1   Running head: Drivers of key seagrass inhabitants

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3   Title: Environmental drivers of seagrass-associated nekton abundance across the northern Gulf

4   of Mexico

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Acknowledgements

Abstract

29   Small variations in environmental parameters can substantially alter species

30   composition, but the extent to which different species respond to these changes remains

31   obscure. A synoptic survey of seagrass-associated faunal communities was performed across

32   the Gulf of Mexico using otter trawls coupled with seagrass and water quality assessments. The

33   abundance of eight central seagrass inhabitants, representing a range of functional groups,

34   were quantified to identify factors that best predicted their prevalence across environmental

35   gradients and the consistency of these ecological relationships. Seagrass density and drift algal

36   biomass generally had the strongest influence on animal abundance (40-67%), although

37   relationships with drift algae were species-specific and seemingly related to faunal size and

38   mobility. Abundances of free-swimming pinfish, pigfish, and silver perch were negatively

39   related to drift algae biomass (0.7, 0.7, and 1.0% Δ/1 g·m^{-2} drift algae respectively), whereas the

40   abundance of pipefish (*Syngnathus spp.*) and brown/pink shrimp (*Penaeus spp.*) tended to be

41   positively related to algal biomass (0.8 and 1.6% Δ/1 g·m^{-2} drift algae). Shrimp abundances

42   increased by 3.6% per 1% increase in light attenuation while the abundance of a higher-order

43   visual predator, silver perch, negatively responded to light attenuation (1.1% Δ/1% Δ vertical

44   light attenuation). Additionally, bivariate plots of organismal abundance and salinity or canopy

45   height indicated a unimodal relationship with peaks in abundance associated with intermediate

46   values for several species. This study explored the extent species and functional groups

47   responded to variation in key elements of the abiotic and biotic environment, providing insight

48   into community development, and offering resource managers quantitative targets for aspects

49   of habitat quality.

50   Keywords: Habitat complexity, fish, shrimp, community structure, large-scale, plant-animal

51   interactions

52   Introduction

53   Physical characteristics of foundation species and abiotic conditions often interact to

54   influence the structure and function of faunal communities. Yet, understanding the

55   mechanisms that control major contributors to ecological communities remains a persistent

56   challenge for ecologists, in part because of the broad array of species, environmental

57   conditions, and interactions that govern organismal abundances. This challenge is further

58   complicated because many species exhibit idiosyncratic responses. For example, some animal

59   species like fish may be attracted to vegetation or habitat fragmentation, while others

60   simultaneously avoid or ignore the change in landscape (Andrew & Wulder 2011). Identifying

61   the drivers of abundance patterns can be particularly complex in coastal ecosystems (Gasol et

62   al. 1997; Gilbert et al. 2010), where large physicochemical gradients (e.g., temperature, salinity,

63   turbidity, dissolved oxygen) and spatiotemporal dynamism often set limits on species

64   composition and relative abundance (Wellborn et al. 1996; Alofs & Jackson 2015; Martin et al.

65   2021).

66   One common habitat feature that plays a strong role in governing coastal animal

67   communities is structural complexity, which tends to increase biodiversity (Kovalenko 2012) via

68   microhabitat creation (Hortal et al. 2009). Here, the nature of the structure can determine the

69   type of microhabitats formed. For instance, submerged aquatic plants oxygenate the water

70   column and surface sediments in different ways than macroalgae and offers different

71   opportunities for community development than mud flats or oyster reefs (Heck et al. 2003). In

72   particular, seagrass beds are known to support an entirely different nekton community than

73   nearby areas where seagrass is absent, even across small spatial scales (Weinstein & Brooks

74   1983; Mattila et al. 1999). Although seagrass beds are among the most productive coastal

75   ecosystems (Hemminga & Duarte 2000), and are frequently considered a marine analogue to

76   tropical rainforests (Simenstad 1994), understanding how multiple biotic and abiotic factors

77   within these systems combine to drive differences in faunal species' abundances within

78   seagrass beds remains a persistent challenge (Warton et al. 2015; Schrandt et al. 2018).

79   Seagrass beds are structurally complex ecosystems, where seagrass species composition,

80   canopy height, and shoot density are all known to elicit faunal responses at small spatial scales

81   (Ruesink et al. 2019). For instance, increases in canopy height can elicit a variety of predator

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82   responses, ranging from increased abundance to decreased foraging efficiency depending on

83   the species (Horinouchi 2007). However, primarily due to logistical constraints, most large-scale

84   studies which explore the effects of seagrass use only a few metrics, such as plant presence-

85   absence or percent cover, to characterize seagrass dominated seascapes. Few studies examine

86   the effects of fine-scale seagrass features across multiple regions or vast spatial scales which

87   hinders our ability to identify consistent associations between structural attributes and nekton

88   abundance (Dunton et al 2011; Neckles et al. 2012; Handley et al. 2020).

89   The structural complexity of seagrass meadows can be enhanced by filamentous or

90   branching drift macroalgae that can become entrained within seagrass canopies. Although drift

91   macroalgae can increase habitat complexity (e.g. Kingsford 1995), it frequently produces a thick

92   (5–15 cm) fibrous layer within and overtop seagrass meadows that can overshadow underlying

93   plants, inhibit benthic-pelagic coupling, and alter gas and nutrient cycling in extreme

94   circumstances (Sundbäck et al. 1996; Corzo et al. 2009). Drift algae can also exhibit high

95   spatiotemporal variability with 10-fold changes in algal biomass within 100 m or among seasons

96   (Kopecky & Dunton 2006). The biomass of drift algae is strongly dependent on wind-wave and

97   tidal water currents as well as local topography, which frequently interact to limit correlations

98   with seagrass landscape parameters such as seagrass presence, shoot density, and canopy

99   height (Bell & Hall 1997; Kopecky & Dunton 2006). The role of drift algae in structuring

100   seagrass-associated nekton communities remains unclear and understudied across large spatial

101   scales (Dantas et al. 2016), though it is undoubtedly an important driver of organismal

102   abundance, particularly for mobile invertebrates (Norkko et al. 2000) and finfish species

103   (Kulczycki et al. 1981).

104   In addition to structural complexity, water quality parameters such as salinity and

105   temperature are known to govern species composition and abundance (e.g., Wellborn 1996;

106   Horinouchi 2007; Loke & Todd 2016). Yet, rarely do these abiotic and biotic variables act in

107   isolation, and understanding their cumulative effects remains an important goal for ecological

108   understanding and ecosystem management. Quantifying the relative influence the above

109   variables play in governing species' abundances remains limited because variation among these

110   factors is not consistent or correlated, and nonlinearities in species responses to many

111   environmental parameters complicate their role in community development (e.g. Stewart et al.

112   2003). Thus, large-scale, synoptic sampling efforts are necessary to assess similar ecosystems

113   with different combinations of abiotic conditions to determine the effects of multiple influential

114   environmental variables. Such work can have advantages over long-term regional studies as

115   vast spatial scales can allow for a broader range of observed values for predictor variables that

116   will not be constrained by their own system-specific correlations. While a number of studies

117   have examined how certain species respond to some of these variables (e.g. Unsworth et al.

118   2007), encompassing broader geographic scales and comparing how different species respond

119   to environmental variables across multiple gradients can improve our understanding of factors

120   governing species distribution patterns. Moreover, this increased knowledge will aid in efforts

121   to develop a predictive framework for organismal population fluctuations in unsampled regions

122   or in response to environmental change.

123   We therefore performed a large-scale survey of turtlegrass (*Thalassia testudinum)*

124   dominated seagrass communities across the northern Gulf of Mexico to determine which

125   environmental variables contribute most to drive abundances of species representative of key

126 functional groups and to determine the consistency of these relationships across 2000 km. Field

127 sites spanned a range of abiotic gradients and topographical features from open coastline to

128 semi-enclosed lagoons. We focused on eight common nekton species that represent five

129 important functional groups to help identify potential mechanisms driving species' abundance

130 patterns and quantify the extent these relationships vary across space and by species in

131 seagrass ecosystems.

132 <div align="center">Methods</div>

133 *Study Sites*

134 We surveyed six coastal sites across the Gulf of Mexico between May 14 and June 14,

135 2018 (Table 1). These sites encompassed two semi-enclosed bays with major freshwater inputs

136 (Corpus Christi Bay and Redfish Bay -Coastal Bend, TX; Charlotte Harbor -Southern Florida),

137 three open coastline sites (St. George Sound -Florida Panhandle, near Cedar Key -Big Bend of

138 Florida, and Chandeleur Islands, LA), and one semi-enclosed lagoon with no major freshwater

139 inputs (Lower Laguna Madre, TX). Sites were superimposed with tessellated hexagons (500 m

140 edge length) in ArcGIS. Twenty to 25 hexagonal stations, which were perceived to contain ≥50%

141 seagrass coverage from satellite imagery, were randomly selected within each site for nekton

142 community assessment. Prior to sampling, ground truthing confirmed that each station

143 contained turtlegrass (*Thalassia testudinum*) and all sampling efforts were separated by at least

144 500 m (Figures S1 – S6). Mean distance between the farthest sampling stations at each site was

145 22.5 ± 2.4 km (Southern Florida = 25 km, Big Bend of Florida = 25 km, Florida Panhandle = 21

146 km, Chandeleur Islands, LA = 24 km, Coastal Bend, TX = 20 km, Lower Laguna Madre, TX = 20

147   km). At the site level, turtlegrass was the dominant benthic macrophyte; however, in some

148   instances, individual stations were dominated by manatee grass (*Syringodium filiforme*), shoal

149   grass (*Halodule wrightii*), or a mixed assemblage of species, while star grass (*Halophila*

150   *engelmannii*) and widgeon grass (*Ruppia maritima*) comprised only 5.7±7.4 SD and 7.1±5.4 SD

151   percent cover respectively in the few stations (11 total) where growing. Coverage of drift algae

152   ranged from 0–100 % within and overtop the seagrass canopy.

153   *Nekton Sampling*

154   The nekton community at each station was sampled with a 4.9-m flat otter trawl with a

155   3.8-cm stretch mesh body and 1.3-cm stretch mesh bag. The net was towed by boat at ~3.6

156   km·h^{-1} for 1-3 min. Trawl time was varied depending on water depth and drift algal biomass to

157   maintain consistent speed and capture efficiency. To account for differences in trawl times,

158   fishing effort was standardized by area swept by the trawl (abundance/[trawl path distance ×

159   net mouth width]). All captured nekton were counted and identified to the lowest practical

160   taxonomic level.

161   For analyses, we chose eight of the most common species that represent a variety of

162   functional groups to better examine how environmental and seagrass parameters govern

163   abundance of individual species and structure nekton communities (pinfish - *Lagodon*

164   *rhomboides*; pigfish - *Orthopristis chrysoptera*; American silver perch - *Bairdiella chrysoura*;

165   three common pipefish species - *Syngnathus scovelli* (gulf pipefish), *S. floridae* (dusky pipefish),

166   and *S. louisianae* (chain pipefish); and two common penaeid shrimp species - *Penaeus*

167   [*Farfantepenaeus*] *aztecus* (brown shrimp), and *P.* [*Farfantepenaeus*] *duorarum* (pink shrimp))

168   (see Table S1 for species size ranges).

