either late spring and summer (brown shrimp, American silver
295 perch, and pinfish), summer (white shrimp), or late summer and early fall (spotted sea trout).
296 This timing is consistent with the species-specific spawning periods reported in the literature.
297 The entire process from spawning to hatching to larval transport and settlement into shallow
298 coastal systems to juvenile growth up to a size adequate for capture with our gear normally takes
299 between one and two months (Monczak et al. 2022). Accordingly, in all cases our catches
300 ramped up at a time falling between one and two months ahead from a time encompassed by the
301 spawning period reported for the species.

302 Namely blue crabs spawn from spring to fall (Hines 2007, VanderKooy 2013), and we
303 found high catches throughout spring, summer, and fall. Brown shrimp spawn from late summer
304 to spring (Renfro and Brusher 1982, Lassuy 1983), and our catches were highest in late spring
305 and summer. White shrimp spawning occurs from spring to fall (Renfro and Brusher 1982), and

306 we found our highest catches in summer. American silver perch spawning mostly takes place in
307 spring, possibly extending into summer (Grammer et al. 2009), and we obtained our highest
308 catches in late spring and summer. Pinfish spawning occurs from winter to early spring (Nelson
309 1998, McDonald et al. 2016), and our catches were highest in late spring and summer. Spotted
310 sea trout spawn from spring to summer (Rutherford et al. 1982, Brown-Peterson and Warren
311 2001), and our catches were highest in late summer and early fall. In addition, our catches
312 generally decreased drastically towards late fall for all six species, pointing to the migration of
313 large juveniles to deeper waters as temperature drops significantly. At any rate, the exact timing
314 for spawning can vary substantially within species, and the temporal oscillations in juvenile
315 catches observed here may well differ from those occurring in other locations and from those
316 occurring in other years within these locations.

317 Importantly, here we examine the use of fringing marsh over adjacent seagrass habitat by
318 juveniles of the six species studied in a situation where, due to gear limitations, we cannot
319 directly compare values of juvenile abundance per unit effort, water volume or bottom area
320 between the two habitats as a proxy for habitat selectivity. Ideally, gear for which values of water
321 volume or bottom area covered can be calculated, and also for which values of efficiency exist or
322 can be accurately estimated, should be employed to allow for direct comparison of nekton
323 abundance per unit effort, water volume or bottom area between habitats and inferences on
324 habitat selectivity by nekton (Paterson and Whitfield 2000, Baker and Minello 2011, Hollweg et
325 al. 2019). However, this is not always possible because such information cannot be obtained for
326 some gear best suited for certain types of habitat and physical conditions, for instance fyke nets
327 for sampling nekton that use the marsh edge and platform during flooding tide, or cast nets to
328 sample nekton in small water basins inaccessible with other gear, among others (Hollweg et al.

329 2019, Cebrian et al. 2020). Here we present an index, the habitat use index (HUI_S), that gets
330 around this problem and still allows for sound comparison of habitat use by nekton between
331 habitats where we cannot derive abundance values per unit effort, water volume or bottom area
332 for one or the two habitats. Besides facilitating field work, this index can also facilitate
333 comparisons in meta-analysis and reviews of the literature.

334 The HUI_S denotes how much more one species uses habitat A over habitat B in relation
335 to the species with the least use of habitat A over habitat B. Thus, it does provide a means to rank
336 species according to their use of habitat A over habitat B from the baseline established by the
337 species with the least use of habitat A over habitat B. In addition, it allows to compare any pair
338 of species along the ranking. For instance, if a species has a HUI_S value of 20 and a second
339 species has a HUI_S value of 5, we can surmise that the first species uses habitat A over habitat B
340 four more times than the second species. As long as specimens can be sampled in the habitats, it
341 should be possible to apply the index to any pairs of habitats and species. An implicit assumption
342 is that each of the gear compared does have the same efficiency (although unknown) for the two
343 species compared.

344 The index is based on the total captures throughout the entire sampling period for the two
345 species compared. Thus, when the study is well replicated through space (i.e., replicated catches
346 in the study site) and time (i.e., catches obtained consistently at adequate frequency over a long
347 period of time), and as long as the assumption above holds, the HUI_S should be a robust indicator
348 of habitat selectivity by nekton species in relation to a benchmark species. When juveniles are
349 considered, the index should include the entire recruitment periods of the species compared. This
350 index adds to a suite of habitat use comparison metrics available in the literature (Heck et al.
351 2003, Rozas et al. 2012, Hollweg et al. 2019, Lefcheck et al. 2019, zu Ermgassen et al., 2021).

