Methodological recommendations for assessing scleractinian and octocoral recruitment to settlement tiles

Leah M Harper Corresp., 1, 2 , **Lindsay K Huebner** 3 , **Elijah D O'Cain** 4, 5 , **Rob Ruzicka** 3 , **Daniel F Gleason** 4 , **Nicole D Fogarty** 1, 6

1 Halmos College of Natural Sciences and Oceanography, Nova Southeastern University, Dania Beach, FL, United States

2 Tennenbaum Marine Observatories Network, MarineGEO, Smithsonian Environmental Research Center, Edgewater, MD, United States

3 Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Saint Petersburg, FL, United States

4 James H. Oliver, Jr., Institute for Coastal Plain Science, Georgia Southern University, Statesboro, GA, United States

5 Coastal Resources Division, Georgia Department of Natural Resources, Brunswick, GA, United States

6 Department of Biology and Marine Biology, Center for Marine Science, University of North Carolina Wilmington, Wilmington, NC, United States

Corresponding Author: Leah M Harper
Email address: harperl@si.edu

Quantifying recruitment of corals is important for evaluating their capacity to recover after disturbances through natural processes, yet measuring recruitment rates *in situ* is challenging due to the minute size of the study organism and the complexity of benthic communities. Settlement tiles are widely used in studies of coral recruitment because they can be viewed under a microscope to enhance accuracy, but methodological choices such as the rugosity of tiles used and when and how to scan tiles for recruits post-collection may cause inconsistencies in measured recruitment rates. We deployed 2880 tiles with matching rugosity on top and bottom surfaces to 30 sites along the Florida Reef Tract for year-long saturations during a three year study. We scanned the top and bottom surfaces of the same tiles for scleractinian recruits before (live scans) and after treating tiles with sodium hypochlorite (corallite scans). Recruit counts were higher in corallite than live scans, indicating that scleractinian recruitment rates should not be directly compared between studies using live scans and those scanning tiles, which have been processed to remove fouling material. Recruit counts also were higher on tile tops in general, but the proportion of settlement to the top and bottom surfaces varied significantly by scleractinian family. Thus, biases may be introduced in recruitment datasets by differences in tile rugosity or by only scanning a subset of tile surfaces. Finally, we quantified octocoral recruitment during live scans and found they preferentially settled to tile tops. We recommend that recruitment tile studies include corallite scans for scleractinian skeletons, deploy tiles with matching rugosity on top and bottom surfaces, and scan all tile surfaces.

1 **Methodological recommendations for assessing scleractinian and octocoral recruitment to**

2 **settlement tiles**

3 Leah M. Harper[1,2*], Lindsay K. Huebner[3], Elijah D. O'Cain[4,5], Rob Ruzicka[3], Daniel F.

4 Gleason[4], Nicole D. Fogarty[1,6]

5 [1]Nova Southeastern University, Halmos College of Natural Sciences and Oceanography, 8000 N

6 Ocean Drive, Dania Beach, FL 33004

7 [2]Present address: Tennenbaum Marine Observatories Network, MarineGEO, Smithsonian

8 Environmental Research Center, Edgewater, Maryland 21037

9 [3]Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 100

10 8th Ave SE, Saint Petersburg, FL 33701

11 [4]James H. Oliver, Jr., Institute for Coastal Plain Science, P.O. Box 8042, Georgia Southern

12 University, Statesboro, GA 30460-8042

13 [5]Present address: Georgia Department of Natural Resources, Coastal Resources Division, 1

14 Conservation Way, Brunswick, GA 31520-8687

15 [6]Present address: Department of Biology and Marine Biology, Center for Marine Science,

16 University of North Carolina Wilmington, 5600 Marvin K. Moss Lane, Wilmington, NC 28412

17 *Contact email: harperl@si.edu

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24 **Abstract**

25 Quantifying recruitment of corals is important for evaluating their capacity to recover after

26 disturbances through natural processes, yet measuring recruitment rates *in situ* is challenging due

27 to the minute size of the study organism and the complexity of benthic communities. Settlement

28 tiles are widely used in studies of coral recruitment because they can be viewed under a

29 microscope to enhance accuracy, but methodological choices such as the rugosity of tiles used

30 and when and how to scan tiles for recruits post-collection may cause inconsistencies in

31 measured recruitment rates. We deployed 2880 tiles with matching rugosity on top and bottom

32 surfaces to 30 sites along the Florida Reef Tract for year-long saturations during a three year

33 study. We scanned the top and bottom surfaces of the same tiles for scleractinian recruits before

34 (live scans) and after treating tiles with sodium hypochlorite (corallite scans). Recruit counts

35 were higher in corallite than live scans, indicating that scleractinian recruitment rates should not

36 be directly compared between studies using live scans and those scanning tiles, which have been

37 processed to remove fouling material. Recruit counts also were higher on tile tops in general, but

38 the proportion of settlement to the top and bottom surfaces varied significantly by scleractinian

39 family. Thus, biases may be introduced in recruitment datasets by differences in tile rugosity or

40 by only scanning a subset of tile surfaces. Finally, we quantified octocoral recruitment during

41 live scans and found they preferentially settled to tile tops. We recommend that recruitment tile

42 studies include corallite scans for scleractinian skeletons, deploy tiles with matching rugosity on

43 top and bottom surfaces, and scan all tile surfaces.

44 **Introduction**

45 Settlement tiles are often used to evaluate variation in coral recruitment through time and space

46 (Rogers et al., 1984; Edmunds, 2017; Davidson et al., 2019). Tiles can be removed from study

47   sites and examined under a microscope, facilitating identification of small recruits and allowing

48   an assessment of recruitment during a defined time period. However, various methodological

49   options exist for conducting settlement tile studies which can influence the resultant recruitment

50   rates, making interstudy comparisons problematic and ecological interpretations inconsistent

51   (Table S1).

52   One such methodological decision that can affect quantified recruitment is the technique

53   used to scan tiles for settled corals. Tiles can be scanned for living recruits shortly after retrieval,

54   typical for studies estimating recruit survivorship (e.g., Arnold, Steneck, & Mumby, 2010) or for

55   sampling recruit tissue for molecular identification (O'Cain et al., 2019; Guerrini et al., 2020).

56   Alternatively, tiles can be soaked in sodium hypochlorite to reveal corallite morphology (Harriott

57   & Fisk, 1987), which can be used to more accurately identify recruits than is possible during live

58   visual scans, and to remove encrusting organisms that potentially obscured recruits which

59   experienced post-settlement mortality.