169   The species selected for inclusion in this study represent a wide range of trophic niches,

170   behaviors, and life history characteristics. Pinfish are an omnivorous mid-trophic level species

171   that consumes algae, seagrass, and small invertebrates, and are frequently the most abundant

172   fish in seagrass beds by an order of magnitude (Darcy 1985). For comparison with a species that

173   occupies a similar ecological niche, we also examined pigfish which have a similar body shape

174   and size to pinfish. Both species utilize the same microhabitat, but pigfish incorporate less

175   vegetation in their diet and feed more frequently on benthic invertebrates (Sutter & McIlwain

176   1987). We also examined the American silver perch, which occupies a higher trophic level (3.71

177   versus 3.2 and 2.9 for pigfish and pinfish; Geers et al. 2016), feeding on small fish as well as

178   crustaceans, and has a more streamlined body than the laterally compressed pinfish or pigfish

179   (Grammer et al. 2009). Pipefish, which primarily feed on zooplankton, were selected for their

180   dependence on seagrass ecosystems, elongated bodies, and slow swim speed, which causes

181   them to primarily rely on camouflage and allows the species to access tighter interstitial spaces

182   than the previous perciform fish species (trophic level = 2.8; Howard & Koehn 1985; Ryer 1988;

183   Christian & Luczkovich 1999). Finally, we examined penaeid shrimp which are commercially-

184   important, benthic prey for a variety of fish species and occupy a different ecological niche and

185   lower trophic level (~2.5; Geers et al. 2016). While the three examined pipefish and two shrimp

186   species were usually found in the same habitats and are known to have similar physiological

187   tolerances and feeding habits among genus members (Pérez Farfante 1969; Howard & Koehn

188   1985; O'Boyle 2011; Geers et al. 2016), the particular species that dominated a location was

189   site-specific. We therefore analyzed the pipefish and shrimp species individually and at the

190   genus level to have sufficient abundance for Gulf-wide assessment. The eight species examined

191   were also chosen because they had a low ability to evade the trawl net and their local

192   abundance was high enough to account for artefacts in capture success due to trawling

193   methods.

194   *Vegetation Measurements*

195   We measured vegetation structural complexity at the beginning, middle, and end of

196   each trawl path. At each location, four 1-m^2 quadrats (each divided into 10-cm x 10-cm grid

197   cells) were laid down haphazardly from the four corners of the boat (~3.5–7.5 meters

198   separation between quadrats at each position; n = 12 quadrats per trawl path). Seagrass cover

199   by species, as well as the cover of attached and drift algae and bare substrate (i.e. total

200   vegetation cover) in the quadrat, was measured by counting the number of grid cells that

201   contained a particular vegetation category (0–100 grids/quadrat), providing a measure of

202   percent occurrence. Shoot density for each seagrass species in each quadrat was quantified by

203   counting the number of shoots within a single quadrat grid cell that contained the species.

204   Although turtlegrass was the dominant seagrass species overall, some quadrats contained

205   mixed species assemblages. In the instances when other seagrass species were present, the

206   number of shoots was counted by species and added together to determine total shoot density.

207   Canopy height for each seagrass species in a quadrat was quantified by measuring from the leaf

208   tip to sediment surface of three randomly selected seagrass leaves. When multiple seagrass

209   species were within a quadrat, the tallest canopy height among the species was also recorded.

210   The mean value for each vegetation category was calculated from all quadrats in a trawl path to

211   provide a metric of vegetation structure (vegetation category % coverage, n = 12 per trawl

212   path; seagrass species shoot density, n = 12 per trawl path; seagrass canopy height, n = 36 per

213   seagrass species per trawl path). The wet weight of all drift macroalgae collected in the trawl

214   was measured in the field using spring scales and similarly standardized by area swept

215   (biomass/[trawl path distance × net mouth length]).

216   *Water Quality Measurements*

217   Water quality was measured at the middle of the trawl path. Water temperature,

218   salinity, and dissolved oxygen concentration (DO mg·L^{-1}) were measured just above the seafloor

219   with a YSI Pro 2030 containing a galvanic DO sensor (Model 2002). Photosynthetically active

220   radiation was quantified with an LI-1500 light sensor logger equipped with two LI-193 spherical

221   underwater quantum sensors separated by a vertical distance of 27-50 cm, as dictated by water

222   depth. Sensors recorded photosynthetically active radiation at 1 Hz and averaged over a 30 s

223   measurement interval. Mean vertical light attenuation coefficient was calculated as a proxy of

224   water turbidity following the equations of Preisendorfer (1961), averaging over three

225   consecutive 30-s measurement intervals. Additionally, we recorded water depth at the

226   beginning, middle, and end of the trawl path.

227   *Statistical Analysis*

228   To screen for potential predictor variables, multivariate classification and regression

229   trees (CART analyses) were run using all quantified environmental characteristics (turtlegrass,

230   manatee grass, shoal grass, star grass, widgeon grass, attached algae, drift algae, and bare

231   sediment percent cover, drift algae biomass, species-specific shoot densities and canopy

232   heights, total shoot density, tallest canopy height, water temperature, salinity, DO, attenuation

233   coefficient, and depth; five trees built; R package "mvpart"). This allowed for the identification

234   of the most promising parameters for further analysis and helped to reduce the complexity of

235   downstream predictive models. As shoot density correlated to percent cover, we regressed

236   these two variables and used the residuals of shoot density to maintain explanatory variable

237   independence (Crawley 2012). To help identify the role particular seagrass species played in

238   governing nekton abundance and ensure that trends were not confounded by any

239   characteristics of a different seagrass species within the same station, we also analyzed the

240   effect of species-specific variables across several different subsets of the data: the full dataset,

241   only stations where that particular seagrass species was present, and stations where that

242   species represented 40% of the vegetation cover present. Additionally, as star grass and

243   sometimes widgeon grass (when reproductive) have substantially different growth forms than

244   the simple blades of turtlegrass, shoal grass, and manatee grass, we also examined species-

245   specific and species-independent metrics (e.g. total shoot density) across the entire dataset

246   (135 stations) and across stations where those two species were absent (123 stations). To test

247   for significant relationships between abundance and environmental parameters, we ran mixed-

248   effects generalized additive models with a quasipoisson distribution for pinfish, pigfish, silver

249   perch, and pipefish, and a zero-inflated poisson distribution for penaeid shrimp due to the large

250   number of stations with no shrimp present (R package "mgcv"). Models included an offset term

251   of trawl path length with a log link to control for differences in trawl distance. Smoothing terms

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252 were added to environmental parameters as many of these relationships were nonlinear.

253 Separate models were used for each species using predictor variables identified in the CART

254 analysis described above. Pinfish, pigfish, and shrimp models had turtlegrass percent cover,

255 turtlegrass shoot density residuals, turtlegrass canopy height, drift algae biomass, temperature,

256 salinity, DO, and attenuation coefficient as fixed effects. Study site was treated as a random

257 effect with random intercept and slopes to control for nonindependence of samples within

258 each station and account for site-dependent effects. Silver perch and pipefish models had the

259 same explanatory variables as the models above, except turtlegrass canopy height was replaced

260 with stations' tallest canopy height as this parameter was found to have a stronger relationship

261 for these species. All statistical analyses were conducted in R v3.5.1 (R Development Core

262 Team, 2018).

263   Results

264 *Pinfish*

265   Pinfish were the most prevalent of all captured species by an order of magnitude with

266 mean ± SD abundance of 0.602 ± 0.788 fish/m^2 across all stations. The three parameters that

267 explained the most variation in pinfish abundance across all the field sites were turtlegrass

268 percent coverage, drift algae biomass, and turtlegrass canopy height (cumulative adjusted R^2 =

269 0.50). While there was a significant positive correlation between pinfish abundance and percent

270 cover (mean slope ± SD = 1.7 ± 0.8% Δ fish density/1% Δ percent cover), drift algae biomass had

271 a significant negative correlation with abundance (-0.7 ± 1.5% Δ fish density/1 g·m^{-2}Δ algal

272 biomass), and canopy height produced a bell-curve with maximum abundances across most

13

273   sites between a canopy height of 320 and 430 mm (Figure 1). The only physical water quality

274   parameter that had a significant relationship with pinfish abundance was oxygen while all

275   vegetative qualities were significant (Table 2).

276   *Pigfish*

277   Pigfish were the second most abundant species collected (0.056 ± 0.170 fish/m^2). Like

278   pinfish, turtlegrass percent cover had a significant positive correlation with pigfish abundance

279   across field sites (2.1 ± 3.9% Δ fish density/1% Δ percent cover; Figure 2). However, turtlegrass

280   shoot density and salinity were also dominant factors that governed pigfish abundance, with

281   both variables producing bell-shaped relationships yielding an abundance maxima (Figure 2;

282   cumulative adjusted R^2 of top three variables = 0.65). Maximum pigfish abundances generally

283   occurred at shoot densities of 300-600 shoots/m^2 and salinities of 22-30. Pigfish abundance

284   declined substantially outside this salinity range (Figure 2c). Dissolved oxygen was also a

285   significant predictor of abundance while canopy height, drift algae biomass, water temperature,

286   and attenuation coefficient were not significant predictors (Table 3).

287   *Silver perch*

288   Silver perch exhibited moderate abundances at 0.024 ± 0.054 fish/m^2. Turtlegrass

289   percent cover, drift algae biomass, and salinity explained the most variation in silver perch

290   abundance (cumulative adjusted R^2 = 0.30). Like pinfish and pigfish, turtlegrass percent cover

291   had a positive effect on silver perch abundance (0.8 ± 1.6% Δ fish density/ 1% Δ percent cover),

292   while drift algae biomass had a negative effect (-0.1 ± 1.5% Δ fish density/1 g·m^{-2} Δ algal

293   biomass), and salinity produced a bell curve with maximum abundances between 21-30 (Figure

294   3). Additionally, silver perch tended to exhibit the greatest abundances in clearer water,

295   although the relationship with turbidity was complex as some sites showed the reverse trend

296   (Supplemental Figure S7). The species was particularly sensitive to environmental conditions as

297   fish abundance varied significantly with all eight analyzed parameters; this sensitivity likely also

298   explains the lower adjusted-R^2 for the final abundance model (Table 2).

299   *Pipefish*

300   Pipefish were the least abundant of the five taxa examined (0.005 ± 0.008 fish/m^2). Gulf

301   pipefish were found at every site except Lower Laguna Madre while dusky pipefish were only

302   found in Florida sites, but were often 2x more abundant than Gulf pipefish when present. Chain

303   pipefish were, on average, 16-33% as abundant as the other pipefish, but were the only species

304   present in Lower Laguna Madre (Figure S8). Turtlegrass percent coverage, drift algae biomass,

305   and salinity were again the three parameters that explained the greatest variation in

306   abundance (cumulative adjusted-R^2 = 0.60). Abundance was positively correlated with seagrass

307   percent cover (3.3 ± 2.8% Δ fish density/1% Δ percent cover) and exhibited a bell-shaped

308   relationship with salinity, with pipefish exhibiting the greatest abundance at the high end of a

309   22–30 salinity range (Figure 4). However, unlike other fish species, pipefish abundance also

310   increased positively with drift algal biomass (0.8 ± 1.0% Δ fish density/1 g·m^{-2} Δ algal biomass;

311   Figure 4b). Turtlegrass shoot density, seagrass canopy height, water temperature, and

312   attenuation coefficient were not significant predictors (Table 2; see Table S2 for species-specific

313   statistics).