352 Critically, all these past metrics are based on the comparison of standardized values of individual
353 abundance between habitats, that is, the comparison of individual abundance per unit effort,
354 water volume, or bottom area between habitats. The HUI_S sets itself apart from all these past
355 metrics in that it allows for sound comparisons of habitat use when standardized values of
356 individual abundance cannot be derived due to gear limitations.

357 Our results showed that juveniles of pinfish consistently showed the lowest HUI_S in all
358 three sites in comparison with juveniles of the other species. This result is consistent with the
359 high preference for seagrass beds by pinfish juveniles reported in other studies (Stoner 1983,
360 Nelson 1998, 2002). Juveniles of spotted sea trout appeared next along the gradient from lesser
361 to higher use of fringing marsh over adjacent seagrass habitat in comparison with the benchmark
362 species of pinfish, having the second lowest HUI_S in Long Island and Marsh Island, and the third
363 lowest HUI_S in West Point-aux-Pins. Past studies have also reported high preference for
364 seagrass beds by spotted sea trout juveniles (Bohaby et al. 2018). Next along this gradient we
365 found American silver perch and brown shrimp, which interchanged their relative ranking across
366 sites. Finally, blue crab showed the fifth highest HUI_S and white shrimp the six highest HUI_S
367 invariably across sites. This relatively higher use of fringing marsh over adjacent seagrass habitat
368 by juveniles of blue crab and white shrimp in relation to the other species is consistent with
369 reports showing high concentrations of these juveniles at the marsh edge (Rozas and Zimmerman
370 2000, Minello and Rozas 2002). Zu Ermgassen et al. (2021) found higher density and
371 productivity enhancement of pinfish in seagrass beds than in marsh edge, and higher density and
372 productivity enhancement of white shrimp in marsh edge than in seagrass beds, in relation to
373 bare surrounding areas.

374 The fact that we sampled the seagrass beds at low tide, thereby possibly restricting
375 nekton access to the marsh, may lead to underestimates for high HUI_S values since the total
376 capture in the seagrass for species with high HUI_S values could have been lower if the samples
377 had been taken at high tide with higher accessibility to the marsh, thereby further increasing the
378 HUI_S value. However, as such underestimation would mostly apply to high HUI_S values, it
379 should not significantly affect the HUI_S -based categorial ranking of the species, in this case
380 pinfish and spotted sea trout with low HUI_S ; American silver perch and brown shrimp with
381 moderate HUI_S ; and blue crab and white shrimp with high HUI_S . The possible underestimation
382 of high HUI_S values should also not significantly affect the observation that, despite similar
383 rankings among species in terms of their HUI_S values in all three sites, HUI_S values varied
384 largely within species across sites. In other words, the extent of larger use of fringing marsh over
385 adjacent seagrass habitat by a species in relation to pinfish and other species seemingly differed
386 remarkably among sites. For instance, white shrimp uses fringing marsh over seagrass habitat
387 94.8 more times than do pinfish in Marsh Island, but 2366.4 more times than do pinfish in Long
388 Island.

389 **Conclusion**

390 Here we propose a metric, the habitat use index (HUI_S), that allows to rank habitat
391 selectivity by nekton species in relation to a benchmark species (i.e., the species with the least
392 use of one habitat over the other) when values of nekton abundance per unit effort, water
393 volume, or bottom area cannot be calculated for one or the two habitats compared. We apply the
394 index to show a consistent habitat selectivity ranking for the juveniles of six important species in
395 the northern Gulf of Mexico where, in relation to pinfish, spotted sea trout shows slightly higher
396 use; American silver perch and brown shrimp moderately higher use; and blue crab and white

