Decoupling the response of an estuarine shrimp to architectural components of habitat structure

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Both the amount and arrangement of structural elements can affect responses to habitat, but it can be difficult to tease the two apart. In order to explore attraction to structure, we examined how the amount and arrangement of artificial stalks affected responses of a shrimp, *Palaemon macrodactylus*, absent other proximate factors such as predation or interspecific competition. In aquaria, we tested the effect of differing densities of both un-branched and branched stalks, where the amount of material in the branched stalk equaled four-times that of the un-branched. The results clearly showed that it was the amount of material, not how it was arranged, that elicited responses from shrimp. Also, although stalks were not purposefully designed to mimic structural elements found in nature, they did resemble biogenic structure such as hydroids, algae, or plants. In order to test shrimp attraction to a different, perhaps more unfamiliar habitat type, we examined responses to plastic "army men." These structural elements elicited similar attraction of shrimp, and, in general, shrimp response correlated well with the fractal dimension of both stalks and army men. Overall, these results indicate that attraction to physical structure, regardless of its nature, may be an important driver of high abundances often associated with complex habitats.

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21   **Abstract**

22   Both the amount and arrangement of structural elements can affect responses to habitat,

23   but it can be difficult to tease the two apart. In order to explore attraction to structure, we

24   examined how the amount and arrangement of artificial stalks affected responses of a shrimp,

25   *Palaemon macrodactylus*, absent other proximate factors such as predation or interspecific

26   competition. In aquaria, we tested the effect of differing densities of both un-branched and

27   branched stalks, where the amount of material in the branched stalk equaled four-times that of

28   the un-branched. The results clearly showed that it was the amount of material, not how it was

29   arranged, that elicited responses from shrimp. Also, although stalks were not purposefully

30   designed to mimic structural elements found in nature, they did resemble biogenic structure such

31   as hydroids, algae, or plants. In order to test shrimp attraction to a different, perhaps more

32   unfamiliar habitat type, we examined responses to plastic "army men." These structural

33   elements elicited similar attraction of shrimp, and, in general, shrimp response correlated well

34   with the fractal dimension of both stalks and army men. Overall, these results indicate that

35   attraction to physical structure, regardless of its nature, may be an important driver of high

36   abundances often associated with complex habitats.

37

38   **1. Introduction**

39   The physical nature of habitats profoundly shapes resident biotic assemblages. Habitat-

40   species relationships underpin basic ecological dynamics (McCoy and Bell, 1991; Matias et al.,

41   2010; Tokeshi and Arakaki, 2012), and also have implications for ecosystem management,

42   conservation, and restoration (e.g., Crooks, 2002; Jimenéz and Conover 2001; Thrush and

43   Dayton, 2002; Byers et al, 2006; St. Pierre and Kovalenko, 2014, Loke et al. 2014).   Despite (or

44   perhaps because of) the ubiquity and importance of habitat-species interactions, there are

45   considerable conceptual and terminological issues associated with even the most fundamental

46   aspects of habitat structure (Matias et al., 2007; Tokeshi and Arakaki, 2012; Kovalenko et al.

47   2013, Loke et al. 2014). In general terms, however, habitat structure is typically considered to be

48   related to two elements: the presence of distinct structural types - habitat heterogeneity; and the

49   absolute abundance and configuration of structural material - structural complexity (Heck and

50   Wetstone 1977; McCoy and Bell, 1991; Sebens, 1991; Beck, 2000). Although this basic

51   framework provides a foundation for considering how the physical nature of habitats shapes

52   communities, these two elements are often confounded in studies examining biotic responses to

53   habitats, making it difficult to quantify the effects of either (Beck, 2000; Matias et al., 2007).

54   The lack of clarity related to habitat structure notwithstanding, numerous studies have

55   demonstrated that "complex" (*sensu lato*) habitats tend to have more individuals and/or species

56   than less complex habitats, a pattern that has been observed across various systems and at

57   various spatial scales (e.g., Krecker, 1939; MacArthur and MacArthur, 1961; Recher, 1969;

58   Orth, 1973; Dean and Connell, 1987; Crooks, 2002; Thomaz et al., 2008). Complex habitats can

59   serve as predation refuges (Crowder and Cooper, 1982; Everett and Ruiz, 1993; Warfe and

60   Barmuta, 2004), and ameliorate competition (Sale, 1975). The structure of habitats can interact

61   with physical conditions such as wind or currents, modulating the supply of resources such as

62   food (Gutiérrez et al., 2011) or altering the distribution of materials to which species might

63   respond (e.g., olfactory cues, Ferner et al., 2009). Structural complexity may increase living

64   space, especially for relatively small organisms, and the fractal dimension of habitats has been

65   found to correlate positively with density and negatively with body size (Gunnarsson, 1992;

66   Morse et al., 1995; McAbendroth et al., 2005). Increased densities and diversities within

67   complex habitats also can be caused by net inward fluxes of individuals. In aquatic systems,

68   planktonic larvae can act as largely passive particles, and settlement rates in habitats such as

69   seagrass beds may be increased due to decreased water velocities (Fonseca et al., 1982).

70   Active behavioral choice is also a proximate mechanism for motile species, and given

71   that behavior can mediate individual-ecosystem interactions, behavioral studies are emerging as

72   a key way to explore responses to human-induced environmental change, including impacts of

73   "novel" habitats (Wright et al. 2010; Sih et al., 2011). In aquatic systems, attraction to objects -

74   any object, regardless of whether it is natural or artificial - is a well-known response of a variety

75   of fish and motile invertebrates (Mortensen, 1917; Carlisle et al., 1964; Salazar, 1973; Druce and

76   Kingsford, 1995; Ingólfsson, 1998; Castro et al., 2002). Further, architectural complexity can

77   play a role in determining magnitude of responses (Dean and Connell, 1987; Hacker and

78   Steneck, 1990). A variety of lab and field experiments have examined behavioral responses to

79   the structural complexity of habitats (e.g., Bell and Westoby, 1986; Jeffries, 1993; Gee and

80   Warwick, 1994; Roberston and Weis, 2007).   Habitat selection is often evaluated in the presence

81   of predation pressure, either by design or as a consequence of field settings (Crowder and

82   Cooper, 1982; Everett and Ruiz, 1993). Fewer studies have looked at habitat choice in the

83   absence of factors such as predation pressure or food supply, but those that have indicate that the

84   physical arrangement of materials alone can play an important role in shaping the distribution

85   and abundance of motile organisms (Stoner 1980; Bell and Westoby 1986; Hacker and Steneck

86   1990).

87   In this study, we examined attraction to the amount and arrangement of structural

88   elements by a motile organism, the shrimp *Palaemon macrodactylus*. This grass shrimp is native

89   to Asia, but has been introduced worldwide (Micu and Nita 2009). It was first reported in San

90   Francisco Bay the 1950's (Newman 1963), and is now one of the most common nektonic

91   organism in the brackish waters there (Hatfield 1985, Crooks pers obs.). Like many motile

92   macrofauna, this shrimp is often found associated with structure, with Newman (1963) noting

93   that it was "frequently found in old tires, tin cans and other artificial structures as well as on

94   pilings, walls and among rocks or calcareous tubes of *Mercierella*" (*Mercierella = Ficopomatus*

95   *enigmatic*us, a non-native, "reef-creating" polychaete worm).

