

2021-01

A global analysis of complexitybiodiversity relationships on marine artificial structures

Strain, EMA

<http://hdl.handle.net/10026.1/17485>

10.1111/geb.13202

Global Ecology and Biogeography

Wiley

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

[Type here]

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

[Type here]

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

[Type here]

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

[Type here]

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).

[Type here]

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

[Type here]

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

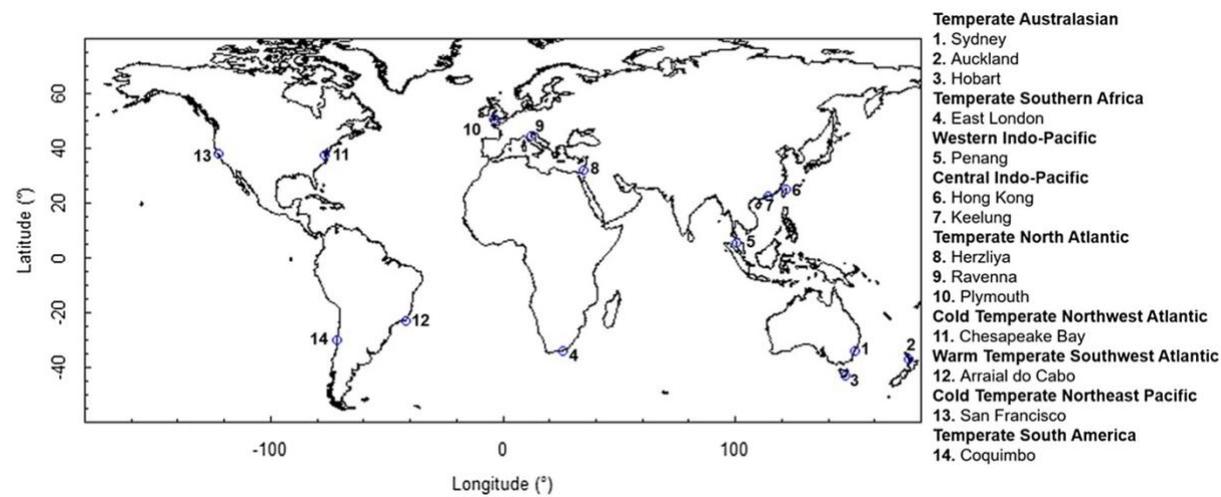
136 **Materials and methods**

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

[Type here]

146 (average, minimum and maximum) and concentration of heavy metals (see Supplementary
147 S1).



148
149
150

151 **Fig 1:** Map showing the experimental locations. Locations are ordered by biogeographic
152 realm.

153

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 m²), 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 m²) 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 m²; 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

[Type here]

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).

172



173
174

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 ($> 500 \mu\text{m}$), using tweezers and by carefully rinsing the tile area with seawater
182 over a $500 \mu\text{m}$ 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

[Type here]

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 ThermoChron iButton data

[Type here]

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 0.5°C 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**

230

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.

[Type here]

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.

[Type here]

260

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

262 offset the sample area (m²), 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**

