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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

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3 25 greatest at lower latitudes, whilst the cover of sessile invertebrates and sessile molluscs
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5 26 responded most strongly to complexity at higher latitudes.
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7

8 27 **Conclusions**

9
10 28 After 12 months, patch-scale relationships between biodiversity and habitat complexity were
11
12 29 not universally positive. Instead, the relationship varied among functional groups and
13
14 30 according to local abiotic and biotic conditions. This result challenges the assumption that
15
16 31 effects of complexity on biodiversity are universally positive. The variable effect of
17
18 32 complexity has ramifications for community and applied ecology, including eco-engineering
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20 33 and restoration that seek to bolster biodiversity through the addition of complexity.
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25 26 27 35 **Introduction:**

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30 36 Habitat complexity the physical structure of environments, is a key driver of variability in the
31
32 37 distribution of biodiversity (Huston, 1979; Kovalenko, Thomaz, & Warfe, 2012). In general,
33
34 38 more complex habitats, with a greater density of spatial elements, support greater species
35
36 39 richness and abundance, across a range of functional groups, than less complex habitats
37
38 40 (McCoy & Bell, 1991; Stein, Gerstner, & Kreft, 2014). Habitat complexity may be derived
39
40 41 from both topographic (e.g. undulations, depressions, and protrusions) or biogenic (e.g., trees,
41
42 42 grasses, seaweeds, ants, corals and bivalves) structures. Complex habitats can influence the
43
44 43 colonisation and subsequent survival of species by determining the area available for
45
46 44 organisms to occupy (Connor & McCoy, 1979), which in turn can influence biotic
47
48 45 interactions (Hixon & Beets, 1993; Holt, 1987). Complex habitats can also have area-
49
50 46 independent effects on niche diversity (Johnson, Frost, Mosley, Roberts, & Hawkins, 2003),
51
52 47 and consequently the availability of refuges from environmental stressors and predators
53
54 48 (Strain, Cumbo, Morris, Steinberg, & Bishop, 2020). At land- and sea-scape scales
55
56 49 complexity enhances biodiversity by increasing habitat heterogeneity and niche space
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3 50 (Kovalenko, Thomaz, & Warfe, 2012). However, at smaller scales, biodiversity and habitat
4
5 51 complexity relationships may vary depending on the type of complexity provided and how it
6
7
8 52 interacts with the environmental and biological setting (Loke & Todd, 2016).
9