96   The goal of our work was to examine how the complexity and density of structural

97   elements would drive behavioral responses of *P. macrodactylus*, while controlling for other

98   proximate factors which might drive shrimp response (e.g., immediate predation risk and

99   presence of food). This consisted of two experiments, one where shrimp could choose between

100   arrays of structural elements in different configurations, and the other where we examined the

101   response to a single array to assess the degree to which habitat complexity, as assessed with total

102   surface area and fractal dimension, could account for position of shrimp in experimental tanks.

103   The structural elements used in the experiments were plastic mesh cut into different

104   configurations. While these artificial structures were not deliberately constructed to resemble

105   any particular species, they did resemble various organisms in benthic communities (Fig. 1A),

106   such as macroalgae, vascular plants, or hydroids. Other researchers have used similar "mimics"

107   to examine responses of aquatic fauna (e.g., Schneider and Mann, 1991; Jeffries 1993; Bourget

108   and Harvey 1998). In order to determine how shrimp would respond to perhaps more unfamiliar

109   structural forms, we also created two "non-mimic" treatments, consisting of plastic "army men"

110   (toy soldiers and equipment; Fig. 1B).

111

112

113 **2.l Methods**

114 *2.1 Location*

115   Asian grass shrimp *Palaemon macrodactylus* were collected from a floating dock at

116 Black Point, where the Petaluma River enters north-western San Francisco Bay.   The shrimp

117 were abundant and easily collected with dip nets, and were transported to the greenhouse facility

118 at Romberg Tiburon Center (San Francisco State University), where they were kept in holding

119 tanks and fed daily with flake fish food. Average-sized shrimp, approx. 4 cm in length, were

120 selected for use in the experiments, and individual shrimp were used only once (Underwood et

121 al. 2004).

122

123 *2.2 Experimental Setup*

124   All experiments were conducted in 10-gallon aquaria (bottom dimensions = 50.8 cm x

125 25.4 cm) with a thin (1-2 cm) layer of sand covering the bottom. The 12 cm-long stalks were cut

126 in two configurations from 1-mm diameter black plastic mesh with approximately 15 x 15-mm

127 openings. Two levels of architectural complexity were used (Figs. 1A and 2). The un-branched

128 stalk was a single strip of mesh with all side branches removed. The branched stalk was cut out

129 of the mesh in such a way that crosspieces were left intact and one branched stalk had the same

130 amount of material and surface area as four un-branched stalks. Two, four, eight, sixteen, and

131 thirty-two stalk configurations were used to assess shrimp responses to structure. Structural

132 material was arrayed uniformly on the 14 x 14-cm PVC plates and fixed in place with hot melt

133 glue. The two non-stalk treatments were created using arrays of toy plastic army men and army

134 equipment (Fig. 1B). These treatments offered different structural types, with less resemblance

135   to naturally-occurring biogenic structure.   There were 8 army men per plate, and 4 pieces of

136   army equipment.

137   Panels were placed on the bottom of the tank with the surfaces buried so that only the

138   stalks or toys were visible above the sand.   The test area was the surface immediately above the

139   entire 14 x 14-cm panel (Fig. 2). All tanks were kept within in a blackout tent to control light

140   exposure, with illumination provided by overhead fluorescent lamps set on a timer with 12 h

141   light / dark cycles. Individual tanks were wrapped on all vertical sides with opaque black plastic

142   to prevent reflections and reactions to shrimp in neighboring tanks.

143   At the beginning of each trial run, five shrimp were placed in each tank and left to

144   acclimate overnight. The next morning, observations were taken every half hour for 6 hours, for

145   a total of 13 observations. Observations were taken by lifting the opaque plastic cover from one

146   long vertical side of each tank and counting the number of shrimp in the test area. Testing before

147   the experiment identified this as the best method for observing shrimp without startling them,

148   and during the course of the experiment we did not notice shrimp respond to our observations.

149   This set-up was used in two experiments.

150

151   *2.3 Choice Between Two Arrays*

152   This experiment assessed shrimp responses when presented with structural arrays of

153   varying architectural complexity on opposite sides of the tanks. Two 14 x 14-cm structural

154   arrays (the test areas) were present in each tank, one on each side, which were randomly chosen

155   (Fig. 2). The shrimp were offered four different pairings. There were two choices between

156   arrays of equal stalk density: 8 un-branched vs. 8 branched, or 32 un-branched vs. 32 branched.

157   There were also two choices with equal surface area of material: 2 branched vs. 8 un-branched,

158   or 8 branched vs. 32 un-branched. The response variable was the average number of shrimp in

159   the each 14 x 14-cm test area over the course of a trial run. The experiment was a Randomized

160   Complete Block Design, blocked in time and with tanks with each treatment pairing running

161   simultaneously. This was repeated 10 times, with a re-randomization of treatment allocation to

162   tank each time.

163

164   *2.3 Response to a Single Array*

165   This experiment examined shrimp responses to the presence of a single structural array of

166   varying architectural complexity on one randomly-chosen side of each tank, with nothing on the

167   other side. Treatments consisted of 5 densities of un-branched stalks and 5 densities of branched

168   stalks. The response variable was the average number of shrimp in the single 14 x 14-cm test

169   area over the course of a trial run. The experiment was again blocked in time, with 8 blocks and

170   a re-randomization of treatment allocation to tank each time. Also, the two non-stalk treatments

171   (plastic army men and army equipment) were included in each block.

172

173   *2.5 Analyses*

174   All shrimp density data were log-transformed prior to analysis, and a constant of 0.077

175   was added to all values. This represents the smallest non-zero number that could be obtained

176   (e.g., Warton and Hui, 2009): one shrimp in one test area during one observation period. In the

177   *Choice Between Arrays* experiment, each pairing was analyzed separately using paired t-tests.

178   For the *Response to a Single Array* experiment, the effects of stalk density, type, and block were

179   analyzed as a three-factor ANOVA without replication. Comparisons between arrays of equal

180   surface area were conducted using paired t-tests.

181   For the assessment of the effect of toys, the number of shrimp in the test area (out of the

182   five total) were compared to what would be expected if shrimp were randomly distributed on the

183   tank floor using a t-test (i.e., an average of 0.69 shrimp would be expected in the 14x14-cm test

184   area, which constitutes 13.8% of the total tank bottom). Number of shrimp in the test area was

185   also plotted against fractal dimension of each array type, including the toys. This was done using

186   the program Fractal Dimension Calculator (http://paulbourke.net/fractals/fracdim/), which uses

187   the box-counting method as an estimate of fractal dimension (Morse et al. 1985, Jeffries 1993).

188   In this procedure, a grid is superimposed upon a digitized image and the number of cells

189   occupied by the image is calculated iteratively for progressively smaller cell sizes. Images for

190   this analysis were taken from the sides of three replicate arrays for each array type. In order to

191   assess if shrimp responded to the toys similarly as the stalks, we determined the degree to which

192   individual points affected the relationship between fractal dimension and number of shrimp using

193   Cook's D (Fox, 1991). A cutoff for "influential" points of $4 / (n - k -1)$ was used (Fox, 1991),

194   where $n = 12$ (number of observations) and $k = 1$ (number of independent variables), resulting in

195   a value of 0.40.

