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Recruitment enhancement varies by taxonomic group and oyster reef habitat characteristics

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17

18 **Abstract**

19   The rapid loss of coastal and estuarine biogenic habitats has reduced the delivery of

20 valuable ecosystem services, resulting in calls for increased habitat restoration. Yet, a lack of

21 information on how key habitat characteristics (e.g., area, vertical relief, age) influence the

22 ability of restored habitats to deliver these ecosystem services hinders efforts to maximize the

23 return on restoration investments. We conducted a meta-analysis to assess the influence of reef

24 type (natural or restored), taxa, and restored reef size, vertical relief, age, and tidal zone on the

25 presence and magnitude of recruitment enhancement for nekton (i.e. fish and swimming crabs).

26 Both intertidal and subtidal reefs, as well as restored and natural reefs, enhanced nekton

27 recruitment, though there was variation among taxonomic groups with reef types. Recruitment

28 enhancement was more common across taxa on restored (six families) than on natural (one

29 family) reefs. Resident nekton families were more consistently enhanced than transient families.

30 Nekton enhancement varied with a number of restored reef characteristics. Recruitment

31 enhancement increased with greater reef size across taxa, decreased with higher vertical relief for

32 two families, and showed maximum recruitment around a single intertidal reef age for one

33 family, and minimum recruitment around a single subtidal reef age for three families.

34 Understanding variation across species in response to key design elements will improve

35 restoration success and enhance return on investment. Moving forward, we recommend studies

36 that vary reef habitat characteristics independently and in combination to identify how variation

37 in these characteristics interact to influence nekton recruitment enhancement by oyster reefs.

38

39 ***Keywords***: *habitat restoration, meta-analysis, nekton, oyster reef, recruitment enhancement, reef*

40 *size, reef age, design, vertical relief*

41

42

Introduction

43

44   Coastal ecosystems consist of landscapes of biogenic habitats (e.g*.,* oyster reefs, corals,

45 salt marshes, mangroves, and seagrasses) that provide a range of ecosystem functions. They

46 serve as nursery and foraging grounds for fish and invertebrates (Coen et al. 1999; Beck et al.

47 2001; Soniat et al. 2004), regulate energy flow and nutrient fluxes (Dame et al. 1984; Piehler and

48 Smyth 2011; Kellogg et al. 2013), stabilize shorelines and slow erosion (Meyer et al. 1997;

49 Piazza et al. 2005), reduce storm surge water levels (Krauss et al. 2009), and enhance biological

50 diversity (Wells 1961; Bahr and Lanier 1981; functions are reviewed in Powers and Boyer

51 2014). These ecosystem functions result in a host of associated services, such as enhancing

52 economically valuable fisheries (Peterson et al. 2003, zu Ermgassen et al. 2016), protecting

53 shorelines and infrastructure (Meyer et al. 1997; Krauss et al. 2009; Scyphers et al. 2011),

54 enhancing water quality by removing excess nitrogen (Piehler and Smyth 2011), and providing

55 cultural benefits such as enhancing recreational opportunities (Carlton et al. 2016; services are

56 reviewed in Barbier et al. 2011; Martin et al. 2016). However, degradation and loss of biogenic

57 habitats are intensifying as human populations continue to grow and exert more pressure on

58 coastal systems, leading to reduced aerial extent and complexity of these biogenic habitats and

59 threatening the critical ecosystem functions they provide (Alongi 2002; Waycott et al. 2009; zu

60 Ermgassen et al. 2012, 2013). To combat these impacts and restore ecosystem functions, habitat

61 restoration is increasingly employed as a tool (Peterson and Lipcius 2003). Although there are

62 many examples of successful habitat restoration efforts (e.g., oysters in protected areas, Powers

63 et al. 2009; seagrasses in Chesapeake Bay, Lefcheck et al. 2018), overall success rates for many

64 projects, including those in coastal habitats, are moderate (Bayraktarov et al. 2016), and

65 ecosystem functions may remain reduced in restored versus intact habitats (Rey Benayas et al.

66 2009). Understanding how particular ecosystem functions vary across a range of restored habitat

67 characteristics (e.g., areal extent, age) can inform future habitat restoration efforts by helping

68 decision-makers better predict how restoration design elements may influence service delivery.

69   Re-establishing biodiversity is a common goal of habitat restoration (Peterson and

70 Lipcius 2003; Rey Benayas et al. 2009), yet distribution patterns of fauna among patchy habitats

71 are difficult to predict because they are shaped by processes occurring at various scales of space,

72 time, and ecological organization that often differ from the scales at which patterns are observed

73 (Levin 1992). Understanding how restoration design influences faunal abundances across

74 multiple taxa will enhance the ability of restoration practitioners to increase the return on

75 investments made by future conservation and restoration efforts. Oyster reefs are broadly

76 distributed and augment populations of many faunal species (Zimmerman et al. 1989; Coen et al.

77 1999; Rodney and Paynter 2006). Although many studies have documented augmented faunal

78 abundances by oyster reefs, the degree of enhancement varies considerably among studies,

79 species, and ocean basins (e.g., Robillard et al. 2010; Kingsley-Smith et al. 2012; Nevins et al.

80 2014; synthesized in zu Ermgassen et al. 2016). This variation in recruitment enhancement could

81 stem from several differences among studies due to varying habitat characteristics, including reef

82 areal extent, vertical relief, tidal zone (e.g., subtidal vs. intertidal) tidal elevation, salinity, or

83 landscape setting (Lenihan 1999; Lenihan et al. 2001; Lehnert and Allen 2002; Grabowski et al.

84 2005), but the potential role of these factors has yet to be thoroughly examined.