314   *Penaeid shrimp*

315   Penaeid shrimp had relatively low overall abundances (0.013 ± 0.036 shrimp/m^2), partly

316   due to their restricted distribution (only Texas Coastal Bend and the Chandeleur Islands had

317   substantial numbers; Figure 5). Brown shrimp were primarily found in sites west of Florida

318   while pink shrimp were only found within the three Florida sites (Figure S9). Additionally, brown

319   shrimp were 12x more abundant on average than pink shrimp in their respective domains

320   (0.012 vs 0.001 shrimp/m^2). Turtlegrass percent cover, drift algal biomass, and attenuation

321   coefficient were the three most important variables explaining penaeid shrimp abundance

322   (cumulative adjusted R^2 = 0.77). As with all other species examined, shrimp abundances

323   correlated positively with percent cover of turtlegrass (0.3 ± 0.8% Δ shrimp density/1% Δ

324   percent cover); whereas the abundance pattern with drift algae differed from the perciform

325   species and was similar to the positive relationship found for pipefish (1.6 ± 1.2% Δ shrimp

326   density/1 g·m^{-2} Δ algal biomass). Interestingly, attenuation coefficient also had a positive

327   correlation with shrimp abundance in sites where shrimp were abundant (3.6± 2.5% Δ

328   shrimp/1% Δ coefficient; Figure 5c). Turtlegrass canopy height, water temperature, and

329   dissolved oxygen also were significant predictors of shrimp abundance, while shoot density and

330   salinity were not significant (Table 2; see Table S2 for species-specific statistics).

331   *Vegetation Measurements*

332   All six sites were dominated by turtlegrass, which had a total average percent cover of

333   63-92% depending on the site, and was the most abundant species at all but 12 (9%) stations.

334   Manatee grass was the second most common species with a mean coverage of 1-52%, followed

335   by shoal grass at 0-15% (Table 3). Manatee grass shoot density and canopy heights were

336   relatively similar to turtlegrass as manatee grass was only 22% denser and 21% taller than

337   turtlegrass. In contrast, shoal grass shoots were 117% denser and 29% shorter than turtlegrass

338   (Table 3). The only significant correlations among vegetation characteristics were between

339   turtlegrass percent cover and its relationship with turtle grass shoot density and total shoot

340   density (r = 0.61 and r = 0.35 respectively; p < 0.0001) while there was a positive trend between

341   drift algae biomass and turtlegrass percent cover in the Chandeleur Islands (r = 0.47; p =

342   0.0783). Both the Florida Panhandle and Big Bend of Florida contained high mixtures of

343   turtlegrass (>80% average coverage) and manatee grass (>40% average coverage) with less than

344   2% coverage of shoal grass. Southern Florida and Coastal Bend Texas had high concentrations

345   of turtlegrass (>60% average coverage) with modest coverage of both manatee and shoal grass

346   (between 10-15%). Both Chandeleur Islands, LA and Lower Laguna Madre, TX also had high

347   levels of turtlegrass (>80% average coverage), but while the Chandeleur Islands had low

348   manatee grass coverage and modest shoal grass coverage, Laguna Madre had modest manatee

349   coverage and low shoal grass coverage (Table 3). Seagrass shoot density was generally highest

350   in the Chandeleur Islands and lowest in Southern Florida while canopy height was usually tallest

351   in the Big Bend of Florida and shortest in Lower Laguna Madre.

352

353   Discussion

354   Even similar ecological systems can be characterized by large differences in species

355   composition and abundance (Tokeshi 1993) as seemingly minor nuances in seagrass and

356   conditions can drive important species trends. Our findings demonstrate the value of

357   simultaneously investigating a suite of biotic and abiotic drivers across multiple systems to

358   identify common drivers of species abundance, which together inform our concept of nekton

359   community development in subtropical seagrass ecosystems. Many of the seagrass structure

360   and abiotic variables we examined had consistent relationships with a particular taxon across

361   broad geographical distances and coastal attributes and could frequently be associated with

362   specific traits (e.g. free-swimming fish species negative relationship with drift algae). However,

363   some species-environment relationships were remarkably different spatially, and sometimes

364   opposite, depending on the nekton species and environmental parameter. In particular,

365   environmental parameters that had linear relationships with abundance usually remained

366   relatively constant across all field sites despite the sites spanning a diverse array of estuarine

367   features. In contrast, environmental parameters that produced non-linear relationships often

368   had site-specific abundance patterns (e.g., pigfish abundance increased with salinity in

369   Louisiana at one end of the salinity spectrum and decreased with salinity in the Florida

370   panhandle at the other end of the spectrum due to their physiological tolerance and unimodal

371   relationship with salinity; Figure 2c; Ohs et al. 2011). Such results help quantify limits on how

372   much species with different specializations are expected to change across various

373   environmental conditions and provide information on potential mechanisms behind differences

374   in faunal community composition within seagrass beds.

375   Multiple seagrass characteristics were linked to local (within-site) and regional (across-

376   site) differences in nekton abundance. Seagrass percent cover likely correlated to increased

377   individual abundance for every focal species and across every site where a species appeared

18

378   because the presence of seagrass tends to increase resource abundance (Diehl 1993), refuge

379   access (Klecka & Boukal 2014), and niche availability (Unsworth et al. 2007), which are well-

380   established ecosystem functions provided by seagrasses. However, the strength of species'

381   positive response to seagrass coverage varied dramatically. While pinfish exhibited modest and

382   relatively consistent increases in abundance with seagrass cover (1.7 ± 0.8% Δ density per 1% of

383   seagrass cover), pigfish and silver perch exhibited dramatic fluctuations in their relationship

384   with seagrass cover across sites (mean ± SD = 2.1% Δ ± 3.9% and 0.8% Δ ± 1.6%, respectively).

385   This is likely because pigfish were more strongly dependent on turtlegrass shoot density than

386   other species and silver perch were sensitive to turbidity, which also tended to vary across site

387   (Tables 1 and 2). Indeed, pigfish abundances and positive relationship with seagrass cover were

388   greatest in the Florida Panhandle where turtlegrass shoot density varied the most while the

389   silver perch relationship with turtlegrass was weakest in sites that had wide fluctuations in

390   turbidity (Southern Florida, Big Bend of Florida, Coastal Bend, TX). Remarkably, pipefish

391   densities increased 1.6 - 8x faster than other species with increases in seagrass cover, further

392   highlighting that these fish are habitat specialists (Howard & Koehn 1985, Ryer 1988).

393   Conversely, shrimp abundances only increased slightly (0.3% Δ density) with changes in

394   seagrass cover, far less than the 1.6% and 3.6% density changes observed with drift algae and

395   water turbidity respectively, suggesting that small shifts in these two variables play a much

396   stronger role in governing shrimp abundances.

397   In contrast to the linear relationship between seagrass cover and species abundance,

398   shoot density and canopy height varied enough to reveal unimodal relationships with

399   abundance for several species, allowing for a quantitative description of niche space with

400   respect to seagrass structure (Figure 2b and Supplemental Figure S10). Importantly, all of the

401   nekton species examined appeared to have their maximum abundances centered around the

402   same range of turtlegrass canopy heights (290–450 mm; Supplemental Figure S10). Two

403   plausible explanations for such nonlinearity are that advantages in structural complexity could

404   be lost due to movement inhibition in dense canopies or competitive exclusion by habitat

405   specialists (Gause 1934; Bartholomew et al. 2000). Experiments on caridean shrimp in seagrass

406   found that as seagrass habitat complexity increased, there was a shift from habitat generalists

407   to habitat specialists (Unsworth et al. 2007). If competitive exclusion was the primary driving

408   source behind these patterns, then the maximum abundance of different species would be

409   offset across the spectrum of seagrass canopy heights. However, the nekton species evaluated

410   here had maximum abundances within the same range of shoot characteristics (with the

411   exception of pipefish which maintained high abundances in dense seagrass and are habitat

412   specialists; Howard & Koehn 1985), while other common nekton species caught in the trawl

413   also showed similar patterns in maximum abundance (data not shown). This suggests that

414   changes in abundance due to structural complexity were not driven by competition for space,

415   but ability to access increasingly smaller interstitial spaces. Further, these findings indicate that

416   denser seagrass beds were not conducive to supporting nekton in the size range caught by the

417   trawl (individuals > 3 cm), although benthic species or individuals of smaller sizes may have

418   benefited. Indeed, individual size is often an important aspect of abundance patterns as species

419   will often form size gradients in concert with habitat gradients (e.g. Holmgren & Appelberg

420   2000; Supplemental Figure S11).

421   While seagrass coverage produced similar relationships with individual abundance

422   across every species examined, drift algae had species-specific relationships with abundance

423   that were dependent on functional group. Abundances of all three perciform fish species

424   (pinfish, pigfish, and silver perch) varied inversely with drift macroalgal biomass, whereas the

425   more closely seagrass-associated pipefish and shrimp abundances increased with algal biomass,

426   consistent with previous findings on drift algae in estuarine systems (Kulczycki et al. 1981; Bell

427   & Westoby 1987). One likely mechanism underpinning these differences is that the drift algae

428   filled the interstitial spaces between seagrass blades that perciform fish normally utilize. This

429   may have provided a habitat that was more beneficial to pipefish and shrimp as their

430   morphology better permit access to tighter, more complex interstitial spaces, similar to what

431   has been found for some seagrass-associated species (Stoner 1982; Ryer 1988). Alternatively, it

432   is possible that the drift algae encountered here may have produced secondary metabolites or

433   biofilms that attracted or repelled certain species (Norri & Fenical 1982; Höckelmann et al.

434   2004), or may have contained more invertebrate prey for shrimp and pipefish (Norkko et al.

435   2000). Future studies are needed to determine the mechanism(s) driving these patterns.