397 shrimp greatly higher use of fringing marsh over adjacent seagrass habitat. These results suggest
398 that, according to the benchmark set by pinfish, the conservation of fringing marsh habitat, and
399 restoration whenever lost, in the northern Gulf of Mexico is paramount to preserve white shrimp
400 and blue crab (Rozas et al. 2007, Colombano et al. 2021). Brown shrimp and American silver
401 perch show a lower use of fringing marsh over adjacent seagrass habitat than do white shrimp
402 and blue crab, but fringing marsh also seems to be important habitat for these species (Moody et
403 al. 2013, Sharma et al 2016). The results also indicate that seagrass is an important habitat for all
404 six species studied, apparently more so at low than high tide for white shrimp and blue crab than
405 for the rest of the species studied due to the relatively higher use of the marsh at high tide by
406 those two species. At a larger scope, studies examining relative habitat use across numerous
407 species and habitats could do much to inform policies of coastal habitat conservation and
408 restoration. Indeed, such studies could identify specific combinations of habitats sheltering the
409 highest abundance and diversity of nekton, i.e., “hot spots for habitat provision”, which in turn
410 would indicate priority areas for conservation as well as templates for restoration elsewhere
411 (Sheaves et al. 2015, Gilby et al. 2020).

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425

426 **Author declaration**

427 Just Cebrian is an Associate Editor for the journal “Estuaries and Coasts”

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569

570 **Figure Legends**

571 Figure 1. Map of the study sites

572 Figure 2. Blue crab catches in the fringing marsh and adjacent seagrass habitat throughout the
573 study. Values are expressed in number of individuals per fyke net or trawl, respectively. Bars
574 correspond to mean values and lines on the bars to standard error

575 Figure 3. Brown shrimp catches in the fringing marsh and adjacent seagrass habitat throughout
576 the study. Values are expressed in number of individuals per fyke net or trawl, respectively. Bars
577 correspond to mean values and lines on the bars to standard error

578 Figure 4. White shrimp catches in the fringing marsh and adjacent seagrass habitat throughout
579 the study. Values are expressed in number of individuals per fyke net or trawl, respectively. Bars
580 correspond to mean values and lines on the bars to standard error

581 Figure 5. American silver perch catches in the fringing marsh and adjacent seagrass habitat
582 throughout the study. Values are expressed in number of individuals per fyke net or trawl,
583 respectively. Bars correspond to mean values and lines on the bars to standard error

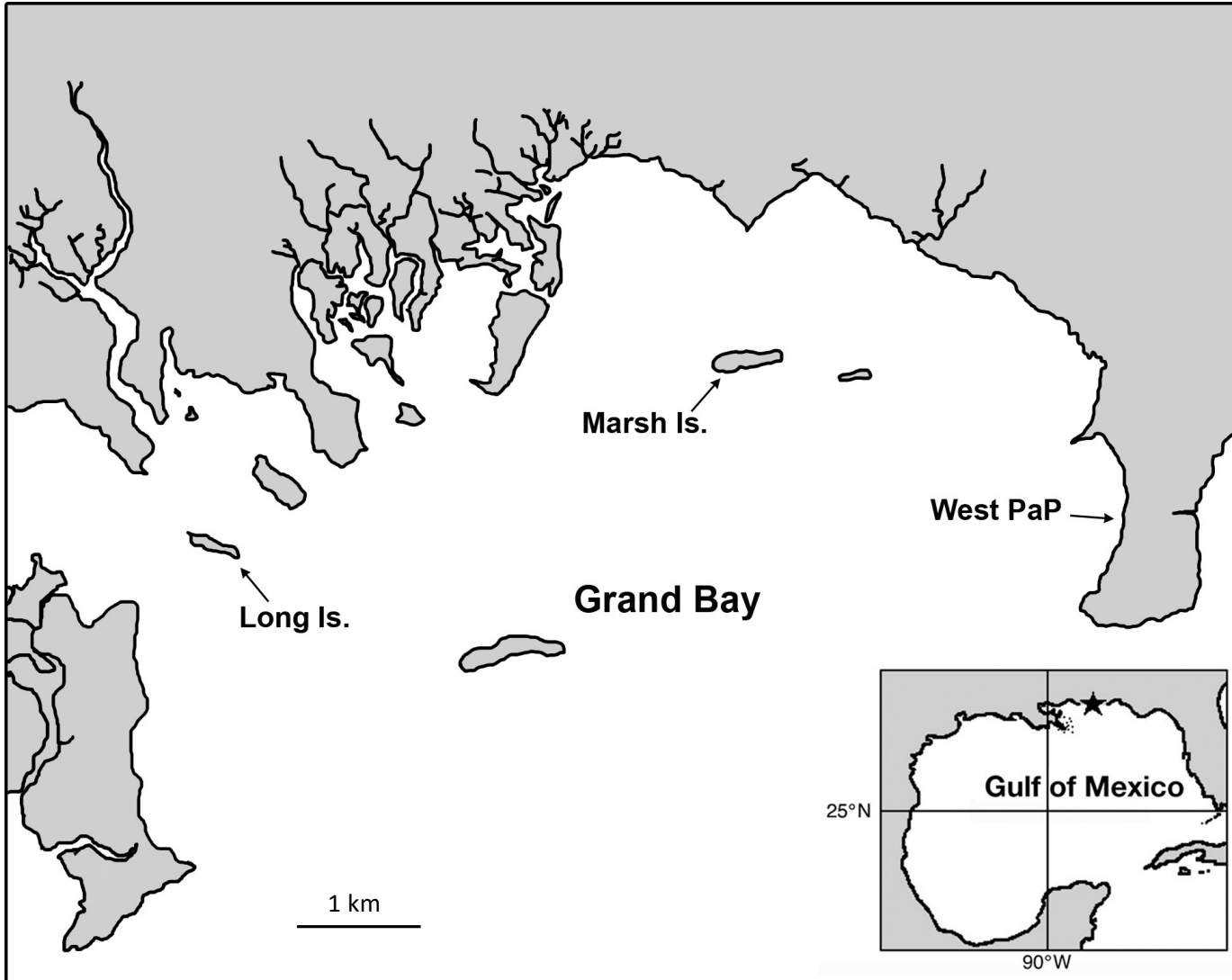
584 Figure 6. Pinfish catches in the fringing marsh and adjacent seagrass habitat throughout the
585 study. Values are expressed in number of individuals per fyke net or trawl, respectively. Bars
586 correspond to mean values and lines on the bars to standard error