273

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

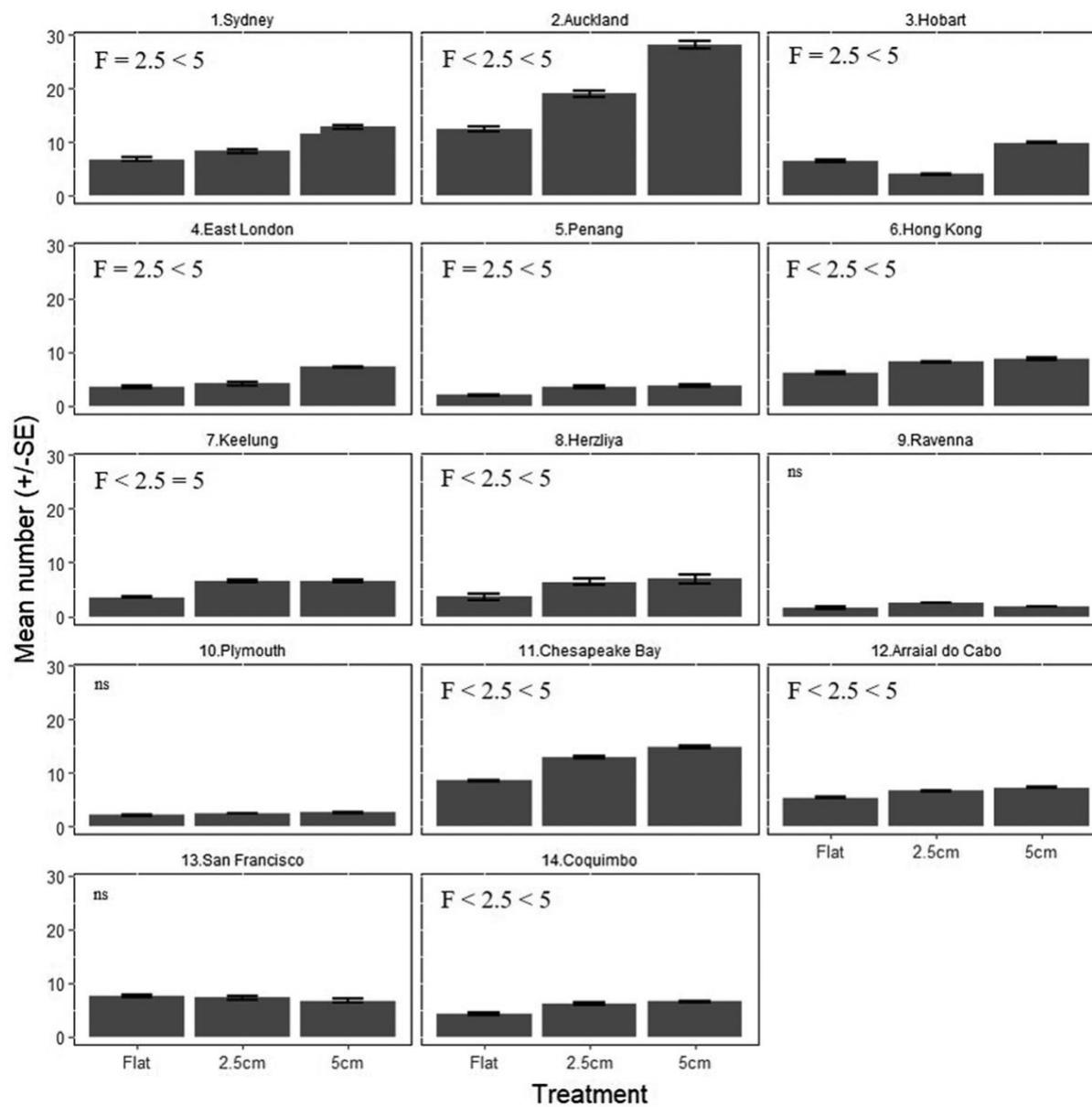
283 no significant effect of complexity at the other 12 locations (Table 1, Supplementary S5).

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

[Type here]

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).

291



292
293

[Type here]

294 **Fig 3:** Effect of complexity (flat and 2.5 cm or 5 cm complex tiles) on the mean (\pm SE) total
295 taxa richness at each of fourteen locations by realm (n = 1 or 2 sites per location). Significant
296 differences (at $\alpha = 0.05$) 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.

[Type here]

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 $\alpha = 0.05$) 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)		
	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

303

304

305

306

307

308

[Type here]

309

310 **Effect of complexity on abundances**

311

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

[Type here]

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

[Type here]

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

334

[Type here]