436   Variation in total nekton abundance appeared to be exacerbated by whether or not the

437   species-specific response to seagrass presence and macroalgal biomass were coincident or

438   countervailing. These results show that the moderate abundances of some species at specific

439   stations (or "noise" in relationships between a parameter and individual abundance) was a

440   product of the species balancing out the opposing effects of seagrass and drift algae presence,

441   while other species would be found at high abundance (representing data outliers) where the

442   two trends coincided. For example, pinfish might have moderate abundances in substations

443   with high seagrass coverage because of large amounts of drift algae while pipefish might

444   simultaneously exhibit exceptionally high abundance at the station because the positive effects

445   of both seagrass and drift algae were acting synergistically. In fact, the high amounts of drift

446   algae in some stations of the Big Bend of Florida and the Florida Panhandle are likely partially

447   responsible for these sites supporting the greatest abundances of pipefish. Similarly, the strong

448   positive relationship between seagrass and drift algae in the Chandeleur Islands and the fact

449   that drift algae was 34 – 300% greater in Coastal Bend than other sites may be why these two

450   locations supported shrimp abundances that were nearly an order of magnitude greater than

451   elsewhere in the study. Relatively low salinities in the Chandeleur Islands also help explain low

452   pipefish abundances there relative to Florida sites. This demonstrates the value of multivariate

453   CART analysis and multiple regression of explanatory variables for predicting community

454   composition in slightly different habitats, especially when environmental relationships can be

455   associated with the abundance of multiple species grouped by a particular trait or specific

456   characteristics (e.g., trophic level or movement ability).

457   Abiotic factors also had strong effects on abundances that help explain differences

458   across stations as these parameters could test the physiological limits of species. For instance,

459   light availability caused modest changes in community trophic structure by increasing the

460   prevalence of lower trophic level species (i.e. penaeid shrimp) and slightly decreasing the

461   prevalence of upper trophic level species (i.e. silver perch). Light attenuation was actually the

462   most important variable for predicting shrimp abundances when they were present, and

463   changes in this parameter produced 8x greater changes in shrimp abundance than relative

464   changes in seagrass percent cover while silver perch exhibited larger changes with light

465   attenuation than seagrass cover at sites that had both exceptionally clear and turbid stations

466   (Southern Florida, Big Bend of Florida, Coastal Bend, TX). The effect of light availability may be

467   the product of dominant predatory mode: visual or olfactory. Visual predators, like silver perch,

468   are less successful foragers in elevated turbidity, thereby releasing chemosensing prey species

469   from predation pressure in turbid regions while simultaneously encouraging visual hunters to

470   avoid such regions (Lunt & Smee 2014; Lunt & Smee 2020). Likewise, mid-trophic level species

471   that do not rely on seeing great distances for foraging were largely unaffected by the level of

472   turbidity encountered (i.e. pinfish, pigfish, and pipefish; Table 2). Broader community level

473   research is necessary, however to verify that these patterns are retained across hunting modes

474   and species groups.

475   Salinity was a principal driver of regional, between-site differences in species

476   abundances as this parameter varied 2.7-fold over the study area with each site exhibiting a

477   distinct salinity regime. Most of the nekton species had abundance maxima at salinities

478   between 20–30, indicative of an optimal range (Jennings & Weyers 2003; Martino & Able 2003).

479   Indeed, the exceptionally high salinities in the Lower Laguna Madre (>36 for every substation)

480   likely contributed to low abundances for every trawled species. Similarly, the Chandeleur

481   Islands and Southern Florida showed moderate increases in species abundance with salinity as

482   these sites spanned the lower limits of some species' tolerances (10 -15 ppt; Larson et al. 1989;

483   Criales et al. 2011; Ohs et al. 2011). In fact, the euryhaline tolerances of pinfish helps explain

484   the relatively high abundance of this species at every station (Darcy 1985). Although salinity is

485   commonly associated with changes in fish assemblages (Gelwick et al. 2001; Schrandt et al.

486   2018), our results with salinity and seagrass characteristics underscore the importance of

487   conducting studies that investigate multiple factors over larger geographical areas as the nature

488   of the relationship between species abundance and these characteristics could change across

489   sites. For instance, many of the species-specific relationships with these variables would often

490   be difficult to detect within a particular site due to the relatively narrow range of parameter

491   variation encompassed within a site and the wide variety of other variables that are

492   simultaneously affecting community composition. By examining the effects of a variable across

493   the entire spectrum of parameter values, researchers gain a broader perspective on the biotic

494   and abiotic interactions structuring communities which can help inform predictions of species

495   prevalence across wider geographic areas through interpolation.

496   Variation in community structure is the norm rather than the exception in natural

497   systems (Gelwick et al. 2001; Alofs & Jackson 2015; Dantas et al. 2016; Lunt and Smee 2020;

498   Martin et al. 2021). We were able to explain much of the spatial variability in component

499   species abundance by simultaneously examining multiple environmental parameters assessed

500   across a broad range of parameter values. Our findings demonstrate how key species or group

501   level examinations of communities with modern statistical approaches can help identify

502   probable and readily testable processes controlling key components of community structure

503   within complex systems. By consistently sampling across a large geographical scale and

504   investigating a range of biotic and abiotic parameters, we were able to describe several

505   environmental relationships with animals representing a variety of functional groups that may

506   not be readily captured at a single site or through disparate studies. Thus, this work

507   demonstrates the importance of large-scale projects for developing unified ecological theory

508   and species management programs that can be applied to a wide variety of situations.

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675   Table Legend

676   **Table 1:** Study site locations with maximum and minimum abiotic conditions.

677   **Table 2:** Statistical results from generalized additive mixed models examining the influence of

678   turtlegrass percent cover, shoot density, canopy height, and drift algae biomass as well as

679   water temperature, salinity, dissolved oxygen (DO), and light attenuation coefficient on the

680   abundance of pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), silver perch

681   (*Bairdiella chrysoura*), pipefish (*Syngnathus* spp.), and penaeid shrimp (*Penaeus* spp.). [a]indicates

682   that turtlegrass canopy height was replaced with values from the tallest observed species

683   present in quadrates. [b] denotes F-values were replaced with X^2 values.

684   **Table 3:** Mean ± SD seagrass morphological characteristics of turtlegrass (*Thalassia*

685   *testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*) in six

686   sites across the northern Gulf of Mexico (n = 20 – 25 stations/site).

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693   Figure Legends

694   **Figure 1:** Pinfish (*Lagodon rhomboides*) density (individuals/m^2) as a function of the top three

695   drivers **a)** turtlegrass percent cover (%), **b)** drift algae biomass (g/m^2), and **c)** turtlegrass canopy

696   height (mm) across six field sites spanning the Gulf of Mexico (Southern Florida, n = 25; Big

697   Bend of Florida, n = 25; Florida Panhandle, n = 21; Chandeleur Islands, LA, n = 24; Coastal Bend,

698   TX, n = 20; Lower Laguna Madre, TX, n = 20).

699   **Figure 2:** Pigfish (*Orthopristis chrysoptera*) density (individuals/m^2) as a function of the top

700   three drivers **a)** turtlegrass percent cover (%), **b)** turtlegrass shoot density (shoots/m^2), and **c)**

701   salinity across six field sites spanning the Gulf of Mexico.

702   **Figure 3:** Silver Perch (*Bairdiella chrysoura*) density (individuals/m^2) as a function of the top

703   three drivers **a)** turtlegrass percent cover (%), **b)** drift algae biomass (g/m^2), and **c)** salinity

704   across six field sites spanning the Gulf of Mexico.

705   **Figure 4:** Pipefish (*Syngnathus* spp.) density (individuals/m^2) as a function of the top three

706   drivers **a)** turtlegrass percent cover (%), **b)** drift algae biomass (g/m^2), and **c)** salinity across six

707   field sites spanning the Gulf of Mexico.

708   **Figure 5:** Penaeid shrimp (*Penaeus* spp.) density (individuals/m^2) as a function of the top three

709   drivers **a)** turtlegrass percent cover (%), **b)** drift algae biomass (g/m^2), and **c)** water attenuation

710   coefficient across six field sites spanning the Gulf of Mexico.

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713   Table 1

Site Locations	Latitude	Longitude	Temperature (°C)	Salinity	Dissolved Oxygen (mg/L)	Attenuation Coefficient	Depth (cm)
Southern Florida	26°69' - 26°88' N	82°06' - 82°25' W	28.2–32.8	10.5–34.0	4.6–8.7	0.3–4.1	55–280
Big Bend of Florida	29°08' 29°63' N	82°92' - 83°63' W	27.7–30.8	21.5–32.7	5.3–11.1	0.3–5.4	75–175
Florida Panhandle	29°82' - 29°91' N	84°45' - 84°79' W	27.7–31.5	22.0–29.5	6.2–8.5	0.5–8.1	40–180
Chandeleur Islands, LA	29°78' - 29°99' N	88°83' - 88°88' W	28.1–33.0	12.1–20.4	5.6–17.6	0.1–2.4	65–155
Coastal Bend, TX	27°75' - 27°97' N	97°08' - 97°18' W	26.3–29.2	32.7–36.8	3.8–9.2	0.1–4.8	43–285
Lower Laguna Madre, TX	26°08' - 26°24' N	97°18' - 97°28' W	26.4–29.4	36.1–37.2	5.0–11.9	0.1–2.2	95–240

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731   Table 2

Species	Environmental Parameters															
	Turtle grass percent cover		Turtle grass shoot density		Turtle grass canopy height		Drift algae biomass		Temperature		Salinity		DO		Attenuation coefficient	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Pinfish	7.26	**0.0073**	3.01	**0.0089**	11.21	**<0.0001**	7.60	**0.0068**	1.47	0.1721	0.08	0.7854	5.11	**0.0257**	2.79	0.0977
Pigfish	3.73	**0.0012**	6.01	**0.0001**	2.48	0.0589	2.11	0.1575	1.43	0.2306	7.88	**0.0001**	5.75	**<0.0001**	1.33	0.3008
Silver Perch	8.76	**<0.0001**	9.08	**0.0033**	13.05	**0.0005**[a]	2.97	**0.0148**	3.89	**0.0496**	6.94	**0.0001**	12.27	**<0.0001**	2.69	**0.0243**
Pipefish	3.96	**0.0037**	0.02	0.9007	1.06	0.3513[a]	8.21	**0.0001**	0.21	0.6498	4.14	**0.0150**	2.64	**0.0006**	1.80	0.1380
Shrimp[b]	9.07	**0.0026**	6.21	0.1180	109.9	**<0.0001**	26.53	**0.0004**	44.10	**0.0001**	1.12	0.8420	52.87	**<0.0001**	165.5	**<0.0001**

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758   Table 3

Site	Grass species	Percent Cover	Shoot density (shoots/m^2)	Canopy height (mm)
Southern Florida	Turtlegrass	69 ± 21	339 ± 141	296 ± 55
	Manatee grass	11 ± 21	888 ± 273	420 ± 91
	Shoal grass	16 ± 26	817 ± 468	222 ± 72
Big Bend of Florida	Turtlegrass	82 ± 24	573 ± 226	413 ± 89
	Manatee grass	42 ± 38	596 ± 388	412 ± 90
	Shoal grass	2 ± 3	471 ± 191	390 ± 153
Florida Panhandle	Turtlegrass	87 ± 18	605 ± 427	327 ± 70
	Manatee grass	52 ± 41	811 ± 420	347 ± 69
	Shoal grass	0 ± 0	NA	NA
Chandeleur Islands, LA	Turtlegrass	80 ± 26	837 ± 281	319 ± 58
	Manatee grass	1 ± 3	1600 ± 1418	287 ± 58
	Shoal grass	14 ± 21	921 ± 558	191 ± 47
Coastal Bend, TX	Turtlegrass	63 ± 29	570 ± 254	363 ± 91
	Manatee grass	15 ± 20	646 ± 399	483 ± 104
	Shoal grass	11 ± 20	2583 ± 1075	188 ± 71
Lower Laguna Madre, TX	Turtlegrass	92 ± 16	508 ± 171	226 ± 90
	Manatee grass	11 ± 21	232 ± 125	337 ± 95
	Shoal grass	1 ± 6	3067 ± 686	131 ± 29
Overall	Turtlegrass	79 ± 24	571 ± 300	324 ± 93
	Manatee grass	22 ± 32	684 ± 521	393 ± 103
	Shoal grass	8 ± 18	1238 ± 1037	229 ± 106

