

1 **Title:** Time-dependent effects of orientation, heterogeneity and composition determines benthic biological  
2 community recruitment patterns on subtidal artificial structures

3  
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10

11 **Running Head:** Manipulating recruitment on to artificial structures

12

### 13 **Highlights**

- 14 • Surface orientation, roughness and chemical composition alter recruitment over time
- 15 • Orientation (light) an early primary driver of community structure
- 16 • Roughness mitigates effects of surface orientation over time
- 17 • Addition of chemical cues may facilitate 'selection' of ecosystem engineers
- 18 • Surface modifications enhance biodiversity, habitat function and service provision

19

### 20 **ABSTRACT**

21 Worldwide, coastlines are becoming increasingly hardened by infrastructure in response to population growth,  
22 need for space, and coastal protection. Coastal and marine infrastructure (CMI) supports fewer species and  
23 lower abundance and diversity than analogous natural rocky habitats, which can alter community composition  
24 and ecosystem functioning. Efforts to develop ecological engineering solutions that offset these negative  
25 consequences on biodiversity while retaining engineering function abound, but to date few studies have  
26 investigated the role of multiple factors simultaneously in driving patterns of biotic colonisation. Here, the role  
27 of surface heterogeneity, chemical composition and surface orientation was evaluated over a 6-month period.  
28 An increase in habitat heterogeneity, the replacement of shale for ground oyster shell (cue) and downward  
29 orientation was predicted to increase species richness, diversity and abundance. Orientation and heterogeneity  
30 greatly affected species richness, abundance, and community composition, and the inclusion of ground oyster  
31 shell (cue) increased bivalve recruitment but had only a marginal effect in community structure. Community  
32 formation was facilitated by low light but inhibited by sedimentation. On upward-facing surfaces, sediment  
33 accumulation on high complexity surfaces expanded niche heterogeneity, and supported communities  
34 comprised of burrowing polychaetes and predatory species. Surface orientation and heterogeneity are key  
35 factors influencing larval recruitment, and in supporting diverse benthic assemblages on artificial structures.  
36 These factors should be considered during the design phase of new engineering projects if the negative  
37 consequences of artificial structures are to be minimised while ensuring engineering function is maintained.

38

39 **KEY WORDS:** ecological engineering; urban sprawl; dynamics; intelligent design; selection; succession

## 40 INTRODUCTION

41 Almost half the human population (Crossland et al. 2005) and three quarters of all large cities are located  
42 within 100km of the coast (Firth et al. 2016b; Neumann et al. 2015). With the growing trend of coastal  
43 migration and population growth rates expected to exceed 9.5 billion by 2050 (Gerland et al. 2014),  
44 anthropogenic pressures are placing increasing demands on coastal marine ecosystems (Airoidi and Beck 2007;  
45 Knights et al. 2015). As a result, increases in coastal and marine infrastructure (CMI), particularly associated  
46 with coastal protection and urbanisation (breakwaters, seawalls, piers and pontoons), and marine industry  
47 (shipping, renewable energy technologies, aquaculture), are dominating coastlines at the expense of natural  
48 habitats (Chapman 2003; Chee et al. 2017; Firth et al. 2016b).

49  
50 Coastal hardening - the replacement of soft substrata with hard artificial structures - inevitably provides habitat  
51 for benthic communities (Airoidi and Bulleri 2011; Chapman 2003; Strain et al. 2018) and are known to alter  
52 connectivity patterns (Airoidi et al. 2015; Bishop et al. 2017). Artificial structures typically support lower  
53 abundance and richness of species than natural rocky habitats (Connell and Glasby 1999; Firth et al. 2013;  
54 Underwood and Anderson 1994) and have been reported to facilitate the establishment and spread of non-  
55 native species, which can threaten native communities (Airoidi et al. 2015; Bracewell et al. 2012; Glasby et al.  
56 2007). Recent focus has consequently been placed on ecological engineering (eco-engineering) which is the  
57 design of sustainable ecosystems for the mutual benefit of society and nature (Mitsch 2012). Experiments have  
58 incorporated natural reef features into CMI design, in attempts to offset the unfavourable impacts of artificial  
59 structures on marine ecosystems, whilst retaining structural integrity e.g. (Collins et al. 2002; Firth et al. 2016a;  
60 Loke and Todd 2016).

61  
62 It has long been known that there is a positive relationship between biodiversity and habitat complexity  
63 (Hauser et al. 2006; Huston 1979; Underwood and Anderson 1994). In the marine environment, natural  
64 features, such as crevices, pits and water-retaining features, increase surface area, entrap nutrients, sediments  
65 and water and expand the range of niches available for colonisation and shelter (Crisp and Ryland 1960; Hauser  
66 et al. 2006; Loke et al. 2015). This complexity is paramount to supporting a diverse range of organisms. The  
67 physical complexity of natural reefs can also alter environmental conditions, such as exposure to light,  
68 temperature and water flow rates that result from the orientation of the surface (Thorson 1964). Shade is  
69 increasingly recognised as a key factor in the structure and functioning of intertidal and shallow subtidal  
70 benthic communities (Davies et al. 2014; Miller and Etter 2008; Vermeij and Bak 2002). Horizontal surfaces  
71 exposed to light typically promote algal growth, enhancing primary production but can be negatively affected  
72 by high sediment loading (Airoidi 2003). In contrast, shaded horizontally-oriented surfaces are typically  
73 dominated by invertebrates, such as ascidians, barnacles and bryozoans, where there is less competition for  
74 space with algae (Anderson and Underwood 1994; Knott et al. 2004).

75  
76 The complexity of natural marine features can also alter water flow and boundary layer dynamics, potentially  
77 modifying larval supply and settlement (Knights and Walters 2010; Roberts et al. 1991). Reduced heterogeneity

78 and the reduction in microhabitats provided by CMI may therefore be fundamental in explaining reduced  
79 species richness and differences in community composition simply as a result of altered physical drivers, when  
80 compared to natural reefs (Firth et al. 2016a; Moschella et al. 2005). An increasing number of studies are  
81 showing that CMI material and design modifications, which increase complexity without compromising the  
82 primary engineering function of the structure, can enhance recruitment, species richness, and diversity  
83 (Chapman and Blockley 2009; Evans et al. 2016; Firth et al. 2016a; Firth et al. 2014a).

84

85 Biogenic habitats are created by oysters, bivalves and polychaete worms (Cole and Knight Jones 1939; Dubois  
86 et al. 2002; Knights et al. 2012). Several factors can influence the settlement of larvae on biogenic habitats,  
87 including noise (Lillis et al. 2013), conspecific chemical cues (Browne and Zimmer 2001; Hadfield and Koehl  
88 2001; Hay 2009), biofilms (Barnes et al. 2010; Pawlik 1992), and proteins and organic compounds in shell  
89 matrices (Crisp 1967; Vasquez et al. 2013). Biofilms are created by the accumulation of micro-organisms on  
90 clean surfaces when initially submerged. They coat hard casings and shells of pioneer species such as molluscs  
91 and polychaete worms, and significantly contribute to nutrient turnover and productivity (Sawall et al. 2012).  
92 Chemicals in the bacteria are strongly depended on for the settlement of larvae, particularly polychaete and  
93 mollusc species (Hadfield and Koehl 2001; Hay 2009; Pawlik 1992), and may be almost entirely responsible for  
94 the larval attraction of fouling community species (Paul et al. 2011). Bacterial biofilms formed by the bacterium  
95 *Alteromonas colwelliana* on oyster shells (Turner et al. 1994), are thought to produce metabolites that induce  
96 settlement of oyster larvae, enabling chemically-induced settlement to work on shells of both live and dead  
97 oysters (Tamburri et al. 1992). Larvae of many mollusc species will also settle in response to heterospecific cues  
98 (Neo et al. 2009; Vasquez et al. 2013), settling on hard shells of other species in the absence of primary hard  
99 substrata (Diederich 2005).

