2021-01

A global analysis of complexitybiodiversity relationships on marine artificial structures

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1   **Aim**

2   Topographic complexity is widely accepted as a key driver of biodiversity, but at the patch-

3   scale, complexity-biodiversity relationships may vary spatially and temporally according to

4   the environmental stressors complexity mitigates, and the species richness and identity of

5   potential colonists. Using a manipulative experiment, we assessed spatial variation in patch-

6   scale effects of complexity on intertidal biodiversity.

7   **Location**

8   27 sites within 14 estuaries/bays distributed globally

9   **Time period**

10   2015-2017

11   **Major taxa studied**

12   Functional groups of algae, sessile and mobile invertebrates

13   **Methods**

14   Concrete tiles of differing complexity (flat; 2.5 cm or 5 cm complex) were affixed at low-

15   high intertidal elevation on coastal defence structures, and the richness and abundance of the

16   colonising taxa were quantified after 12 months.

17   **Results**

18   The patch-scale effects of complexity varied spatially and among functional groups.

19   Complexity had neutral to positive effects on total, invertebrate and algal taxa richness, and

20   invertebrate abundances. However, effects on the abundance of algae ranged from positive to

21   negative, depending on location and functional group. The tidal elevation at which tiles were

22   placed accounted for some variation. The total and invertebrate richness were greater at low

23   or mid than at high intertidal elevations. Latitude was also an important source of spatial

24   variation, with the effects of complexity on total richness and mobile mollusc abundance

25   greatest at lower latitudes, whilst the cover of sessile invertebrates and sessile molluscs

26   responded most strongly to complexity at higher latitudes.

27   **Conclusions**

28   After 12 months, patch-scale relationships between biodiversity and habitat complexity were

29   not universally positive. Instead, the relationship varied among functional groups and

30   according to local abiotic and biotic conditions. This result challenges the assumption that

31   effects of complexity on biodiversity are universally positive. The variable effect of

32   complexity has ramifications for community and applied ecology, including eco-engineering

33   and restoration that seek to bolster biodiversity through the addition of complexity.

34

35   **Introduction:**

36   Habitat complexity the physical structure of environments, is a key driver of variability in the

37   distribution of biodiversity (Huston, 1979; Kovalenko, Thomaz, & Warfe, 2012). In general,

38   more complex habitats, with a greater density of spatial elements, support greater species

39   richness and abundance, across a range of functional groups, than less complex habitats

40   (McCoy & Bell, 1991; Stein, Gerstner, & Kreft, 2014). Habitat complexity may be derived

41   from both topographic (e.g. undulations, depressions, and protrusions) or biogenic (e.g., trees,

42   grasses, seaweeds, ants, corals and bivalves) structures. Complex habitats can influence the

43   colonisation and subsequent survival of species by determining the area available for

44   organisms to occupy (Connor & McCoy, 1979), which in turn can influence biotic

45   interactions (Hixon & Beets, 1993; Holt, 1987). Complex habitats can also have area-

46   independent effects on niche diversity (Johnson, Frost, Mosley, Roberts, & Hawkins, 2003),

47   and consequently the availability of refuges from environmental stressors and predators

48   (Strain, Cumbo, Morris, Steinberg, & Bishop, 2020). At land- and sea-scape scales

49   complexity enhances biodiversity by increasing habitat heterogeneity and niche space

50   (Kovalenko, Thomaz, & Warfe, 2012). However, at smaller scales, biodiversity and habitat

51   complexity relationships may vary depending on the type of complexity provided and how it

52   interacts with the environmental and biological setting (Loke & Todd, 2016).

53

54   The environmental variation among sites at local and biogeographic scales may influence

55   patch-scale habitat complexity (hereafter complexity) - biodiversity relationships by

56   determining resource availability, environmental conditions, as well as the species pool on

57   which complexity can act (Johnson et al., 2003; Bracewell et al., 2018). The stress gradient

58   hypothesis (Bertness & Callaway, 1994) proposes that positive interactions among species

59   (e.g. between habitat-forming and dependent taxa) will be most prevalent in environmentally

60   stressful environments, where local habitat amelioration is critical to organismal survival

61   (Bracewell, Clark, & Johnston, 2018; McAfee, Cole, & Bishop, 2016). Hence, microhabitats

62   that ameliorate extreme temperatures and/or desiccation stressors could increase in

63   importance with increasing tidal elevation (Bateman & Bishop, 2016) and decreasing latitude

64   (Bracewell et al., 2018). Conversely, the patch-scale effects of complexity may be consistent

65   across latitude if the local species are adapted to their local conditions or could have a greater

66   influence in locations where there is a greater difference between the air and sea

67   temperatures.

68

69   Additionally, complexity may be expected to have greatest patch-scale effects on biodiversity

70   in environments where there is a diverse species pool on which it can act. Whereby, the

71   effects of complexity may vary across latitudinal gradients in species richness (Bracewell et

72   al., 2018). At local scales, anthropogenic stressors such as contaminants may over-ride the

73   effects of complexity where they create conditions that are inhibitory to the survival of most

74 species (Mayer-Pinto, Matias, & Coleman, 2016). How species abundance and, hence,

75 richness responds to complexity may also vary according to the dominant functional groups

76 present at a given location (Strain, Olabarria, et al., 2018). Functional groups, defined here as

77 groups of organisms displaying distinct life-forms, that differ in their niche requirements,

78 tolerance to environmental stressors, and susceptibility to predation. While, overall,

79 increasing complexity is expected to enhance microhabitat diversity and niche space, the

80 availability of some microhabitat types will decline and others will increase with different

81 types of complexity (Kelaher, 2003). The taxa whose niche requirements are favoured by

82 increasing complexity will benefit at the expense of other taxa whose niches match

83 microhabitats that decline in abundance or area (Malumbres-Olarte, Vink, Ross, Cruickshank,

84 & Paterson, 2013).

85

86 For example, on intertidal rocky shores, algae can be among the dominant space occupants of

87 well-lit yet moist microhabitats (e.g. rockpools), that prevent desiccation, and allow adequate

88 light for photosynthesis (Wilson, James, Newman, & Myers, 1992). In contrast, invertebrates,

89 particularly sessile invertebrates benefit from microhabitats (e.g. crevices) that provide

90 protection from predators, but are also sufficiently shaded that their algal competitors cannot

91 survive (Glasby, 1999; Miller & Etter, 2008). Stress-sensitive taxa may benefit more than

92 stress-tolerant taxa from microhabitats that ameliorate environmental stressors (Darling et al.,

93 2017). Similarly, taxa that are more susceptible to predation (i.e. lack morphological or

94 behavioural defences) or have body sizes that most closely match the size of the

95 microhabitats may benefit most from complexity-mediated predator amelioration (Strain,

96 Morris, et al., 2018). Experimental research on the effects of increasing complexity on

97 different functional groups (i.e. algae, sessile invertebrates, and mobile invertebrates) is

98 lacking (but see Strain et al. 2020).