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770   Figure 1

Legend:
- ○ Southern Florida, FL
- ● Big Bend of Florida, FL
- ● Florida Panhandle, FL
- ▲ Chandeleur Islands, LA
- ■ Coastal Bend, TX
- ■ Lower Laguna Madre, TX

Panel a: Pinfish abundance (individuals/m²) vs Turtlegrass percent cover (%)
Panel b: Pinfish abundance (individuals/m²) vs Drift algae biomass (g/m²)
Panel c: Pinfish abundance (individuals/m²) vs Turtlegrass Canopy height (mm)
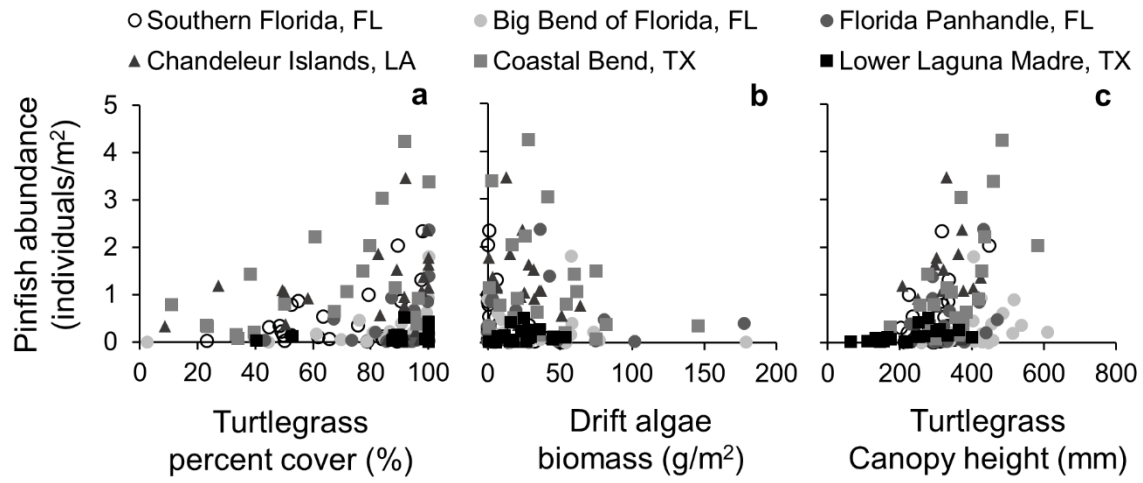
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Legend: ○ Southern Florida, FL   ● Big Bend of Florida, FL   ● Florida Panhandle, FL
▲ Chandeleur Islands, LA   ■ Coastal Bend, TX   ■ Lower Laguna Madre, TX

Panel a: Pigfish abundance (individuals/m²) vs Turtlegrass percent cover (%)
Panel b: Pigfish abundance vs Turtlegrass shoot density (shoots/m²)
Panel c: Pigfish abundance vs Salinity
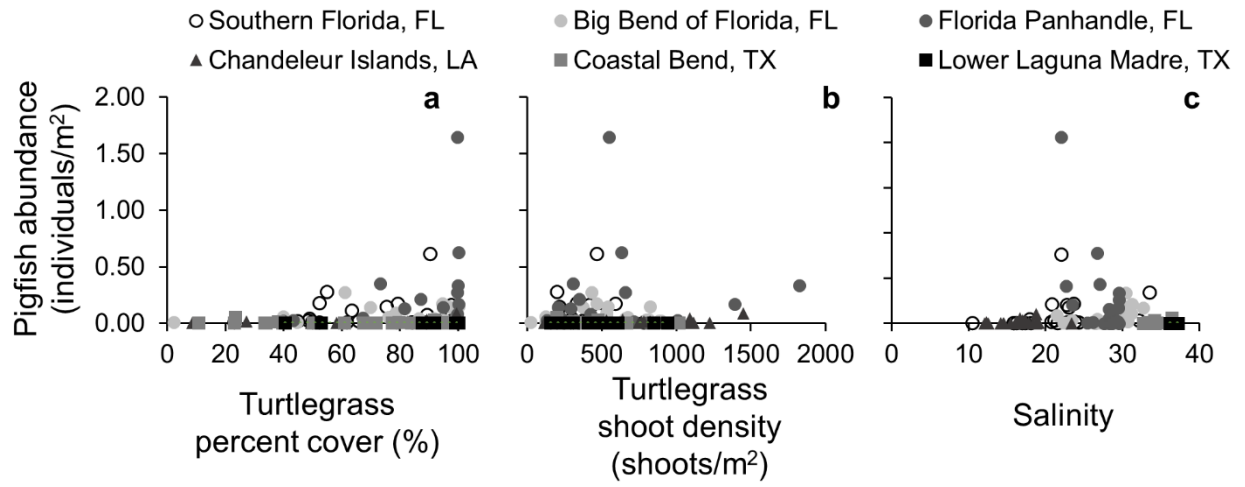
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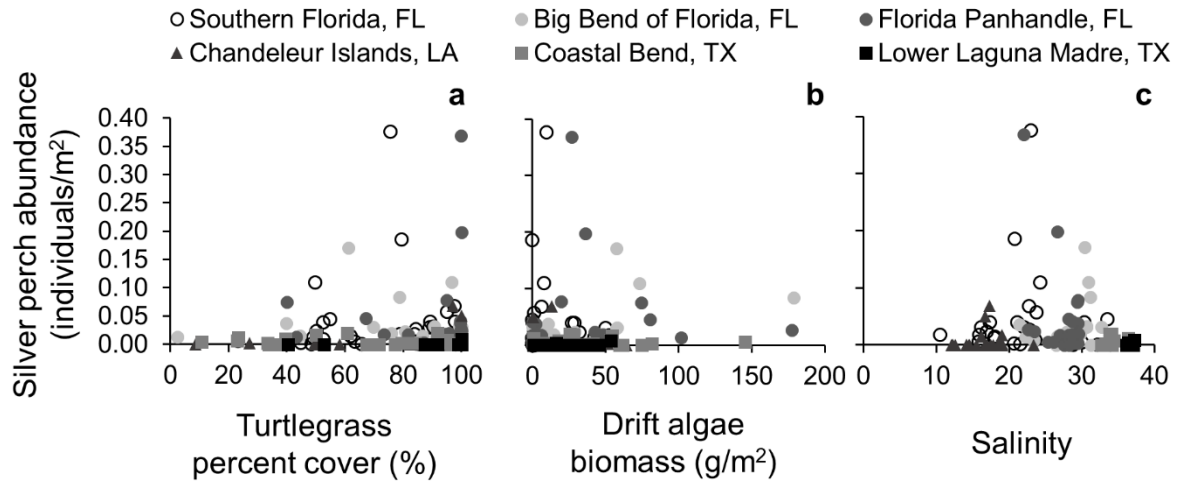
Figure 3

Southern Florida, FL   Big Bend of Florida, FL   Florida Panhandle, FL
Chandeleur Islands, LA   Coastal Bend, TX   Lower Laguna Madre, TX

Silver perch abundance (individuals/m²)

a Turtlegrass percent cover (%)

b Drift algae biomass (g/m²)

c Salinity

830   Figure 4

Legend:
○ Southern Florida, FL   ● Big Bend of Florida, FL   ● Florida Panhandle, FL
▲ Chandeleur Islands, LA   ■ Coastal Bend, TX   ■ Lower Laguna Madre, TX

Y-axis: Pipefish abundance (individuals/m²)

Panel a: Turtlegrass percent cover (%)
Panel b: Drift algae biomass (g/m²)
Panel c: Salinity
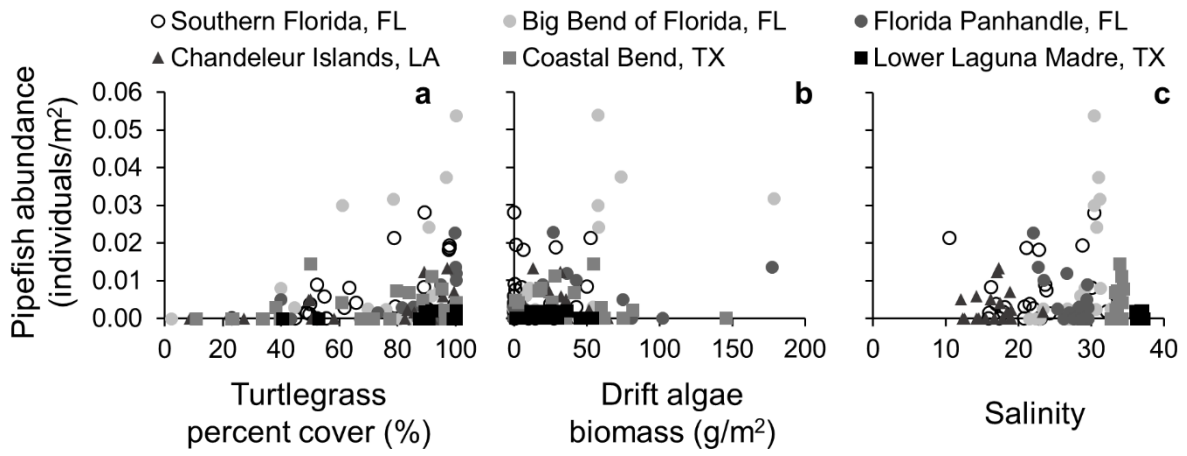
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850   Figure 5

Figure 5
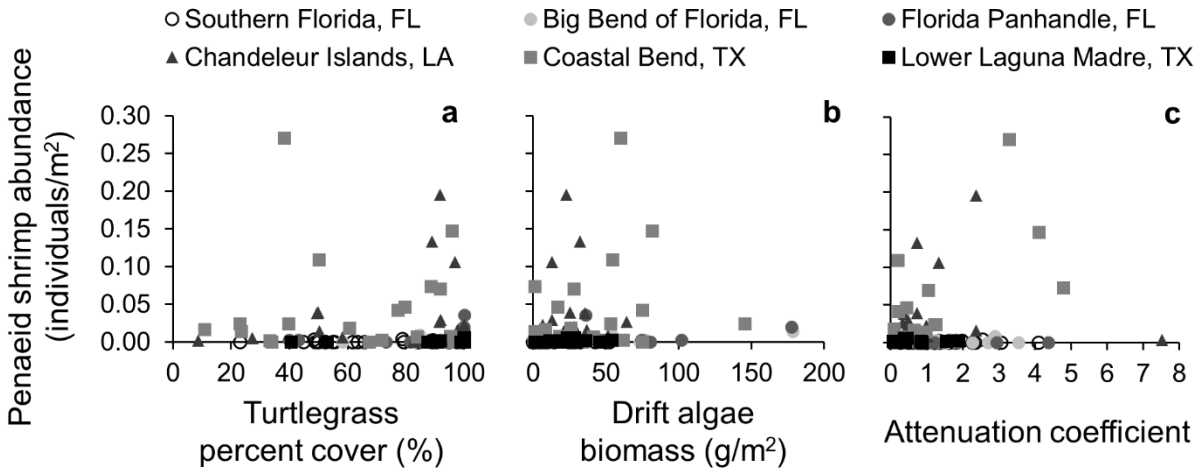
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Electronic Supplemental Material