85   We synthesized information from Eastern Oyster (*Crassostrea virginica*) restoration

86 studies across the U.S. to assess the potential influence of habitat characteristics incorporated

87 into reef restoration designs on the abundance of reef-associated nekton (specifically fish and

88 swimming crabs in association with oyster reefs). Augmentation of nekton can occur through

89 recruitment enhancement of early life stages (which includes improved settlement, growth, and

90 survival of juveniles; Beck et al. 2001), or enhanced growth and reproductive effort of adults

91 (e.g., by concentrating food resources and enhancing foraging and spawning opportunities;

92 Peterson et al. 2003, Powers et al. 2003) relative to unstructured habitats. Because growth

93 enhancement likely contributes far less to lifetime augmented nekton production by oyster reefs

94 than recruitment enhancement (Peterson et al. 2003, zu Ermgassen et al. 2016), our synthesis

95 focused on recruitment enhancement. We specifically examined whether reef recruitment

96 enhancement varies by taxonomic group and 1) reef type (i.e., natural or restored reefs) or 2) the

97 size, vertical relief, or age of restored reefs. Our ultimate goal was to provide information for

98 resource managers to guide future habitat restoration efforts.

99

100 **Methods**

101 *Literature review*

102 First, we determined the variety of reef characteristics reported by studies investigating

103 nekton recruitment enhancement by oyster reefs using citations from the reference list of a

104 recently completed meta-analysis (zu Ermgassen et al. 2016). We identified nekton families that

105 were regularly reported at oyster reef and control habitats, including both resident (i.e., species

106 that feed, breed, and shelter on reefs long after initial recruitment, Coen et al. 1999; Harding and

107 Mann 2000) and transient (i.e., species that recruit to structured habitats but are more widely

108 distributed across multiple habitats after recruitment, Harding and Mann 2001) reef-associated

109 species. We also performed forward searches in Google Scholar on two published syntheses:

110 Peterson et al. (2003) and zu Ermgassen et al. (2016). We retained studies that met the following

111 criteria: 1) authors quantified density or relative abundance of target nekton families at both

112   oyster reefs (or experimental units that contained oyster shell and served as a mimic for reef

113   habitat; e.g., Humphries et al. 2011) and unstructured mud or sand habitats within the same

114   study; 2) restored reefs used oyster shell, including shell piles, cultch, bagged shell, or shell piles

115   from other species (e.g., surf clams) if topped by oyster shell; 3) restored reefs were within the

116   tidal extent of natural reefs (< 10 m deep relative to mean low water [MLW] at the base of the

117   reef; Kennedy and Sanford 1999) , 4) fishing gear(s) quantitatively censused juveniles; and 5)

118   authors reported densities or abundances of target nekton by species or family.

119   *Data Extraction*

120   We extracted densities or abundances, measures of spread (standard deviation or standard

121   error), and sample sizes of each nekton species from oyster reefs and their paired unstructured

122   control habitat patches. We extracted data for nine nekton families, including reef residents:

123   toadfish (Batrachoididae), blennies (Blenniidae), gobies (Gobiidae), and skilletfish

124   (Gobiesocidae, which were later removed due to limited data availability); and reef transients:

125   grunts (Haemulidae), snappers (Lutjanidae), swimming crabs (Portunidae), drums (Sciaenidae),

126   and porgies (Sparidae; Table 1). We normalized densities to mean individuals m^{-2}, abundances to

127   mean individuals per sample (relative abundances), and measures of spread to one standard error

128   of the mean (Appendix B). We extracted tidal zone (subtidal or intertidal), reef type (restored or

129   natural), restoration method (reefs restored with or without live oysters), and when available, reef

130   size (standardized to m^2), vertical relief (distance from bare sediment to the highest point on the

131   reef, standardized to m), tidal elevation (at the base of the reef, in m relative to MLW), adult

132   oyster density (individuals m^{-2} > 75 mm in shell height, or specified as adult by the authors), and

133   the year of restored reef construction, from which we calculated reef age (Table A1; Appendix

134   B).

Analyses

136   To compare nekton recruitment to oyster reefs versus unstructured control habitat, we

137   calculated log response ratios (LRRs, Hedges et al. 1999) with 95% confidence intervals by

138   family (Appendix B). An LRR with CIs > 0 implies that nekton recruitment was enhanced by

139   oyster reefs, an LRR with CIs < 0 implies the opposite, and an LRR with CIs that include 0

140   implies no difference in recruitment between oyster reef and control habitats. For each research

141   question, we assessed data publication bias with funnel plots (Appendix C) and data availability

142   with mosaic and violin plots (Appendix D).

143   To assess whether recruitment enhancement varied as a function of reef type (natural or

144   restored) and nekton family, we conducted linear mixed model analyses separately for intertidal

145   and subtidal reefs that included two categorical factors (reef type and nekton family) and their

146   interaction as fixed effects, with study as a random effect. We conducted mixed model analyses

147   separately by tidal zone since subtidal and intertidal habitats harbor different nekton

148   communities (Lehnert and Allen 2002), and subtidal and intertidal oyster reefs are distributed

149   unevenly in our database: intertidal reefs are more prevalent on the Atlantic coast and subtidal

150   reefs are more common in the Gulf of Mexico (Fig. 1; Tab. A1). Furthermore, the reef

151   characteristics in our database differed across tidal zones (Fig. D1-D12). We removed any family

152   that was represented by fewer than three independent studies and/or fewer than 10 independent

153   LRRs ("NA" on Fig. 2). Results of randomization and resampling in support of these criteria are

154   presented in Appendix E.

155   To evaluate the effects of restored reef characteristics (i.e., reef size, vertical relief, and

156   age) on recruitment enhancement, we focused on restored reefs only, and performed linear mixed

157   effect regression models with orthogonal polynomials (first and second order) for the continuous

158 reef characteristics as fixed effects, and study as a random effect. We conducted separate

159 analyses for each reef characteristic, nekton family, and tidal zone. We did not model families

160 represented by fewer than three independent studies and/or 10 independent LRRs covering

161 different values of the reef characteristics (e.g., reef sizes, vertical reliefs, or ages; "insufficient

162 data" in Figs. 3-8), and results are not reported or plotted for models that did not converge.

163 Since not all families were represented at all values of each reef characteristic (e.g., all vertical

164 reliefs or sizes), we performed separate analyses for each family and included all available data

165 (but for combined-family approaches, see Appendix B for methods and Appendix E for results).