587 Figure 7. Spotted sea trout catches in the fringing marsh and adjacent seagrass habitat throughout
588 the study. Values are expressed in number of individuals per fyke net or trawl, respectively. Bars
589 correspond to mean values and lines on the bars to standard error

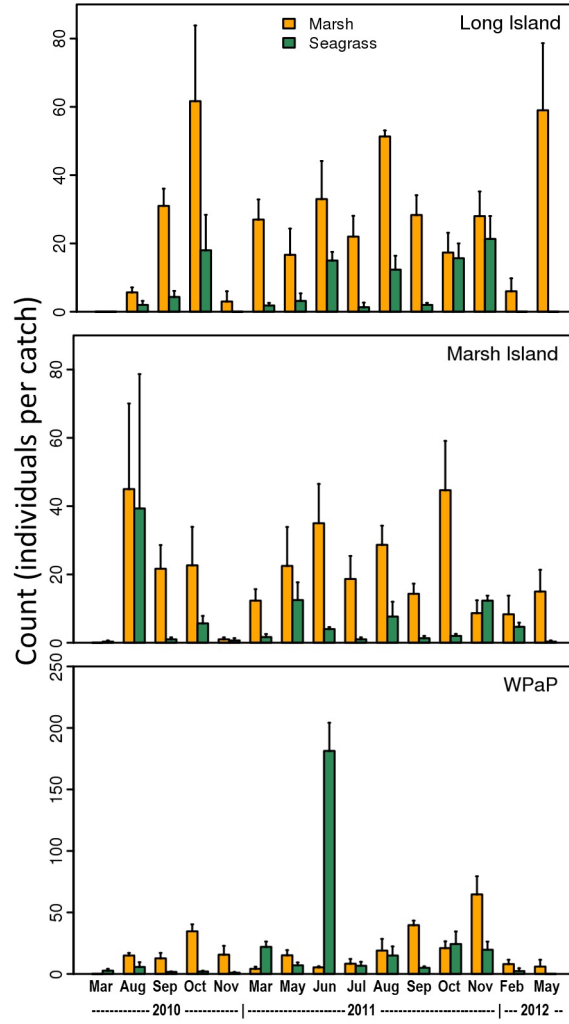
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Table 1. Values of total capture in marsh, total capture in seagrass, their ratio, and HUI_S for the species examined