100

101 The chemical composition of material used for CMI has potential to influence benthic abundance, richness and  
102 diversity (McManus et al. 2017). Substrata comprising differential physical and chemical compositions can  
103 affect initial colonisation rates, succession, and subsequent species interactions (Anderson and Underwood  
104 1994). The most common material used in over 50% of CMI is Portland cement, which offers advantages over  
105 other man-made materials, including high porosity, which is favoured by many species (Anderson and  
106 Underwood 1994; Pomerat and Weiss 1946). It is also easily adaptable to support complex structure designs  
107 and desirable habitat features (Firth et al. 2016a; Firth et al. 2014a; Loke and Todd 2016). However, the lime  
108 content found in concrete creates a highly alkaline surface, which is known to be toxic to some marine life  
109 upon initial submergence (Lukens and Selberg 2004). This can reduce initial rates of species colonisation  
110 (Nandakumar et al. 2003), such that CMI are not like-for-like substitutes for natural habitats (Sella and Perkol-  
111 Finkel 2015).

112

113 This does not mean that CMI does not support life. Concrete is demonstrated to support diverse communities  
114 (Firth et al. 2016a; Sella and Perkol-Finkel 2015). In fact, marine fouling on the surface of concrete has been  
115 shown to enhance the structures durability through thermal protection (Coombes et al. 2017) and by slowing

116 down the corrosive effects of chloride ion penetration (Kawabata et al. 2012). Biogenic build-up, such as the  
117 deposition of calcium carbonate by calcareous colonisers including serpulid worms and oysters, also offers bio-  
118 protection against weathering and erosion, protecting the structure and enhancing its longevity (Coombes et  
119 al. 2013). Therefore, efforts to increase the attractiveness of the structure to recruits may be beneficial to both  
120 ecosystem services and the longevity of the structure.

121  
122 On artificial structures, the emergent composition of fouling communities not only depends on the order of  
123 larval recruitment and species identity, but also the construction material, its design, and the timing of its  
124 placement (Nandakumar 1996; Underwood and Anderson 1994). For example, the addition of organic  
125 materials can lower the pH of the concrete, and potentially encourage settlement of engineering species such  
126 as bivalves, worms and bryozoans (Sella and Perkol-Finkel 2015). To date, few eco-engineering designs have  
127 experimented with the incorporation of organic materials into CMI (but see Neo et al. 2009). The negative  
128 implications of creating artificial substrate and its replacement of natural habitats may potentially be offset  
129 through novel design and material choice, potentially reducing the negative consequences for biodiversity  
130 (Airoldi and Bulleri 2011) without compromising the original purpose of CMI, but a better understanding of  
131 succession and functioning of communities on artificial structures is needed.

132  
133 Here, we compare recruitment onto concrete tiles manufactured with/without (i) ground oyster shell to  
134 replace shale, and (ii) habitat heterogeneity. Tiles were submerged for a period of 6 months and colonisation,  
135 succession and diversity assessed using a combination of monthly non-destructive sampling for the first 5  
136 months and destructive sampling after 6 months. We hypothesised that (1) habitat complexity would support  
137 greater species richness and diversity; and (2) the replacement of shale with organic replacement would  
138 support different taxonomic and community composition compared to standard concrete. A final objective was  
139 to test if change in the orientation of the surface (upward or downward-facing used as a proxy for light) would  
140 alter recruitment patterns on to tile of different composition and heterogeneity.

141

## 142 **MATERIALS AND METHODS**

### 143 **Tile construction and deployment**

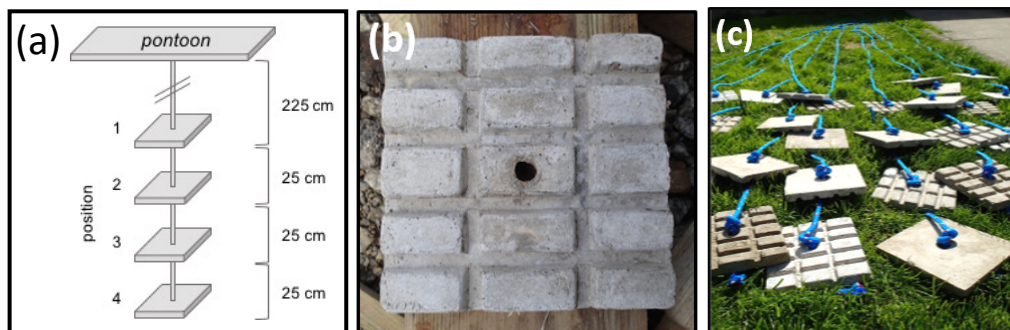
144 Individual concrete tiles (15cm × 15cm × 1cm) were constructed with a patterned surface (1cm wide; 1cm  
145 deep) on one side, and a smooth surface on the other (Fig 1). This tile size was chosen as it represents a  
146 manageable experimental unit in terms of construction, deployment and taxonomic analysis. The block pattern  
147 increased surface area by 25% over the smooth tile surface and represents a simple, cheap and easy to  
148 implement modification to a standard artificial structure surface. Tiles were made using either: (i) standard  
149 concrete mix of 1.5:1.5:1 (sand:shale:Portland cement), or (ii) with complete replacement of the shale  
150 component of the mix for ground oyster (*Magallana* (formerly *Crassostrea*) *gigas*) cultch, which may provide  
151 an olfactory cue for larval settlement (e.g. O'Connor et al. 2008). Other materials may also provide a cue but  
152 are not tested here. All tiles were reinforced with an internal plastic-coated metal mesh grid and cured for 2-  
153 wk. Twenty replicates of each tile type were made and randomly allocated to four treatments (N=80): smooth-

154 surface, standard concrete (SO-); smooth-surface with oyster shell (SO+); patterned-surface, standard concrete  
155 (PO-); and patterned-surface with oyster shell (PO+).

156

157 Tiles were suspended from floating pontoons at Port Pendennis Marina, Falmouth, UK (50°9'6.54" N,  
158 5°3'39.21" W) on 3 m lengths of polyethylene rope. The marina is located in a sheltered position at the mouth  
159 of the River Fal and the moorings are adjacent to moorings for international cruise ships and a dockyard. Four  
160 tiles (one of each type) were randomly assigned to 1 of 4 positions on a rope (Fig. 1a), and spaced 25 cm apart,  
161 resulting in tiles at 2.25, 2.5, 2.75 and 3m below the sea surface. A preliminary test of light intensity at the  
162 surface of each tile revealed no differences between positions. Ten tiles of each type (see above) were  
163 orientated with the patterned surface facing upward (flat surface down) and ten with the patterned surface  
164 facing downward (flat surface up).