10 53
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12
13 54 The environmental variation among sites at local and biogeographic scales may influence
14
15 55 patch-scale habitat complexity (hereafter complexity) - biodiversity relationships by
16
17 56 determining resource availability, environmental conditions, as well as the species pool on
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19
20 57 which complexity can act (Johnson et al., 2003); Bracewell et al., 2018). The stress gradient
21
22 58 hypothesis (Bertness & Callaway, 1994) proposes that positive interactions among species
23
24 59 (e.g. between habitat-forming and dependent taxa) will be most prevalent in environmentally
25
26
27 60 stressful environments, where local habitat amelioration is critical to organismal survival
28
29 61 (Bracewell, Clark, & Johnston, 2018; McAfee, Cole, & Bishop, 2016). Hence, microhabitats
30
31 62 that ameliorate extreme temperatures and/or desiccation stressors could increase in
32
33
34 63 importance with increasing tidal elevation (Bateman & Bishop, 2016) and decreasing latitude
35
36 64 (Bracewell et al., 2018). Conversely, the patch-scale effects of complexity may be consistent
37
38 65 across latitude if the local species are adapted to their local conditions or could have a greater
39
40 66 influence in locations where there is a greater difference between the air and sea
41
42
43 67 temperatures.
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49 69 Additionally, complexity may be expected to have greatest patch-scale effects on biodiversity
50
51 70 in environments where there is a diverse species pool on which it can act, whereby, the
52
53 71 effects of complexity may vary across latitudinal gradients in species richness (Bracewell et
54
55 72 al., 2018). At local scales, anthropogenic stressors such as contaminants may over-ride the
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58 73 effects of complexity where they create conditions that are inhibitory to the survival of most
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3 74 species (Mayer-Pinto, Matias, & Coleman, 2016). How species abundance and, hence,
4
5 75 richness responds to complexity may also vary according to the dominant functional groups
6
7 76 present at a given location (Strain, Olabarria, et al., 2018). Functional groups, defined here as
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9
10 77 groups of organisms displaying distinct life-forms, that differ in their niche requirements,
11
12 78 tolerance to environmental stressors, and susceptibility to predation (Micheli & Halpern,
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14 79 2005). While, overall, increasing complexity is expected to enhance microhabitat diversity
15
16 80 and niche space, the availability of some microhabitat types will decline and others will
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19 81 increase with different types of complexity (Kelaher, 2003).
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25 83 The taxa whose niche requirements are favoured by increasing complexity will benefit at the
26
27 84 expense of other taxa whose niches match microhabitats that decline in abundance or area
28
29 85 (Malumbres-Olarte, Vink, Ross, Cruickshank, & Paterson, 2013). For example, on intertidal
30
31 86 rocky shores, algae can be among the dominant space occupants of well-lit yet wet
32
33 87 microhabitats (e.g. rockpools), that prevent desiccation, and allow adequate light for
34
35 88 photosynthesis (Wilson, James, Newman, & Myers, 1992). In contrast, mobile invertebrates,
36
37 89 particularly sessile invertebrates benefit from microhabitats (e.g. crevices) that provide
38
39 90 protection from predators, but are also sufficiently shaded that their algal competitors cannot
40
41 91 survive (Glasby, 1999; Miller & Etter, 2008). Stress-sensitive taxa may benefit more than
42
43 92 stress-tolerant taxa from microhabitats that ameliorate environmental stressors (Darling et al.,
44
45 93 2017). Similarly, taxa that are more susceptible to predation (i.e. lack morphological or
46
47 94 behavioural defences) or have body sizes that most closely match the size of the
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49 95 microhabitats may benefit most from complexity-mediated predator amelioration (Strain,
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51 96 Morris, et al., 2018). Experimental research on the effects of increasing complexity on
52
53 97 different functional groups (i.e. algae, sessile invertebrates, and mobile invertebrates) is
54
55 98 lacking (but see Strain et al. 2020).
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3 99 Few studies have examined the effects of complexity at large spatial scales, across functional
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5 100 groups and the influence of varying environmental contexts, to test the generality of patch-
6
7 101 scale complexity-biodiversity relationships. Understanding how complexity underpins
8
9 102 richness and abundance of different taxa and functional groups across a range of
10
11 103 environmental conditions is of particular importance, given accelerating habitat loss and
12
13 104 homogenisation (Kovalenko et al., 2012). In urban marine environments, natural habitats are
14
15 105 being replaced by artificial structures (e.g. seawalls, groynes, breakwaters and wharves) with
16
17 106 reduced complexity (Airoldi, Connell, & Beck, 2009; Bulleri & Chapman, 2010). Such
18
19 107 habitat homogenisation often occurs simultaneously with other anthropogenically-derived
20
21 108 environmental changes, such as pollution and/or species invasions (McKinney, 2008). The
22
23 109 smooth, relatively homogenous, surfaces of artificial structures typically support fewer native
24
25 110 species and individuals (Chapman, 2003), but more non-native species (Airoldi & Bulleri,
26
27 111 2011) compared to the more complex natural habitats they replace.
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37 113 There has been increasing interest in how complexity might be incorporated into the design
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39 114 of marine urban structures so as to enhance their ecological value (O'Shaughnessy et al.,
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41 115 2020). The addition of complexity to topographically homogenous marine urban structures
42
43 116 has been proposed as a mechanism by which the overall richness and abundances of key
44
45 117 functional groups might be enhanced (Strain et al. 2018). However, the manner in which
46
47 118 complexity acts will be context dependent and researchers have recommended that latitudinal
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49 119 and biogeographic considerations are taken into account prior to design or construction
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51 120 (Mayer-Pinto, Dafforn, & Johnston, 2019).
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3 122 Using standardised experiments on a global scale, we investigated how manipulating one
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5 123 form of complexity (crevices/ridges) on tiles affected the richness and abundance of
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7 124 colonising taxa at fourteen urban estuaries or bays spread across nine biogeographic realms.
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10 125 We predicted that patch-scale complexity would have a positive influence on the taxa
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12 126 richness and abundances of all sessile and mobile invertebrates functional groups but not
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14 127 algae, which have higher light requirements, because of greater shading in the crevices
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16
17 128 (Strain et al., 2020). Furthermore, we expected that the positive effects of increased
18
19 129 complexity on richness and abundances of sessile and mobile invertebrates would increase
20
21 130 with tidal elevation and with decreasing latitude, as desiccation stress and extreme high
22
23 131 temperatures increase, respectively. Finally, we hypothesised that complexity would have a
24
25 132 reduced effect on the richness and abundances of sessile and mobile invertebrates in highly
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27 133 polluted environments such as those located near marinas or ports, where the effects of
28
29 134 pollution can over-ride the effects of complexity (Mayer-Pinto et al. 2018).
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34 135