166 We also examined the influence of tidal elevation on recruitment enhancement for each family

167 using linear mixed effect regression models with orthogonal polynomials (first and second order)

168 for tidal elevation as a fixed effect and study as a random effect (Appendix E). Where models

169 indicated that predictor variables are on substantially different scales (i.e. reef size) we rescaled

170 using natural log transformation.

171 All models were weighted by sample size (Appendix B). All analyses were conducted in

172 R 3.6.1 (R Core Team, 2019) on the RStudio IDE 1.2.1335 (RStudio Team, 2019).

173

174 **Results**

175 We extracted density or relative abundance comparisons from 28 studies (Table A1) that

176 generated 1,820 LRRs across eight target nekton families (excluding skilletfish), represented by

177 51 species (Table 1). Studies were distributed along the Atlantic and Gulf of Mexico coastlines

178 from New Jersey to Texas, USA, across 25 embayments (Fig. 1). Funnel plots indicated no

179 evidence of publication bias (Fig. C1).

180 ***Restored vs. natural reefs (reef type)***

181   Recruitment enhancement on intertidal reefs varied interactively by family and reef type

182   (Fig. 2a; family * reef type, $F_{4,790} = 8.25$ p < 0.001). In the intertidal, recruitment was frequently

183   enhanced on restored reefs (i.e., LRR > 0 for two resident families: toadfish and blennies and

184   three transient families: grunts, snappers and porgies; Fig. 2a), but not on natural oyster reefs

185   (i.e., LRR = 0; Fig. 2a). Recruitment enhancement on subtidal reefs varied by family and was

186   marginally related to reef type, but not their interaction (Fig. 2b; family, $F_{3,513} = 8.19$, p < 0.001;

187   reef type, $F_{1,11} = 3.53$ p = 0.09; family * reef type, $F_{3,513} = 1.81$, p = 0.15). Five families (three

188   resident: toadfishes, blennies, and gobies; two transient: grunts and porgies) were enhanced at

189   subtidal restored reefs (Fig. 2b), and one resident family (blennies) was enhanced on subtidal

190   natural reefs (Fig. 2b). Swimming crabs were more abundant on unstructured sedimentary habitat

191   than natural reefs in both intertidal and subtidal zones (i.e., LRR < 0; Fig. 2a-b), though they did

192   not differ between restored reefs and unstructured habitat in either zone (Fig. 2a-b). In the

193   subtidal zone, drums were more abundant on unstructured sedimentary habitat than restored reefs

194   but did not differ between natural reefs and controls (Fig. 2b).

195   *Restored reef characteristics (reef size, vertical relief, and age)*

196   Recruitment enhancement differed with reef size for only one family (blennies; Fig. 3-4).

197   On intertidal reefs, there was no relationship between blenny recruitment and reef size (natural

198   log transformed). On subtidal reefs, there was a marginal U-shaped relationship between blenny

199   recruitment enhancement and subtidal reef size ($t_{54.7} = 1.78$, p = 0.08), with recruitment

200   enhancement decreasing from 0.5 m^2 to 28.3 m^2 and increasing from 28.3 m^2 to 50.3 m^2 (Fig.

201   4b).

202   Recruitment enhancement of several families (grunts, drums, and blennies) varied with

203   reef vertical relief (Fig. 5-6). Drum enhancement varied with vertical relief on intertidal reefs in

204   a U-shaped pattern (Fig. 5g, $t_{6.9}$ = 2.66, p = 0.03), though a single experiment, at a vertical relief

205   of 0.48 m with 20 independent replicates, appears to drive this relationship (Fig. 5g).

206   Enhancement of blennies on subtidal reefs tended to decrease with increasing vertical relief (Fig.

207   6b; $t_{6.6}$ = -1.96, p = 0.09). On subtidal reefs, drum enhancement decreased as vertical relief

208   increased (Fig. 6g; $t_{7.44}$ = -2.52, p = 0.04).

209   Recruitment enhancement of some families was also correlated with reef age (Figs. 7-8).

210   On subtidal reefs, toadfish enhancement varied with reef age in a U-shaped pattern, decreasing

211   from reefs that were between 0 and approximately 4 years of age, and then increasing from reefs

212   aged approximately 4 to 6 years ($t_{77.6}$ = 2.43, p = 0.02; Fig. 8a). Drum enhancement responded

213   similarly to reef age on subtidal reefs ($t_{126.8}$ = 7.25, p < 0.0001; Fig. 8g), decreasing from 0- to 4-

214   year-old reefs, then increasing on six-year-old reefs (Fig. 8g). Porgy enhancement on subtidal

215   reefs also varied similarly with reef age ($t_{56.2}$ = 2.56, p = 0.01; Fig. 8h), decreasing on reefs

216   between 0- to 3-years old, and then increasing on six-year-old reefs (Fig. 8h). Porgy

217   enhancement on intertidal reefs tended to vary with reef age in a hump-shaped pattern (Fig. 7h,

218    $t_{17.7}$ = -2.04, p = 0.06), with recruitment enhancement increasing from 0 to 7 years, and

219   decreasing from 7 to 13 years.

220

221   **Discussion**

222   Our analyses confirmed that both natural and restored oyster reefs enhance nekton

223   recruitment, and we further demonstrate that the magnitude of this enhancement is as strong or

224   stronger on restored reefs as natural reefs for five nekton families (Fig. 2). The magnitude of

225   enhancement also varied by family and tidal zone and key characteristics of restored reef design

226   (i.e., reef size, reef vertical relief, and reef age) also influenced recruitment enhancement of

227 fishes and swimming crabs. Nekton recruitment enhancement tended to increase with intertidal

228 reef size, though increases in vertical relief decreased enhancement, particularly at subtidal reefs.

229 Enhancement of many nekton species occurred immediately, though enhancement of porgies

230 peaked around 6 years on intertidal reefs, and enhancement of toadfish, drums and porgies was

231 lowest at intermediate ages (about 3-4 years) on subtidal reefs. Further data are needed to

232 examine whether recruitment enhancement is sustained over longer time periods.