165



166

167 **Figure 1.** (a) Schematic of tile arrangement on a rope; (b) a tile with an embedded pattern design; and (c)  
168 assembled tile ropes.

169

### 170 **Sampling**

171 Tiles were deployed in April 2016 and colonisation and community assemblage changes were monitored over a  
172 6-month period. Tile introduction was timed to capture the main recruitment window for many marine species  
173 in the UK (Knights et al. 2016). For months 1-5, all tiles were removed from the water, the upward and  
174 downward-facing surfaces of each tile photographed with a digital camera, then returned to the water (within  
175 10 minutes to minimise stress to plants and animals on the tiles between sampling periods). Given an aim was  
176 to evaluate succession on tiles, species identification in months 1-5 could not be done using destructive  
177 sampling. As such, the resolution of the sampling limited the identification of organisms to phyla and  
178 percentage live cover per phyla, which were estimated using image analysis in ImageJ (Abramoff et al. 2004).  
179 After 6 months, all tiles were removed from the water and transported to Plymouth University Marine Station,  
180 where they were suspended in aerated, ambient sea temperature flow-through seawater tanks (salinity = 35)  
181 until they were destructively sampled. Tiles were removed after 6-months due to logistical constraints. On both  
182 tile surfaces, the identity of all organisms was assessed to their lowest operational taxonomic unit (OTU) using  
183 standard taxonomic keys, and their abundance enumerated. Quantification of live cover of species on each tile  
184 was determined using a 1cm × 1cm grid. Data recorded included: (i) percent cover of colonial organisms and

185 single-species dominated assemblages (e.g. clusters of barnacles and serpulid worms, sponges, bryozoans), and  
186 (ii) individual counts (total abundance) of solitary sessile and mobile organisms.

187

## 188 **Statistical Analyses**

189 All analyses were performed using the open-source software package, R Version 3.4.3 (R Development Core  
190 Team 2017). All data were normal and variances were homogeneous. Evidence of temporal autocorrelation as  
191 a result of repeated measurement of tiles over time was tested using the ACF function in the *nlme* package,  
192 and where relevant, an autoregressive-1 (AR1) or ARMA (autocorrelation-moving average) autocorrelation  
193 structure was included in the model. Akaike Information Criterion (AIC) was used to differentiate between  
194 model fits.

195

### 196 *Month 1-5*

197 A generalised least squares (GLS) model tested for differences in the number of phyla and percent cover across  
198 all treatments. Tukey HSD post-hoc pairwise comparisons were used to determine differences between levels  
199 within factors. Localised regression (LOESS) was used to plot changes in mean number of phyla and abundance  
200 (% live cover) for each tile surface over time.

201

### 202 *Month 6*

203 To standardise data for the effect of the increased surface area on patterned tiles, abundance counts were  
204 converted to densities. ANOVA was used to test for differences in species number, density, and Shannon-  
205 Wiener diversity (H') between tile treatments. Significant differences between levels within factors were  
206 assessed using Tukey HSD posthoc pairwise comparisons.

207

208 Rank clocks (the *coord\_polar()* function in *ggplot2*) were used to illustrate change in mean species abundance  
209 within treatment combinations over time. A 3-factor permuted multivariate ANOVA (PERMANOVA) with 9999  
210 permutations (Anderson 2003) was used to test differences in community structure using the following fixed  
211 factors (levels): orientation (up; down); heterogeneity (flat; patterned); and shale-oyster replacement (shale;  
212 oyster). Bray-Curtis index was used to construct dissimilarity matrices (Clarke and Warwick 1998). Analyses  
213 were performed using ADONIS ('vegan' package, Oksanen et al. 2016) to test hypotheses and SIMPROF  
214 (Similarity percentages) used to determine species most influential in causing similarity among tiles within  
215 treatments and dissimilarity among different treatments. Non-metric multidimensional scaling (nMDS) was  
216 used to graphically represent trends in multivariate data.

217

## 218 **RESULTS**

### 219 **Month 1-5**

220 A total of 18 taxa from 8 phyla were identified on tiles using non-destructive sampling methods. Orientation  
221 had a significant effect on the number of OTUs present on tiles over time (Table 1;  $p < 0.0001$ ). Downward-  
222 facing tiles were colonised rapidly, with the number of OTUs after 5 months (~5) not significantly different to

223 month 1. In contrast, upward-facing tiles were slower to be colonised (~3 OTUs after 1 month), but the number  
224 of OTUs gradually increased in over time (Fig. 2a) to the point where they were comparable to downward-  
225 facing tiles after 5 months submersion. Adding heterogeneity also led to a small but significant increase in the  
226 number of OTUs in comparison to a flat substrate ( $p < 0.001$ , Table 1, Fig. 2b).

227

228 A combination of tile orientation and heterogeneity led to markedly different live percentage cover on tiles  
229 over time (Table 1;  $p < 0.05$ ). Downward-facing tiles had significantly more live cover than upward-facing tiles  
230 at any given time and cover rapidly increased between sampling periods (Fig. 2c), although heterogeneity had  
231 little effect on percentage cover on these tiles. In contrast, the addition of heterogeneity on upward-facing tiles  
232 led to nearly 50% increases in percentage cover for each time point (Fig. 2c). After 5 months, percentage cover  
233 on downward-facing tiles was ~4x greater than on upward-facing tiles.

234

235 The communities on downward and upward-facing tiles differed to some extent, although both were  
236 dominated by the Ascidian (*Ciona intestinalis*) which represented, on average, 94.4% of the total assemblage  
237 across all tile surfaces after 3 months (Fig. 3). The growth of this taxa in particular led to rapid covering of  
238 downward-facing tiles, in addition to relatively large abundances of Annelids (*Pomatoceros lamarkii*), the non-  
239 native barnacle (*Austrominius modestus*) and bryozoan (*Bugula neritina*). Upward-facing tiles also supported  
240 these dominant species as well as the red algae (*Pterothamnion plumula*), but in general, abundances tended  
241 to be much lower (Fig. 3). Replacement of shale with ground oyster shell had no effect on either the number of  
242 OTUs or percentage cover of flora and fauna on tiles (Table 1).

243

#### 244 **Month 6**

245 After 6 months, tiles were destructively sampled and 81 species from 14 phyla were identified (Supplemental  
246 Material). There was no significant difference in Shannon-Wiener diversity ( $F_{7,72} = 1.66$ ,  $p > 0.05$ ) irrespective of  
247 orientation, heterogeneity or shale replacement. There was, however, highly significant differences in mean  
248 species richness ( $F_{7,72} = 986$ ,  $p < 0.0001$ ) (Fig. 4) among treatments. Maximum richness occurred on downward-  
249 facing tiles (~25 spp. per tile), but heterogeneity had no effect (Fig. 4a). In contrast, richness was generally  
250 lower on upward-facing tiles, although the addition of heterogeneity led to significant increases in species  
251 richness of ~5 spp. per tile. This pattern was mirrored for percentage live cover estimates (Fig. 4b).