335

336 **Correlates of spatial variation in effects of complexity**

337

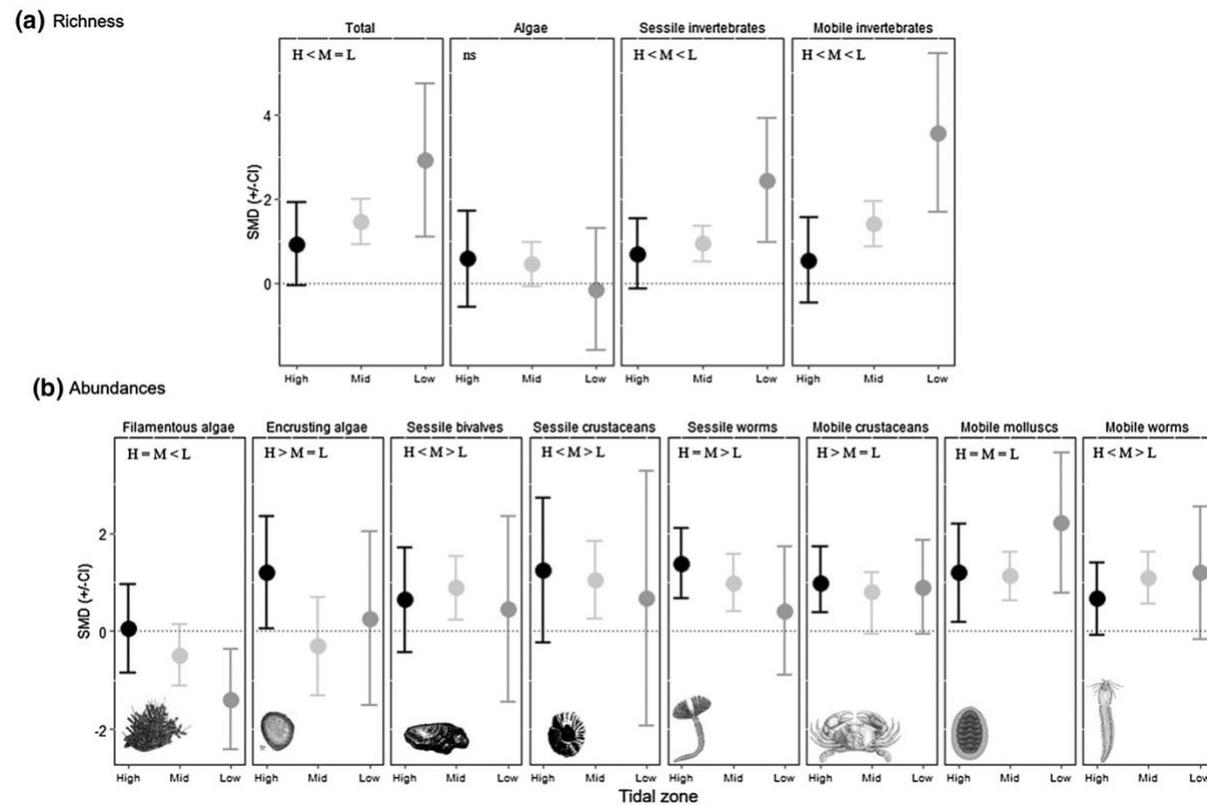
338 The standard mean difference (SMD) of total, sessile invertebrate and mobile invertebrate
339 richness, the percentage cover of filamentous/filiform macroalgae, encrusting algae, sessile
340 bivalves, sessile crustaceans, sessile worms and the abundances of mobile worms on the 5 cm
341 compared to 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

[Type here]