233   Review of past restoration projects suggest that enhancement of nekton recruitment is

234 generally greater on restored than on natural reefs. The enhancement by restored reefs supports

235 earlier findings that nekton communities respond rapidly to oyster reef restoration efforts

236 (Lenihan et al.2001; Grabowski et al. 2005; La Peyre et al. 2014) and highlights the utility of reef

237 restoration as a technique to recover nekton abundances. We do not know why restored reefs

238 more consistently augmented nekton than natural reefs, but past or current exposure of natural

239 reefs to destructive harvesting practices that reduced their habitat quality may have contributed

240 to this difference. Given the dramatic losses of oyster populations to overharvesting and other

241 contributing factors (reviewed in Kirby 2004), remaining natural reefs may be degraded and

242 exhibiting reduced function (zu Ermgassen et al. 2012; 2013), whereas restored reefs are often

243 protected from harvest (e.g., Dunnigan 2015). Only 10 of 29 studies in our analysis reported

244 susceptibility to harvest, with even fewer providing specific harvest methods and amounts,

245 precluding an analysis of the effects of harvest on nekton recruitment enhancement in this study.

246   Habitat patch size can mediate the population dynamics of mobile species (Hanski 1999):

247 larger habitat patches have lower metapopulation extinction rates (MacArthur and Wilson 1967,

248 Hanski 1999) and alleviate negative edge effects in fragmented landscapes (Reis 2004). Thus, we

249 expected enhancement of fish and mobile crustacean recruitment to increase with restored reef

250 (patch) size. Our analyses of individual families were not significant but there were positive

251 trends at intertidal reefs, and our combined-family analysis provided additional support that

252 recruitment enhancement increases with intertidal reef size (Fig. E2a). For subtidal reefs, the

253 influence of reef size was taxon-dependent (Fig E2b), consistent with findings from the habitat

254 fragmentation literature (Eggleston et al. 1999; Johnson and Heck 2006). Relationships between

255 fish recruitment enhancement and reef size may be more consistent within a region than across

256 regions. For instance, the density of commercial fishes within marine reserves increased with

257 reserve size when marine reserves within a single region were compared to unprotected spaces

258 (Edgar and Barrett 1997; Claudet et al. 2008), yet Lester et al. (2009) found no relationship

259 between density enhancement and MPA size when synthesizing MPAs globally. Additionally, an

260 over-representation of small reef sizes in our analysis, as in the global analysis of MPAs (Lester

261 et al. 2009), may have hindered our ability to detect an impact of habitat size. Reefs in our

262 analysis ranged in size over four orders of magnitude (0.45 to > 8000 m^2), though greater than

263 70% of restored reefs that reported sizes were ≤ 50 m^2 (Fig. D3). Given the magnitude of

264 degradation that has occurred in many estuaries in the U.S. and elsewhere, extensive restoration

265 efforts are necessary. Studies that include larger (i.e., ~ 100 – 1000 m^2) restored reefs are needed

266 to better define the relationship between reef size and recruitment enhancement and determine

267 whether there are optimal or minimum sizes necessary to benefit target species.

268   The vertical relief of a reef can influence oyster survival (Taylor and Bushek 2008;

269 Colden et al. 2017). We expected that greater relief would also increase augmentation of fish and

270 mobile crustacean abundances, as taller reefs are less likely to be influenced by bottom-water

271 hypoxia (Lenihan et al 2001), more likely to avoid sedimentation and sustain oyster populations

272 (Taylor and Bushek 2008; Colden et al. 2017), and potentially provide greater reef complexity

273 and refuge quality. Recruitment enhancement of individual families did not vary consistently

274 with vertical relief on intertidal reefs, which may be more strongly influenced by seldom-

275 reported tidal emersion (determined by a combination of vertical relief, tidal elevation, and tidal

276 range in the embayment; Fodrie et al. 2014; Walles et al. 2016) than vertical relief alone. On

277 subtidal reefs, we found evidence that increasing reef vertical relief decreased recruitment

278 enhancement of two families. Perhaps greater vertical relief on these reefs provided more

279 accessible area to support a wider variety of predators, leading to these negative relationships.

280 Prior studies have described thresholds in initial height of subtidal restored oyster reefs (~0.2 –

281 0.45 m) for the persistence of oyster growth (Lenihan 1999; Powers et al. 2009; Schulte et al.

282 2009; Lipcius et al. 2015; Grizzle and Ward 2016; Colden et al. 2017). Our results suggest a

283 threshold under which nekton recruitment is enhanced (< 1 m) by greater reef height; from 0 to 1

284 m reef height, small gains in reef height can lead to substantial increases in nekton recruitment

285 enhancement until they reach a maximum and then decline above around 1 m reef height. Thus,

286 designing reefs to optimize oyster recruitment will likely influence enhancement of fish families.

287 Although the mechanisms driving this relationship are not clear, if reefs are preferentially

288 restored in areas that are not typically subjected to hypoxia, then reefs with higher vertical relief

289 may not be necessary. Given that constructing high relief reefs is more expensive and requires

290 greater amounts of shell material, restoration decision-makers could increase the aerial extent of

291 restored reefs in areas where low-relief reefs will be effective.

292   Variability in recruitment enhancement across families may also be attributable to their

293 degree of reef fidelity (e.g., reef residents vs. transients). Oyster habitat is considered an essential

294 habitat for resident species long after initial recruitment (Coen et al. 1999; Harding and Mann

295 2000), whereas transient species spend less time on reefs and are more widely distributed across

296 multiple structured habitats (Harding and Mann 2001). In our database, some intriguing potential

297 differences between residents and transients emerged. Each resident species we examined

298 demonstrated recruitment enhancement, whereas only two families of transient species were

299 enhanced (grunts and porgies), and two demonstrated lower recruitment at some oyster reefs

300 (drums and crabs; Fig. 2). Drums are transient among estuarine habitats and utilize oyster reefs

301 over non-vegetated habitat in some studies (Lenihan et al. 2001; Kingsley-Smith et al. 2012),

302 though they utilize marsh edges and subtidal areas over oyster reefs in other studies (Stunz et al.