252

253 After 6 months submersion, there were significant differences in community composition due to heterogeneity  
254 and orientation (orientation  $\times$  heterogeneity:  $F_{1,72} = 6.68$ ,  $p < 0.01$ ). Differences were largely driven by four  
255 species; the abundance of the annelid *Pomatoceros lamarkii*, saddle oyster *Anomia ephippium*, ascidian  
256 *Asciella scabra*, and barnacle *Austrominius modestus* (Table 2c). The emergent communities on upward-  
257 facing tiles were more variable than downward-facing tiles (Fig. 5) and dependent on heterogeneity.

258 Rhodophyta, Chlorophyta and Nemertea were strongly correlated with upward-facing flat surfaces (Fig. 5),  
259 whereas platyhelminthes and arthropods were more associated with upward-facing patterned surfaces. Adding  
260 heterogeneity had no effect on the community composition on downward-facing surfaces. Protozoa (e.g.

261 *Folliculina* sp.) were most strongly associated with downward-facing surfaces as well as Chordata, Cnidaria, and  
 262 Echinoderms. A number of phyla (Annelida, Porifera, Mollusca) were ubiquitous on all tiles but tended more  
 263 strongly toward downward-facing surfaces (Fig. 5).

264

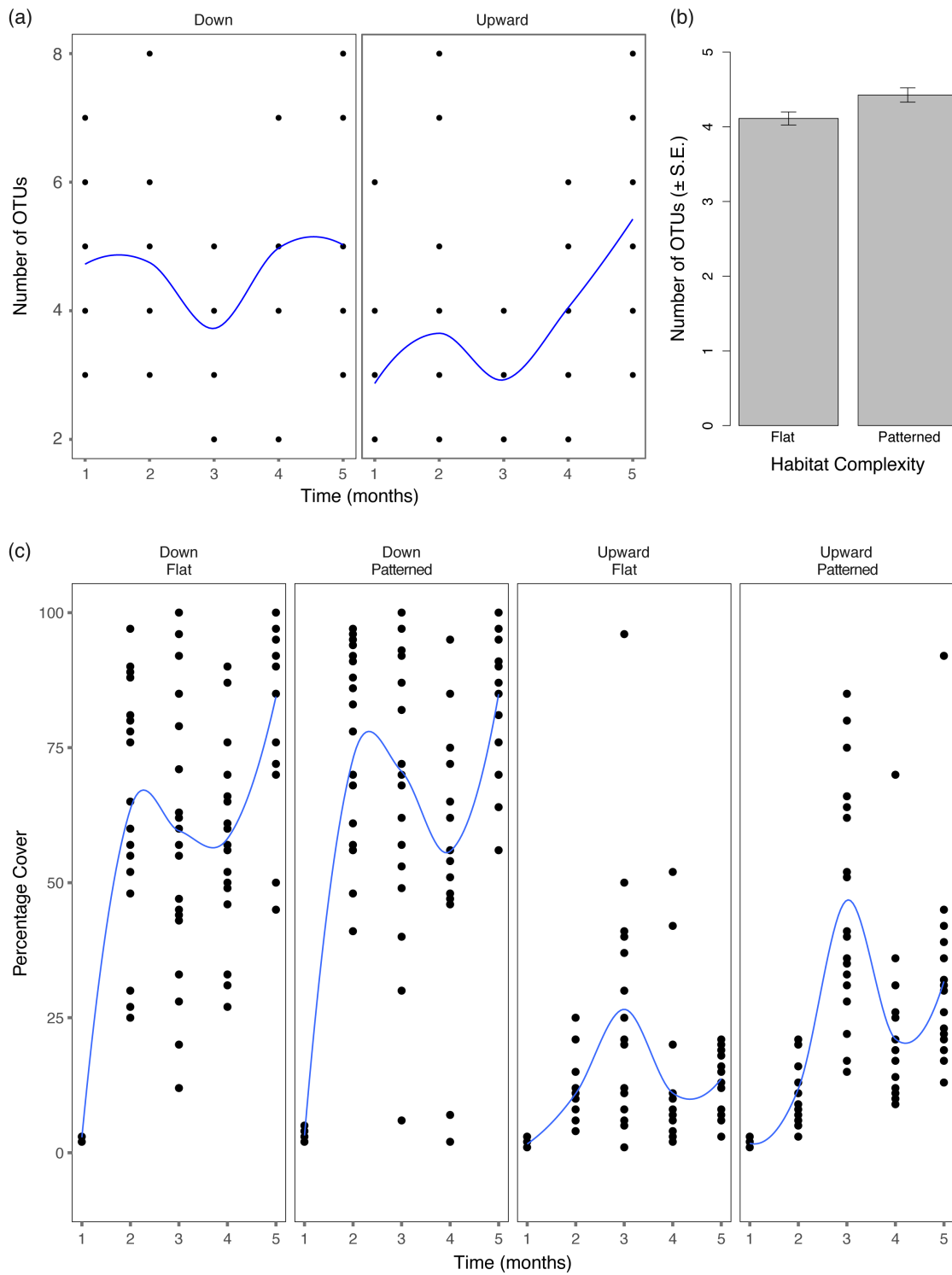
265 The replacement of shale with ground oyster shell led to modest differences in the emergent community  
 266 structure ( $F_{1, 72} = 3.11$ ,  $p < 0.05$ ,  $R^2 = 0.03$ ) in addition to orientation and the addition of heterogeneity,  
 267 although there was no obvious and clear pattern to the dissimilarity as a result of this factor. Restricting the  
 268 analyses to a comparison of Molluscan abundance (specifically *A. ephippium*, *Hiatella arctica*, and *Musculas*  
 269 *costulatas*; no *M. gigas* recruited) revealed some pattern; Mollusc abundance on surfaces constructed with  
 270 oyster shell was 37.6% higher than on tiles constructed using shale. Importantly, no invasive species (including  
 271 *M. gigas*) were recorded on any tiles during the experiment.

272

273 **Table 1.** Generalised least square regression (GLS) comparing mean number of OTUs and mean abundance  
 274 (percentage cover) across orientation, heterogeneity, and shale-replacement treatments over time from  
 275 months one to five. Significant *P*-values are shown in bold.