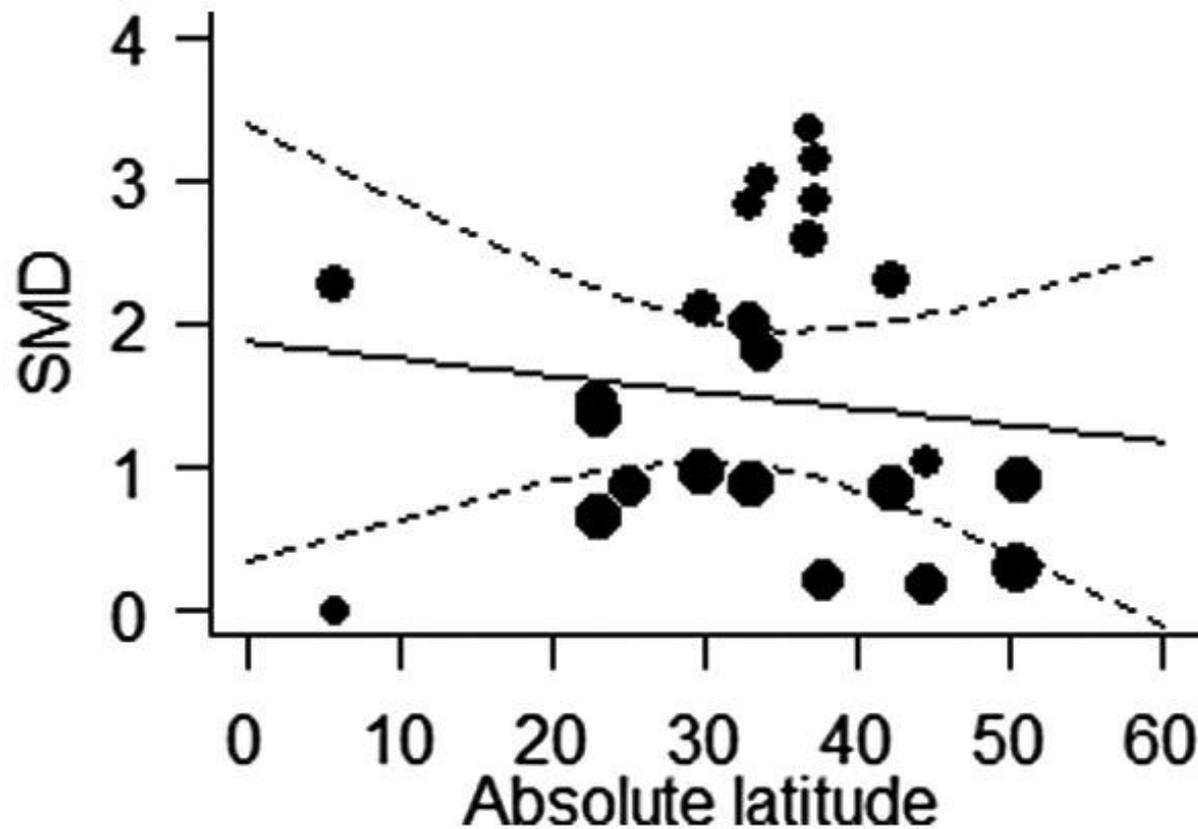
359
360

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

367

368

[Type here]



369
370

371 **Fig. 5:** Effects of absolute latitude on the standard mean differences SMD in total taxa
372 between 5 cm complex and flat tiles ($n = 27$ sites), where the size of the circle varies
373 according to the variance.

374

375

376 Discussion

377

378 The incorporation of complexity into artificial structures is increasingly being advocated as a
379 mechanism to maintain or enhance native biodiversity, but most studies to date have
380 examined effects of complexity on marine built structures over a relatively narrow range of
381 environmental conditions (reviewed by Strain et al. 2018). Our study, spanning 27 sites from
382 14 locations across the globe, provided the first experimental test of how effects of patch-
383 scale complexity on artificial structures vary across very large spatial scales. After 12

[Type here]

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 crevices,
405 were often absent, suggesting a greater role of microhabitat identity and diversity than surface
406 area in driving the patterns.

407

[Type here]

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

[Type here]

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

[Type here]

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

[Type here]

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

[Type here]

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**

528 We thank the many people that helped in deploying and monitoring the experiment and
529 funding bodies (see Supplementary S9 for full details).