99   Few studies have examined the effects of complexity at large spatial scales, across functional

100   groups and the influence of varying environmental contexts, to test the generality of patch-

101   scale complexity-biodiversity relationships. Understanding how complexity underpins

102   richness and abundance of different taxa and functional groups across a range of

103   environmental conditions is of particular importance, given accelerating habitat loss and

104   homogenisation (Kovalenko et al., 2012). In urban marine environments, natural habitats are

105   being replaced by artificial structures (e.g. seawalls, groynes, breakwaters and wharves) with

106   reduced complexity (Airoldi, Connell, & Beck, 2009; Bulleri & Chapman, 2010). Such

107   habitat homogenisation often occurs simultaneously with other anthropogenically-derived

108   environmental changes, such as pollution and/or species invasions (McKinney, 2008). The

109   smooth, relatively homogenous, surfaces of artificial structures typically support fewer native

110   species and individuals (Chapman, 2003), but more non-native species (Airoldi & Bulleri,

111   2011) compared to the more complex natural habitats they replace.

112

113   There has been increasing interest in how complexity might be incorporated into the design

114   of marine urban structures so as to enhance their ecological value (O'Shaughnessy et al.,

115   2020). The addition of complexity to topographically homogenous marine urban structures

116   has been proposed as a mechanism by which the overall richness and abundances of key

117   functional groups might be enhanced (Strain et al. 2018). However, the manner in which

118   complexity acts will be context dependent and researchers have recommended that latitudinal

119   and biogeographic considerations are taken into account prior to design or construction

120   (Mayer-Pinto, Dafforn, & Johnston, 2019).

121

122   Using standardised experiments on a global scale, we investigated how manipulating one

123   form of complexity (crevices/ridges) on tiles affected the richness and abundance of

124   colonising taxa at fourteen urban estuaries or bays spread across nine biogeographic realms.

125   We predicted that patch-scale complexity would have a positive influence on the taxa

126   richness and abundances of all sessile and mobile invertebrates functional groups but not

127   algae, which have higher light requirements, because of greater shading in the crevices

128   (Strain et al., 2020). Furthermore, we expected that the positive effects of increased

129   complexity on richness and abundances of sessile and mobile invertebrates would increase

130   with tidal elevation and with decreasing latitude, as desiccation stress and extreme high

131   temperatures increase, respectively. Finally, we hypothesised that complexity would have a

132   reduced effect on the richness and abundances of sessile and mobile invertebrates in highly

133   polluted environments such as those located near marinas or ports, where the effects of

134   pollution can over-ride the effects of complexity (Mayer-Pinto et al. 2018).

135

136   **Materials and methods**

137   **Study sites**

138   Experimental manipulations were conducted at 27 sites, distributed across 14 locations

139   globally (Fig. 1). There were two sites at each location, except for Herzliya Marina, Israel,

140   which hosted a single site. The locations were all in estuaries or bays situated along urbanised

141   coastlines, and were partners in the World Harbour Project (www.worldharbourproject.com).

142   Each had a semi-diurnal tidal regime and well mixed marine waters. Within locations, each

143   site comprised a vertical seawall or breakwater that extended from the shallow subtidal or the

144   low intertidal to the high intertidal zone. Sites at least 0.1 km apart, were of variable

145   proximity to port facilities or marinas, and varied in tidal height, tidal range, temperature

146 (average, minimum and maximum) and concentration of heavy metals (see Supplementary

147 S1).
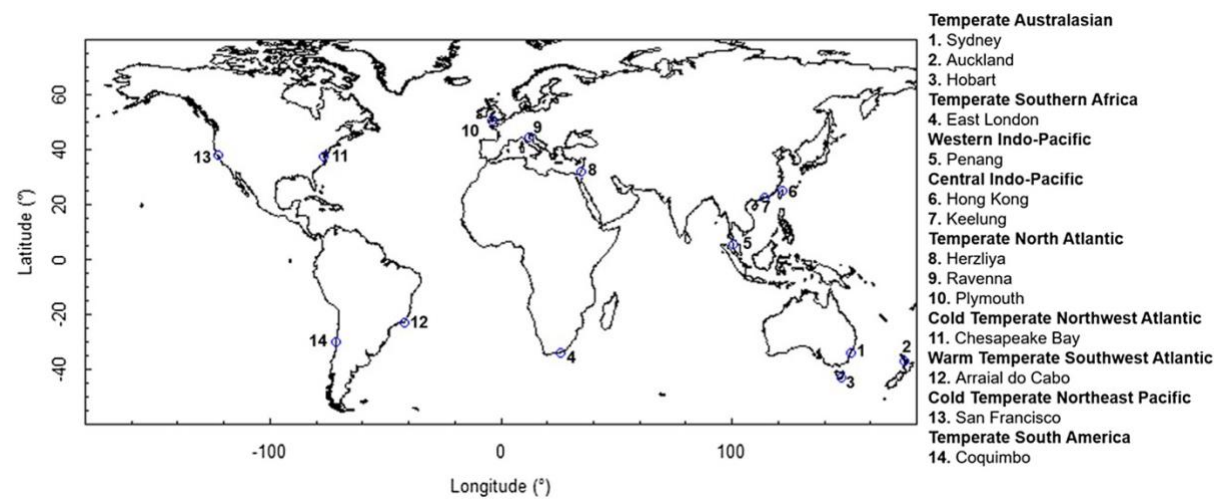
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151 **Fig 1:** Map showing the experimental locations. Locations are ordered by biogeographic

152 realm.

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154 **Experimental design**

155 At each site, 0.25×0.25 m concrete tiles were affixed to the coastal defence structures (i.e.

156 seawalls, or breakwaters). The tiles allowed manipulation of intertidal habitat complexity by

157 provisioning crevices and ridges as well as associated increase in surface area. The tiles,

158 designed and manufactured by Reef Design Lab (Melbourne, Australia), were flat (surface

159 area = 0.0625 m^2), had 0.025 m high ridges separated by 0.015 to 0.05 m wide crevices

160 (hereafter '2.5 cm complex'; surface area = 0.090 m^2) or had 0.05 m high ridges, each

161 separated by 0.015 to 0.05 m wide crevices (hereafter '5 cm complex'; surface area = 0.136

162 m^2; Fig. 2). At each site, five tiles of each design were either directly attached to the

163 structures, in the centre of 0.3×0.3 m patches cleared of pre-existing flora and fauna, or

164 attached to wood backing boards that were suspended off the top of the structures using rope

165 or nails. Tiles were attached to the structures, backing boards or steel frames using bolts that

166   were placed through a drilled hole in two to four corners of the tiles. At each site, the tiles

167   were deployed in a single horizontal row, from a low to high intertidal elevation, depending

168   on the location. Tiles were deployed in random order with respect to the experimental

169   treatments, with the complex tiles positioned so that the crevices and ridges were orientated

170   vertically. In temperate locations, the tiles were deployed between early spring to late autumn

171   during the period of greatest species recruitment and growth (Table S1).