Source of Variation	df	Number of OTU		Percentage Cover	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cue	1	3.65	0.057	0.17	0.68
Heterogeneity	1	11.27	<b>&lt;0.001</b>	15.24	<b>&lt;0.0001</b>
Orientation	1	53.58	<b>&lt;0.0001</b>	173.75	<b>&lt;0.0001</b>
Time	1	35.75	<b>&lt;0.0001</b>	100.50	<b>&lt;0.0001</b>
Cue × Heterogeneity	1	0.03	0.87	0.12	0.73
Cue × Orientation	1	3.07	0.08	0.73	0.39
Heterogeneity × Orientation	1	1.50	0.22	10.29	<b>&lt;0.01</b>
Cue × Time	1	0.102	0.75	0.18	0.67
Heterogeneity × Time	1	0.64	0.42	2.10	0.15
Orientation × Time	1	39.29	<b>&lt;0.0001</b>	45.07	<b>&lt;0.001</b>
Cue × Heterogeneity × Orientation	1	1.47	0.23	0.003	0.96
Cue × Heterogeneity × Time	1	0.001	0.98	0.33	0.57
Cue × Orientation × Time	1	0.065	0.79	0.71	0.39
Heterogeneity × Orientation × Time	1	3.62	0.057	4.29	<b>&lt;0.05</b>
Cue × Heterogeneity × Orientation × Time	1	0.351	0.55	0.74	0.39
Residual	367				



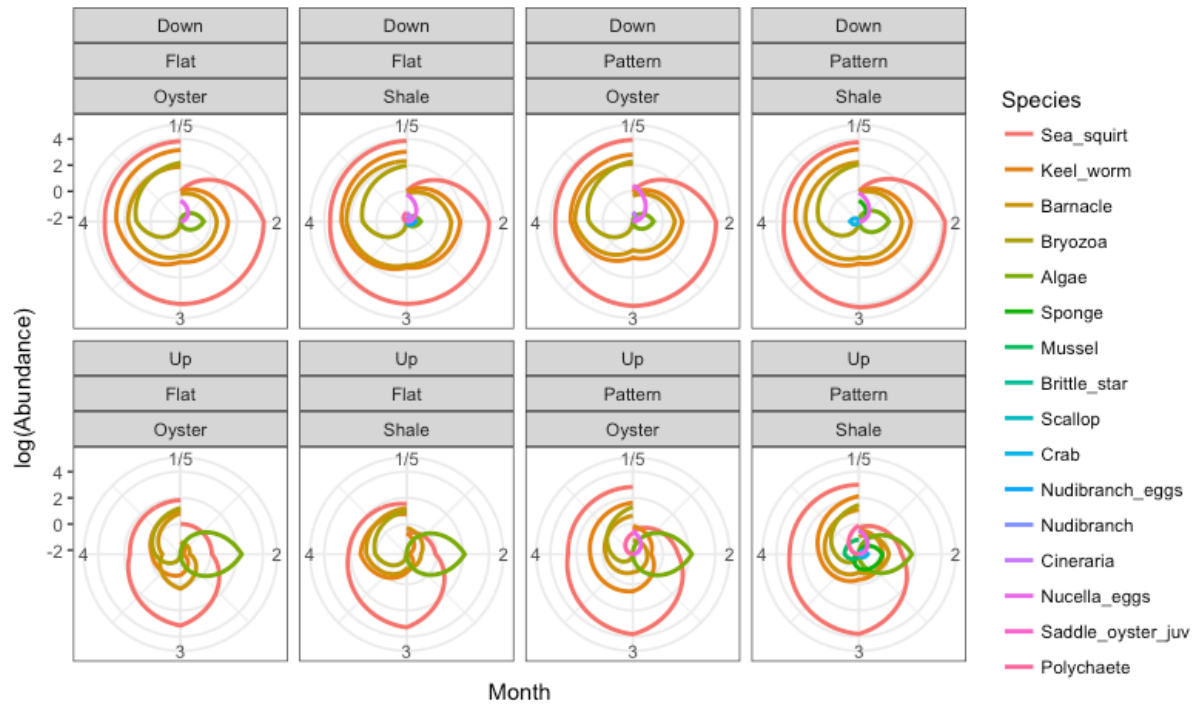


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278 **Figure 2.** Number of OTUs (a) by tile orientation over time, (b) heterogeneity (mean  $\pm$  S.E.), and (c) change in  
 279 percentage cover over time on downward and upward-facing tiles of differing heterogeneity (flat; patterned).  
 280 Significant regression lines are shown and fitted using smoothed localised regression (LOESS).

281

282



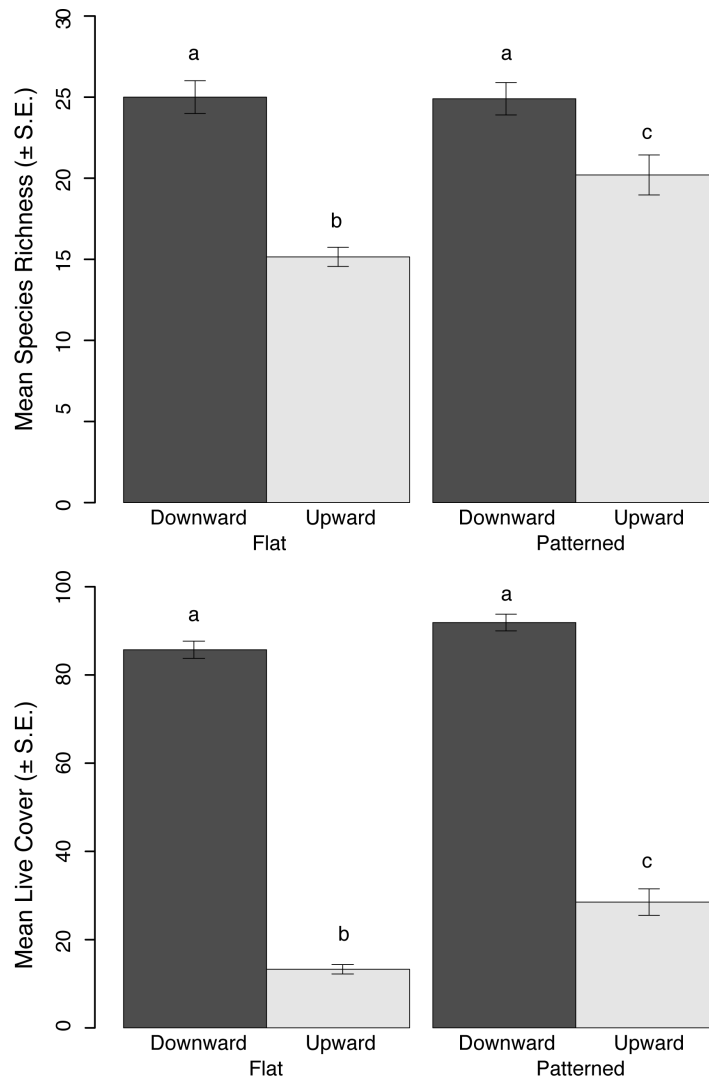
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284 **Figure 3.** Rank clocks of mean log(abundance) of species across treatments (orientation (down/up);

285 heterogeneity (flat/pattern); shale replacement (oyster/shale) at monthly intervals (1-5 months) after

286 submersion (April – September 2016) ( $N = 400$ ). The species list is ordered by relative contribution.

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**Figure 4.** Comparison of species richness (top) and mean percent live cover (bottom) between treatments after six months submersion (N=80). Error bars show standard error. Letters above bars indicate outcomes of posthoc pairwise comparisons (Tukey HSD), where same letters indicate no difference between group means ( $p > 0.05$ ).

297 **Table 2.** (a) ANOVA comparing mean number of Operational Taxonomic Units (OTUs) and mean live cover  
 298 among orientations, heterogeneities and concrete composition after 6 months. Post-hoc pair-wise comparisons  
 299 of orientation and heterogeneity groupings. Significant *P*-values are shown in bold.