Environmental drivers of seagrass-associated nekton abundance across the northern Gulf of Mexico

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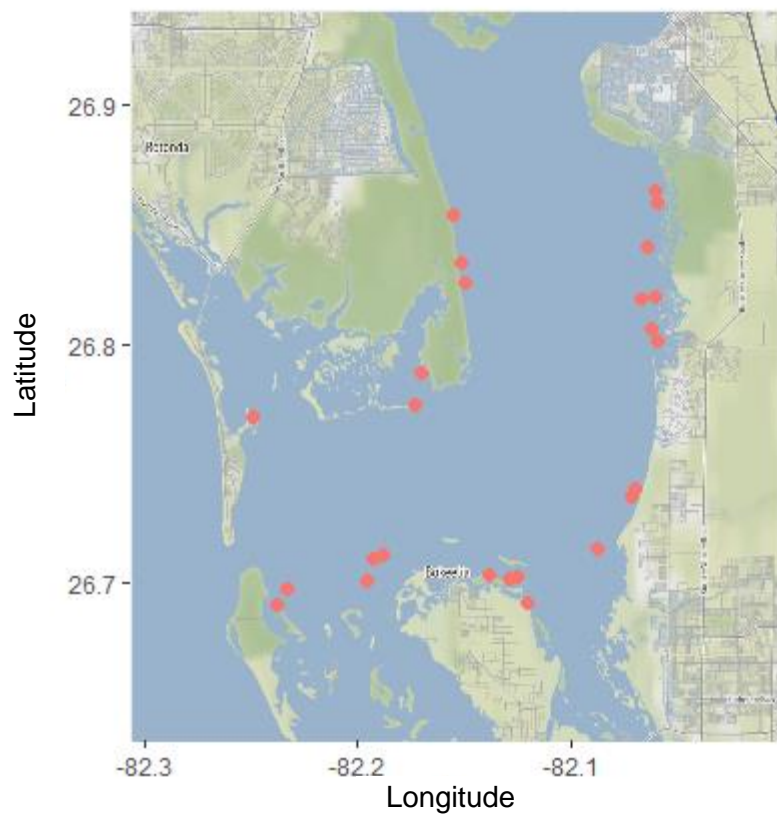
Figure S1: Location of sampling stations in Southern Florida (Charlotte Harbor; n = 25).
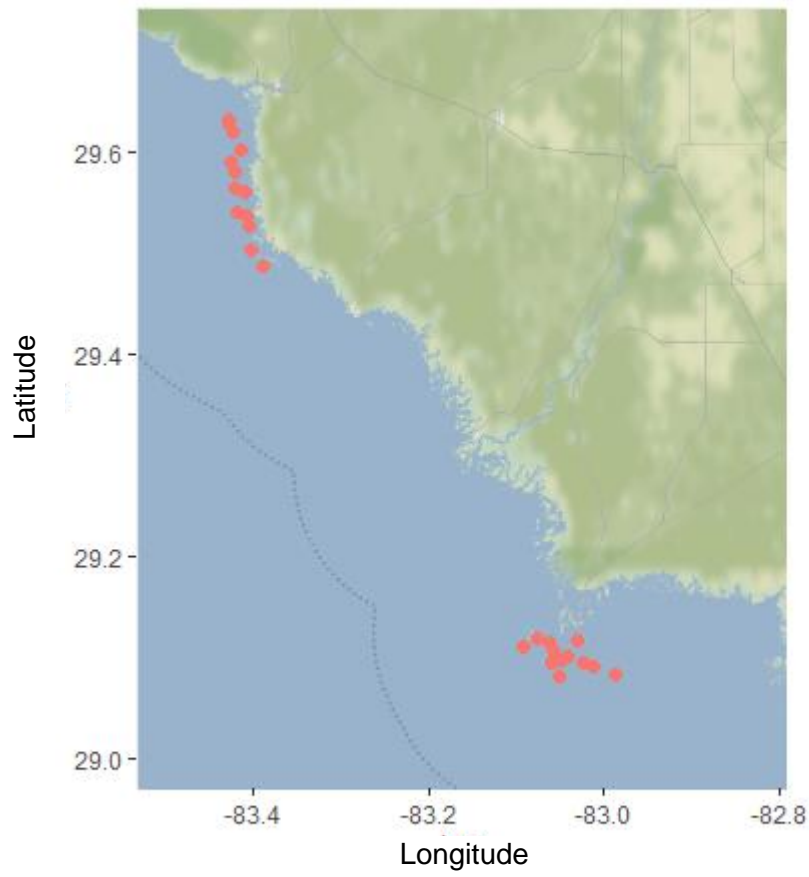
Figure S2: Location of sampling stations in Big Bend of Florida (Cedar Key; n = 25).
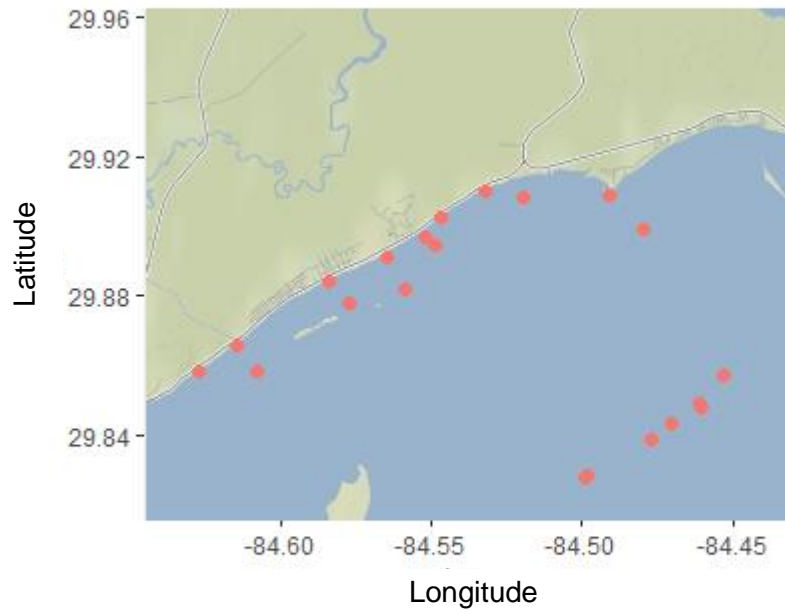
Figure S3: Location of sampling stations in Florida Panhandle (Apalachicola Bay; n = 21).

Chandeleur Islands, LA
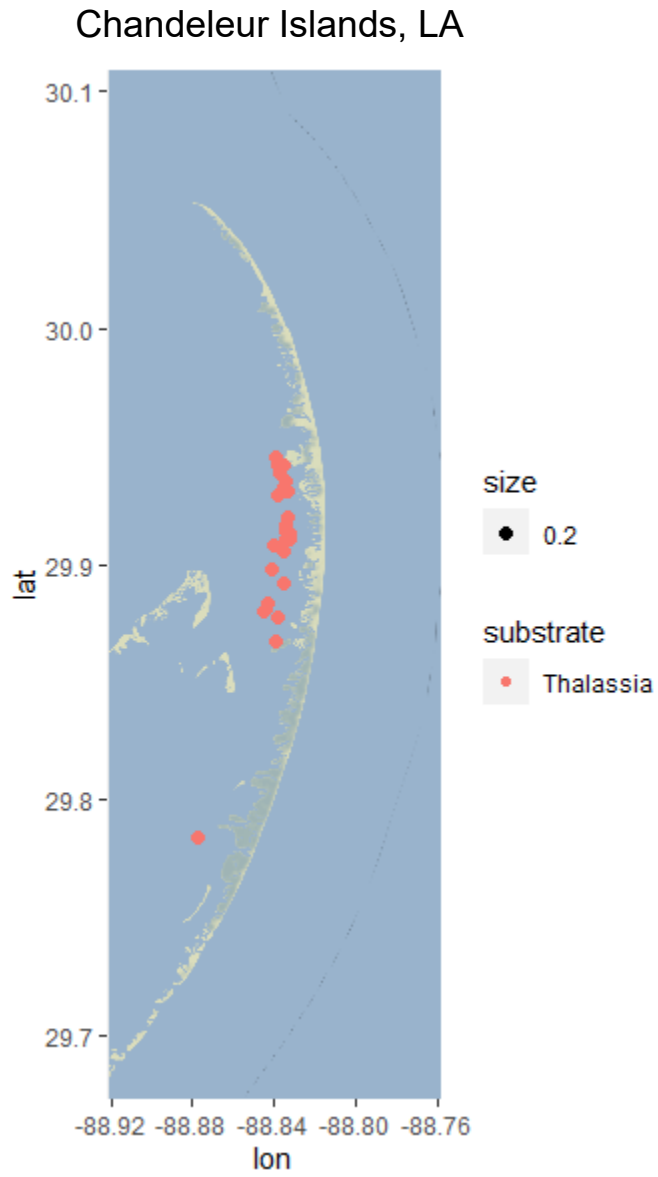
Figure S4: Location of sampling stations in Louisiana (Chandeleur Islands; n = 24).
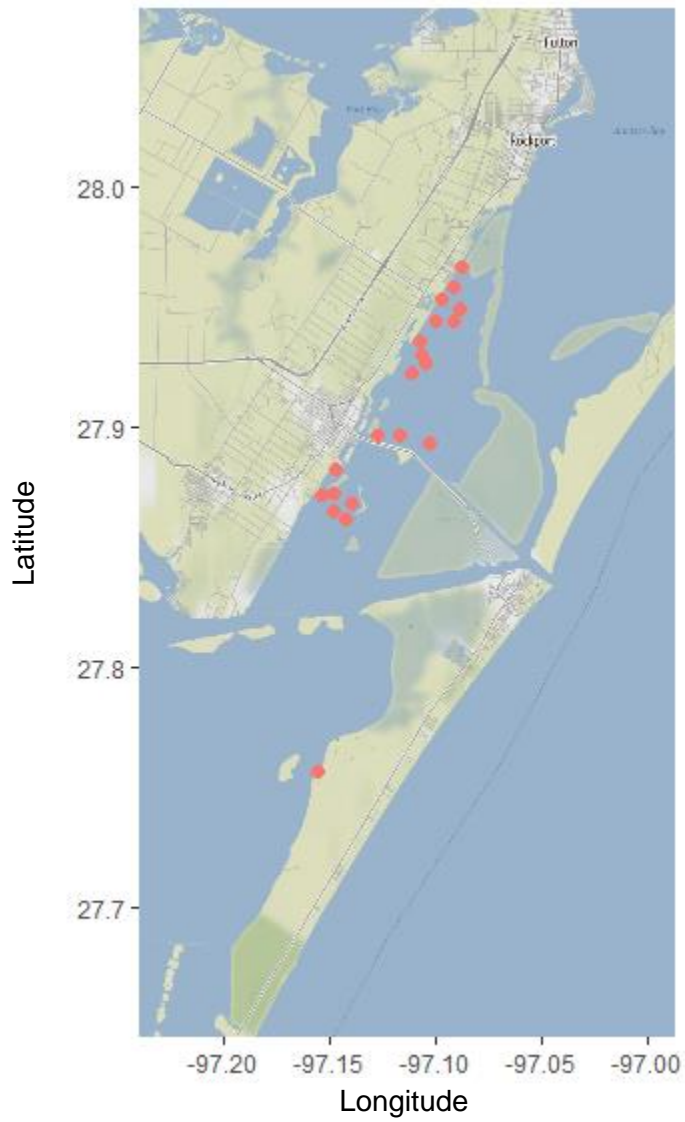
Figure S5: Location of sampling stations in Coastal Bend Texas (Corpus Christi Bay; n = 20).