60   Whether to scan all tile surfaces (top, bottom, and sides) or only a subset represents

61   another methodological choice. For most studies that have compared tile surfaces, >90% of

62   recruits were found on the bottom surface (Green & Edmunds, 2011; Edmunds, Nozawa, &

63   Villanueva, 2014; Humanes & Bastidas, 2015). Consequently, some studies exclude the top

64   surface from analysis (Chong-Seng, Graham, & Pratchett, 2014; Burt & Bauman, 2020; Gouezo

65   et al., 2020). However, commonly there are differences in rugosity on tile surfaces used in

66   recruitment studies (Green & Edmunds, 2011; Edmunds, 2017; Lal et al., 2018), with tops being

67   smooth and bottoms bearing textures which provide microhabitat refugia for recruits. Tile

68   rugosity may mimic heterogenous natural substratum and enhance rates of scleractinian

69   recruitment and survivorship on tiles (Nozawa, 2008; Edmunds, Nozawa, & Villanueva, 2014;

70   Randall et al., 2021); if the top surface of the tile is also textured, the proportion of settlement

71   there can be increased (Edmunds, Nozawa, & Villanueva, 2014). Thus, rugosity differences

72   between tile top and bottom surfaces may confound recruitment data, as can scanning only a

73   subset of tile surfaces.

74   Most coral reef settlement tile literature focuses on scleractinian recruitment. However,

75   as scleractinians have declined throughout the Caribbean, octocoral densities have remained

76   stable or increased (Ruzicka et al., 2013; Edmunds & Lasker, 2016; Lasker et al., 2020).

77   Octocoral recruitment is typically quantified *in situ* (Lasker, 2013; Lasker & Porto-Hannes,

78   2021) and rarely on tiles, potentially leaving gaps in understanding the spatial and temporal

79   variation in octocoral recruitment.

80   During a study initially designed to investigate the spatial and temporal variation in

81   scleractinian and octocoral recruitment on 2,778 settlement tiles deployed throughout the Florida

82   Reef Tract (Harper et al., in prep.), we observed methodological inconsistencies in the coral

83   recruitment literature (Table S1). We therefore designed our study to also collect companion data

84   on our methodological choices, in an effort to critically examine the potential implications of

85   these choices, and of those made in other studies, on the ecological results. Specifically, we

86   present here an assessment of recruitment tile methods in which we 1) compare scleractinian

87   recruitment rates quantified through live and corallite scans on the same tiles, 2) compare

88   scleractinian recruitment overall and by taxonomic family to the tops and bottoms of tile surfaces

89   with matching rugosity, and 3) quantify live octocoral recruits on the top and bottom surfaces of

90   the same tiles. We conclude with recommendations for future coral recruitment studies on tile

91   rugosity, and when and how to scan tiles for scleractinian and octocoral recruits.

92   **Methods**

93   Tiles were deployed at 30 sites along the Florida Reef Tract, from Broward County in the north

94   to Key West in the south, with depths ranging from 1.5 to 18m (Fig. 1, Table S2), in accordance

95   with the following authorizations: Florida Keys National Marine Sanctuary Permit FKNMS-

96   2013-058-A1, Department of the Army Permit SAJ-2014-01396, and Broward County

97   Environmental Resource License DF14-1048. Tiles were unglazed terracotta (15x15x1cm),

98   consistent with many previous studies of coral recruitment (Mundy, 2000; Arnold & Steneck,

99   2011; Green & Edmunds, 2011; Edmunds, Nozawa, & Villanueva, 2014; van Woesik, Scott, &

100   Aronson, 2014; Humanes & Bastidas, 2015). Because each tile was smooth on one surface and

101   grooved on the other, tiles were deployed in back-to-back pairs, with grooved surfaces facing

102   outward, to provide consistent rugosity on the top and bottom of each tile pair (Fig. 2A-B).

103   At each of 30 sites (Fig. 1, Table S2), we haphazardly deployed 32 tile pairs by attaching

104   them to the substratum. Tile pairs were arranged along four permanent transects ~22m in length

105   at each site, with eight tile pairs per transect. The distance between nearest neighboring tiles was

106   $\cong$1-10m. Using a pneumatic drill attached to a SCUBA cylinder, we drilled holes in the

107   substratum with a carbide drill bit (1.25-1.59cm diameter), into which we placed 1.25cm

108   diameter ribbed plastic drywall anchors. Tile pairs were secured, generally parallel to the

109   substratum, using a stainless steel lag screw (0.64cm diameter, 5-13cm length, depending on

110   substratum rugosity) inserted through pre-drilled center holes in the paired tiles and screwed into

111   the drywall anchor (Fig. 2A-B). Tile deployments occurred from February to April in 2015,

112   2016, and 2017 (Table S2), allowing a minimum of four weeks for settlement tiles to condition

113   before expected *Porites astreoides* planulation (Edmunds, Gates, & Gleason, 2001). Tiles were

114   retrieved approximately 12 months after deployment (range 11.5-13.5 months) in each of 2016,

115   2017, and 2018 (Table S2). Tiles were removed from the substratum and transported on racks

116 made from two layers of egg crate material with bolts to hold the tiles in place and nuts to space

117 the tiles from the racks, preventing possible damage to recruits (Fig. 2C).

118   The grooved top and bottom of tile pairs were submerged in trays of seawater while

119 examined under a dissecting microscope for living scleractinian and octocoral recruits (Fig.

120 2D,F). Subsequently, tiles were submerged in 10% sodium hypochlorite solution for 24-48h to

121 remove live tissue, then dried for scleractinian corallite scans (octocorals do not leave skeletal

122 material behind). During corallite scans, the grooved top and bottom surfaces were examined a

123 second time to locate scleractinian recruit skeletons (Fig. 2E,G). We additionally scanned the tile

124 sides (edges) for corallites, which was not possible during live scans with the tiles submerged in

125 trays. To determine whether taxonomic groups of scleractinians settled in different proportions

126 across tile surfaces, corallites were identified to the family level using diagnostic characteristics

127 such as shape, calice diameter at budding stage, columella development, and septal arrangement

128 and dentition (Smith, 1971; Budd et al., 2001; Budd & Stolarski, 2011; Humblet, Hongo, &

129 Sugihara, 2015). Corallites that were damaged, underdeveloped, or did not meet diagnostic

130 criteria were classified as unidentified. Diagnostic characteristics were supported with molecular

131 evidence using a single-step nested multiplex PCR assay designed to identify Caribbean

132 scleractinian recruits, developed from a subset of recruits sampled during live scans (O'Cain et

133 al., 2019). Further, we conducted blind inter-observer comparisons of corallite identifications to

134 ensure standardization.