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175   **Fig 2:** The three experimental treatments: a) flat, b) 2.5 cm complex, c) 5 cm complex.

176

177   **Colonising taxa**

178   After 12 months, all tiles were removed from the field, individually bagged and frozen until

179   analysis. On each tile, we recorded the identity and percentage cover (pooling across primary

180   and secondary growth) of all sessile algae and invertebrate taxa and removed all mobile

181   invertebrates (> 500 µm), using tweezers and by carefully rinsing the tile area with seawater

182   over a 500 µm sieve from the whole tile or two subsamples, depending on location

183   (Supplementary S1). At locations where subsampling was conducted, these were from one

184   pre-determined crevice (0.016 m^2) and one ridge (0.013 m^2) of each complex tile, that were

185   not adjacent to each other, but were pooled for the purposes of the analyses. On flat tiles, two

186   areas of similar size were subsampled and pooled. A pilot study conducted using Sydney data

187   revealed similar treatment effects on the richness and abundance of colonising taxa,

188   irrespective of whether a subsample or the full tile was sampled (Supplementary S2). All taxa

189   were identified to species or morphospecies using dissecting microscopes and then classified

190   into three coarser-level functional groups (hereafter 'functional groups') including algae,

191   sessile invertebrates and mobile invertebrates as well as nineteen finer-level functional

192   groups (Supplementary S2) based on the CATAMI classification guide (Althaus et al., 2015);

193   hereafter 'CATAMI groups.

194

195   **Environmental parameters**

196   To test hypotheses about potential sources of variability in complexity effects, we estimated

197   the tidal elevation, temperature, and proximity to boating facilities of tiles at each study site.

198   For tidal elevation we recorded the inundation period (proportion of time underwater) of the

199   tiles using a pressure logger. At each site, one pressure logger was attached to the top of a flat

200   tile and programmed to record water depth every 20 min for a period of one-month.

201   Measurements were made using either a Sensus Ultra (Reefnet Pty Ltd; +/- 0.03 m accuracy),

202   a Hobo Onset (Onsetcomp; +/- 0.02 m accuracy) or EasyTREK SP-300 (NIVELCO; +/-

203   0.05% of the measured range accuracy). Based on these measurements, the tidal elevation

204   was categorised as either high (inundated for <33% of the tidal cycle), mid (inundated for

205   >34 to 65% of the tidal cycle) or low (inundated for >66% of the tidal cycle; Supplementary

206   S1).

207

208   Throughout the 12-month experiment, we took measurements of temperature at 21 sites

209   (Supplementary S1). At each site, we deployed three DS1921G Themochron iButton data

210   loggers (Thermodata Pty. Ltd. Warrnambool, Australia) haphazardly on flat tiles. The

211   iButtons were waterproofed with Plastidip rubber coating (Plasti Dip International, Blaine,

212   Minnesota, USA). The iButtons were programmed to record temperatures at 20 min intervals,

213   across a one-month period, with 0.5ºC accuracy. The iButtons were attached to the tiles using

214   cable ties so that they could easily be removed, downloaded, and replaced each month. Mean

215   (both aerial and in water), maximum (aerial) and minimum (aerial) temperature were

216   negatively correlated with absolute latitude at the 21 sites (Supplementary S4). Hence, to

217   avoid issues with collinearity between these two predictor variables, subsequent analyses

218   were run only on latitude of study sites.

219

220   At the end of the experiment, we measured the distance from the centre of each site to the

221   nearest boating facility (port or marina) using satellite images in Google Earth. For 17 sites,

222   we also obtained information on the concentration of copper from sediment sampling

223   (Supplementary S1). Increasing distance of study sites to the nearest boating facility was

224   negatively correlated (but not significantly) with the amount of copper (historically used as

225   an antifouling agent; Dafforn et al. 2011) in sediment at the 17 sites for which both sets of

226   data were available (Supplementary S4). Hence, distance to the nearest boating facility,

227   which could be measured for all 27 sites, was used as a proxy for contamination.

228

229   **Analyses**

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231   We used multivariate generalised linear modelling to test the effects of complexity (fixed, 3

232   levels: flat, 2.5 cm or 5 cm), location (fixed, 14 levels) and site nested within location (fixed

233   1-2 levels) on the abundances of each of the 19 CATAMI groups. These data were modelled

234   using a negative binomial distribution due to overdispersion from the Poisson distribution.

235   Where multivariate analyses indicated a significant main effect of treatment, or an interaction

236   of treatment with location or site(location) univariate post hoc test statistics and p-values

237   were calculated for each group separately adjusting for multiple comparisons. For those

238   groups found to have significant effects of treatment (either occurring independently of or

239   interacting with spatial factors), pairwise differences between treatment levels, were assessed

240   using univariate linear models (LMs). Where both the treatment $\times$ location and treatment $\times$

241   site (location) were significant, only the treatment $\times$ location interaction was interpreted as its

242   significance demonstrates effects of location that are apparent over smaller site-scale

243   variability. Similarly, we used LMs or generalised linear models (GLMs) with the factors

244   complexity, location and site nested within location to compare the richness and abundances

245   (cover or counts) of total taxa, algae, sessile invertebrates and mobile invertebrates across

246   treatments, at 12 months.

247

248   To test hypotheses about whether the effects of complexity on the richness and abundances of

249   the key functional groups on the tiles, varied by tidal elevations, latitude and distance from

250   the nearest marina or port, we used analyses on the standard mean difference (SMD) between

251   the 5 cm and flat tile. The Hedge's G SMD was calculated at the scale of site, using the

252   average and standard deviation of the five tiles sampled within each site, for each treatment.