Figure S6: Location of sampling stations in Lower Laguna Madre Texas (n = 20).

Table S1: Total abundance and size range (mm) of eight common species caught in trawls throughout the northern Gulf of Mexico, May 2018.

| Species	Total Abundance	Size Range (mm)
Pinfish - *Lagodon rhomboides*	38,383	20-245
Pigfish - *Orthopristis chrysoptera*	3,064	16-268
Silver Perch - *Bairdiella chrysoura*	1,369	25 - 190
Gulf pipefish - *Syngnathus scovelli*	99	65-199
Dusky pipefish - *Syngnathus floridae*	146	40-244
Chain pipefish - *Syngnathus louisianae*	29	85-215
Brown shrimp - *Penaeus aztecus*	733	12-98
Pink shrimp - *Penaeus duorarum*	55	35-93
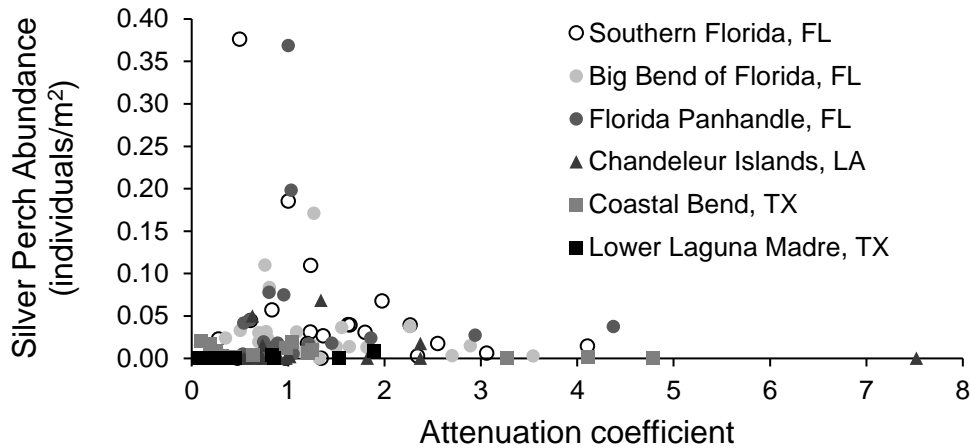
Figure S7: Silver Perch (*Bairdiella chrysoura*) density (individuals·m^{-2}) as a function of water attenuation coefficient across six field sites spanning the Gulf of Mexico.
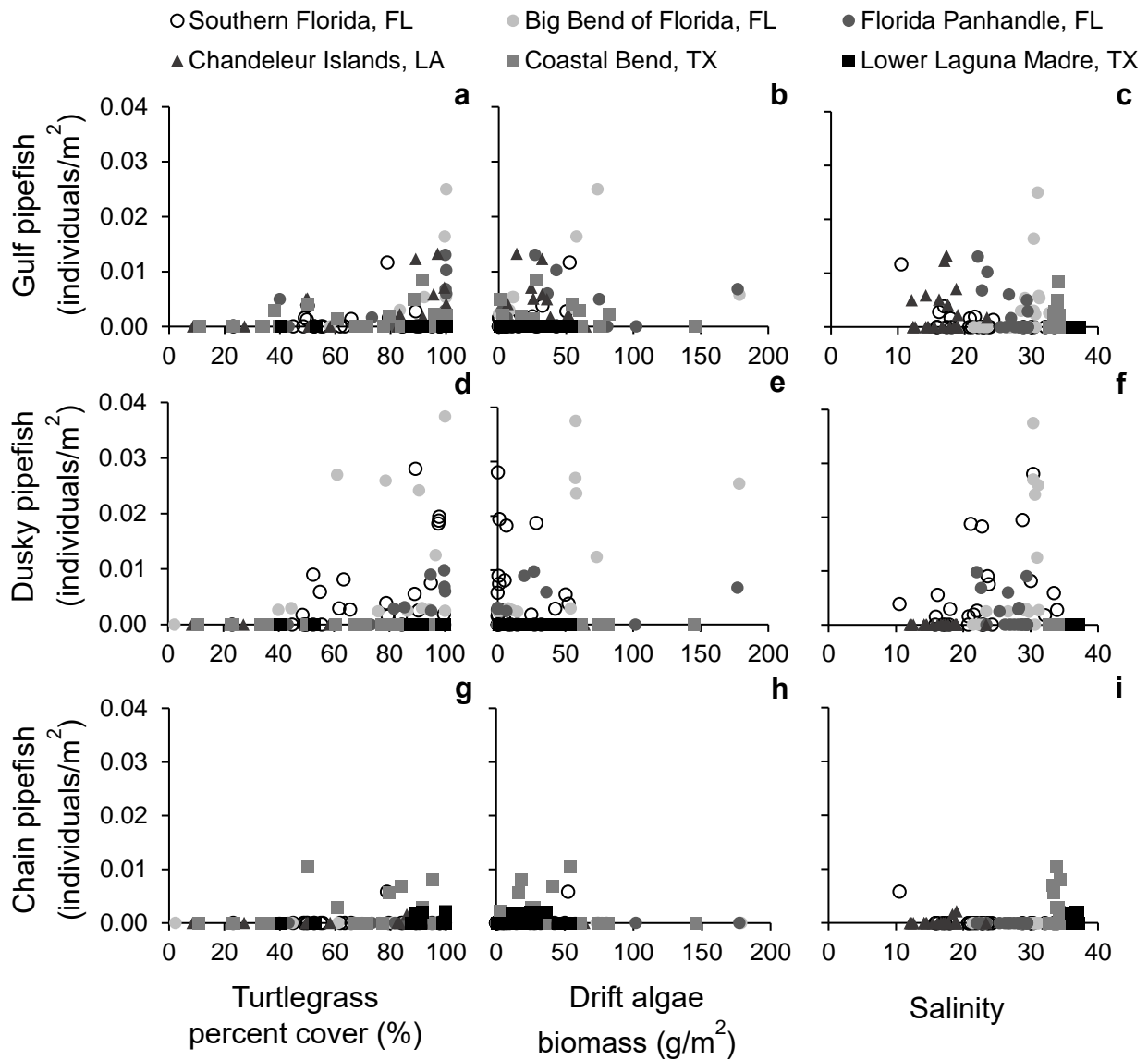
Figure S8: Gulf (*Syngnathus scovelli*), dusky (*Syngnathus floridae*), and chain pipefish

(*Syngnathus louisianae*) density (individuals·m^{-2}) as a function of the top three drivers **a,d,g)**

turtlegrass percent cover (%), **b,e,h)** drift algae biomass (g·m^{-2}), and **c,f,i)** salinity across six field

sites spanning the Gulf of Mexico (n = 20 - 25 per site).
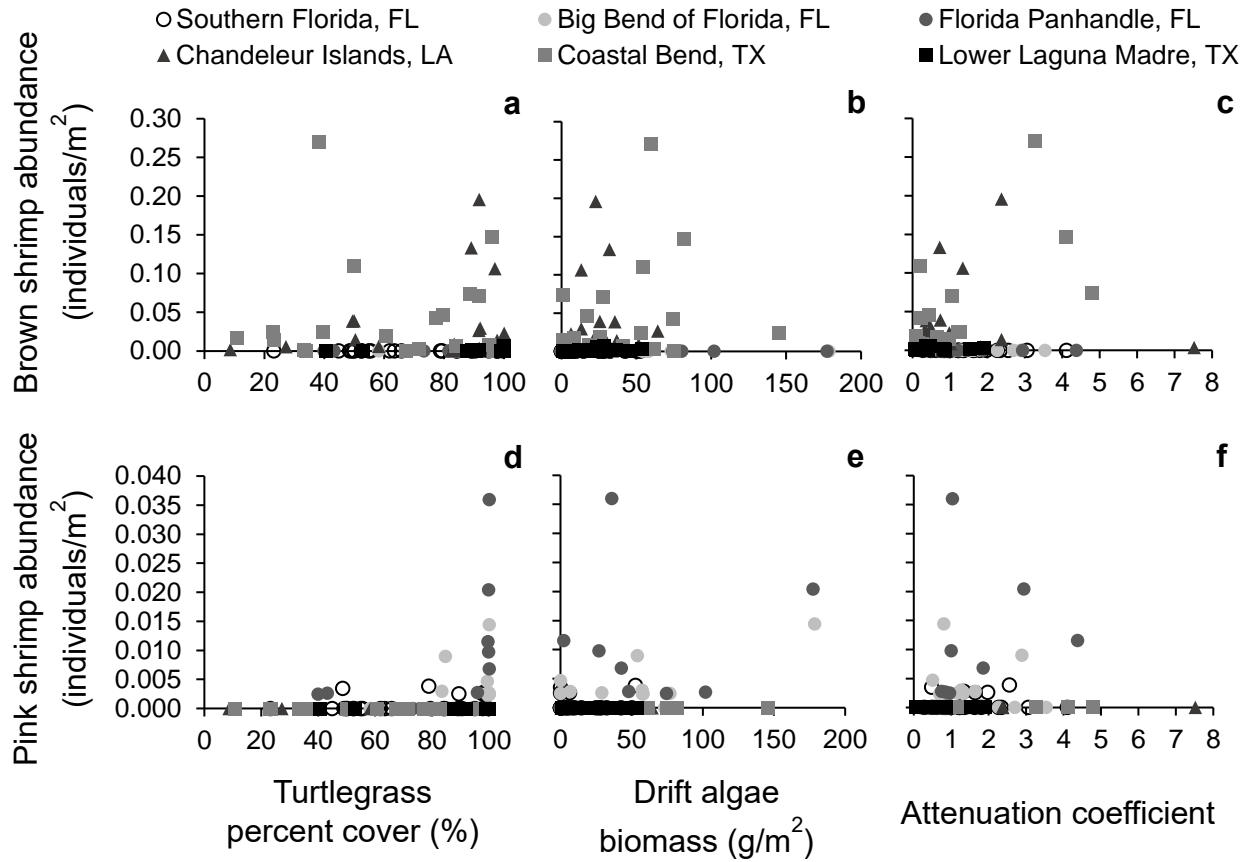
Figure S9: Brown shrimp (*Penaeus aztecus*) and pink shrimp (*Penaeus duorarum*) density (individuals·m^{-2}) as a function of the top three drivers **a,d)** turtlegrass percent cover (%), **b,e)** drift algae biomass (g·m^{-2}), and **c,f)** attenuation coefficient across six field sites spanning the Gulf of Mexico (n = 20 - 25 per site).