196

197   **3. Results**

198   *3.1 Choice Between Two Arrays*

199   In the case where shrimp in a single tank had a choice between two arrays with differing

200   structural arrangements, the total amount of material, and not how it was arranged, was the

201   primary driver of shrimp response (Fig. 3). In tanks with test areas with equal amounts of

202   material but differing stalk density, no statistically significant differences in number of shrimp

203   were found ($P \geq 0.39$). At equal stalk density, however, shrimp preferred test areas with branched

204   stalks, choosing areas with more structure over those with less (Fig. 3). This effect was

205   particularly apparent at the highest stalk densities, with over 8 times as many shrimp found with

206   branched stalks than with un-branched (P<0.001).

207

208

209   *3.2. Response to a Single Array*

210   When presented with a single array per tank, the quantity of structure again had marked

211   effects on shrimp location within tanks (Fig. 4). Both stalk density and stalk type (branched vs.

212   un-branched) were statistically significant. For both stalk types, number of shrimp increased

213   approximately 500% from the lowest to the highest stalk densities. However, there were no

214   significant differences in shrimp densities in test areas with equal amounts of material but

215   differing stalk density (Fig. 4 – dashed lines), as also observed in the choice experiment (Fig. 3).

216   In general, total stalk surface area, irrespective of stalk type, was an excellent predictor of

217   number of shrimp within the test area (Fig. 5)

218   The shrimp also displayed marked responses to the non-stalk habitat treatments. The

219   army men treatment had a mean density of 2.3 (± 0.2) shrimp per 14x14-cm test area, and the

220   army equipment treatment had a mean density of 1.6 (± 0.4). Both of these are significantly

221   different than what would be expected if shrimp were randomly distributed on the tank bottom

222   (army men: $t_7 = 11.5$, p<0.001; army equipment: $t_7 = 3.22$, p=0.015). Also, these shrimp

223   densities are comparable to the two highest values found using branched stalk treatments.

224   Fractal dimension, as assessed with the box-counting method, was again an excellent

225   predictor of number of shrimp within the test area (Fig. 6). Although stalks and toys represent

226   quite different structural forms (as well as textures and colors), fractal dimension accounted for

227 93% of the variability to shrimp number ($R^2 = 0.93$, P<0.001).   The values for Cook's D, which

228 assesses outliers (or "influential points") in regressions, all fell below the cut-off of 0.4 (although

229 the value for the army equipment approached this at D = 0.37). Also, for the stalk treatments, it

230 is important to note that the amount of material was also very closely related to the fractal

231 dimension of the arrays (logarithmic regression, $R^2 = 0.98$, P<0.001).

232

233 **4. Discussion**

234   These experiments demonstrate that shrimp responded to the presence of structure in the

235 absence of proximate factors such as predation pressure and food supply, and that an excellent

236 predictor of shrimp location was the amount of material available. These findings support

237 previous suggestions that surface area tends to be a good measure of complexity (Stoner, 1980;

238 Stoner and Lewis, 1985; Beck, 2000). For example, Attrill et al. (2000) found that macro-

239 invertebrate community structure in seagrass beds was associated with the amount of plant

240 available, and Dean and Connell (1987) showed that intertidal invertebrates chose algal clumps

241 of based on biomass rather than species identity. Not surprisingly, however, exceptions to this

242 relationship are found, and morphologically different structures with constant surface areas have

243 been shown to elicit differing responses (Loke and Todd 2016), such as artificial macrophyte

244 beds with many thin blades having higher fish abundance than beds with fewer, thicker blades

245 (Jenkins and Sutherland, 1997).   In other cases, surface area might underestimate the number of

246 individuals and species found within increasingly complex habitats (Hauser et al. 2006), or,

247 conversely, there might be negative relationships between amount of material and invertebrate

248 communities (Kelahar 2003). Together, these emphasize that other processes are at work beyond

249   just surface area, and it is necessary to consider factors such as scale and environmental context

250   (Kovalenko et al. 2013; Matias 2013).

251   Fractal dimension also was a powerful predictor of shrimp response. Although it is

252   possible that shrimp were also responding to differing cues (such as material or color), fractal

253   dimension explained much of the variability in shrimp response to the two stalk types as well as

254   army toys (Fig. 6). Like other experiments that explicitly attempted comparisons of fractal

255   dimension and surface area (Beck 2000 and references therein), our results have similarly

256   resulted in a limited ability to recommend one over the other given that surface area and fractal

257   dimension were correlated. It is worth noting, though, that fractal dimension, assessed with the

258   box-counting method, is easier to assess than surface area for irregular structures (Beck 2000),

259   but can be difficult to apply in the context of applied conservation or restoration activities (Loke

260   et al. 2014). Although several studies have shown that fractal surfaces offer more usable space

261   for smaller organisms than larger ones, producing a positive relationship between abundance and

262   complexity (Morse et al., 1985; Shorrocks et al. 1991), this argument does not apply here as the

263   shrimp were all comparably-sized (approximately 4-cm).

264   Our results also agree with other studies indicating that behavioral choice is an important

265   factor shaping the distribution and abundance of motile organisms (e.g., Stoner, 1980; Rooke,

266   1984; Bell and Westoby, 1986). In the laboratory setting of these experiments, shrimp were

267   attracted to branched and un-branched structures that generally resembled materials such as

268   hydroids, algae, or plants. In addition, the shrimp responded to forms that might be less typical

269   of natural systems, the plastic army toys. Together, these responses suggest that for these shrimp

270   choice is largely based on the presence of structure of any sort, and not just a response to familiar

271   forms.

272   Despite the potentially strong effect of choice on patterns of distribution and abundance,

273   more work is needed on underlying mechanisms, including habitat choice in response to specific

274   behaviors being displayed, such as mating, navigation, feeding, or predator escape (Shumway,

275   2008; Kovalenko et al. 2013; Roever et al., 2014).   Many inter-related factors could potentially

276   drive attraction to structure, including thigmotactic movement oriented by contact or touch

277   (Olyslager and Williams, 1993; Uryu et al., 1996; Webster and Laland 2011), or structure

278   offering a visual reference point for activities such as breeding or feeding (e.g., Dagorn and

279   Fréon, 1999).   For some organisms, such as birds and mammals, it has been suggested that

280   psychological factors, such as aversion or attraction to novel conditions, serve to structure

281   behaviors and distributional patterns (Greenberg, 1984). Also, although predators were not

282   immediately involved in our experiments, there is likely recognition that complex habitats may

283   afford escape from predation (Bell and Westoby, 1986, Shumway, 2008), and species might alter

284   behavior according to the perceived protective value of habitats even in the absence of

285   immediate predation risk (Ingrum et al., 2010).

286   The response of species to the physical nature of habitats, and the general tendency to

287   choose more complex over simpler structures, has a number of implications for applied ecology.