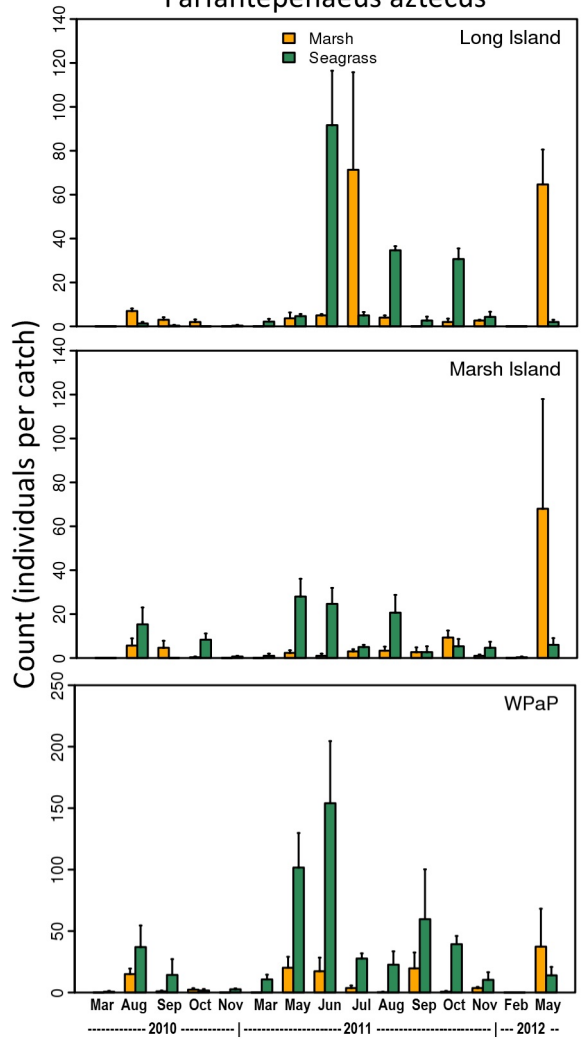
	Long Island				Marsh Island				West Point-aux-Pins			
	TC Marsh	TC Seagrass	TC Marsh/ TC Seagrass	HUIs	TC Marsh	TC Seagrass	TC Marsh/ TC Seagrass	HUIs	TC Marsh	TC Seagrass	TC Marsh/ TC Seagrass	HUIs
Pinfish	1	408	0.002	1	11	320	0.034	1	2	455	0.004	1
Spotted sea trout	10	61	0.164	66.9	26	90	0.289	8.4	13	237	0.055	12.5
American silver perch	318	352	0.903	368.6	535	186	2.876	83.7	9	895	0.010	2.3
Brown shrimp	507	560	0.905	369.4	311	452	0.688	20.0	424	1794	0.236	53.8
Blue crab	1301	306	4.252	1734.7	1000	321	3.115	90.6	866	910	0.952	216.5
White shrimp	551	95	5.800	2366.4	590	181	3.260	94.8	1316	432	3.046	693.0