Table S2: Statistical results from generalized additive mixed models examining the influence of turtlegrass percent cover, shoot density, canopy height, drift algae biomass, water temperature, salinity, dissolved oxygen (DO), and light attenuation coefficient on the abundance of gulf (*Syngnathus scovelli*) and dusky pipefish (*Syngnathus floridae*) as well as brown (*Penaeus aztecus*) and pink shrimp (*Penaeus duorarum*). There were not enough captured chain pipefish (*Syngnathus louisianae*) for statistics. [b] denotes X^2 values were replaced with F-values.

|	Environmental Parameters															
Species	Turtlegrass percent cover		Turtlegrass shoot density		Turtlegrass canopy height		Drift algae biomass		Temperature		Salinity		DO		Attenuation coefficient	
	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p
Gulf Pipefish[b]	5.60	**0.0198**	1.63	0.1543	1.17	0.3330	2.62	0.0637	1.77	0.1073	3.74	**0.0120**	1.32	0.2607	0.36	0.5499
Dusky Pipefish[b]	3.62	**0.0094**	2.18	0.1431	2.72	**0.0488**	6.47	**0.0015**	1.17	0.2828	3.35	**0.0187**	2.86	**0.0303**	2.55	**0.0492**
Brown Shrimp	22.23	**<0.0001**	6.90	**0.0087**	67.8	**<0.0001**	62.6	**<0.0001**	54.8	**0.0001**	5.75	**0.0165**	36.7	**<0.0001**	49.5	**<0.0001**
Pink Shrimp	16.36	**0.0184**	0.08	0.7819	5.45	0.1739	16.9	**0.0030**	3.06	0.0805	15.0	**0.0337**	2.53	0.1114	8.11	**0.0346**
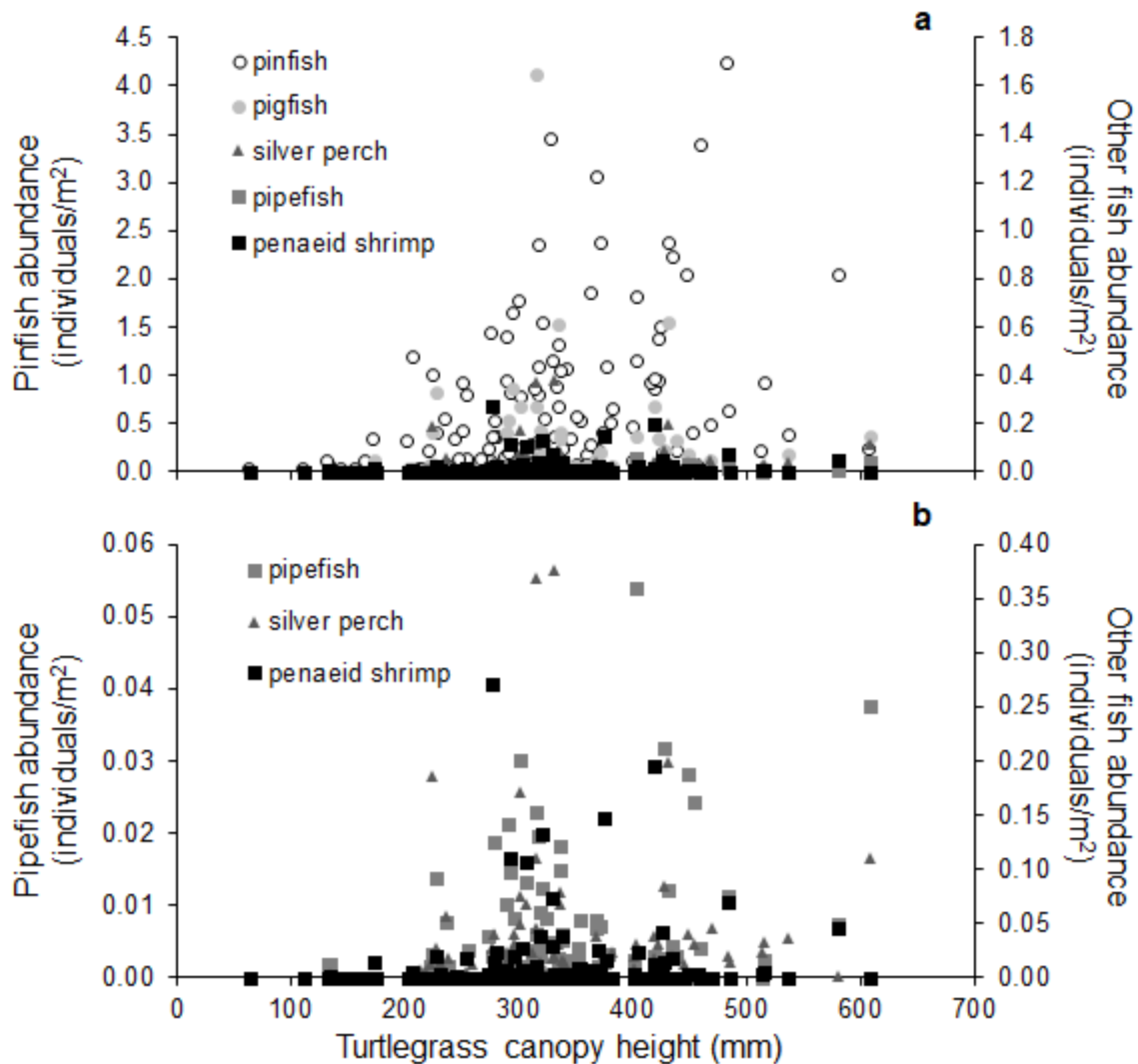
Figure S10: a) Density (individuals·m^{-2}) of pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), silver perch (*Bairdiella chrysoura*), Pipefish (*Syngnathus* spp.), and penaeid shrimp (*Penaeus* spp.) across turtlegrass canopy height (mm). Panel **b)** contains only silver perch, pipefish, and penaeid shrimp abundances to better illustrate abundance similarities (n = 134 for each species).
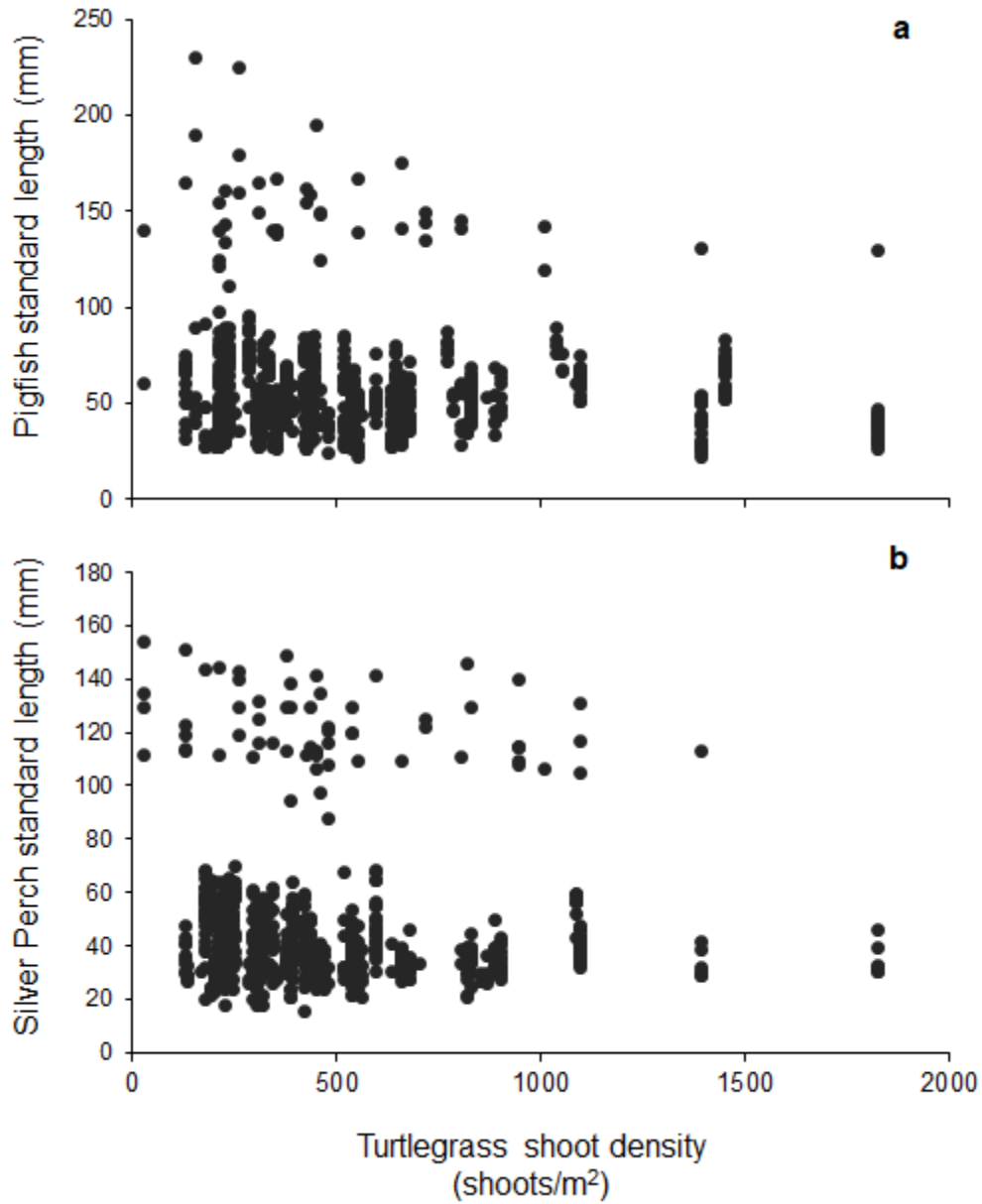
Figure S11: Individual standard length (mm) of randomly measured **a)** pigfish (*Orthopristis chrysoptera*), and **b)** silver perch (*Bairdiella chrysoura*) collected across turtlegrass shoot density (shoots·m^{-2}) within six field sites spanning the Gulf of Mexico (n = 988 and 829 respectively).

Figures showing site coordinates were created using the R package: ggmap. (Kahle and Wickham, 2013).

References

Kahle, D. and Wickham, H. 2013. ggmap: Spatial Visualization with ggplot2. *The R Journal* 5: 144-161.