288   For example, a better understanding of the behavioral responses to structure can improve design

289   of artificial reefs (Gratwicke and Speight, 2005; Perkol-Finkel et al., 2006) and fish aggregating

290   devices (Dagorn and Fréon, 1999; Castro et al., 2001, Girard et al., 2004). The generality of

291   behavioral responses to structure also allows prediction of the effects of habitat-modifying exotic

292   species, as invasive ecosystem engineers may create unfamiliar, novel habitat types that tend to

293   benefit at least some resident biota regardless of the exact type of structure being created

294   (Crooks, 2002). Clearly, there will be exceptions to the pattern of positive relationships between

295   complexity and species responses (Crooks, 2002, Gutiérrez and Iribarne, 2004). For example,

296   complex habitats can impair visual fields (Rilov et al., 2007) or interfere with foraging, such as

297   the invasive alga *Caulerpa* interfering with feeding of native mullet (Levi and Francour, 2004).

298   Given the potential importance of the recognition and response of organisms to habitat

299   complexity, more research is needed on this subject (Shumway, 2008). In general, it will be

300   valuable to examine habitat preferences in the absence of other extrinsic factors in a wide range

301   of species, as understanding such interspecific differences may help explain community-level

302   patterns (e.g., Greenberg 1984). For *P. macrodactylus*, which has been shown to demonstrate a

303   high degree of correlation between habitat complexity and magnitude of response (this study), it

304   would be interesting to determine whether responses are innate rather than learned (which might

305   be accomplished by examining lab-reared versus field-caught individuals), as well as to conduct

306   experiments with varying densities of conspecifics in order to determine the potential role of

307   density-dependent, intraspecific interactions in shaping distribution. It also would be valuable to

308   compare results of artificial structures to natural ones, including carefully-controlled field

309   experiments to explore shrimp responses in the presence of other factors that would affect

310   distribution in natural settings (Underwood et al. 2004).

311

312   **Conclusions**

313   The results of these and other experiments demonstrate that attraction to physical

314   structure in the absence of proximate mechanisms such as food supply and predators can explain

315   patterns of increased densities within complex habitats. However, it is clear that the habitat

316   structure affects resident biota in many other fundamental ways, including active and passive

317   accumulation of individuals (Fonseca et al., 1982), amelioration of competition (Sale, 1975) and

318   environmental conditions (Bruno and Bertness, 2001), and predator avoidance (Everett and Ruiz,

319   1993). As many of these factors will tend to promote higher densities within complex habitats, it

320   can be difficult to tease out the relative importance of each when all are potentially operating.

321   Nevertheless, it is likely this synergism that drives attraction to complex structure.

322

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326

327

328   **References**

329   Attrill, M.J., Strong, J.A., and Rowden, A.A. (2000). Are macroinvertebrate communities

330   influenced by seagrass structural complexity? *Ecography* 23, 114–121.

331   Beck, M., 2000. Separating the elements of habitat structure: independent effects of habitat

332   complexity and structural components on rocky intertidal gastropods. *J. Exp. Mar. Biol.*

333   *Ecol.* 249, 29–49.

334   Bell, J.D., Westoby, M., 1986. Abundance of macrofauna in dense seagrass is due to habitat

335   preference, not predation. *Oecologia* 68, 205–209.

336   Bourget, E. and Harvey, M., 1998. Spatial analysis of recruitment of marine invertebrates on

337   arborescent substrata. *Biofouling*, 12, 45–55.

338   Bruno, J.F., Bertness, M.D. 2001. Habitat modification and facilitation in benthic marine

339   communities, in: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.) Marine Community

340   Ecology, Sinauer Associates, Inc, Massachusetts, pp. 201-218.

341 Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks,

342   J.A., Wilson, W.G., 2006. Using ecosystem engineers to restore ecological systems. *Trends*

343   *Ecol. Evol*. 21, 493–500.

344 Carlisle, J.G. Jr., Turner, C.H., Ebert, E.E., 1964. Artificial habitat in the marine environment.

345   California Department of Fish and Game, Fish Bulletin 124.

346 Castro, J.J., Santiago, J.A., Santana-Ortega, A.T., 2001. A general theory on fish aggregation to

347   floating objects: An alternative to the meeting point hypothesis. *Rev. Fish. Biol. Fisheries*

348   11, 255–277.

349 Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the

350   role of ecosystem engineers. *Oikos* 97, 153–166.

351 Crowder, L.B., Cooper, W.E., 1982. Habitat structural complexity and the interaction between

352   bluegills and their prey. *Ecology* 63, 1802–1813.

353 Dagorn, L., Fréon, P., 1999. Tropical tuna associated with floating objects: a simulation study of

354   the meeting point hypothesis. *Can. J. Fish. Aquat. Sci.* 56, 984–993.

355 Dean, R.L., Connell, J.H., 1987. Marine invertebrates in an algal succession. III. Mechanisms

356   linking habitat complexity with diversity. *J. Exp. Mar. Biol. Ecol.* 109, 249–273.

357 Druce, B.E. and Kingsford, M.J. 1995. An experimental investigation on the fishes associated

358   with drifting objects in coastal waters of temperate Australia. *Bulletin of Marine Science*, 57:

359   378-392.

360 Everett, R.A., Ruiz, G.M., 1993. Coarse woody debris as a refuge from predation in aquatic

361   communities. An experimental test. *Oecologia* 93, 475–486.

362 Ferner, M., Smee, D., Weissburg, M., 2009. Habitat complexity alters lethal and non-lethal

363   olfactory interactions between predators and prey. *Mar. Ecol. Prog. Ser.* 374, 13–22.

364   Fonseca, M.S., Fisher, J.S., Zieman, J.C., Thayer, G.W., 1982. Influence of the seagrass, *Zostera*

365   *marina* L., on current flow. *Estuar. Coast. Shelf S.* 15, 351–364.

366   Fox, J. 1991. Regression Diagnostics. SAGE Publications, Inc, Thousand Oaks, California, USA.

367   Gee, J.M., Warwick, R.M., 1994. Metazoan community structure in relation to the fractal

368   dimensions of marine macroalgae. *Mar. Ecol. Prog. Ser.* 103, 141–150.

369   Girard, C., Benhamou, S., Dagorn, L., 2004. FAD: Fish Aggregating Device or Fish Attracting

370   Device? A new analysis of yellowfin tuna movements around floating objects. *Anim. Behav.*

371   67, 319–326.

372   Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance

373   and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish*

374   *Biology* 66, 650–667.

375   Greenberg, R., 1984. Neophobia in the foraging-site selection of a neotropical migrant bird: an

376   experimental study. *P. Natl. Acad. Sci. USA* 81, 3778–3780.

377   Gunnarsson, B., 1992. Fractal dimension of plants and body size distribution in spiders.

378   *Functional Ecology* 6: 636–641.

379   Gutiérrez, J., Iribarne, O., 2004. Conditional responses of organisms to habitat structure: an

380   example from intertidal mudflats. *Oecologia* 139, 572–582.

381   Gutiérrez, J.L., Jones, C.G., Byers, J.E., Arkema, K.K., Berkenbusch, K., Commito, J.A., Duarte,

382   C.M., Hacker, S.D., Lambrinos, J.G., Hendriks, I.E., Hogarth, P.J., Palomo, M.G., Wild, C.,

383   2011. Physical ecosystem engineers and the functioning of estuaries and coasts, in:

384   Wolanski, E., McLusky, D.S. (Eds.) Treatise on Estuarine and Coastal Science, Vol 7.

385   Academic Press, Waltham, Massachusetts, pp. 53–81.

386 Hacker, S.D. and Steneck, R.S. 1990. Habitat architecture and the abundance and body-size-

387   dependent habitat selection of a phytal amphipod. *Ecology* 71: 2269-2285.