300

(a) Univariate ANOVA of total percent cover and species richness

Source	Number of OTUs			Percentage Live Cover	
	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<b>Orientation</b>	1	53.48	<b>&lt;0.0001</b>	1035.05	<b>&lt;0.0001</b>
<b>Heterogeneity</b>	1	1.77	0.18	25.69	<b>&lt;0.0001</b>
Cue	1	6.19	<b>&lt;0.05</b>	2.07	0.15
<b>Orientation x Heterogeneity</b>	1	0.006	0.94	4.62	<b>&lt;0.05</b>
Orientation x Cue	1	6.70	<b>&lt;0.05</b>	0.005	0.94
Heterogeneity x Cue	1	0.87	0.36	0.48	0.49
Orientation x Heterogeneity x Cue	1	0.006	0.94	0.08	0.77
Residual	72				

301

302 (b) PERMANOVA of species percent cover (colonial species) and abundance (singular individuals)

Source	df	MS	<i>F</i>	<i>P</i>	R <sup>2</sup>
<b>Orientation</b>	1	5.35	47.67	<b>&lt;0.001</b>	0.35
<b>Heterogeneity</b>	1	0.53	4.68	<b>&lt;0.05</b>	0.03
<b>Cue</b>	1	0.31	2.78	<b>&lt;0.05</b>	0.02
<b>Orientation x Heterogeneity</b>	1	0.42	3.72	<b>&lt;0.01</b>	0.03
Orientation x Cue	1	0.16	1.46	0.15	0.01
Heterogeneity x Cue	1	0.09	0.84	0.50	<0.01
Orientation x Heterogeneity x Cue	1	0.09	0.81	0.52	<0.01
Residual	72	0.1169			

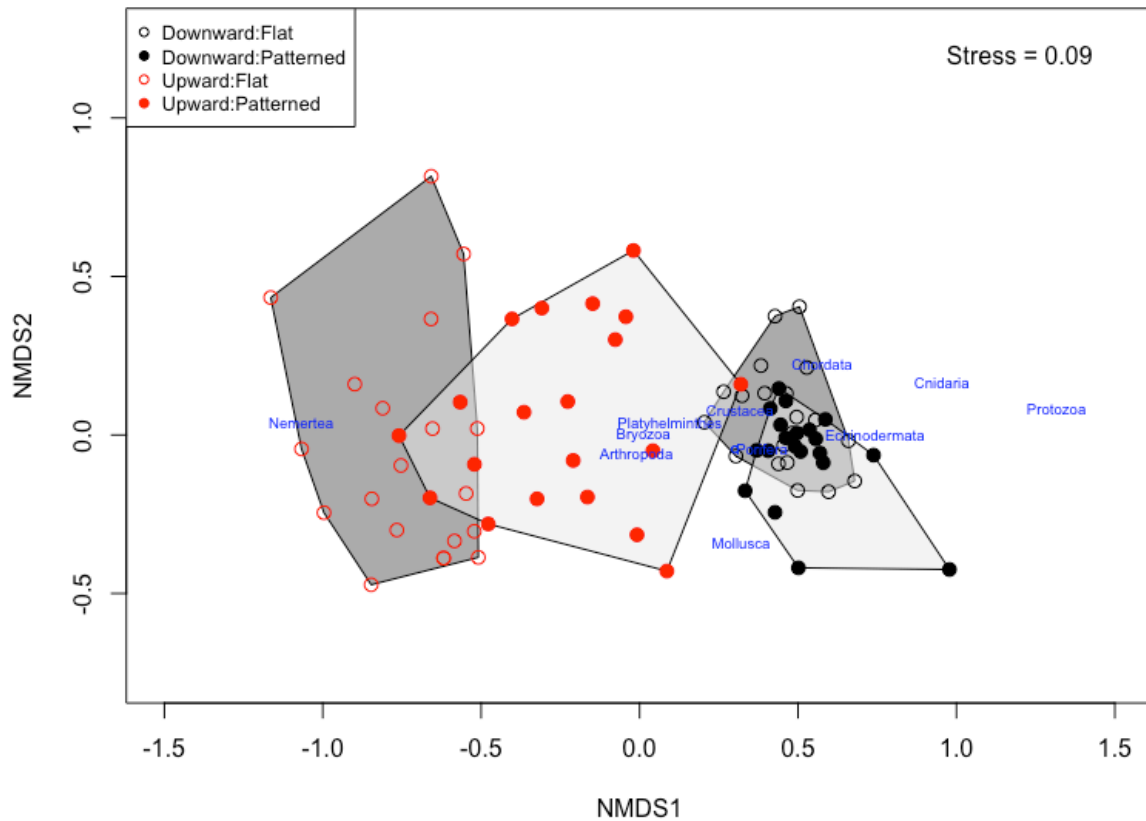
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304 (c) SIMPROF analysis of the most influential phyla and species contributing to the differences in community  
 305 assemblages between levels within complexity and orientation treatments after 6-months.

Phyla	Heterogeneity	Orientation	Species	Heterogeneity	Orientation
Chordata	29.1%	30.1%	<i>Ciona instestinalis</i>	16.5%	21.0%
Mollusca	52.2%	-	<i>Anomia ephippium</i>	30.4%	35.9%
Annelida	71.2%	51.0%	<i>Pomatoceros lamarckii</i>	40.2%	48.0%
Mollusca	-	71.2%	<i>Ascidella scabra</i>	47.4%	-
			<i>Austrominius modestus</i>	53.8%	55.6%

306

307



308  
 309 **Figure 5.** nMDS plot of dissimilarity in phyla composition after 6 months of submersion (N = 80). Points shapes  
 310 and colour definitions are shown in the legend. Polygons indicate the dispersion of points within orientation.  
 311 NB Centroids (xy coordinates) for Chlorophyta (-5.04, 0.19) and Rhodophyta (-4.64, 0.05) are not shown for  
 312 clarity.

313  
 314 **DISCUSSION**

315 The replacement of natural habitats with artificial structures in the marine environment has led to concerted  
 316 effort to enhance biodiversity using a combination of design and material modifications (Strain et al. 2018).  
 317 Here, the change in community composition over a 6-month period on recruitment tiles in response to addition  
 318 of surface heterogeneity (pits/crevices), a change in the composition of the construction material, and  
 319 orientation of the surface (a proxy for light) was simultaneously tested. The importance of orientation and  
 320 surface heterogeneity on species richness, percentage live cover and abundance changed over time, but the  
 321 replacement of shale by ground oyster had limited effect.

322  
 323 It is well known that substratum orientation can alter the environmental conditions around the substrate such  
 324 as temperature, light and disturbance (Davies et al. 2014; Firth et al. 2014a; Firth et al. 2016c; Irving and  
 325 Connell 2002; Miller and Etter 2008) resulting in differences in community structure. In this experiment,  
 326 downward-facing tiles were, in the first 4 months, characterised by different communities and more rapid

327 colonisation and greater percentage of live cover than upward-facing tiles. Upward-facing surfaces, especially  
328 those without added heterogeneity, were colonised by red and green algae, which in shallow subtidal  
329 ecosystems is unsurprising as direct illumination favours photosynthesis and growth (Irving and Connell 2002;  
330 Miller and Etter 2008, but see Hansson 1995). In contrast, downward-facing shaded surfaces were dominated  
331 by a diverse range of sessile invertebrates; the early life-history stages of which are typically sciaphilic, and use  
332 a combination of synchronous spawning and negative phototaxis to facilitate recruitment into shaded habitat  
333 (Svane and Havenhand 1993).