253   We chose the SMD effect size rather than the log response ratio because these data contained

254   many zeros (i.e. no species observed and/or no variance observed between replicates within

255   the same treatment) (Borenstein, Hedges, Higgins, & Rothstein, 2010). We tested the effects

256   of tidal zone, latitude and distance to the nearest marina or port using the Hedges random

257   effects estimator (Hedges, 1981) with the package metafor (Viechtbauer, 2010). For the

258   analyses testing the effects of tidal zone, we adjusted for the effects of location, by adding

259   location as a moderator in a multilevel random effects model.

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261   All statistical analyses were undertaken in R 3.5.0 (R Core Team, 2016). For all models we

262   offset the sample area (m^2), to separate the effects of complexity from surface area.

263   Generalised linear models were undertaken in the package MASS and figures were produced

264   using the package ggplot 2 (Wickham, 2016). The multivariate analyses were undertaken

265   with the packages mvabund and boral (Hui, 2016). All models were checked for over-

266   dispersion and spatial and temporal autocorrelation with plots, and the residuals were visually

267   inspected for heteroscedasticity. Where appropriate, post hoc comparisons were undertaken

268   using the package emmeans (Lenth, Singmann, & Love, 2018) to identify sources of

269   treatment effects.

270

271   **Results**

272   **Effect of complexity on richness**

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274   The effect of complexity on total taxa richness and the richness of each of the three coarse-

275   level functional groups (algae, sessile invertebrates, and mobile invertebrates) varied among

276   locations (Fig. 3, Table 1, Supplementary S5). Where significant effects were seen, the 2.5

277   cm and/or the 5 cm complex tiles (i.e. with cervices/ridges) supported greater taxa richness

278   than the flat tiles (Table 1). Total taxa richness was greater on the 5 cm complex tiles than the

279   flat tiles (by 0.8 – 2.7 times) at 10 of the 14 locations and on the 2.5 cm complex relative to

280   the flat tiles at eight locations, with no effect of complexity on total richness at four locations

281   (Fig. 3, Table 1, Supplementary S5). Algal richness was greater on 5 cm complex tiles (by

282   1.1-2.4 times) than on the 2.5 cm complex tiles or the flat tiles at two locations, but displayed
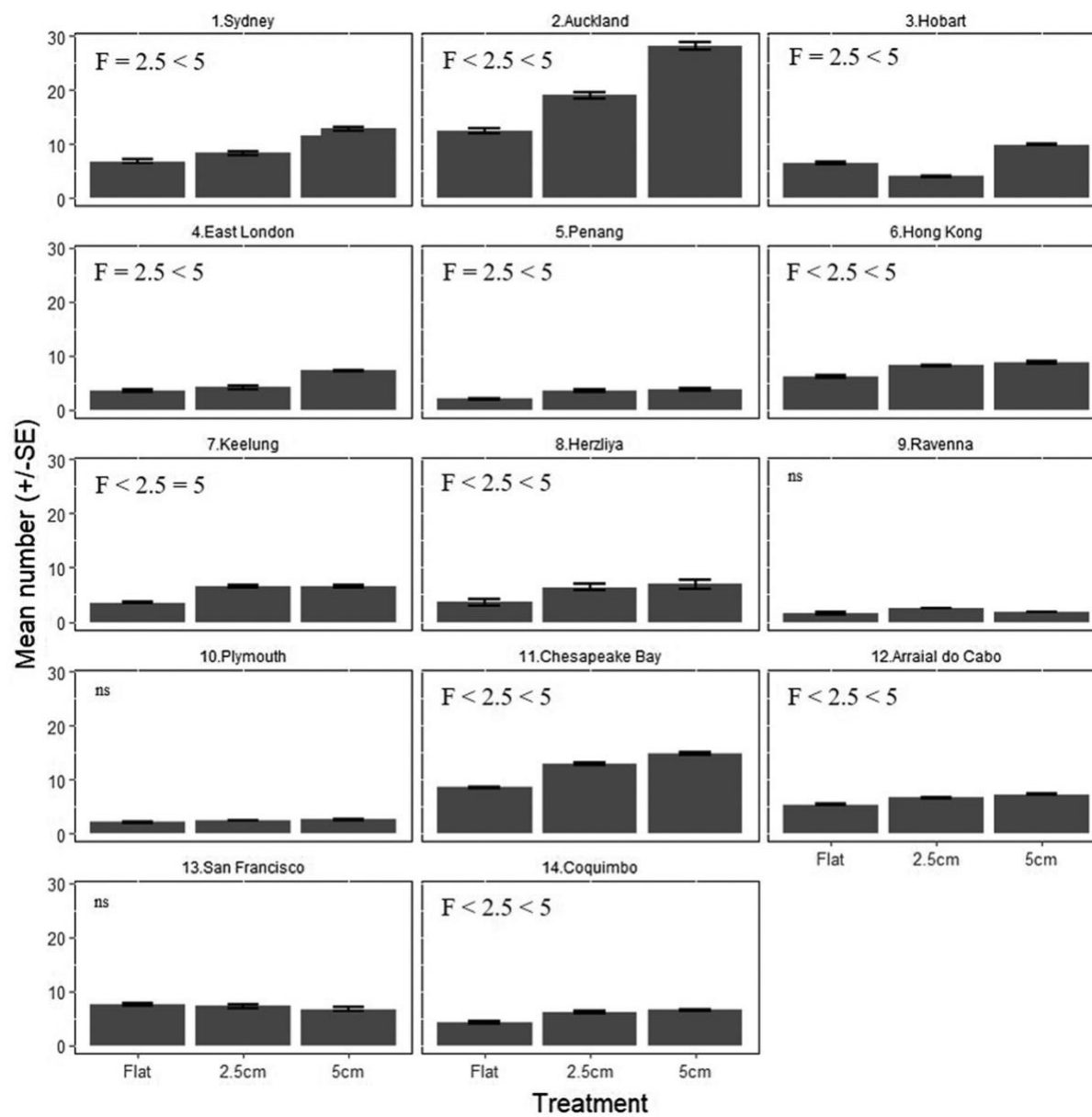
283   no significant effect of complexity at the other 12 locations (Table 1, Supplementary S5).

284   Sessile invertebrates were more speciose on the 5 cm complex tiles than on flat tiles at nine

285   locations (by 1.0-1.8 times), and more speciose on the 2.5 cm complex than flat tiles at seven

286   locations, but did not differ among treatments at the other five locations (Table 1,

287   Supplementary S5). There were more mobile species on the 5 cm complex tiles compared

288   with the flat tiles at eight locations (1.0-2.4 times), and on the 2.5 cm complex tiles relative to

289   flat tiles at five locations, with no significant differences for the other nine locations (Table 1,

290   Supplementary S5).

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294   **Fig 3:** Effect of complexity (flat and 2.5 cm or 5 cm complex tiles) on the mean (+/-SE) total

295   taxa richness at each of fourteen locations by realm (n = 1 or 2 sites per location). Significant

296   differences (at α = 0.05) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are

297   indicated by '>' or '<', with 'ns' or '=' denoting treatments that did not significantly differ.