388 Hauser, A., Attrill, M.J., Cotton, P.A., 2006. Effects of habitat complexity on the diversity and

389   abundance of macrofauna colonising artificial kelp holdfasts. *Mar. Ecol. Prog. Ser.* 325, 93–

390   100.

391 Heck, K.L., Wetstone, G.S., 1977. Habitat complexity and invertebrate species richness and

392   abundance in tropical seagrass meadows. *J. Biogeogr.* 4, 135.

393 Ingólfsson, A. 1998. Dynamics of macrofaunal communities of floating seaweed clumps off

394   western Iceland: a study of patches on the surface of the sea. *Journal of Experimental*

395   *Marine Biology and Ecology* 231: 119-137.

396 Ingrum, J., Nordell, S.E., Dole, J., 2010. Effects of habitat complexity and group size on

397   perceived predation risk in goldfish (*Carassius auratus*). *Ethol. Ecol. Evol.* 22, 119–132.

398 Jeffries, M., 1993. Invertebrate colonization of artificial pondweeds of differing fractal

399   dimension. *Oikos* 67, 142–148.

400 Jenkins, G.P., Sutherland, C.R., 1997. The influence of habitat structure on nearshore fish

401   assemblages in a southern Australian embayment: colonisation and turnover rate of fishes

402   associated with artificial macrophyte beds of varying physical structure. *J. Exp. Mar. Biol.*

403   *Ecol.* 218, 103–125.

404 Jenkins, G., Walker-Smith, G., Hamer, P., 2002. Elements of habitat complexity that influence

405   harpacticoid copepods associated with seagrass beds in a temperate bay. *Oecologia* 131,

406   598–605.

407 Jiménez, J.E., Conover, M.R., 2001. Ecological approaches to reduce predation on ground-

408   nesting gamebirds and their nests. *Wildlife Soc. B.* 29, 62–69.

409   Kelaher, B.P., 2003. Changes in habitat complexity negatively affect diverse gastropod

410   assemblages in coralline algal turf. *Oecologia* 135, 431–441.

411   Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2011. Habitat complexity: approaches and future

412   directions. *Hydrobiologia* 685, 1–17.

413   Krecker, F.H., 1939. A comparative study of the animal population of certain submerged aquatic

414   plants. *Ecol.* 20, 553–562.

415   Levi, F., Francour, P., 2004. Behavioural response of *Mullus surmuletus* to habitat modification

416   by the invasive macroalga *Caulerpa taxifolia*. *J. Fish Biol.* 64, 55–64.

417   Loke, L.H.L., Jachowski, N.R., Bouma, T.J., Ladle, R.J. & Todd, P.A., 2014. Complexity for

418   Artificial Substrates (CASU): Software for creating and visualising habitat complexity. *PLoS*

419   *ONE* 9, e87990.

420   Loke, L.H.L., Todd, P.A., 2106. Structural complexity and component type increase intertidal

421   biodiversity independently of area. *Ecology* 97, 383-393.

422   MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity *Ecol.* 42, 594–598.

423   Matias, M.G., 2013. Macrofaunal responses to structural complexity are mediated by

424   environmental variability and surrounding habitats. *Mar. Biol.* 160, 493–502.

425   Matias, M.G., Underwood, A.J., Coleman, R.A., 2007. Interactions of components of habitats

426   alter composition and variability of assemblages. *J. Anim. Ecol.* 76, 986–994.

427   Matias, M.G., Underwood, A.J., Hochuli, D.F., Coleman, R.A., 2010. Independent effects of

428   patch size and structural complexity on diversity of benthic macroinvertebrates. *Ecol.* 91,

429   1908–1915.

430 McAbendroth, L., Ramsay, P.M., Foggo, A., Rundle, S.D., Bilton, D.T., 2005. Does macrophyte

431   fractal complexity drive invertebrate diversity, biomass and body size distributions? *Oikos*

432   111, 279–290.

433 McCoy, E.D., Bell, S.S., 1991. Habitat structure: the evolution and diversification of a complex

434   topic, in: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat structure: the physical

435   arrangement of objects in space. Chapman and Hall, London, pp. 3–21.

436 Morse, D.R., Lawton, J.H., Dodson, M.M., Williamson, M.H., 1985. Fractal dimension of

437   vegetation and the distribution of arthropod body lengths. *Nature* 314, 731–733.

438 Mortensen, T., 1917. Observations on protective adaptation and habits, mainly in marine

439   animals, in: Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. Vidensk.

440   *Medd. Dansk Naturhist. Forem.* 69, pp. 57–96.

441 Newman, W.A. 1963. On the introduction of an edible oriental shrimp (Caridea, Palaemonidae)

442   to San Francisco Bay. Crustaceana 5:119-132.

443 Olyslager, N.J., Williams, D.D., 1993. Microhabitat selection by the lotic amphipod Gammarus

444   pseudolimnaeus Bousfield: mechanisms for evaluating local substrate and current suitability.

445   *Canadian Journal of Zoology* 71, 2401–2409.

446 Orth, R.J., 1973. Benthic infauna of eelgrass,Zostera marina, beds. *Chesapeake Science* 14, 258–

447   269.

448 Perkol-Finkel, S., Shashar, N., Benayahu, Y., 2006. Can artificial reefs mimic natural reef

449   communities? The roles of structural features and age. *Mar. Environ. Res.* 61, 121–135.

450 Recher, H.F., 1969. Bird species diversity and habitat diversity in Australia and North America.

451   *Am. Nat.* 103: 75–80.

452   Rilov, G., Figueira, W.F., Lyman, S.J., Crowder, L.B., 2007. Complex habitats may not always

453   benefit prey: linking visual field with reef fish behavior and distribution. *Mar. Ecol. Prog.*

454   *Ser.* 329, 225–238.

455   Robertson, T.L., Weis, J.S., 2007. Interactions between the grass shrimp Palaemonetes pugio and

456   the salt marsh grasses *Phragmites australis* and *Spartina alterniflora. Biol. Invasions* 9, 25–

457   30.

458   Roever, C.L., Beyer, H.L., Chase, M.J., van Aarde, R.J., 2014. The pitfalls of ignoring behaviour

459   when quantifying habitat selection. *Divers. Distrib.* 20, 322–333.

460   Rooke, J.B., 1984. The invertebrate fauna of four macrophytes in a lotic system *Freshwater*

461   *Biol.* 14, 507–513.

462   Salazar, M.H., 1973. Animal attraction to sunken submarines. *Oceans* 6: 68-70.

463   Sale, P.F., 1975. Patterns of use of space in a guild of territorial reef fishes. *Mar. Biol.* 29, 89–97.

464   Schneider, F.I., Mann, K.H., 1991. Species specific relationships of invertebrates to vegetation in

465   a seagrass bed. I. Experiments on the importance of macrophyte shape, epiphyte cover and

466   predation. *Journal of Experimental Marine Biology and Ecology*, 145, 119-139.

467   Sebens, K.P., 1991. Habitat structure and community dynamics in marine benthic systems, in:

468   Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure and Community

469   Dynamics in Marine Benthic Systems. Chapman and Hall, London, pp. 211–234.

470   Shorrocks, B., Marsters, J., Ward, I., Evennett, P.J., 1991. The fractal dimension of lichens and

471   the distribution of arthropod body lengths. *Funct. Ecol.* 5, 457-460.