135   To determine whether scan method (live vs. corallite) influenced recruit count, we fit a

136 negative binomial generalized linear model with a log link (GLM) in R v.4.0.3 (R Core Team,

137 2020) using the package MASS (Venables & Ripley, 2002). We modeled the effects of the fixed

138 factors of site, year, location on tile, and scan method (allowing for an interaction between

139   location and scan method) on the response variable recruit count. Model assumptions were

140   assessed visually. We evaluated the significance of fixed effects with Type II analysis of

141   deviance using the 'car' package (Fox & Weisberg, 2019). In addition, we modeled the effects

142   of scan method, location on tile, and interaction within each year and applied Tukey's pairwise

143   contrasts to assess within-year differences in recruit count between groups using the 'emmeans'

144   package (Lenth, 2021).

145   The majority (99.9%) of recruits identified to family level in the corallite scans were in

146   the families Siderastreidae, Poritidae, Agariciidae, and Faviidae (membership in Faviidae as

147   assigned in Budd and Stolarski 2011). For these identified recruits, we used a negative binomial

148   GLM with a log link to assess the effects of coral family and tile surface (top, side, and bottom)

149   on recruit count from corallite scans. We also included year and site as fixed factors, to account

150   for temporal and spatial autocorrelation, and included area of tile surfaces as an offset variable.

151   Because site depth potentially drives the tile surface of scleractinian recruitment (Rogers et al.,

152   1984), we included depth as a covariate. The model allowed for interactions between coral

153   family, location on tile, and depth. We tested for significance of fixed effects with Type II

154   analysis of deviance and evaluated significant differences in settlement orientation within

155   families using Tukey's pairwise contrast. To test the significance of individual scleractinian

156   families' relationships between recruitment location on tile and depth, we used simple linear

157   regressions with site-wide proportions of each family on tops, bottoms, and sides of tiles as

158   response variables and depth as the explanatory variable. For regressions revealing significant

159   relationships, we calculated Pearson's product moment correlation coefficients.

160   Finally, for octocorals, we used a generalized linear model (quasipoisson family with a

161   log link) to regress total live recruit count against the factors of tile surface (top and bottom) and

162   year, with depth as a covariate, allowing for interaction between tile surface and depth. After

163   assessing model assumptions visually, we tested for significance of fixed effects with Type II

164   analysis of deviance and evaluated significant differences in tile surface within each year using

165   Tukey's pairwise contrast. For all analyses, extreme values were trimmed from figures where

166   necessary for readability (as reported in figure legends) but were incorporated in statistical

167   analyses.

168   **Results**

169   Over three years, we deployed 2880 tile pairs and retrieved 2778 (96% retrieval). Most of the

170   unretrieved tile pairs (93 of 102) were lost during the 2017-2018 deployment, when Hurricane

171   Irma made landfall in the Florida Keys. In all three years, significantly more scleractinians were

172   found in corallite than live scans on both the top and bottom tile surfaces (ANOVA p<0.001;

173   Fig. 3, Table 1), with a significant interaction between scan method and tile surface (ANOVA

174   p=0.008). Overall, we found 379% more recruits in corallite than live scans (excluding those

175   found on tile sides, which were not scanned live).

176   Corallite scans found significantly higher numbers of scleractinian recruits on top

177   compared to bottom surfaces of tiles in each year (Tukey p<0.001 for 2016 and 2018; Tukey

178   p=0.001 for 2017; Fig. 3, Table 1). When the data were pooled across all three years, our recruit

179   community was dominated by siderastreids, which settled in vastly higher numbers on tile tops,

180   followed by sides and bottoms (Tukey's p<0.001 for top-side and top-bottom contrasts; Fig. 4,

181   Table 2). Poritids were our second most common group, and they also showed a strong

182   preference for tile tops (Tukey's, top-bottom p<0.001), followed by bottoms (Tukey's, side-

183   bottom p <0.001). Agariciids preferentially settled on tile bottoms (Tukey's, bottom-side

184   p<0.001, bottom-top p<0001), but were our third most common family. Faviid settlement was

185 low overall, with significantly more recruits found on tops and bottoms than tile sides each

186 (Tukey's, side-top p=0.007, side-bottom p=0.002).

187   Tile surface interacted with site depth and coral family (ANOVA p<0.001, Table 2),

188 though depth alone did not have a significant effect on the number of recruits. Simple linear

189 regression determined that the proportion of siderastreid recruits on the tops of tiles increased

190 with increasing depth (p=0.042, r=0.24; Fig. 5). Additionally, the proportion of faviids (p=0.028,

191 r=0.33) and poritids (p<0.001, r=0.37) that settled on the sides of tiles increased with increasing

192 site depth (Fig. 5).

193   Live octocoral recruit counts varied significantly by year, and tile surface (ANOVA, year

194 p<0.001, tile surface p=0.003; Fig. 6, Table 3), with site-level density ranging from $0m^{-2}$ to

195 $182.6m^{-2}$. In 2016, mean site-level octocoral recruit density was $3.8 \pm 1.8m^{-2}$, but mean densities

196 rose to $16.6 \pm 6.3m^{-2}$ in 2017 and $8.1 \pm 4.0m^{-2}$ in 2018. Overall, 67% of octocorals were on tile

197 tops, though the pairwise within-year difference between top and bottom surfaces was only

198 significant in 2018 (Tukey's, 2018 top-bottom contrast p<0.001). While overall octocoral

199 recruitment did not vary with site depth, the interaction between depth and location on tile was

200 significant (p<0.001).

201 **Discussion**

202 In our three year study of coral recruitment to the Florida Reef Tract, we counted scleractinian

203 recruits in both live and corallite scans and found significantly more recruits in corallite scans

204 overall. While others have acknowledged that removing tissue of corals and fouling organisms

205 may result in a higher recruit count (Arnold & Steneck, 2011), this difference has rarely been

206 quantified. We attribute the difference between corallite and live scan counts to recruits that were

207 overgrown, smothered by sediment, otherwise dead, and/or very small (<0.5mm) and likely

208   obscured during live scans. The significant interaction between scan method and tile surface may

209   reflect the difficulty in locating small recruits during live scans on heavily sedimented top

210   surfaces of tiles. This large discrepancy in numbers on the same tiles indicates that scleractinian

211   recruitment rates should not be directly compared between studies only performing live scans

212   and those quantifying recruitment on tiles that have been post-processed to remove fouling

213   material. These results also suggest that for studies focusing on overall scleractinian recruitment

214   without concern for the effect of post-settlement survivorship, soaking tiles in sodium

215   hypochlorite provides a more accurate estimate than live scans.