530 **Data Availability**

531 The data are available as Supporting Information

532

533 **References**

- 534 Adamo, P., Arienzo, M., Imperato, M., Naimo, D., Nardi, G., & Stanzione, D. (2005).
535 Distribution and partition of heavy metals in surface and sub-surface sediments of
536 Naples city port. *Chemosphere*, 61(6), 800-809.
- 537 Airoidi, L., & Bulleri, F. (2011). Anthropogenic disturbance can determine the magnitude of
538 opportunistic species responses on marine urban infrastructures. *PLoS One*, 6(8),
539 e22985.
- 540 Airoidi, L., Connell, S. D., & Beck, M. W. (2009). The loss of natural habitats and the
541 addition of artificial substrata. In *Marine Hard Bottom Communities* (pp. 269-280):
542 Springer.
- 543 Airoidi, L., Turon, X., Perkol-Finkel, S., & Rius, M. (2015). Corridors for aliens but not for
544 natives: effects of marine urban sprawl at a regional scale. *Diversity and*
545 *Distributions*, 21(7), 755-768.
- 546 Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C. H., . . .
547 Colquhoun, J. (2015). A standardised vocabulary for identifying benthic biota and
548 substrata from underwater imagery: the CATAMI classification scheme. *PLoS One*,
549 10(10), e0141039.
- 550 Bateman, D., & Bishop, M. J. (2016). The environmental context and traits of habitat-
551 forming bivalves influence the magnitude of their ecosystem engineering. *Marine*
552 *Ecology Progress Series*, 563, 95-110.
- 553 Beck, M. W. (1998). Comparison of the measurement and effects of habitat structure on
554 gastropods in rocky intertidal and mangrove habitats. *Marine Ecology Progress*
555 *Series*, 169, 165-178.
- 556 Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in*
557 *Ecology and Evolution*, 9(5), 191-193.
- 558 Bertness, M. D., Yund, P. O., & Brown, A. F. (1983). Snail grazing and the abundance of
559 algal crusts on a sheltered New England rocky beach. *Journal of Experimental*
560 *Marine Biology and Ecology*, 71(2), 147-164.
- 561 Borenstein, M., Hedges, L. V., Higgins, J., & Rothstein, H. R. (2010). A basic introduction to
562 fixed-effect and random-effects models for meta-analysis. *Research Synthesis*
563 *Methods*, 1(2), 97-111.
- 564 Bracewell, S. A., Clark, G. F., & Johnston, E. L. (2018). Habitat complexity effects on
565 diversity and abundance differ with latitude: an experimental study over 20 degrees.
566 *Ecology*, 99(9), 1964-1974.
- 567 Bulleri, F., & Chapman, M. G. (2010). The introduction of coastal infrastructure as a driver
568 of change in marine environments. *Journal of Applied Ecology*, 47(1), 26-35.
- 569 Chapman. (2003). Paucity of mobile species on constructed seawalls: effects of urbanization
570 on biodiversity. *Marine Ecology Progress Series*, 264, 21-29.
- 571 Chapman, & Blockley, D. J. (2009). Engineering novel habitats on urban infrastructure to
572 increase intertidal biodiversity. *Oecologia*, 161(3), 625-635.
- 573 Chapman, Underwood, A., & Browne, M. A. (2018). An assessment of the current usage of
574 ecological engineering and reconciliation ecology in managing alterations to habitats
575 in urban estuaries. *Ecological Engineering*, 120, 560-573.
- 576 Connell, J. (1961). The influence of interspecific competition and other factors on the
577 distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42(4), 710-723.

[Type here]