472   Shumway, C.A., 2008. Habitat complexity, brain, and behavior. *Brain Behav. Evol.* 72, 123–134.

473   Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-

474   induced rapid environmental change. *Evolutionary Applications* 4, 367–387.

475 St Pierre, J.I., Kovalenko, K.E., 2014. Effect of habitat complexity attributes on species richness.

476   *Ecosphere* 5, art22.

477 Stoner, A.W., 1980. The role of seagrass biomass in the organization of benthic macrofaunal

478   assemblages. *B. Mar. Sci.* 30, 537–551.

479 Stoner, A.W., Lewis, F.G.I., 1985. The influence of quantitative and qualitative aspects of

480   habitat complexity in tropical seagrass meadows. *J. Exp. Mar. Biol. Ecol.* 94, 19–40.

481 Thomaz, S.M., Dibble, E.D., Evangelista, L.R., Higuti, J., Bini, L.M., 2008. Influence of aquatic

482   macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons.

483   *Freshwater Biology* 53, 358–367.

484 Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and

485   dredging: Implications for marine biodiversity. *Annu. Rev. Ecol. Syst.* 33, 449–473.

486 Tokeshi, M., Arakaki, S., 2012. Habitat complexity in aquatic systems: fractals and beyond.

487   *Hydrobiologia* 685, 27–47.

488 Underwood, A.J., Chapman, M.G., Crowe, T.P., 2004. Identifying and understanding ecological

489   preferences for habitat or prey. *Journal of Experimental Marine Biology and Ecology* 300,

490   161–187.

491 Uryu, Y., Iwasaki, K., Hinoue, M., 1996. Laboratory experiments on behaviour and movement

492   of a freshwater mussel, *Limnoperna fortunei* (Dunker). *J. Molluscan Studies* 62, 327–341.

493 Warfe, D., Barmuta, L., 2004. Habitat structural complexity mediates the foraging success of

494   multiple predator species. *Oecologia* 141, 171-178.

495 Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: the analysis of proportions in ecology.

496   *Ecology* 92:3–10.

497 Webster, M.M., Laland, K.N., 2011. Reproductive state affects reliance on public information in

498   sticklebacks. *P. Roy. Soc. B.-Biol. Sci.* 278, 619–627.

499 Wright, J.T., Byers, J.E., Koukoumaftsis, L.P., Ralph, P.J., Gribben, P.E., 2010. Native species

500   behaviour mitigates the impact of habitat-forming invasive seaweed. *Oecologia* 163, 527–

501   534.

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Table 1. ANOVA table for the Choice experiment, examining the average number of shrimp in

the test areas with differing combinations of stalk density and type.

Source of Variation	df	MS	F	P-value
Density (n=5)	4	1.37	12.2	<0.001
Stalk Type: Unbranched vs. Branched (n=2)	1	2.75	24.4	<0.001
Block (n=8)	7	0.21	1.9	0.11
Block * Density	28	0.06	0.5	0.95
Block * Stalk Type	7	0.26	0.2	0.98
Density * Stalk Type	4	0.08	0.7	0.60
Residual	28	0.11		

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Figure 1. Examples of experimental treatments. A) Unbranched and branched stalks, showing a configuration with equal surface area. B) The novel, "non-mimic" habitat - plastic army men and equipment.
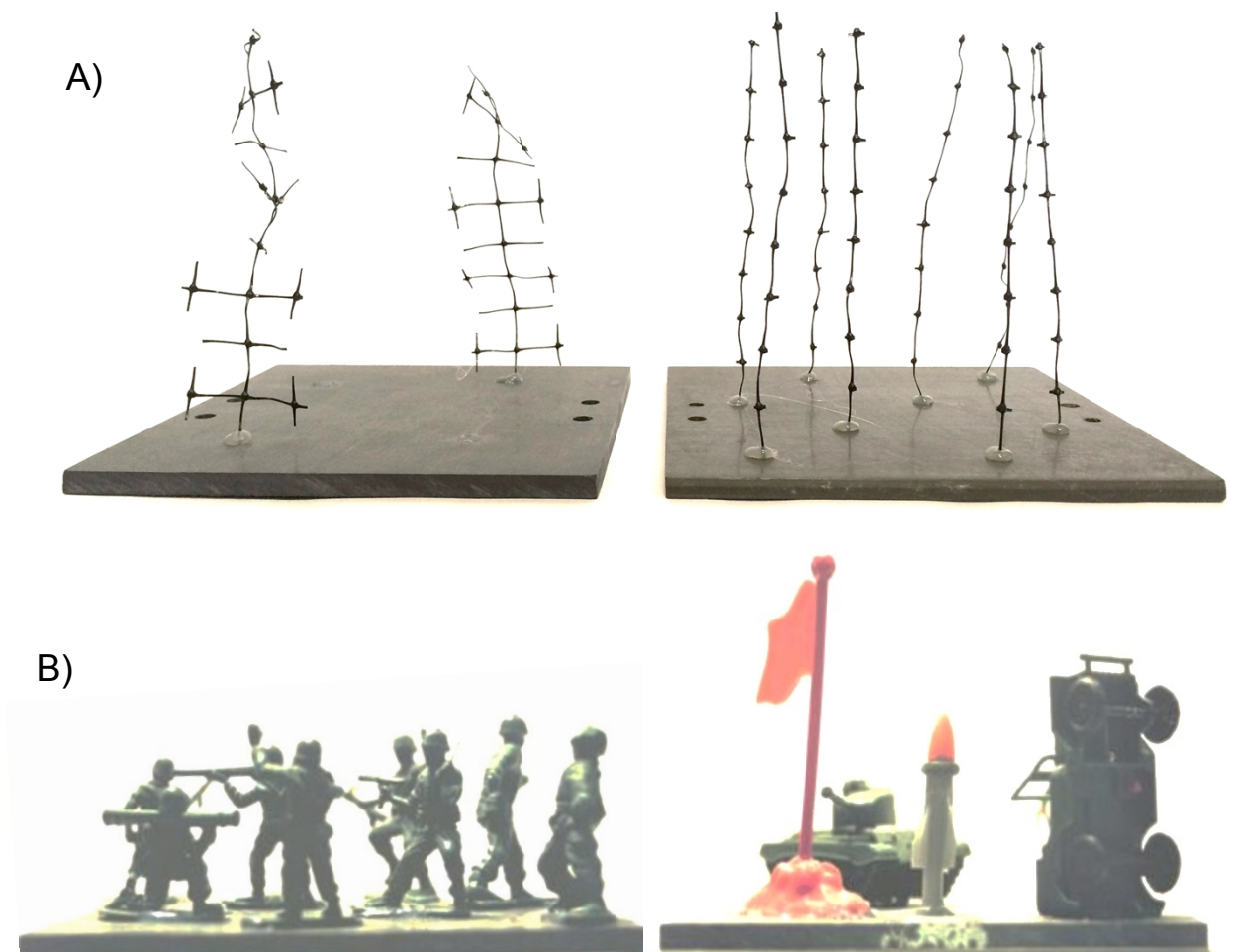
Figure 2. The experimental design. Stalks were constructed so that four un-branched stalks had the same surface area as one branched stalk. Two experiments were run, one where shrimp could choose between structural arrays on opposite sides of the tank, and one where shrimp responded to a single structural array on a randomly-selected side.