216   Contrary to most assessments of scleractinian settlement orientation in shallow water, we

217   found the majority of recruit corallites on the top surfaces of our settlement tiles in every year of

218   our study (Fig. 3). Scleractinians have been reported to settle predominantly on bottom surfaces

219   of tiles because that side of the tile mimics the natural cryptic microhabitats preferred for

220   settlement (Green & Edmunds, 2011; Humanes & Bastidas, 2015). Further, studies that include

221   sites deeper than 10m tend to reveal a shift in settlement orientation from tile bottoms and sides

222   to tops with increasing depth (Rogers et al., 1984; Babcock & Mundy, 1996). While our study

223   identified some shifts in the proportion of recruits that settled to tile top (siderastreids) and side

224   surfaces (poritids and faviids) with increasing site depth, these shifts were modest and not

225   consistent across the coral families (Fig. 5). Because increasing site depth does not explain the

226   overall majority of settlement to tile tops observed in our study, we propose that including

227   rugosity on tile tops in this study may have enhanced recruitment to that surface (Nozawa,

228   Tanaka, & Reimer, 2011; Edmunds, Nozawa, & Villanueva, 2014). Thus, biases are introduced

229   in recruitment studies when top and bottom tile surfaces differ in rugosity and/or quantification is

230   limited to tile bottoms.

231   Regardless of site depth, the proportion of settlement to top and bottom surfaces varied

232   by scleractinian family. Siderastreids and poritids settled predominantly on tile tops, while

233   agariciids settled predominantly on tile bottoms. Therefore, biases introduced by differences in

234   tile rugosity or by only scanning tile bottoms may over- or underestimate the relative

235   contributions of scleractinian families to overall recruitment. Agariciids usually settle cryptically

236   (Morse et al., 1988) and often dominate Caribbean recruit communities (Rogers et al., 1984;

237   Arnold and Steneck, 2011). Had we only quantified recruits on tile bottoms, we would have

238   concluded that agariciids were the dominant member of our recruit community, consistent with

239   prior studies. We also would have significantly underestimated recruitment by siderastreids,

240   reducing it to a level comparable to that of faviids. Thus, our decision to scan tile tops in addition

241   to bottoms has profound implications for any ecological conclusions on the relative recruitment

242   of these coral families in our study region.

243   As with scleractinians, we found more octocoral recruits on tile tops (67% of the three

244   year total) compared to bottoms; although this difference was only significant in 2018, it

245   emphasizes the importance of scanning all tile surfaces. This majority of recruits on the top

246   surfaces is unlikely to be explained by a survivorship advantage there, as studies which have

247   deployed lab-reared recruits *in situ* have found low survivorship on tile tops (Lasker, Kim, &

248   Coffroth,1998; Evans, Coffroth, & Lasker, 2013). Without the ability to measure overall

249   recruitment (i.e., conducting a corallite scan) as can be done for scleractinians, counts of living

250   octocoral recruits on tiles, regardless of surface, include some level of post-settlement mortality.

251   The abundance per survey area of octocoral recruits *in situ* is highly variable, making the

252   assessment of post-settlement mortality on octocoral recruit densities difficult (Lasker & Porto-

253   Hannes, 2021), compounded with the difficulty of seeing very small recruits. However, tiles can

254   be examined under a microscope, likely allowing for smaller recruits to be counted than through

255   *in situ* surveys. The densities of live octocoral recruits in our study were on par or higher than

256   those that have been found during *in situ* surveys (Privitera-Johnson, Lenz, & Edmunds, 2015;

257   Lasker & Porto-Hannes, 2021), indicating the viability of settlement tiles for the study of

258   octocoral recruitment. While assessments of recruit survivorship were beyond the scope of our

259   study, researchers may be able to use tiles to more clearly assess the effects of post-settlement

260   mortality on octocoral recruitment than can be done during *in situ* surveys. For example, tiles can

261   be collected, scanned for even very small living recruits under a microscope, and redeployed for

262   repeated live recruit scans, as has been done for scleractinians (Arnold, Steneck, & Mumby

263   2010; Arnold & Steneck, 2011)

264   **Conclusions**

265   Our three-year, region-wide recruitment study provided an opportunity to evaluate

266   methodological considerations that may confound efforts to compare coral recruitment rates

267   between studies that used different methods. First, we found higher densities of scleractinian

268   recruits in corallite than live scans, indicating that while live scans can have useful applications

269   such as quantifying post-settlement survival or allowing for molecular identification of recruits,

270   they are likely to underestimate overall scleractinian recruitment rates when directly compared to

271   studies that examine tiles treated with sodium hypochlorite. We recommend that, for

272   comparisons of global scleractinian recruitment, tiles should be scanned after being processed for

273   the removal of sediment and benthic organisms that could obscure the detection of small recruits.

274   Second, we found more scleractinian recruits on tile tops than bottoms, indicating that rugosity

275   should be uniform on both surfaces, to ensure that differences in recruitment rates to these

276   surfaces are due to ecological and not methodological factors. Further, scanning all surfaces of

277   the tiles will avoid mischaracterizing the relative contribution of identified scleractinian recruit

278   taxa to the overall recruitment rate. Finally, we propose that tiles also can be used to enumerate

279   living octocoral recruits, and studies that do so should abide by the same recommendations for

280   uniform tile rugosity and scanning both tops and bottoms of the tiles.