303 2010). Low or no recruitment of drums to oyster reefs may therefore reflect functional

304 redundancy of structured habitats (Grabowski et al. 2005; Geraldi et al. 2009) and/or alternative

305 habitat selection, particularly in intertidal zones where alternative structured habitats are often

306 readily available. Understanding the influence of coastal habitat landscapes, rather than just

307 individual habitats, on faunal abundance is a key research priority for informing habitat

308 restoration efforts (Gilby et al. 2018). In the case of the Blue crab, *Callinectes sapidus*, previous

309 studies found blue crab to be enhanced by oyster reef in the Gulf of Mexico, but not in the

310 Atlantic coast (zu Ermgassen et al. 2016). It is possible that by using data from both regions in

311 this analysis, this regional enhancement was masked in our results.

312   Several other factors not included in our analysis likely influence nekton recruitment

313 enhancement by oyster reefs. For instance, nekton densities on oyster reefs, including many of

314 our target families, fluctuate seasonally (Lehnert and Allen 2002; Shervette and Gelwick 2008).

315 Many studies in our synthesis reported densities pooled across repeated time points, precluding

316 an analysis of seasonality. Further, our synthesis included studies conducted across different

317 latitudes where seasonality effects may differ. Although we were not able to explicitly evaluate

318   the effects of seasonality, assuming nekton do not change their relative use of oyster vs.

319   unstructured habitats by season, this omission should not confound our results.

320   We are often forced to make assumptions about whether ecosystem services from

321   restored habitats are consistent over time because of the lack of temporal data on service delivery

322   (Barbier et al. 2011; Grabowski et al. 2012). While many studies reviewed in this meta-analysis

323   have documented that fish and invertebrate communities respond quickly to restoration efforts,

324   ecological theory predicts that recruitment enhancement will vary through time. For example, as

325   restored reefs age, we expect their associated communities will undergo succession (Connell and

326   Slatyer 1977; Manley et al. 2010; Quan et al. 2012). Recruitment was reported at intertidal

327   restored reefs 0 – 13 years old in our study. Though reef age was not a strong predictor of

328   recruitment enhancement in our analyses, porgies provided some evidence for a maximum

329   recruitment enhancement at intermediate reef ages, while recruitment enhancement data for

330   intertidal reefs aged 8 – 12 years are not available for any family and represent a data gap (Fig.

331   7). For restored reefs in the subtidal, a minimum recruitment enhancement value at reefs aged 3 –

332   4 years were represented by data from a single study that reported annual recruitment on reefs >

333   1 year old (Lenihan et al. 2001). Additional studies are needed to provide further evidence for

334   this relationship and address the data gap beyond 6 years old for subtidal reefs. Several studies

335   pooled densities across years (4 of 21 studies that reported reef construction date, Appendix A),

336   indicating that services were consistent over the time these studies were sampled (e.g., La Peyre

337   et al. 2014). However, the limited data for nekton recruitment enhancement over a decadal

338   timescale (but see Ziegler et al. 2018) challenges our ability to project whether ecosystem service

339   delivery remains constant or varies temporally at the scale of several years to decades. Thus,

340 long-term studies investigating the degree to which nekton enhancement varies with reef age

341 would be particularly useful.

342   Reef habitat complexity (the physical structure of an environment) is predicted to

343 increase with reef age as oysters settle atop one another and grow vertically in the water column

344 (Bahr and Lanier 1981; Grabowski et al. 2005; Rodriguez et al. 2014; Ziegler et al. 2018). Such

345 habitat complexity has been linked to habitat quality for associated communities, with interstitial

346 refuges that decrease interaction strengths (i.e., predation, Humphries et al. 2011) and increase

347 rugosity, which alters water flow and enhances larval settlement opportunities (Breitburg et al.

348 1995). Oyster density and biomass are often used as quantitative measures of reef complexity

349 (Baggett et al. 2015); thus, we expected augmentation of fish and mobile crustaceans to increase

350 with oyster density and biomass on oyster reefs, even in the absence of explicit information

351 about reef age. However, we could not assess nekton responses to oyster density, as only five out

352 of the 22 studies of restored reefs in our database reported oyster density, and fewer yet reported

353 biomass.

354   Syntheses across restoration efforts can identify potential influences of reef

355 characteristics on recruitment enhancement, determine restoration designs that are most

356 beneficial to target species, and help assess tradeoffs among targeted services. Future

357 experiments that manipulate multiple restoration design factors orthogonally will further our

358 understanding and predictive capacity of how they potentially interact to influence ecosystem

359 service delivery by restored habitats, including nekton recruitment enhancement at oyster reefs.

360 Such manipulations are difficult at scales relevant for restoration, so data syntheses are also a

361 critical tool for advancing restoration science. Future synthesis efforts will be facilitated by

362 consistent reporting across restoration efforts; therefore, we highlight Baggett et al.'s (2015)

363   recommendations for reporting universal oyster reef metrics (project footprint and reef area, reef

364   vertical relief, oyster density, and oyster size-frequency distribution) and environmental variables

365   (water temperature, salinity, and for subtidal reefs, dissolved oxygen) from all oyster restoration

366   projects, in addition to densities of target species when reefs are intended to benefit nekton. We

367   also support Walles et al. (2016)'s recommendation to add tidal emersion for intertidal reefs to

368   this set of recommendations, and we further suggest that tidal elevation, reef age at the time of

369   sampling, and exposure to oyster harvest be reported for effective comparisons across restored

370   reefs. Given the magnitude of restoration needed to recover lost ecosystem services from

371   biogenic habitats, experimental and synthetic efforts aimed at guiding restoration decision-

372   making are critical.

373   **Acknowledgments**

384

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Supporting Information

Supporting information may be found in the online version of this article.

Appendix A. Key features and citations for studies included in the meta-analysis.

Appendix B. Detailed description of methods including additional comparisons of mean LRRs.

Appendix C. Assessment of publication bias.

Appendix D. Assessment of data availability.

Appendix E. Additional results: Resampling and additional comparisons of mean LRRs.