334

335 Species prevalent on the downward-facing surfaces early on, such as the fast-growing ascidian *Ciona*  
336 *intestinalis*, are often considered opportunistic (i.e. r-strategists). They can rapidly form dense single-species-  
337 dominated assemblages (Bracewell et al. 2013) that dominate competitive interactions (Jackson 1977) but also  
338 experience intense intraspecific competition that leads to rapid die-off (*sensu* “boom-bust” species; Price  
339 1999). This “boom-bust” cycle was clearly evident in the change in number of OTUs and percentage live cover,  
340 where rapid increases in percentage live cover in Month 2 led to marked reduction in the number of OTUs in  
341 Month 3 and percentage live cover in Month 4. Following this “bust” phase, newly available space was  
342 gradually occupied by less opportunistic and long-lived species (k-strategists).

343

344 The addition of surface heterogeneity using relatively simple uniform channels led to a greater number of  
345 species overall, as well as increasing percentage cover by colonial organisms on upward-facing surfaces.  
346 Surface heterogeneity is well known to facilitate recruitment of species depending on its scale (Firth et al.  
347 2014b; Moschella et al. 2005). At larger spatial scales (cm to m), the introduction of pits (Sella and Perkol-Finkel  
348 2015), water retaining features (e.g. Chapman and Blockley 2009; Evans et al. 2016; Firth et al. 2016a) and  
349 grooves (Borsje et al. 2011; Coombes et al. 2015) can provide suitable habitat and refuge for larger species. At  
350 the sub-centimetre scale, species such as barnacles, rock borers and oysters, have been shown to utilise small  
351 imperfections such as the tiny air pockets created during concrete manufacture as habitat. This fine-scale  
352 rugosity, although not explored here, can facilitate recruitment of rugophilic species by providing an initial key  
353 for biological glues or providing increased protection (Coombes et al. 2015).

354

355 Adding heterogeneity to upward-facing surfaces led to increased sediment loading not present on flat surfaces  
356 (Nadine Hanlon, *pers. obs.*) indicating alteration of the boundary layer dynamics flowing over the surface of the  
357 concrete. Surface roughness has been shown to increase drag, reduce maximum water flow speed and create  
358 turbulent eddies over biogenic reefs (Loke et al. 2017; Whitman and Reidenbach 2012). These processes can  
359 facilitate the retention and aggregation of abiotic propagules (e.g. sediment) on upward-facing or sheltered  
360 substrates, effectively creating a layer of sedimentary habitat in an environment usually characterised by high  
361 shear (Airoldi and Cinelli 1997). This created a fundamentally different niche to that on low heterogeneity  
362 upward-facing surfaces that did not retain sediment. It is therefore unsurprising that the relative importance of  
363 heterogeneity in affecting community structure on upward and downward-facing surfaces was different.

364 Species characteristic of hard-bottom subtidal substrates were absent from higher heterogeneity, sediment-

365 dominated upward-facing surfaces, and soft-bottom species were absent from downward-facing surfaces.  
366 Changes in boundary layer dynamics may also alter biotic interactions with the substrate. Reductions in flow  
367 velocity can increase contact or 'hitting' time (McNair et al. 1997) leading to a greater probability of successful  
368 attachment to the surface (Crimaldi et al. 2002), increase propagule abundance and retention (Abelson and  
369 Denny 1997; Knights et al. 2012; Knights and Walters 2010) and enhance preferential habitat selection (North  
370 et al. 2008), especially in bivalves and other encrusting species.

371

372 Chemical cues and biofilms are also considered important drivers of population and community dynamics,  
373 affecting conspecific and heterospecific settlement (Crisp 1967; Turner et al. 1994; Vasquez et al. 2013), or  
374 predator-prey interactions (Dixson et al. 2010; Weissburg et al. 2014). We expected the inclusion of ground  
375 oyster shell to enhance bivalve recruitment; the hypothesis being that the shell would introduce a chemical cue  
376 that increases recruitment (e.g. Browne and Zimmer 2001; Vasquez et al. 2013). The replacement of shale with  
377 ground oyster shell had only a marginal effect on the emergent communities as a whole although there was a  
378 significant increase in the abundance of molluscs recruited on tiles. Bivalves, in particular, have been shown to  
379 settle in response to heterospecific cues within the same family (Vasquez et al. 2013) suggesting that the  
380 replacement of shale for ground oyster shell may be a viable approach for enhancing oyster recruitment on  
381 CMI. For other taxa, the perception of, or response to, chemical cues may be in part overridden by the  
382 chemical properties of the concrete. Concrete is typically characterised by a high pH (~13), which is toxic to  
383 some marine life (Lukens and Selberg 2004) and has been shown to inhibit settlement, growth and survival of  
384 benthic organisms (Connell and Glasby 1999; Lee et al. 2017). Perkol-Finkel and Sella (2014) demonstrated that  
385 reducing alkalinity by the use of different composites in the concrete could increase percentage live cover and  
386 enhance the recruitment of ecosystem engineers. Conversely, increasing acidity has also been shown to change  
387 'perception' of chemical cues, significantly altering predator-prey dynamics in larval fish (Dixson et al. 2010)  
388 and bivalves (Sadler et al. 2018), and the recruitment of meiofauna (Lee et al. 2017). Oyster settlement can be  
389 induced by the glycyl-glycyl-L-arginine (GGR) protein, produced within the shell (Crisp 1967), but it is only  
390 effective once larvae are within close proximity (cm-mm) of the surface bound cue (Browne and Zimmer 2001).  
391 In nature, detection and reaction to that cue is reliant on the concentration of waterborne cues from live  
392 conspecifics (Crisp 1967), conspecific noise (Lillis et al. 2013), and flow regimes (Knights and Walters 2010;  
393 Turner et al. 1994). As such, while these data suggest there may be some benefit of the use of cues for  
394 attracting some taxa, it remains unclear as to how extensive the effects might be for whole communities.

395

396 Our results show multiple recruitment drivers affect the emergent communities of artificial structures, and the  
397 effect of those drivers is time-dependent. Disentangling the effects of multiple recruitment drivers can be  
398 difficult, and mechanisms may not be clear-cut. Both sessile invertebrates and algae are known to respond  
399 (negatively or positively) to light and clear differences in the communities were apparent here; although other  
400 factors including disturbance, sedimentation (Irving and Connell 2002) or interspecific competition for space  
401 (Anderson and Underwood 1994; Miller and Etter 2008) are also likely to play important roles. In this study, we  
402 did not explicitly test for the effects of light, disturbance or boundary layer conditions on community dynamics,

403 which we can only infer as possible contributing drivers of community patterns. Neither can we determine the  
404 relative weighting of these processes in the emergent community structure. Understanding the contribution of  
405 multiple drivers to community structure remains a challenge to ecology (Martorell and Freckleton 2014;  
406 Widder et al. 2016), affecting our ability to predict outcomes of interactions, such that the emergent outcomes  
407 are often context specific or time-sensitive.