281

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285   **Conflict of Interest Statement**

286   On behalf of all authors, the corresponding author states that there is no conflict of interest.

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392   **Figure legends**

393   **Figure 1. Map of Florida Reef Tract study sites.** Point color is scaled to depth in meters. Sites

394   spanned four regions of the reef tract: Southeast Florida and the Upper, Middle, and Lower Keys,

395   and are labeled with numbers corresponding to Table S2. Map tiles by Stamen Design, under CC

396   BY 3.0. Data by OpenStreetMap, under ODbL.

397   **Figure 2. Settlement tiles before, during and after deployment.** Terracotta tiles were

398   configured in pairs, grooved sides facing outward, yielding consistent rugosity on the top and

399   bottom surfaces of the pair. Tiles were deployed by installing a green plastic drywall anchor into

400   a hole drilled into the substratum; stainless steel lag screws were used to fasten the tile pairs into

401   the anchor (A). A tile pair deployed to the reef (B) and transport racks after retrieval of tiles,

402   before surfacing (C). Tiles were submerged in trays filled with seawater for scans of living

403   recruits (D,F), then soaked in sodium hypochlorite and scanned for corallites (E,G). Images D

404   and E depict the same individual from the family Siderastreidae before and after tissue removal.

405   Images F and G depict the same individual from the family Poritidae before and after tissue

406   removal. Scale bars represent 1mm. Photo credits: (A) Rob Ruzicka, (B) Lindsay Huebner, (C)

407   Lauren Stefaniak, (D-G) Leah Harper.

408   **Figure 3. Density of scleractinian recruits on top and bottom tile surfaces by scan method**

409   **(live and corallite) across N = 30 Florida Reef Tract sites for each of three years of tile**

410   **deployment.** Boxplots show mean density of recruits at each study site, and display the median

411   (horizontal line), the first and third quartiles (interquartile range [IQR]), 1.5 × IQR (whiskers),

412   and outliers (black dots). Two outliers with density values greater than 1500m^{-2} were trimmed

413   from the plot for readability (2164m^{-2}, 4128m^{-2}; both from top surface, corallite scan, 2018).

414   Letters denote significant pairwise difference of recruit count between top and bottom tile

415   surfaces, as well as live and corallite scans of each tile surface, within each year (Tukey's

416   p<0.05).

417   **Figure 4. Density of scleractinian recruits found on tile surfaces during corallite scans**

418   **across N = 30 Florida Reef Tract sites and three years of deployments.** Boxplots show mean

419   density of recruits at each study site; N = 90 site-years surveyed. Boxes display the median

420   (horizontal line), the first and third quartiles (interquartile range [IQR]), 1.5 × IQR (whiskers),

421   and outliers (black dots). Five outliers with density values greater than 100m^{-2} were trimmed

422   from the plot for readability (198m^{-2}, 215m^{-2}, 295m^{-2}, 442m^{-2}, 723m^{-2}; all from top surface,

423   Siderastreidae). Letters denote significant differences of recruit count within scleractinian family

424   (Tukey's p<0.05).

425   **Figure 5. Relationships between site depth in meters (x-axes) and proportion of corallites**

426   **found on each tile surface (y-axes) per scleractinian coral family.** Significant linear

427   relationships are denoted with asterisks (* denotes p<0.01; *** denotes p<0.0001) and the

428   Pearson product-moment correlation coefficient is shown for significant relationships.

429   **Figure 6. Density of octocoral recruits found on top and bottom tile surfaces during live**

430   **scans across N = 30 Florida Reef Tract sites for each of three years of deployment.** Boxplots

431   show the mean density of recruits at each study site within each year. Boxes display the median

432   (horizontal line), the first and third quartiles (interquartile range [IQR]), 1.5 × IQR (whiskers),

433   and outliers (black dots). Two outliers with density values greater than 200m^{-2} were trimmed

434   from the plot for readability (240m^{-2}; top surface 2018, and 340m^{-2}; top surface 2017). Asterisks

435   denote significant pairwise differences of recruit count within year (*** denotes $p<0.001$).

436   **Table legends**

437   **Table 1. Type II Analysis of Deviance of a negative binomial generalized linear model**

438   **regressing the number of scleractinian recruits found on the top and bottom surfaces of**

439   **tiles (location) in live and corallite scans (method).** Site and year are fixed factors. The chi-

440   square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

441   **Table 2. Type II Analysis of Deviance of a negative binomial generalized linear model**

442   **regressing the number of scleractinian recruits against family, tile surface, and depth.** Year

443   is a fixed factor. The chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq])

444   are shown.

445   **Table 3. Type II Analysis of Deviance of a quasipoisson generalized linear model regressing**

446   **the number of octocoral recruits against tile surface and depth.** Year is a fixed covariate. The

447   chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

448

449

Figure 1

Map of Florida Reef Tract study sites.

Point color is scaled to depth in meters. Sites spanned four regions of the reef tract: Southeast Florida and the Upper, Middle, and Lower Keys, and are labeled with numbers corresponding to Table S2. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

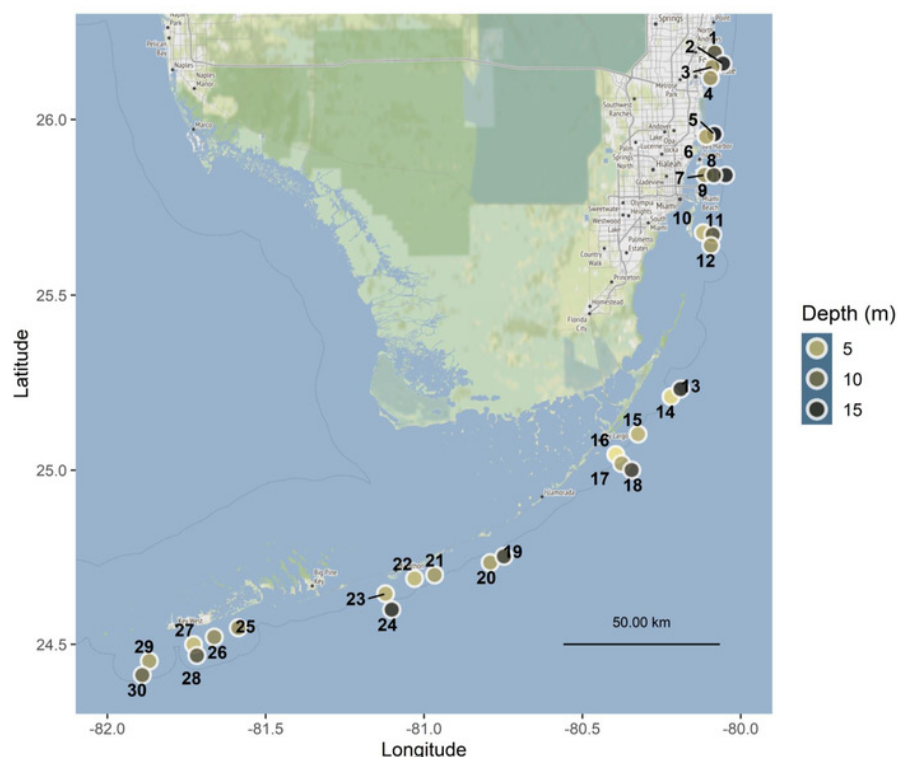



Figure 2

Settlement tiles before, during and after deployment.