298   **Table 1:** Overview of the posthoc tests for significant complexity by location interactions in

299   the total richness and the richness and abundance of functional groups. Significant

300   differences (at α = 0.05) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are

301   indicated by '>' or '<', with 'ns' or '=' denoting treatments that did not significantly differ.

302   Locations are ordered by realm. Details of these analyses are given in Appendices S4.

Response	Richness			Abundances (percentage cover or counts)		
Functional group	Algae	Sessile invertebrate	Mobile invertebrate	Algae	Sessile invertebrates	Mobile invertebrates
1. Sydney	F=2.5<5	F=2.5<5	F<2.5=5	ns	F=2.5<5	F=2.5<5
2. Auckland	ns	F<2.5<5	F<2.5=5	ns	F<2.5=5	F<2.5=5
3. Hobart	ns	F=2.5<5	F=2.5<5	ns	F<2.5=5	F=2.5<5
4. East London	ns	ns	F=2.5<5	ns	ns	F=2.5<5
5. Penang	ns	F<2.5=5	Ns	ns	ns	Ns
6. Hong Kong	ns	F<2.5=5	F<2.5=5	ns	F<2.5=5	F<2.5=5
7. Keelung	ns	ns	F<2.5=5	ns	Ns	F=2.5<5
8. Herzliya	ns	F<2.5=5	Ns	ns	F<2.5=5	F<2.5=5
9. Ravenna	ns	F<2.5=5	Ns	ns	Ns	ns
10. Plymouth	ns	ns	Ns	ns	F<2.5=5	ns
11. Chesapeake Bay	ns	F<2.5=5	F=2.5<5	F<2.5=5	F<2.5=5	F<2.5=5
12. San Francisco	ns	ns	Ns	ns	Ns	ns
13. Arraial do Cabo	F=2.5<5	F<2.5=5	Ns	ns	Ns	F=2.5<5
14. Coquimbo	ns	ns	F<2.5=5	F<2.5=5	F<2.5=5	F<2.5=5

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Effect of complexity on abundances

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312 The effects of complexity varied among functional groups (algae, sessile and mobile

313 invertebrates) and the 19 CATAMI groups, and within these groupings, according to location

314 and/or site (Table 1, Table 2, Supplementary S5-S6). The abundances (i.e. percentage cover

315 or counts) of algae, sessile and mobile invertebrates (Table 1, Supplementary S5) as well as

316 that of encrusting macroalgae, bryozoans, sessile and mobile crustaceans, sessile and mobile

317 molluscs and sessile worms each displayed significant positive effects of the 2.5 cm and/or

318 the 5 cm complex tiles relative to the flat tiles, at one or more locations, with non-significant

319 effects at the remaining (Table 2, Supplementary S5).

320 The abundances of mobile crustaceans and mobile molluscs showed significant positive

321 effects of either the 2.5 cm and/or 5 cm tiles compared with the flat tiles, at some sites, but

322 these differences were not consistent between sites within locations (Tables 2, Supplementary

323 S6). The effects of complexity were, among locations, spatially variable in both occurrence

324 and direction for filamentous/filiform macroalgae cover and mobile worm abundances and

325 between sites for foliose macroalgae cover (Table 2, Supplementary S6). Although present on

326 tiles, globose saccate macroalgae, articulated calcareous macroalgae, ascidians, cnidarians,

327 sponges, hexapods, arthropods and echinoderms displayed patterns in abundance that did not

328 respond to complexity, at any of the sites or locations (Table 2, Supplementary S6).

329

330

331 **Table 2:** Overview of the posthoc tests for significant complexity by location or complexity by site(location) interactions in the abundance of

332 CATAMI groups. Significant differences (at $\alpha = 0.05$) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are denoted with '>' or '<',

333 with 'ns' or '=' denoting treatments that did not differ. Locations are ordered by realm. Details of these analyses are given in supplementary S5.

Response	Abundances (percentage cover or counts)									
Functional group	Filamentous filiform algae (%)	Foliose algae (%)	Encrusting algae (%)	Bryozoans (%)	Sessile crustaceans (%)	Sessile molluscs (%)	Sessile worms (%)	Mobile crustacea (counts)	Mobile molluscs (counts)	Mobile worms (counts)
1. Sydney	F=2.5<5	Site 1 F<2.5<5 Site 2 ns	F=2.5<5	F=2.5<5	F=5<2.5	F<2.5<5	F=2.5<5	Site 1 F=2.5<5 Site 2 F<2.5<5	F<2.5<5	F=2.5<5
2. Auckland	ns	Site 1 F>2.5>5 Site 2 ns	ns	ns	F<2.5<5	ns	F=2.5<5	Site 1 F<2.5<5 Site 2 F<2.5<5	F<2.5<5	F=2.5<5
3. Hobart	ns	Site 1 F=5<2.5	ns	ns	F<2.5<5	F<2.5<5	ns	Site 1 F=5<2.5 Site 2 ns	F<2.5<5	F>2.5<5
4. East London	ns	Site 1 F>2.5>5 Site 2 F=2.5<5	F=2.5<5	ns	ns	ns	ns	ns	F<2.5<5	ns
5. Penang	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
6. Hong Kong	ns	ns	ns	ns	F<2.5<5	F=5<2.5	ns	Site 1 F<2.5<5 Site 2 F<2.5<5	F<2.5<5	ns
7. Keelung	F>2.5>5	ns	ns	ns	ns	ns	F=2.5<5	Site 1 ns Site 2 F<2.5<5	F<2.5<5	ns
8. Herzliya	ns	ns	ns	F<2.5<5	F=2.5<5	ns	F=2.5<5	ns	ns	ns
9. Ravenna	ns	ns	ns	ns	F=5<2.5	F<2.5<5	ns	ns	ns	ns

10. Plymouth	ns	Site 1 F=5<2.5 Site 2 ns	ns	F=5<2.5	F<2.5<5	F=2.5<5	ns	ns	ns	ns
11. Chesapeake Bay	ns	ns	ns	ns	ns	F<2.5<5	ns	Site 1 F<2.5<5 Site 2 F=2.5<5	ns	F<2.5<5
12. San Francisco	ns	ns	ns	ns	F<2.5<5	ns	ns	Site 1 F>2.5>5 Site 2 ns	F>2.5>5	ns
13. Arraial do Cabo	ns	ns	F<2.5<5	ns	F<2.5<5	ns	F<2.5<5	ns	F<2.5<5	ns
14. Coquimbo	F>2.5>5	Site 1 F>2.5>5 Site 2 ns	ns	ns	F<2.5<5	ns	ns	ns	F<2.5<5	ns

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Correlates of spatial variation in effects of complexity

337

338   The standard mean difference (SMD) of total, sessile invertebrate and mobile invertebrate

339   richness, the percentage cover of filamentous/filiform macroalgae, encrusting algae, sessile

340   bivalves, sessile crustaceans, sessile worms and the abundances of mobile worms on the 5 cm

341   compared to the flat tiles varied significantly among tidal zones (Fig. 4, Supplementary S7).