- 578 Connell, S. D., & Anderson, M. J. (1999). Predation by fish on assemblages of intertidal
579 epibiota: effects of predator size and patch size. *Journal of Experimental Marine*
580 *Biology and Ecology*, 241(1), 15-29.
- 581 Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area
582 relationship. *The American Naturalist*, 113(6), 791-833.
- 583 Dafforn, K. A., Lewis, J. A., & Johnston, E. L. (2011). Antifouling strategies: history and
584 regulation, ecological impacts and mitigation. *Marine Pollution Bulletin*, 62(3), 453-
585 465.
- 586 Darling, E. S., Graham, N. A., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., &
587 Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and
588 reef fish assemblages. *Coral Reefs*, 36(2), 561-575.
- 589 Dean, R. L., & Connell, J. H. (1987). Marine invertebrates in an algal succession. III.
590 Mechanisms linking habitat complexity with diversity. *Journal of Experimental*
591 *Marine Biology and Ecology*, 109(3), 249-273.
- 592 Ewel, J. J. (1987). Restoration is the ultimate test of ecological theory. *Restoration ecology: a*
593 *synthetic approach to ecological research*. Cambridge University Press, Cambridge,
594 UK, 31-33.
- 595 Freestone, A. L., & Osman, R. W. (2007). COS 1-3: Latitudinal diversity gradient drives
596 community response to heterogeneity and shapes marine biodiversity patterns at small
597 scales.
- 598 Glasby, T. (1999). Effects of shading on subtidal epibiotic assemblages. *Journal of*
599 *Experimental Marine Biology and Ecology*, 234(2), 275-290.
- 600 Harley, C. D. (2003). Abiotic stress and herbivory interact to set range limits across a two-
601 dimensional stress gradient. *Ecology*, 84(6), 1477-1488.
- 602 Hedges, L. V. (1981). Distribution theory for Glass's estimator of effect size and related
603 estimators. *Journal of Educational and Behavioral Statistics*, 6(2), 107-128.
- 604 Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American*
605 *Naturalist*, 163(2), 192-211.
- 606 Hixon, M. A., & Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef
607 fish assemblages. *Ecological Monographs*, 63(1), 77-101.
- 608 Holt, R. D. (1987). Prey communities in patchy environments. *Oikos*, 276-290.
- 609 Hui, F. K. (2016). boral-Bayesian ordination and regression analysis of multivariate
610 abundance data in R. *Methods in Ecology and Evolution*, 7(6), 744-750.
- 611 Huston, M. (1979). A general hypothesis of species diversity. *The American Naturalist*,
612 113(1), 81-101.
- 613 Janssen, A., Sabelis, M. W., Magalhães, S., Montserrat, M., & Van der Hammen, T. (2007).
614 Habitat structure affects intraguild predation. *Ecology*, 88(11), 2713-2719.
- 615 Johnson, M. P., Frost, N. J., Mosley, M. W., Roberts, M. F., & Hawkins, S. J. (2003). The
616 area-independent effects of habitat complexity on biodiversity vary between regions.
617 *Ecology Letters*, 6(2), 126-132.
- 618 Kelaher, B. (2003). Changes in habitat complexity negatively affect diverse gastropod
619 assemblages in coralline algal turf. *Oecologia*, 135(3), 431-441.
- 620 Kinsella, C. M., & Crowe, T. P. (2016). Separate and combined effects of copper and
621 freshwater on the biodiversity and functioning of fouling assemblages. *Marine*
622 *Pollution Bulletin*, 107(1), 136-143.
- 623 Kovalenko, K. E., Thomaz, S. M., & Warfe, D. M. (2012). Habitat complexity: approaches
624 and future directions. *Hydrobiologia*, 685(1), 1-17.
- 625 Lenth, R., Singmann, H., & Love, J. (2018). Emmeans: Estimated marginal means, aka least-
626 squares means. *R package version*, 1(1).

[Type here]