Terracotta tiles were configured in pairs, grooved sides facing outward, yielding consistent rugosity on the top and bottom surfaces of the pair. Tiles were deployed by installing a green plastic drywall anchor into a hole drilled into the substratum; stainless steel lag screws were used to fasten the tile pairs into the anchor (A). A tile pair deployed to the reef (B) and transport racks after retrieval of tiles, before surfacing (C). Tiles were submerged in trays filled with seawater for scans of living recruits (D,F), then soaked in sodium hypochlorite and scanned for corallites (E,G). Images D and E depict the same individual from the family Siderastreidae before and after tissue removal. Images F and G depict the same individual from the family Poritidae before and after tissue removal. Scale bars represent 1mm. Photo credits: (A) Rob Ruzicka, (B) Lindsay Huebner, (C) Lauren Stefaniak, (D-G) Leah Harper.

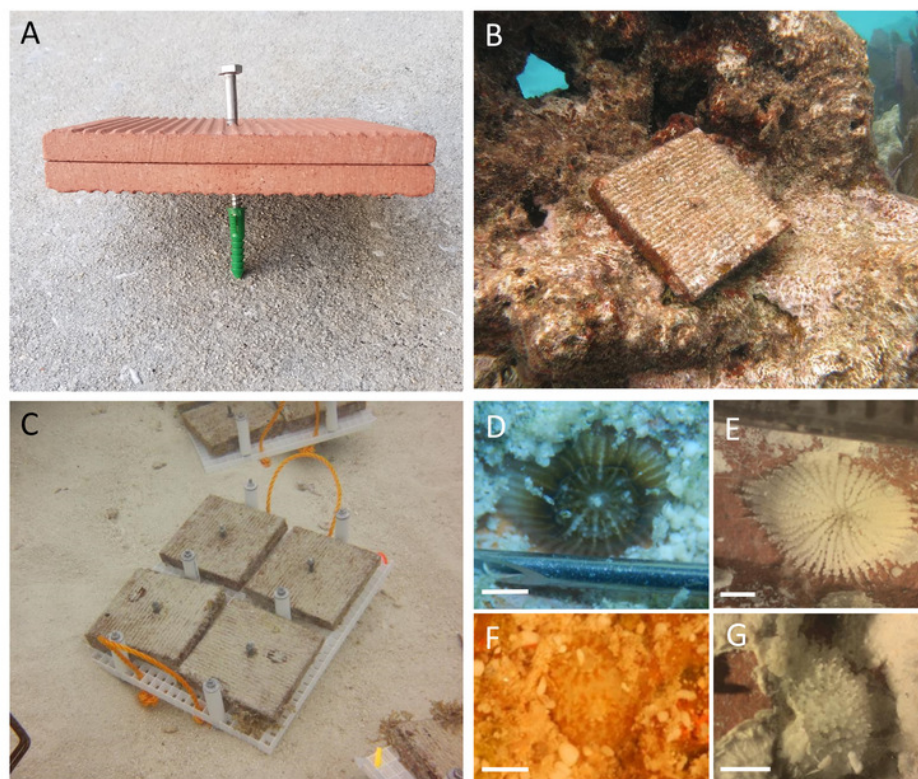



Figure 3

Density of scleractinian recruits on top and bottom tile surfaces by scan method (live and corallite) across N = 30 Florida Reef Tract sites for each of three years of tile deployment.

Boxplots show mean density of recruits at each study site, and display the median (horizontal line), the first and third quartiles (interquartile range [IQR]), 1.5 × IQR (whiskers), and outliers (black dots). Two outliers with density values greater than 1500m^{-2} were trimmed from the plot for readability (2164m^{-2}, 4128m^{-2}; both from top surface, corallite scan, 2018). Letters denote significant pairwise difference of recruit count between top and bottom tile surfaces, as well as live and corallite scans of each tile surface, within each year (Tukey's p<0.05).

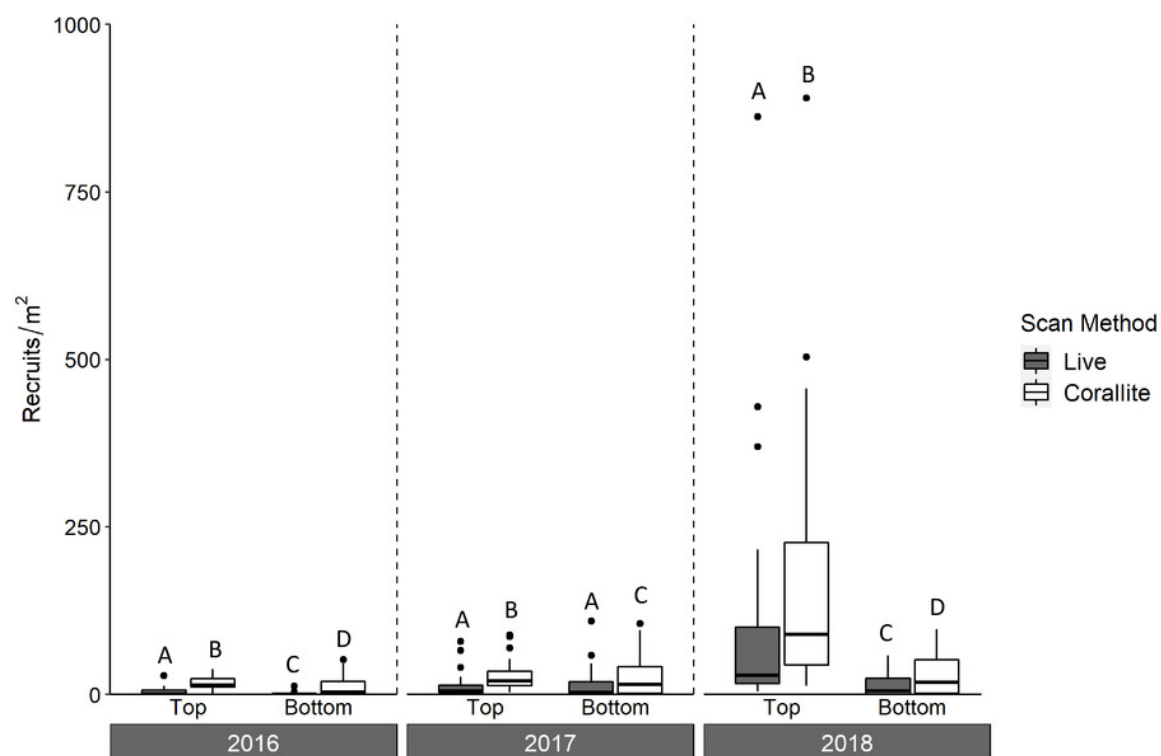



Figure 4

Density of scleractinian recruits found on tile surfaces during corallite scans across N = 30 Florida Reef Tract sites and three years of deployments.