342   Significant differences in the SMDs were found in the mid and low tidal zone for each of

343   total and sessile and mobile invertebrate richness and in the high, mid and low tidal zone for

344   the abundances of mobile molluscs (Fig. 4, Supplementary S7). In contrast, the difference in

345   the SMD was only significant in the high tidal zone for the percentage cover of encrusting

346   algae and in the mid and high tidal zones for the percentage cover of sessile worms and the

347   abundances of mobile crustaceans. The percentage cover of sessile bivalves and sessile

348   crustaceans and the abundances of mobile worms displayed differences in the SMDs that

349   were only significant in the mid-tidal zone and in the low tidal zone for the percentage cover

350   of filamentous algae (Fig. 4, Supplementary S7).

351

352   The SMD in the richness of sessile invertebrate species between the 5 cm complex and flat

353   tiles increased with distance from the nearest marina or port. However, the SMD for other

354   groups was unaffected by this variable (Supplementary S7). The SMD of total taxa richness

355   significantly decreased with latitude (Fig. 5), as did abundance of molluscs, while conversely,

356   SMD of percentage cover of sessile bivalves increased with latitude (Supplementary S7). All

357   other groups were unaffected by latitude (Supplementary S7).

358
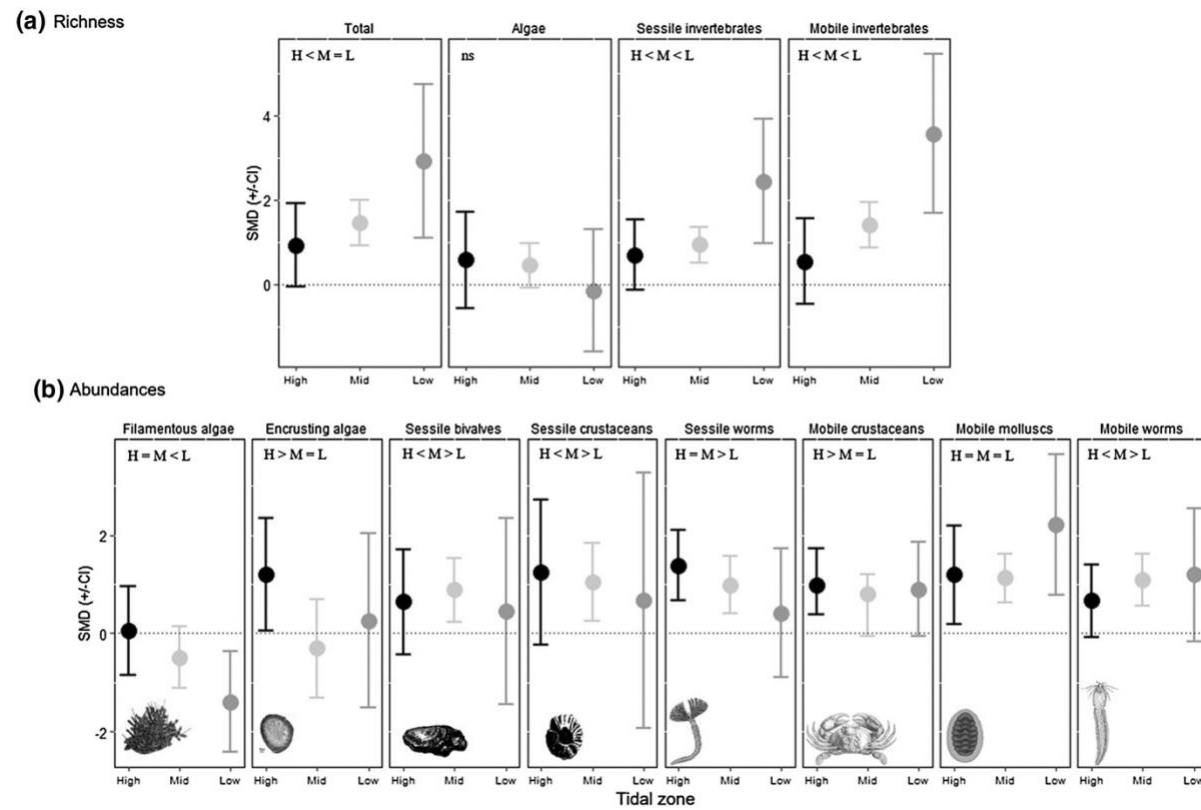
(a) Richness

(b) Abundances

Fig. 4: Effects of tidal zones on the standard mean difference SMD (+/-CI) in a) richness of total taxa, algae, sessile invertebrates and mobile invertebrates and b) abundances (percentage cover or abundance) of key CATAMI groups between 5 cm complex and flat tiles (high n = 5 sites, mid n = 18 sites, and low n = 4 sites). Effects are significant if the confidence intervals do not overlap zero (dashed line). Significant differences (at α = 0.05) between high (H), and mid (M) or low (L) tidal zones are indicated by '>' or '<'.
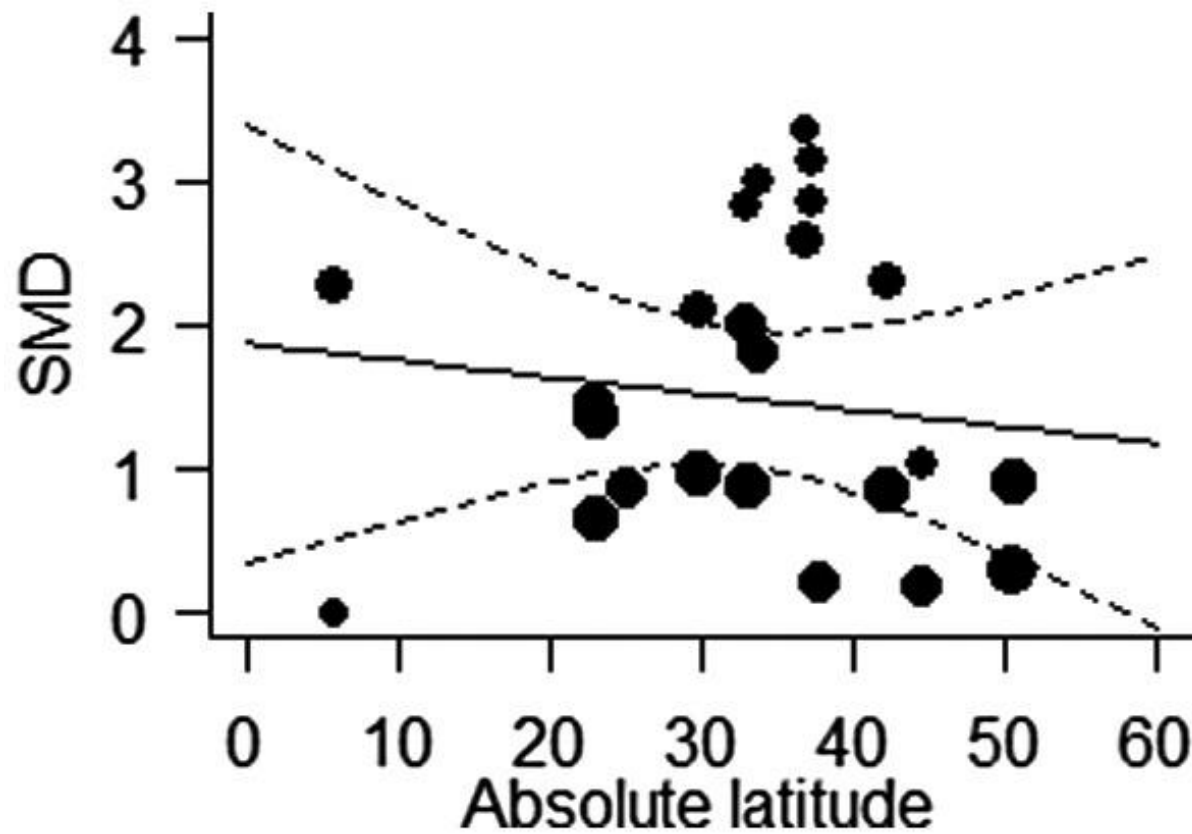
Fig. 5: Effects of absolute latitude on the standard mean differences SMD in total taxa

between 5 cm complex and flat tiles (n = 27 sites), where the size of the circle varies

according to the variance.

Discussion

The incorporation of complexity into artificial structures is increasingly being advocated as a

mechanism to maintain or enhance native biodiversity, but most studies to date have

examined effects of complexity on marine built structures over a relatively narrow range of

environmental conditions (reviewed by Strain et al. 2018). Our study, spanning 27 sites from

14 locations across the globe, provided the first experimental test of how effects of patch-

scale complexity on artificial structures vary across very large spatial scales. After 12

384 months, complexity had positive effects on the richness and abundance of the colonising taxa

385 at most (10 out of 14) of the locations tested. Nevertheless, the effects of complexity on the

386 colonisation of individual functional groups, varied spatially according to tidal elevation and

387 latitude. These results challenge the paradigm that environmental that complexity has

388 universally positive effects on biodiversity (Huston, 1979) and instead support the growing

389 assertion (e.g. Beck, 1998) that at the patch-scale effects of complexity on biodiversity can

390 vary in magnitude and direction according to local abiotic and biotic stressors, niche

391 requirements of the dominant taxa and the scale of complexity provided.

392

393 The study, which manipulated a single type of habitat complexity (crevices/ridges), was not