Table 1. List of species represented in the dataset by reef association, family common and

scientific name, and species common and scientific names.

Reef Association	Family (common)	Common Name	Species
Resident		Gulf toadfish	*Opsanus beta*
		Oyster toadfish	*Opsanus tau*
	Toadfish (Batrachoididae)	Stiped blenny	*Chasmodes bosquianus*
		Florida blenny	*Chasmodes saburrae*
		Crested blenny	*Hypleurochilus geminatus*
		Feather blenny	*Hypsoblennius hentz*
		Freckled blenny	*Hypsoblennius ionthas*
		Highfin blenny	*Lupinoblennius nicholsi*
		Blenny species	*Blennidae* spp.
	Skilletfish (Gobiesocidae)	Skilletfish	*Gobiesox strumosus*
	Goby (Gobiidae)	Frillfin goby	*Bathygobius soporator*
		Darter goby	*Ctenogobius boleosoma*
		Freshwater goby	*Ctenogobius shufeldti*
		Emerald goby	*Ctenogobius smaragdus*
		Highfin goby	*Gobionellus oceanus*
		Naked goby	*Gobiosoma bosc*
		Seaboard goby	*Gobiosoma ginsburgi*
		Code goby	*Gobiosoma robustum*
		Clown goby	*Microgobius gulosus*
		Green goby	*Microgobius thalassinus*
		Goby species	*Gobiosoma* spp.; *Microgobius* spp.; Gobiidae
Transient	Grunt (Haemulidae)	Barred grunt	*Conodon nobilis*
		White grunt	*Haemulon plumierii*
		Pigfish	*Orthopristis chrysoptera*
	Snapper (Lutjanidae)	Gray snapper	*Lutjanus griseus*
		Lane snapper	*Lutjanus synagris*
	Swimming crab (Portunidae)	Blue crab	*Callinectes sapidus*
		Lesser blue crab	*Callinectes similis*

	Iridescent swimming crab	*Portunus gibbesii*
	Blotched swimming crab	*Portunus spinimanus*
	Swimming crab species	*Callinectes* spp.; Portunidae
Drum (Sciaenidae)	Silver perch	*Bairdiella chrysoura*
	Sand seatrout	*Cynoscion arenarius*
	Spotted seatrout	*Cynoscion nebulosus*
	Silver seatrout	*Cynoscion nothus*
	Weakfish	*Cynoscion regalis*
	Banded drum	*Larimus fasciatus*
	Spot croaker	*Leiostomus xanthurus*
	Southern kingfish	*Menticirrhus americanus*
	Northern kingfish	*Menticirrhus saxatilis*
	Atlantic croaker	*Micropogonias undulatus*
	Black drum	*Pogonias cromis*
	Red drum	*Sciaenops ocellatus*
	American stardrum	*Stellifer lanceolatus*
	Drum species	*Cynoscion* spp. Sciaenidae
Porgy (Sparidae)	Sheepshead	*Archosargus probatocephalus*
	Spottail seabream	*Diplodus holbrookii*
	Pinfish	*Lagodon rhomboides*

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624

625

626 **Figure 1.** Map of study sites along the Gulf of Mexico and Atlantic Coasts of the USA. States

627 shaded in gray are represented in the dataset. Each point represents an independent study, with

628 shapes representing tidal zone (circles represent intertidal reefs and triangles represent subtidal

629 reefs). Additional study attributes are listed in Table A1.

630

631 **Figure 2a-b.** Mean and 95% confidence intervals of the Log Response Ratios (LRR) of nekton

632 densities at oyster compared to unstructured sedimentary control habitats for each family

633 (toadfish = Batrachoididae, blenny = Blenniidae, goby = Gobiidae, grunt = Haemulidae, snapper

634 = Lutjanidae, crab = Portunidae, drum = Sciaenidae, porgy = Sparidae), at natural vs. restored

635 reefs, for a) intertidal reefs, and b) subtidal reefs. Numbers indicate the total number of LRRs

636 that contributed to the mean LRR for each family. Asterisks indicate 95% confidence intervals

637 that do not overlap 0. NA indicates that data were insufficient to include in analyses, as there

638 were fewer than 10 LRRs included in the mean.

639

640 **Figure 3a-h.** Variation in mean Log Response Ratios (LRR) of nekton densities by reef size (m^2)

641 on intertidal reefs. Point size is weighted by the number of independent replicates for each reef.

642 The model for Toadfish (panel a) has a singular fit and should be interpreted with caution.

643

644 **Figure 4a-h.** Variation in mean Log Response Ratios (LRR) of nekton densities by reef size (m^2)

645 on subtidal reefs. Studies that included multiple experiments with reefs of different sizes are

646 assigned separate points for each reef. Point size is weighted by the number of independent

647 replicates for each reef. For readibility, mean LRRs (0.921 for toadfish, 0.679 for drums and 1.63

648   for porgies) for the study with the largest subtidal reef (> 8000 m^2; Table A1) are not pictured.

649   The model for Gobies (panel c) has a singular fit and should be interpreted with caution.

650

651   **Figure 5a-h.** Variation in mean Log Response Ratios (LRR) of nekton densities by vertical relief

652   (m) on intertidal reefs. Studies that included multiple experiments with reefs of different reliefs

653   are assigned separate points for each reef. Point size is weighted by the number of independent

654   replicates for each reef. Plots with a solid trend line and 95% confidence intervals (gray areas)

655   indicate a significant effect of vertical relief from single-family mixed model analysis. The

656   model for Grunts (panel d) has a singular fit and should be interpreted with caution.

657

658   **Figure 6a-h.** Variation in mean Log Response Ratios (LRR) of nekton densities by vertical relief

659   (m) on subtidal reefs. Studies that included multiple experiments with reefs of different reliefs

660   are assigned separate points for each reef. Point size is weighted by the number of independent

661   replicates for each reef. Plots with a solid trend line and 95% confidence intervals (gray areas)

662   indicate a significant effect of reef age from single-family mixed model analysis. Dashed lines

663   indicate vertical relief effects for which $0.05 \leq P \leq 0.1$.