Boxplots show mean density of recruits at each study site; N = 90 site-years surveyed. Boxes display the median (horizontal line), the first and third quartiles (interquartile range [IQR]), 1.5 × IQR (whiskers), and outliers (black dots). Five outliers with density values greater than 100m^{-2} were trimmed from the plot for readability (198m^{-2}, 215m^{-2}, 295m^{-2}, 442m^{-2}, 723m^{-2}; all from top surface, Siderastreidae). Letters denote significant differences of recruit count within scleractinian family (Tukey's p<0.05).

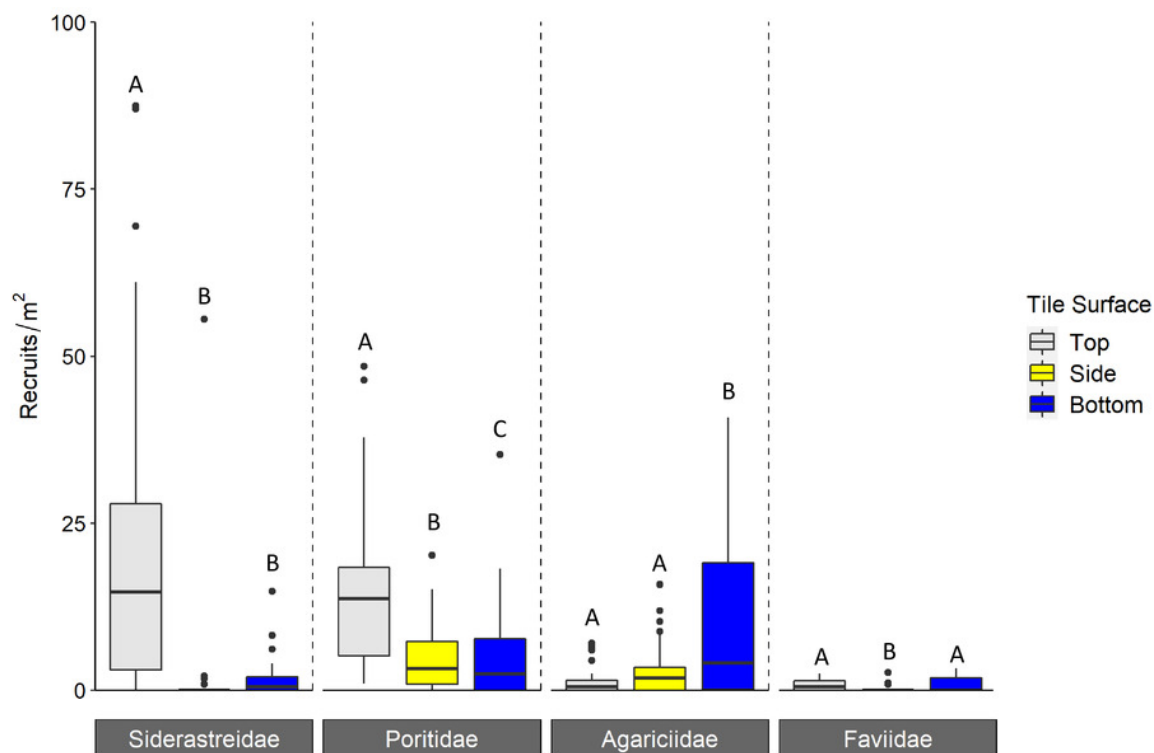



Figure 5

Relationships between site depth in meters (x-axes) and proportion of corallites found on each tile surface (y-axes) per scleractinian coral family.

Significant linear relationships are denoted with asterisks (* denotes p<0.01; *** denotes p<0.0001) and the Pearson product-moment correlation coefficient is shown for significant relationships.