394 designed to disentangle complexity effects arising from enhancement of surface area and

395 microhabitat diversity. The complex tiles not only had greater surface area but, in providing

396 crevices and ridges, provided greater microhabitat diversity than the flat tiles that had only a

397 single microhabitat type. These crevices and ridges have previously been demonstrated to

398 differ in light, humidity, temperature, and predator access (Strain et al. 2018; 2020),

399 supporting distinct communities of algae and invertebrates (Strain et al. 2020). The spatially

400 variable effects of crevices and ridges on biodiversity suggest that differences between

401 complex and flat treatments did not simply reflect the greater surface area of the former, but

402 also modification of environmental conditions and biological interactions by the

403 microhabitats. Further, whereas differences were consistently found between complex and

404 flat tiles, differences between the two complex treatments, with 5 cm or 2.5 cm deep cervices,

405 were often absent, suggesting a greater role of microhabitat identity and diversity than surface

406 area in driving the patterns.

407

408 Whereas effects of the complex tiles on the richness and abundance of invertebrate groups

409 were, where present, positive, effects of the complex tiles on the richness and abundance of

410 algae were highly variable, not only in occurrence, but also direction. The sessile invertebrate

411 groups that responded most positively to the cervices and ridges provided by this study were

412 taxa that are limited to shaded and moist low intertidal and subtidal shore (such as bryozoans)

413 (Miller & Etter, 2008), and taxa commonly targeted by benthic predators (e.g. molluscs,

414 crustaceans, worms) (Janssen, Sabelis, Magalhães, Montserrat, & Van der Hammen, 2007;

415 Strain, Morris, et al., 2018). In contrast, the mobile invertebrates that responded positively

416 were taxa that could rapidly colonise by migration from nearby habitats (e.g. mobile molluscs

417 and crustaceans), (Martins, Thompson, Neto, Hawkins, & Jenkins, 2010). These taxa were

418 predominantly found in the protective crevices of the complex tiles, suggesting that the

419 provision of refugia could have played an important role (Strain et al., 2020). Filamentous

420 and foliose macroalgae were negatively affected by complexity at some sites, despite the

421 overall greater surface area of complex tiles. This may be because light in the crevices was

422 insufficient to meet the needs of these taxa that have high light requirements (Markager &

423 Sand-Jensen, 1992), or alternatively because of enhanced top-down control by the abundant

424 grazer communities in the crevices. Encrusting algae, which have low light requirements

425 (Markager & Sand-Jensen, 1992) and a tough thallus that deters grazers (Bertness, Yund, &

426 Brown, 1983) were the only algal group to consistently respond positively to complexity.

427

428 Thermal and desiccation stress have long been implicated in setting the upper distributional

429 limits of organisms intertidally (Harley, 2003; Wolcott, 1973) while classically, the lower

430 distributional limits are thought to be set by biological interactions such as competition and

431 predation (Connell, 1961). Consistent with this thinking and previous within-site comparisons

432 of complexity-biodiversity relationships among elevations (Cordell et al. 2017), we found the

433   effects of added complexity on taxa richness and abundance of colonising organisms differed