408  
409 It is often reported that artificial structures are typically depauperate of species, yet we found a diverse range  
410 of species on the artificial structures. Many of the species that recruited during this experiment were  
411 ecosystem engineers, adding three-dimensional space to the existing surface and facilitating the recruitment of  
412 later arriving invertebrates through the provision of biogenic habitat structure (Thompson et al. 1996). Biogenic  
413 build-up can protect artificial structures from weathering and erosion and enhance their longevity (Coombes et  
414 al. 2013) providing an important regulating ecosystem service. These species tended to be more strongly  
415 associated with downward-facing (shaded) surfaces, although the dissimilarity between downward and  
416 upward-facing communities could be partly mitigated by the addition of heterogeneity to upward-facing  
417 surfaces. Given the increasing prevalence of artificial structures in the marine environment (Firth et al. 2016),  
418 our results show how a simple, cheap and easy to implement modification of the artificial surface, especially on  
419 illuminated (upward-facing) surfaces, can act as important mechanism for promoting recruitment and  
420 colonisation of surfaces by plants and animals that enhances biodiversity and improves the resilience of  
421 artificial structures to weathering without compromising structural integrity. It is suggested that this  
422 modification could be applied to all new structures.

423  
424 The replacement of shale for ground oyster yielded only marginal increases in the abundance of ecosystem  
425 engineers despite previous studies arguing for the importance of olfactory cues during the recruitment process  
426 (e.g. O'Connor et al. 2008). Our findings therefore suggest a number of logical next steps for research. One is to  
427 explore whether the chemical signature of concrete (e.g. its alkalinity; Sella & Perkol-Finkel, 2015) alters the  
428 magnitude of a biological settlement response to a cue i.e. does the alkalinity of the surface alter the  
429 perception of biological cues by potential recruits and thus modify the efficacy of shale replacement in  
430 promoting settlement? Another is to consider the choice of biological material used to replace the shale  
431 component in the concrete. It may be that *M. gigas* is not a particularly important settlement cue. Future trials  
432 should therefore consider the replacement of shale with other biogenic materials (e.g. mussel shell) or  
433 combinations of biogenic materials, which will shed further light on the extent to which the choice of biogenic  
434 material can act as a selection mechanism for certain (targeted) species or biodiversity in general.

435  
436 Overall, it is apparent that innovative engineering design that uses a combination of shade and addition of  
437 heterogeneity can provide a mechanism, not just to provide space for nature on CMI but to facilitate selected  
438 recruitment of certain ecologically-important phyla. Understanding how to design and build CMI that attracts  
439 recruitment by target species is the next step in designing functional artificial structures that also compensate  
440 for the loss of natural habitat as a result of ocean sprawl.



441

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447

448

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660 APPENDICES

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662 **Appendix 1: Species identified during destructive sampling after six months**

Phyla	Species
Porifera	1 <i>Sycon ciliatum</i>
	2 <i>Halichondria panicea</i>
	3 <i>Leucosolenia botryoides</i>
Cnidaria	4 <i>Actinia equina</i>
Platyhelminthes	5 <i>Leptoplana tremallaris</i>
	6 <i>Eurynepta cornuta</i>
	7 <i>Stylostomum ellipse</i>
	8 <i>Plagiostomum sulphueum</i>
	9 Flat worm1 sp.
Nemertea	10 <i>Emplectonema gracile</i>
	11 <i>Nemertea flavida</i>
	12 <i>Lineus albocinctus</i>
	13 <i>Vieitezia luzmurubeeae</i>
Annelida	14 <i>Tetrastemma flavidum</i>
	15 <i>Tetrastemma herouardi</i>
	16 <i>Alentia gelatinosa</i>
	17 <i>Lepidonotus clava</i>
	18 <i>Cirratulus cirratus</i>
	19 <i>Ophryotrocha puerilis</i>
	20 <i>Psamathe fusca</i>
	21 <i>Micronereis variegata</i>
	22 <i>Platynereis species</i>
	23 <i>Phyllodoce mucosa</i>
	24 <i>Nereiphylla rubiginosa</i>
	25 <i>Amblyosyllis formosa</i>
	26 <i>Eupolymnia nebulosa</i>
27 <i>Lanice conchilega</i>	
28 <i>Polycirrus caliendrum</i>	
29 <i>Branchiomma bombyx</i>	
30 <i>Pseudopotamilla reniformis</i>	
31 <i>Sabella pavonina</i>	
32 <i>Pomatoceros lamarcki</i>	
33 <i>Pomatoceros triquiter</i>	

	34 <i>Spirobis sp.</i>
Crustacea	35 <i>Austrominius modestus</i>
	36 <i>Eurydice affinis</i>
	37 <i>Gammarus sp.</i>
	38 <i>Caprella sp.</i>
	39 <i>Cancer pagurus</i>
	40 <i>Rhithropanopeus harrisi</i>
Arthropoda	41 <i>Endeis spinosa</i>
	42 <i>Pycnogonida sp</i>
Mollusca	43 <i>Acanthochitona crinitus</i>
	44 <i>Rissoa parva</i>
	45 <i>Crepidula fornicata</i>
	46 <i>Runcina coronata</i>
	47 <i>Goniodoris castanea</i>
	48 <i>Goniodoris nodosa</i>
	49 <i>Philine aperta</i>
	50 <i>Polycera quadrilineata</i>
	51 <i>Janolus hyalinus</i>
	52 <i>Anomia ephippium</i>
	53 <i>Mytilidae sp.</i>
	54 <i>Mytilus edulis</i>
	55 <i>Musculus costulatas</i>
	56 <i>Pectinidae sp.</i>
	57 <i>Hiatella arctica</i>
	58 <i>Nudibranch sp. egg mass</i>
Bryozoa	59 <i>Crisularia plumosa</i>
	60 <i>Watersipora subtorquata</i>
	61 <i>Membranipora membranacea</i>
	62 <i>Bugula neritina</i>
	63 <i>Bugulina stolonifera</i>
	64 <i>Schizomavella linearis</i>
Echinodermata	65 <i>Asterina gibbosa</i>
	66 Starfish sp. larvae
Chordata	67 <i>Ciona intestinalis</i>
	68 <i>Clavelina lepadiformis</i>
	69 <i>Didemnum maculosum</i>
	70 <i>Diplosoma spongiforme</i>

	71 <i>Asciella aspersa</i>
	72 <i>Asciella scabra</i>
	73 <i>Asterocarpa humilis</i>
	74 <i>Phallusia mammillata</i>
	75 <i>Dendrodoa grossularia</i>
	76 <i>Stolonica socialis</i>
	77 <i>Botrylloides violaceus</i>
	78 <i>Ascidia sp. egg mass</i>
Protozoa	79 <i>Folliculina sp.</i>
Chlorophyta	80 Chlorophyta sp.
Rhodophyta	81 <i>Pterothamnion plumula</i>

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