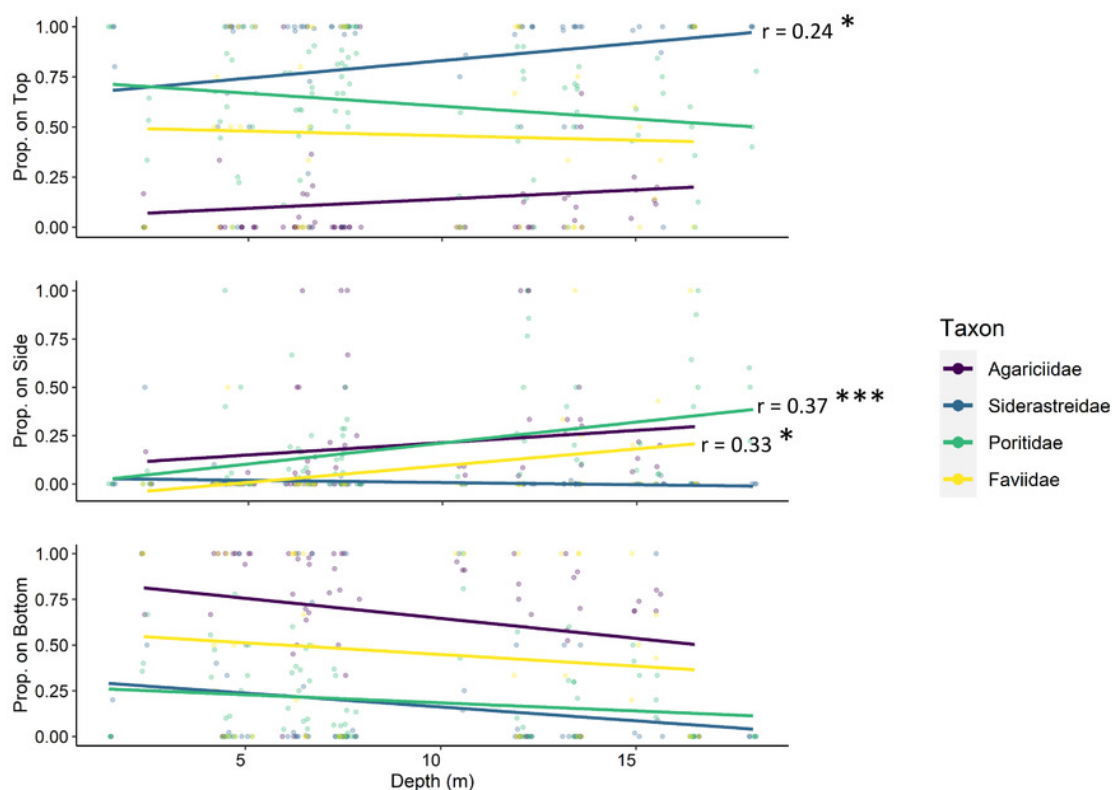
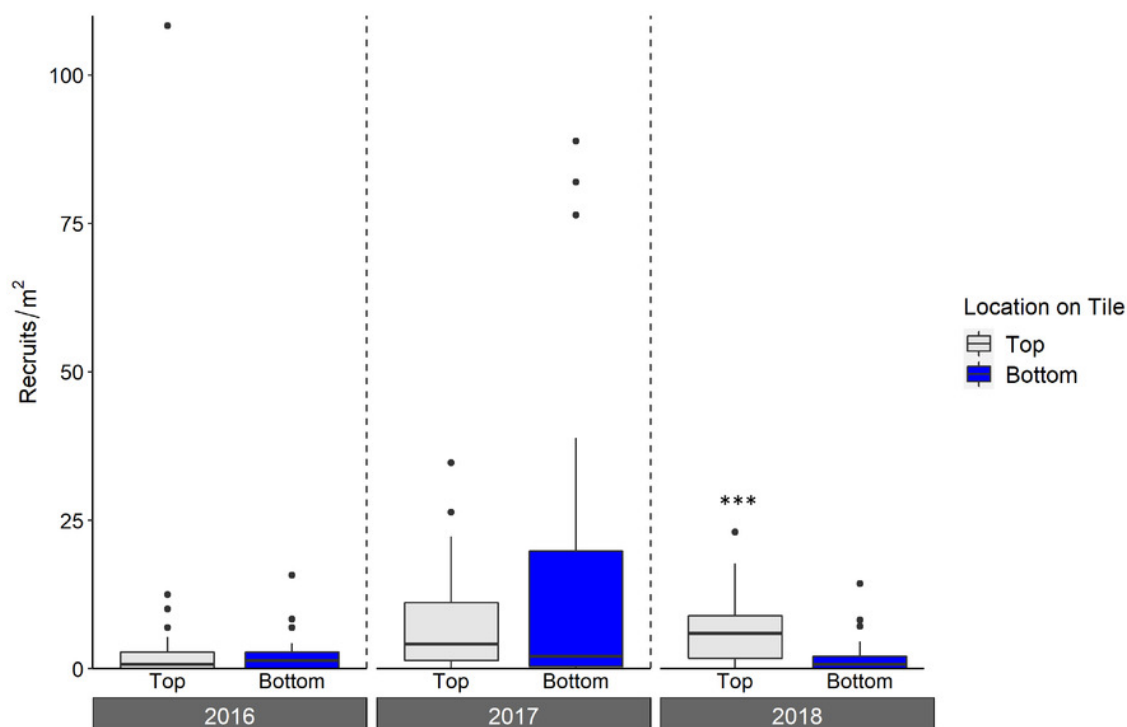



Figure 6

Density of octocoral recruits found on top and bottom tile surfaces during live scans across N = 30 Florida Reef Tract sites for each of three years of deployment.

Boxplots show the mean density of recruits at each study site within each year. Boxes display the median (horizontal line), the first and third quartiles (interquartile range [IQR]), 1.5 × IQR (whiskers), and outliers (black dots). Two outliers with density values greater than $200m^{-2}$ were trimmed from the plot for readability ($240m^{-2}$; top surface 2018, and $340m^{-2}$; top surface 2017). Asterisks denote significant pairwise differences of recruit count within year (*** denotes p<0.001).

Type II Analysis of Deviance of a negative binomial generalized linear model regressing the number of scleractinian recruits found on the top and bottom surfaces of tiles (location) in live and corallite scans (method).

Site and year are fixed factors. The chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

1 **Table 1. Type II Analysis of Deviance of a negative binomial generalized linear model**
2 **regressing the number of scleractinian recruits found on the top and bottom surfaces of**
3 **tiles (location) in live and corallite scans (method).** Site and year are fixed factors. The chi-
4 square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

	Chisq	Df	Pr(>Chisq)
Location on Tile	440.98	1	<0.001
Method	563.02	1	<0.001
Year	1287.02	2	<0.001
Site	1111.11	29	<0.001
Interaction of Location & Method	7.02	1	0.008

Type II Analysis of Deviance of a negative binomial generalized linear model regressing the number of scleractinian recruits against family, tile surface, and depth.

Year is a fixed factor. The chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

1 **Table 2. Type II Analysis of Deviance of a negative binomial generalized linear model**
2 **regressing the number of scleractinian recruits against family, tile surface, and depth.** Year
3 is a fixed factor. The chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq])
4 are shown.

Factor	Chisq	Df	Pr(>Chisq)
Taxon	993.87	3	<0.001
Tile Surface	1001.04	2	<0.001
Depth	2.98	1	0.084
Year	478.82	2	<0.001
Taxon x Tile Surface	1044.3	6	<0.001
Taxon x Depth	56.76	3	<0.001
Tile Surface x Depth	28.57	2	<0.001
Taxon x Tile Surface x Depth	26.16	6	<0.001

Type II Analysis of Deviance of a quasipoisson generalized linear model regressing the number of octocoral recruits against tile surface and depth.

Year is a fixed covariate. The chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

1 **Table 3. Type II Analysis of Deviance of a quasipoisson generalized linear model regressing**
2 **the number of octocoral recruits against tile surface and depth.** Year is a fixed covariate. The
3 chi-square value (Chisq), degrees of freedom (df), and p-value (Pr[>Chisq]) are shown.

	Chisq	Df	Pr(>Chisq)
Location on Tile	43.56	1	<0.001
Depth	3.06	1	0.081
Interaction of Location & Depth	82.35	1	<0.001
Year	120.29	2	<0.001