- 627 Loke, L. H., & Todd, P. A. (2016). Structural complexity and component type increase
628 intertidal biodiversity independently of area. *Ecology*, *97*(2), 383-393.
- 629 Malumbres-Olarte, J., Vink, C. J., Ross, J. G., Cruickshank, R. H., & Paterson, A. M. (2013).
630 The role of habitat complexity on spider communities in native alpine grasslands of
631 New Zealand. *Insect Conservation and Diversity*, *6*(2), 124-134.
- 632 Markager, S., & Sand-Jensen, K. (1992). Light requirements and depth zonation of marine
633 macroalgae. *Marine Ecology-Progress Series*, *88*, 83-83.
- 634 Marraffini, M. L., Ashton, G. V., Brown, C. W., Chang, A. L., & Ruiz, G. M. (2017).
635 Settlement plates as monitoring devices for non-indigenous species in marine fouling
636 communities. *Management of Biological Invasions*, *8*(4), 559-566.
- 637 Martins, G. M., Thompson, R. C., Neto, A. I., Hawkins, S. J., & Jenkins, S. R. (2010).
638 Enhancing stocks of the exploited limpet *Patella candei* d'Orbigny via modifications
639 in coastal engineering. *Biological Conservation*, *143*(1), 203-211.
- 640 Mayer-Pinto, M., Dafforn, K. A., & Johnston, E. L. (2019). A Decision Framework for
641 Coastal Infrastructure to Optimize Biotic Resistance and Resilience in a Changing
642 Climate. *Bioscience*, *69*(10), 833-843.
- 643 Mayer-Pinto, M., Matias, M. G., & Coleman, R. A. (2016). The interplay between habitat
644 structure and chemical contaminants on biotic responses of benthic organisms. *PeerJ*,
645 *4*, e1985.
- 646 McAfee, D., Cole, V. J., & Bishop, M. J. (2016). Latitudinal gradients in ecosystem
647 engineering by oysters vary across habitats. *Ecology*, *97*(4), 929-939.
- 648 McCoy, E. D., & Bell, S. S. (1991). Habitat structure: the evolution and diversification of a
649 complex topic. In *Habitat structure* (pp. 3-27): Springer.
- 650 McKinney, M. L. (2008). Effects of urbanization on species richness: a review of plants and
651 animals. *Urban ecosystems*, *11*(2), 161-176.
- 652 Menge, B. A., & Lubchenco, J. (1981). Community organization in temperate and tropical
653 rocky intertidal habitats: prey refuges in relation to consumer pressure gradients.
654 *Ecological Monographs*, *51*(4), 429-450.
- 655 Miller, R. J., & Etter, R. J. (2008). Shading facilitates sessile invertebrate dominance in the
656 rocky subtidal Gulf of Maine. *Ecology*, *89*(2), 452-462.
- 657 Moschella, P., Abbiati, M., Åberg, P., Airoidi, L., Anderson, J., Bacchiocchi, F., . . . Gacia,
658 E. (2005). Low-crested coastal defence structures as artificial habitats for marine life:
659 using ecological criteria in design. *Coastal Engineering*, *52*(10), 1053-1071.
- 660 O'Shaughnessy, K. A., Hawkins, S. J., Evans, A. J., Hanley, M. E., Lunt, P., Thompson, R.
661 C., . . . Iglesias, G. (2019). Design catalogue for eco-engineering of coastal artificial
662 structures: a multifunctional approach for stakeholders and end-users. *Urban*
663 *ecosystems*, 1-13.
- 664 Piola, R. F., Dafforn, K. A., & Johnston, E. L. (2009). The influence of antifouling practices
665 on marine invasions. *Biofouling*, *25*(7), 633-644.
- 666 R Core Team. (2016). R: A Language and Environment for Statistical Computing. Vienna,
667 Austria: R Foundation for Statistical Computing. Retrieved from [https://www.R-](https://www.R-project.org)
668 [project.org](https://www.R-project.org)
- 669 Rivero, N. K., Dafforn, K. A., Coleman, M. A., & Johnston, E. L. (2013). Environmental and
670 ecological changes associated with a marina. *Biofouling*, *29*(7), 803-815.
- 671 Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver
672 of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866-
673 880.
- 674 Strain, E. M., Cumbo, V., Morris, R., Steinberg, P., & Bishop, M. J. (2020). Interacting
675 effects of habitat structure and seeding with oysters on intertidal biodiversity of
676 seawalls. *PLoS One*. *5*(7): e0230807

[Type here]

- 677 Strain, E. M., Morris, R., Coleman, R., Figueira, W., Steinberg, P., Johnston, E., & Bishop,
678 M. J. (2018). Increasing microhabitat complexity on seawalls can reduce fish
679 predation on native oysters. *Ecological Engineering*, 120, 637-642.
- 680 Strain, E. M., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R. L., Bugnot, A. B., . . .
681 Bishop, M. J. (2018). Eco-engineering urban infrastructure for marine and coastal
682 biodiversity: Which interventions have the greatest ecological benefit? *Journal of*
683 *Applied Ecology*, 55(1), 426-441.
- 684 Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of*
685 *Statistical Software*, 36(3), 1-48.
- 686 Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*: Springer.
- 687 Wilson, J. B., James, R., Newman, J., & Myers, T. (1992). Rock pool algae: species
688 composition determined by chance? *Oecologia*, 91(1), 150-152.
- 689 Wolcott, T. G. (1973). Physiological ecology and intertidal zonation in limpets (Acmaea): a
690 critical look at" limiting factors". *The Biological Bulletin*, 145(2), 389-422.

691

[Type here]