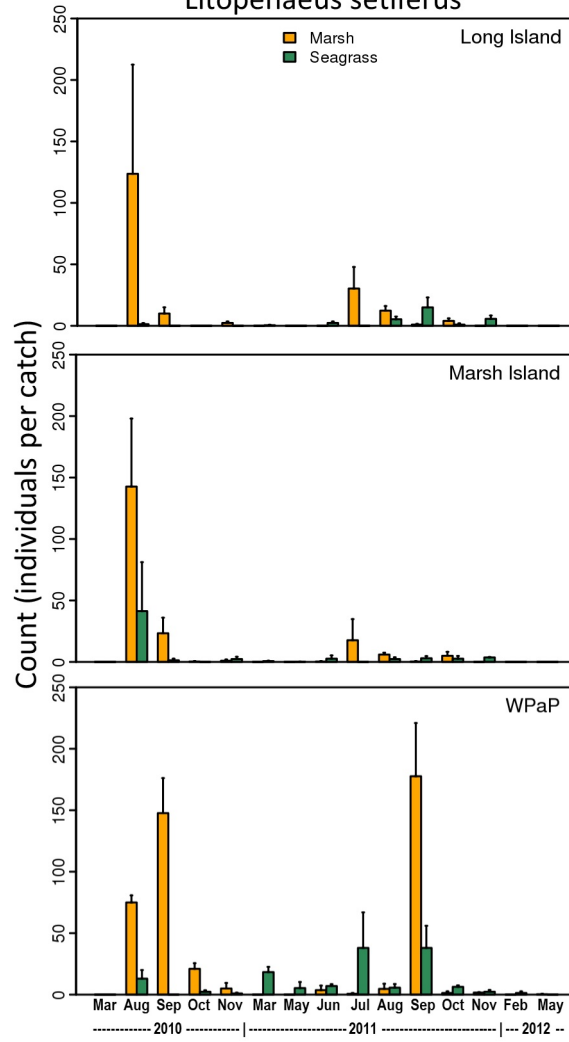
Callinectes sapidus



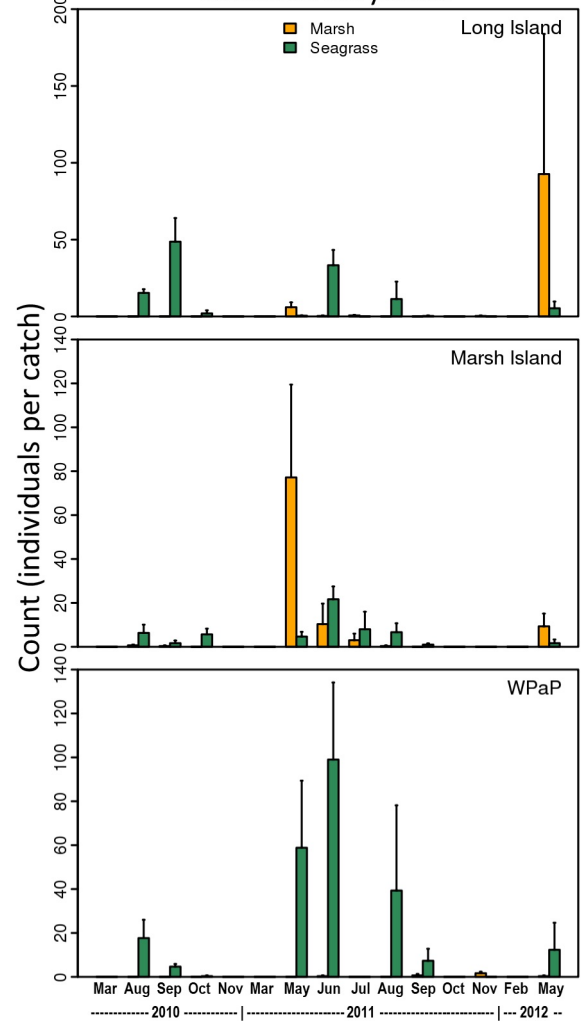
Farfantepenaeus aztecus



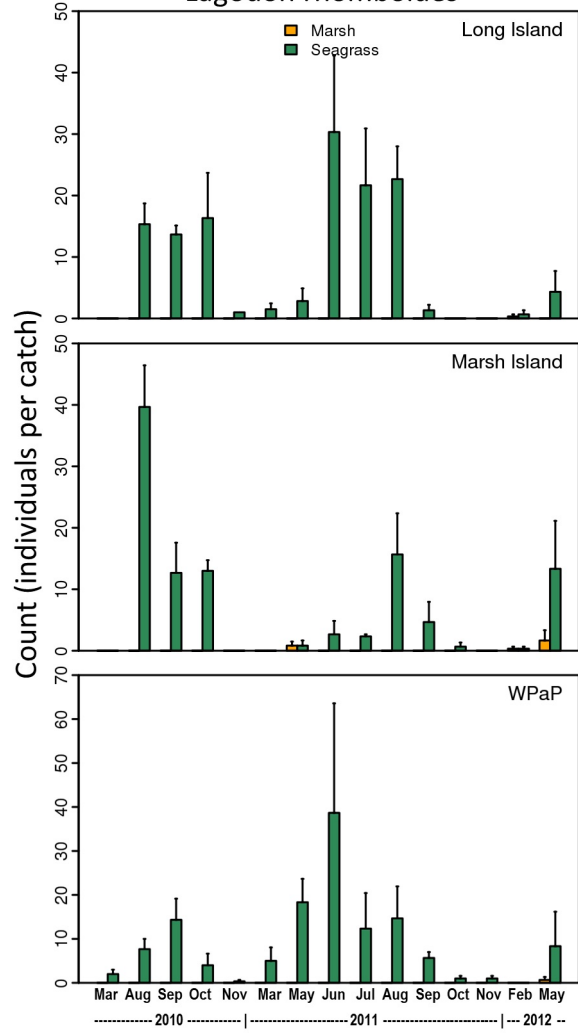
Litopenaeus setiferus



Bairdiella chrysoura



Lagodon rhomboides



Cynoscion nebulosus