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665   **Figure 7a-h.** Variation in mean Log Response Ratios (LRR) of nekton densities by reef age

666   (years) on intertidal reefs. Studies that included multiple experiments with reefs of different ages

667   are assigned separate points for each reef. Point size is weighted by the number of independent

668   replicates for each reef. Plots with a dashed trend line and 95% confidence intervals (gray areas)
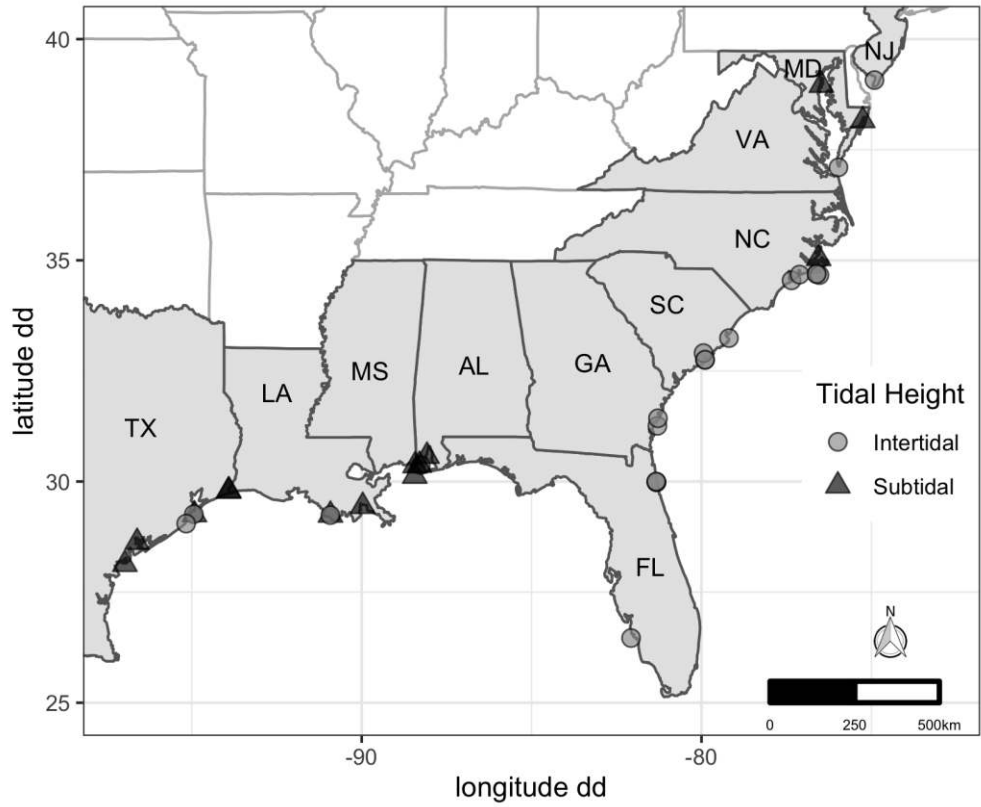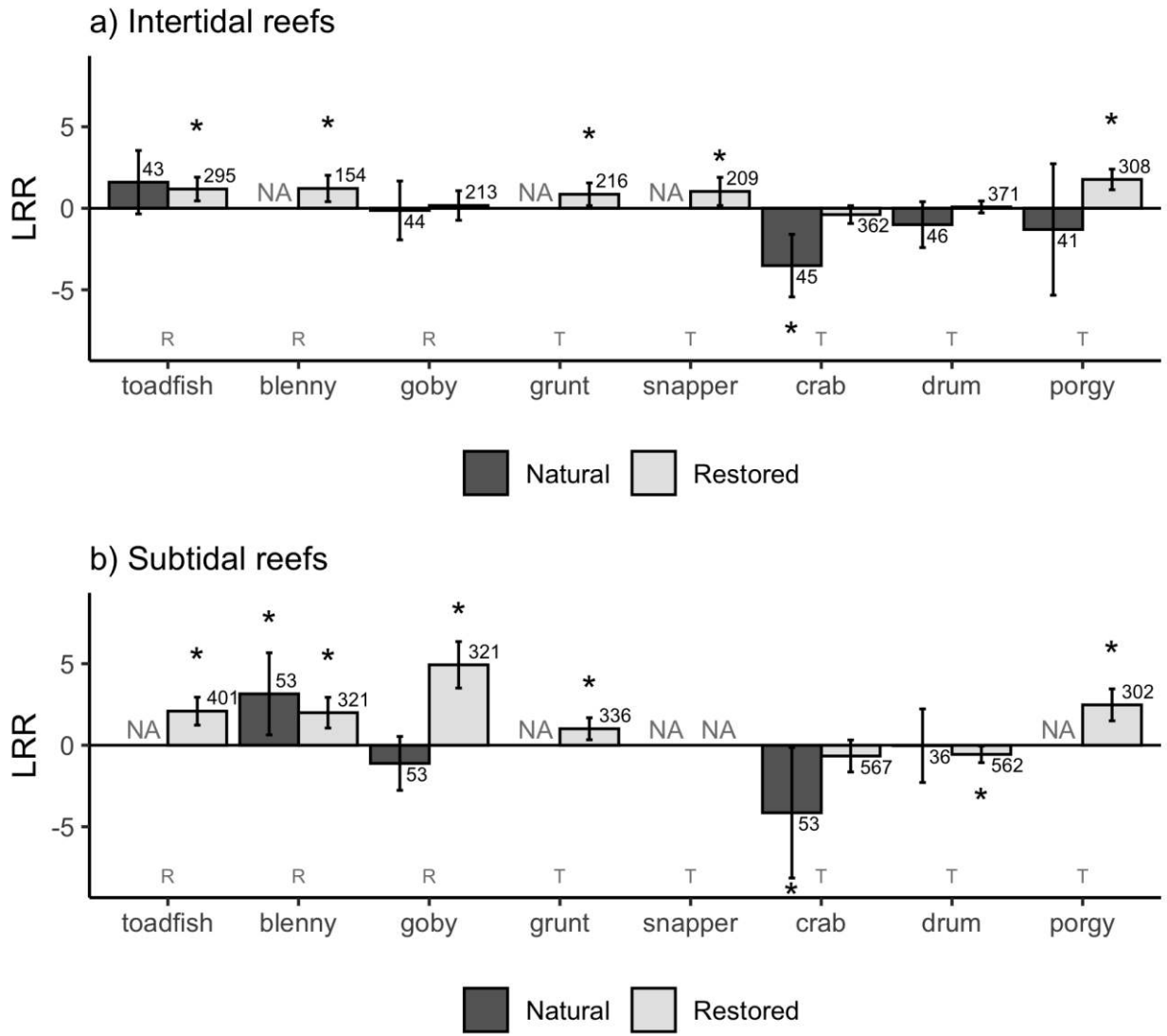
669   indicate a reef age from single-family mixed model analysis for which $0.05 \leq P \leq 0.1$. The model