Stalk Arrays
(per 14 x 14 cm test area)

Total Surface Area (cm²)	Number of Stalks	
	Branched	Unbranched
0.75		2
1.5		4
3.0	2	8
6.0	4	16
12.1	8	32
24.1	16	
48.2	32	

Experimental Set-Up

Choice Between Arrays

Response to Single Array

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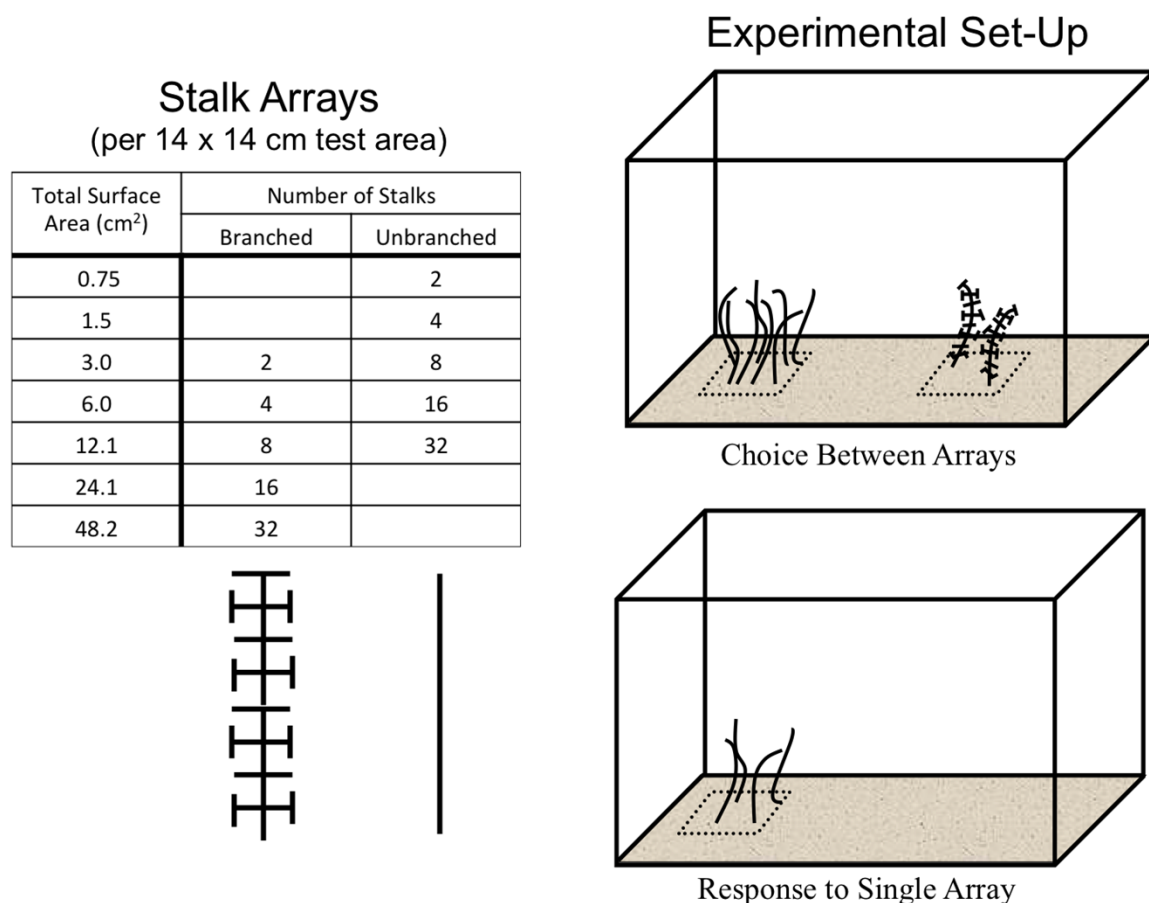
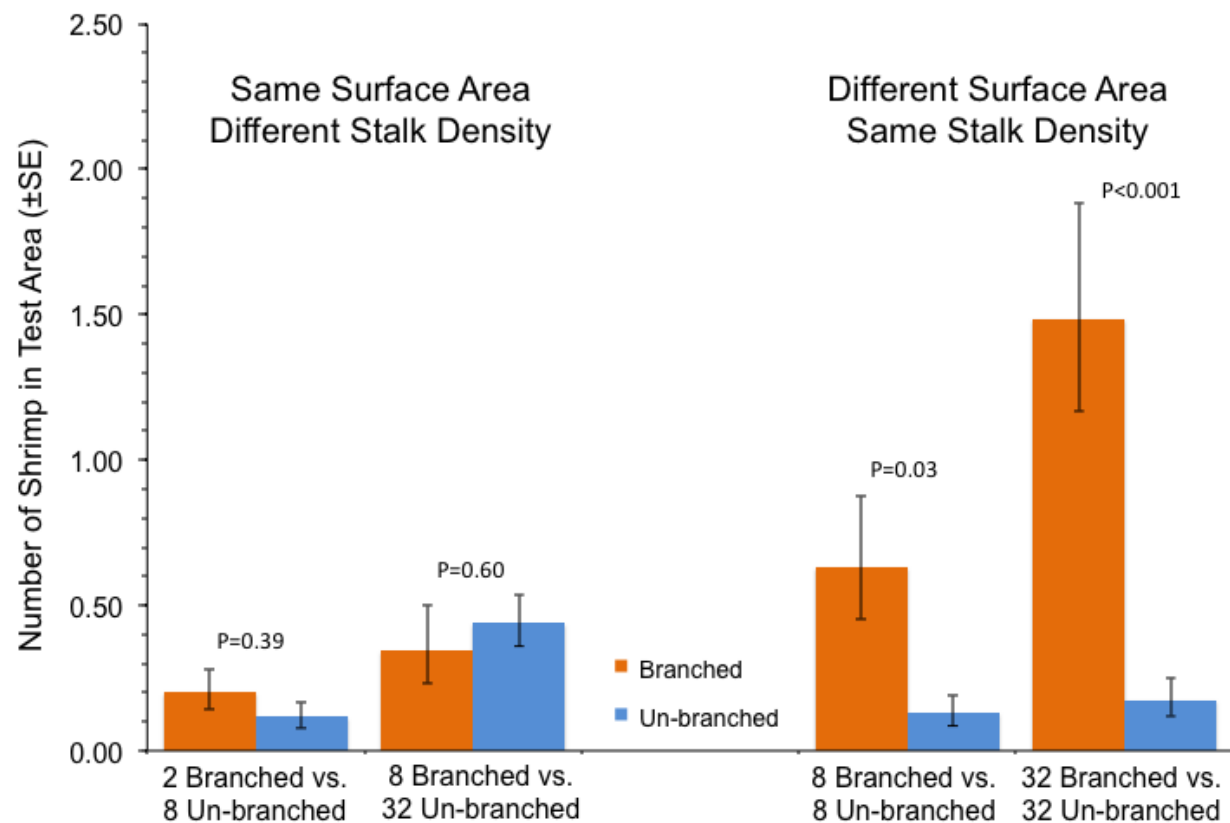

508 Figure 3. Shrimp responses when given a choice between structural arrays with the same surface
509 area or same stalk density.
510

511

Figure 4. Relationship between number of stalks and number of shrimp in the test area in the

tanks with a single array. Also shown with dashed lines are the comparisons between arrays

with equal stalk surface area, which were all statistically non-significant (paired t-tests, 7 df, P-

values > 0.34). See also Table 1.