434   among tidal elevations, as well as among functional groups. Total taxa richness and the

435   richness of sessile and mobile invertebrates responded most strongly to complexity in the low

436   intertidal zone, but the richness and abundances of algae, and abundances of sessile

437   invertebrates responded more strongly in the mid and high intertidal zones. In the low

438   intertidal, the crevices on complex tiles may provide refuge to invertebrate taxa from large-

439   bodied marine predators, such as fish, which can exert considerable top-down control on the

440   communities of coastal structures (Connell & Anderson, 1999) and/or from wave exposure

441   that can challenge the attachment strength of organisms and interfere with feeding behaviour

442   (Bulleri & Chapman, 2010; Moschella et al., 2005). In the high and mid intertidal, on

443   artificial coastal defences as on natural rocky shores, cool and shaded crevices could

444   influence the richness and abundances of algae and the abundances of invertebrates by

445   providing refuge from extreme temperatures and desiccation at low tide (Chapman &

446   Blockley, 2009; Strain et al., 2020).

447

448   Additionally, we found evidence for latitudinal variation in the effects of complexity on total

449   taxa richness and the abundance of some invertebrate groups. Complexity had the greatest

450   effects on the total richness of taxa and the abundances of mobile molluscs at low latitudes,

451   where average temperatures, primary productivity as well as taxa richness and abundance are

452   generally highest (Hillebrand, 2004). However, the cover of sessile molluscs displayed the

453   reverse pattern of greater effects of complexity at higher latitudes, where average

454   temperatures and the percentage cover of sessile invertebrates were lower. These results are

455   consistent with other studies that have demonstrated positive effects of complexity on the

456   richness or diversity of invertebrates at tropical latitudes in intertidal systems (Freestone &

457   Osman, 2007; Menge & Lubchenco, 1981). Latitudinal variation in the effects of complexity

458   likely reflects spatial variation in the local species pool, functional group identity and species

459   recruitment, predation, and growth rates.

460

461   Despite our hypothesis that pollutants would override the effects of complexity, proximity of

462   sites to marinas and port facilities, which are commonly highly contaminated (Adamo et al.,

463   2005; Rivero, Dafforn, Coleman, & Johnston, 2013), explained little of the variation in

464   effects of complexity for most groups of algae and invertebrates. There was, however, a

465   positive effect of the distance to the nearest port or marina on the relationship between

466   complexity and richness of sessile invertebrates. Although our study did not document spatial

467   variation in the size of the species pool of available colonists, the positive relationship

468   between distance from boating facilities and effects of complexity on sessile invertebrates is

469   consistent with the contaminants associated with boating facilities adversely impacting the

470   native species pool on which complexity can act. Heavy metals, such as copper, either

471   historically or presently used in antifouling paints, can negatively impact native biodiversity

472   (Dafforn, Lewis, & Johnston, 2011; Kinsella & Crowe, 2016). Previous studies have

473   demonstrated these contaminants can also enhance the richness and abundances of invasive

474   species (Marraffini, Ashton, Brown, Chang, & Ruiz, 2017; Piola, Dafforn, & Johnston,

475   2009); thus complexity could facilitate the increase of the non-endemic species pool. Studies

476   directly manipulating contamination inside and outside harbours would be required to

477   establish the importance of this factor as a moderator of complexity effects.

478

479   Our results support previous suggestions that the addition of complexity to the homogenous,

480   flat surfaces of coastal defence structures has the potential to improve ecological outcomes

481   (O'Shaughnessy et al., 2020). As compared to the natural habitats they replace,

482   topographically simple artificial structures commonly support reduced native biodiversity

483 (Airoldi, Turon, Perkol-Finkel, & Rius, 2015). Eco-engineering complexity and missing

484 microhabitats on these artificial structures to enhance the biodiversity and ecosystem

485 functioning of their communities, is increasingly common. However, scientific studies

486 providing the evidence base for this rapidly-growing field are often poorly replicated and

487 carried out over small spatial and temporal scales (Chapman, Underwood, & Browne, 2018;

488 Firth, Airoldi et al. 2020). Global integration of small-scale ecological experiments such as

489 those conducted here can be useful in identifying appropriate eco-engineering approaches

490 before they are scaled up. Our study provides the most geographically comprehensive test of

491 the effects of complexity on the biodiversity of coastal defence structures across the globe.

492 We clearly demonstrate that complexity can affect the richness and abundances of colonising

493 taxa, and despite large biogeographic variation in the identity of taxa present, these effects are

494 largely of a consistent and positive direction for particular functional groups, across the

495 globe.

496

497 Despite the generally positive effects of complexity, we found that the magnitude of these

498 varied spatially from negligible to strongly positive (or in the case of some algae, negative).

499 This is an important result as it suggests that economically costly eco-engineering

500 interventions may have negligible benefit at some locations and may even negatively

501 influence some functional groups if applied blindly. Effective eco-engineering requires

502 understanding of the key environmental stressors that may be mitigated and the functional

503 traits of taxa that are being targeted for enhancement (see also Morris et al. 2018). By

504 designing microhabitats with the niches of target functional groups in mind, the benefits of

505 complexity additions to structures may be maximised. Critically, the finding that the effect of

506 complexity varied among locations, tidal zones and with latitude, highlights the importance

507 of understanding how the effects of complexity are shaped by the local abiotic and biotic

508   environments before implementing eco-engineering solutions – one size will not necessarily

509   fit all. Manipulative experiments are now needed to confirm how specific environmental and

510   biological factors mediate complexity-biodiversity relationships, within urbanised marine

511   settings and whether the effects of complexity identified over a 12-month period here persist

512   over longer time scales. Moreover, to fully assess the biodiversity benefits of eco-engineering

513   interventions that add complexity, we would also need to compare the complex tiles to the

514   surface of the coastal defence structure and adjacent natural rocky shores.

515

516   Eco-engineering, like ecological restoration (Ewel, 1987) provides the ultimate test of

517   ecological theory (Mitsch 1996), by reassembling ecosystems from first principles. A

518   cornerstone of community ecology has been the positive relationship between complexity and

519   diversity (Dean & Connell, 1987; Kovalenko et al., 2012). Our global study challenges this

520   paradigm in demonstrating that at patch-scales complexity effects can range from positive to

521   neutral to negative, depending upon location and functional group. General guidelines to

522   enhance biodiversity in coastal constructions will benefit from a grounding in ecological

523   theory that can help developers predict the influence of local environmental and biotic

524   contexts (Mayer-Pinto et al 2019).

525

526

527   **Acknowledgements**

530   **Data Availability**

531   The data are available as Supporting Information

532

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