670   for Toadfish (panel a) has a singular fit and should be interpreted with caution.

671   **Figure 8a-h.** Variation in mean Log Response Ratios (LRR) of nekton densities by reef age

672   (years) on subtidal reefs. Studies that included multiple experiments with reefs of different ages

673   are assigned separate points for each reef. Point size is weighted by the number of independent

674   replicates for each reef. Plots with a trend line and 95% confidence intervals (gray areas) indicate

675   a significant effect of reef age from single-family mixed model analysis.

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681   Figure 1.

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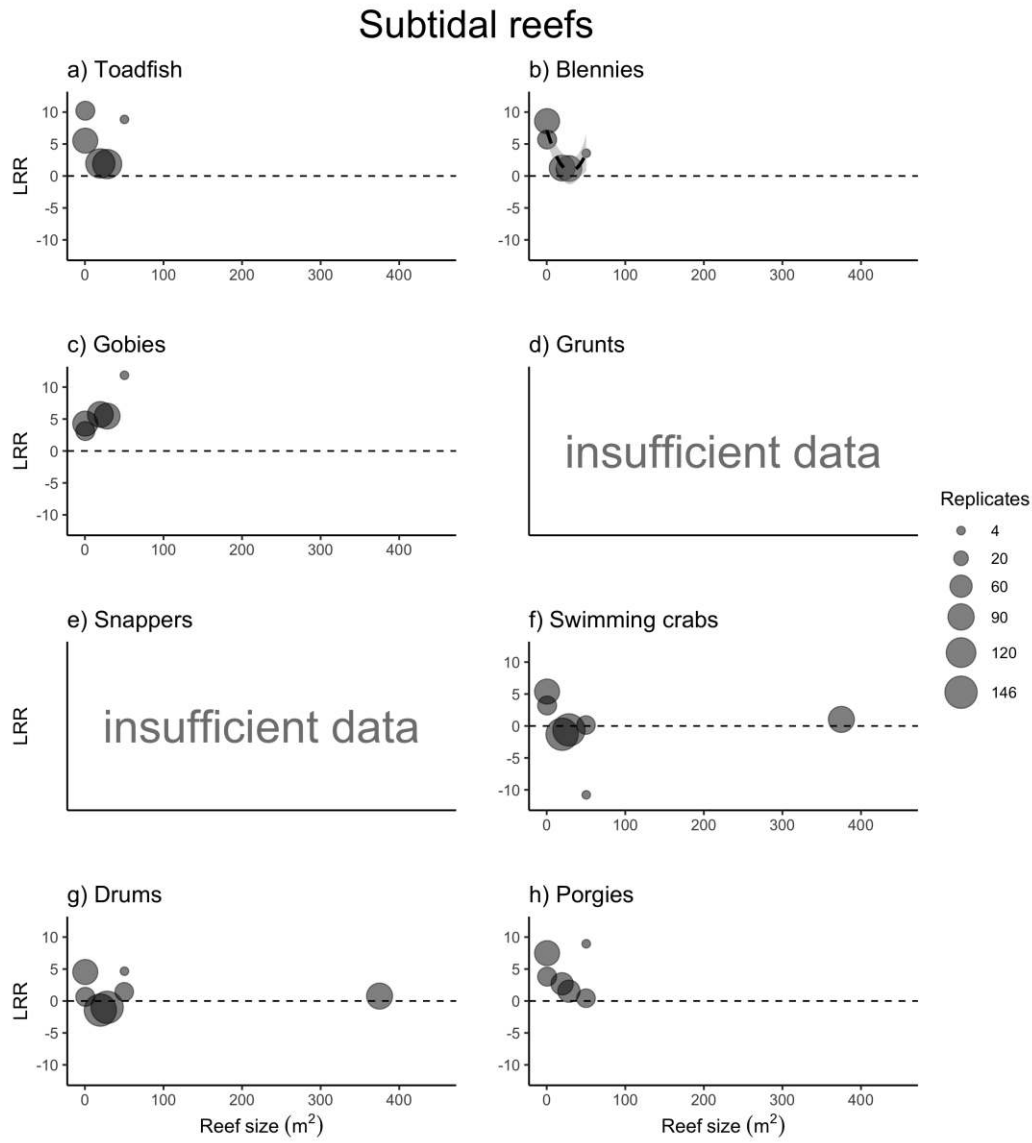683   **Figure 2a-b.**

a) Intertidal reefs

b) Subtidal reefs

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685

Figure 3a-h.

Intertidal reefs

689   **Figure 4a-h.**

Subtidal reefs

a) Toadfish
b) Blennies
c) Gobies
d) Grunts — insufficient data
e) Snappers — insufficient data
f) Swimming crabs
g) Drums
h) Porgies

Replicates: 4, 20, 60, 90, 120, 146

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Figure 5a-h.

Subtidal reefs

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697

Figure 7a-h.

Intertidal reefs

701   **Figure 8a-h.**

Figure 8a-h. Subtidal reefs. a) Toadfish, b) Blennies (insufficient data), c) Gobies (insufficient data), d) Grunts (insufficient data), e) Snappers (insufficient data), f) Swimming crabs (insufficient data), g) Drums, h) Porgies.

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