512

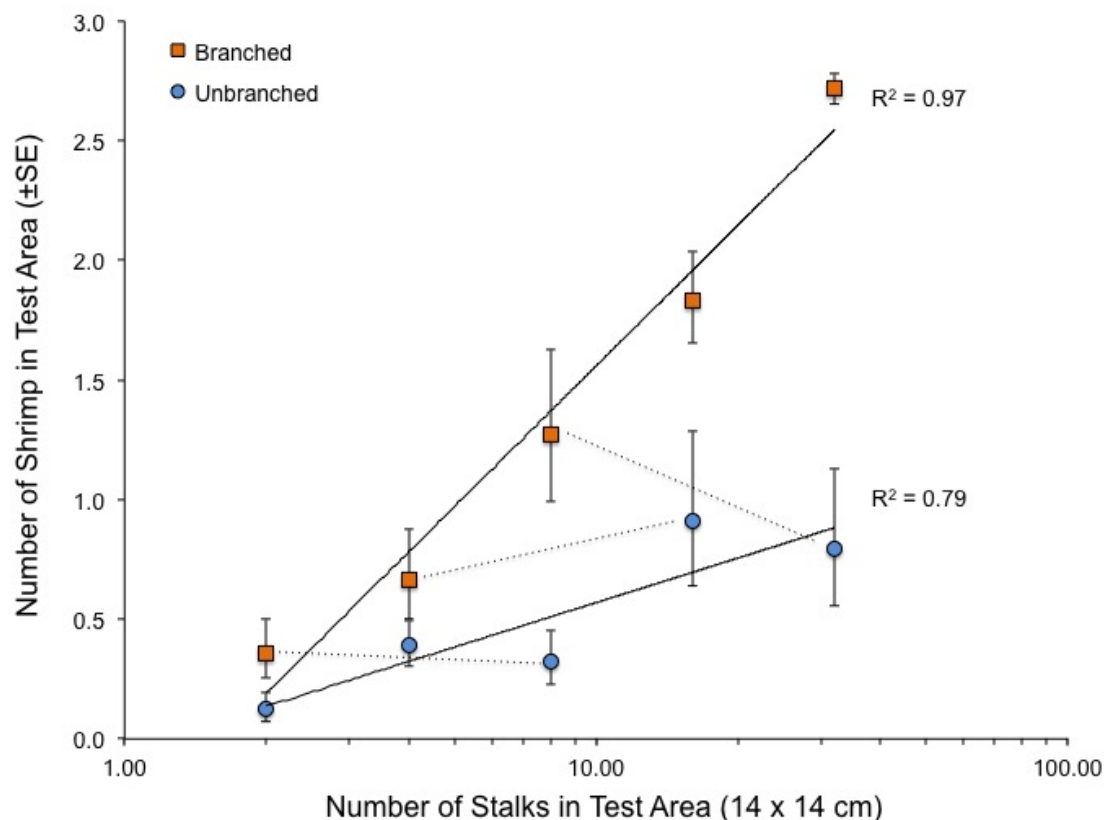



Figure 5. Relationship between total stalk surface area and number of shrimp in the test area in tanks with a single array.

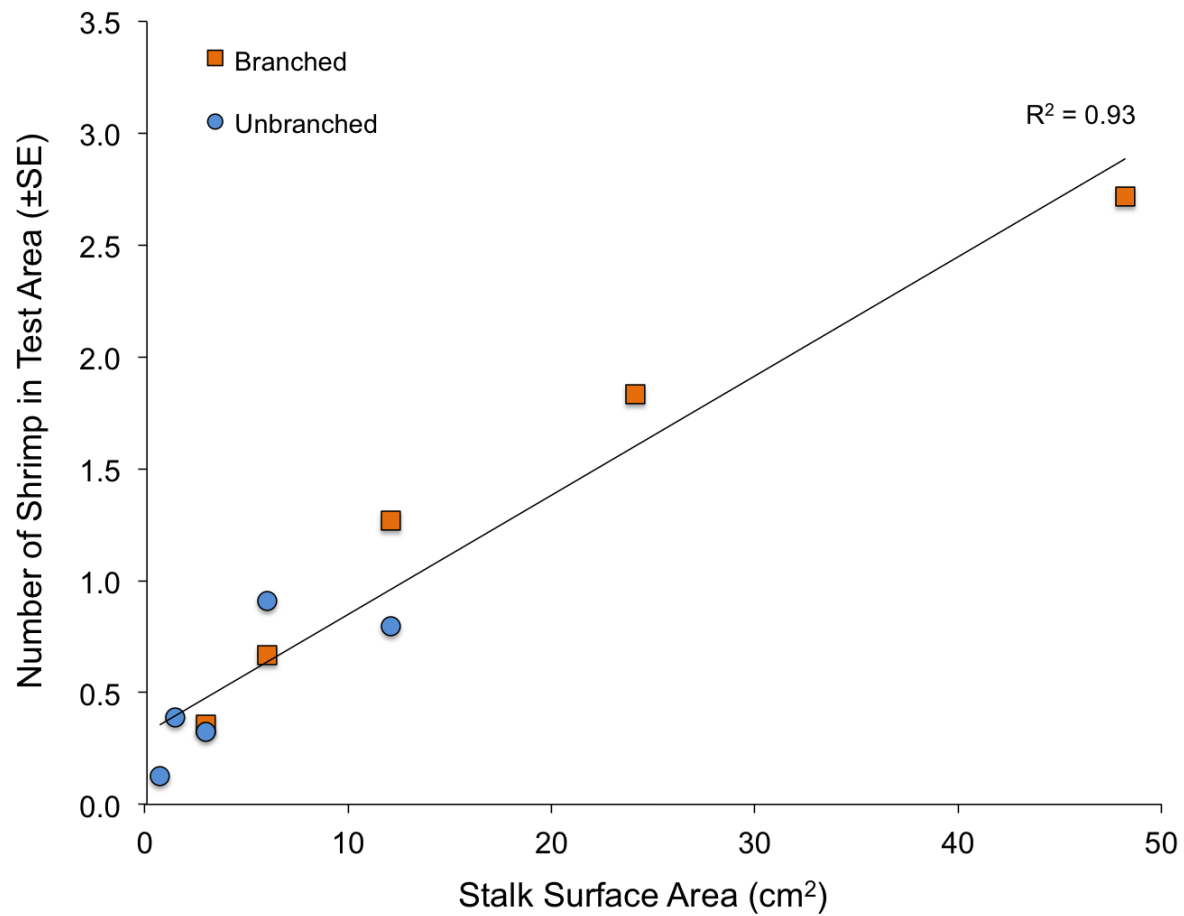



Figure 6. Relationship between the fractal dimension of the stalk arrays and toy treatments with

and number of shrimp the test area.

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