36 136 **Materials and methods**

39 137 **Study sites**

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42 138 Experimental manipulations were conducted at 27 sites, distributed across 14 locations
43
44 139 globally (Fig. 1). There were two sites at each location, except for Herzliya Marina, Israel,
45
46 140 which hosted a single site. The locations were all in estuaries or bays situated along urbanised
47
48 141 coastlines, and were partners in the World Harbour Project (www.worldharbourproject.com).
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50 142 Each had a semi-diurnal tidal regime and well mixed marine waters. Within locations, each
51
52 143 site comprised a vertical seawall or breakwater that extended from the shallow subtidal or the
53
54 144 low intertidal to the high intertidal zone. Sites at least 0.1 km apart, were of variable
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56 145 proximity to port facilities or marinas, and varied in tidal height, tidal range, temperature
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3 146 (average, minimum and maximum) and concentration of heavy metals (see Supplementary
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5 147 S1).

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10 149 **Fig 1:** Map showing the experimental locations. Locations are ordered by biogeographic
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12 realm.
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16 17 152 **Experimental design**

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20 153 At each site, 0.25×0.25 m concrete tiles were affixed to the coastal defence structures (i.e.
21
22 154 seawalls, or breakwaters). The tiles allowed manipulation of intertidal habitat complexity by
23
24 155 provisioning crevices and ridges as well as associated increase in surface area. The tiles,
25
26 156 designed and manufactured by Reef Design Lab (Melbourne, Australia), were flat (surface
27
28 157 area = 0.0625 m²), had 0.025 m high ridges separated by 0.015 to 0.05 m wide crevices
29
30 158 (hereafter ‘2.5 cm complex’; surface area = 0.090 m²) or had 0.05 m high ridges, each
31
32 159 separated by 0.015 to 0.05 m wide crevices (hereafter ‘5 cm complex’; surface area = 0.136
33
34 160 m²; Fig. 2). At each site, five tiles of each design were either directly attached to the
35
36 161 structures, in the centre of 0.3×0.3 m patches cleared of pre-existing flora and fauna, or
37
38 162 attached to wood backing boards that were suspended off the top of the structures using rope
39
40 163 or nails. Tiles were attached to the structures, backing boards or steel frames using bolts that
41
42 164 were placed through a drilled hole in two to four corners of the tiles. At each site, the tiles
43
44 165 were deployed in a single horizontal row, from a low to high intertidal elevation, depending
45
46 166 on the location. Tiles were deployed in random order with respect to the experimental
47
48 167 treatments, with the complex tiles positioned so that the crevices and ridges were orientated
49
50 168 vertically. In temperate locations, the tiles were deployed between early spring to late autumn
51
52 169 during the period of greatest species recruitment and growth (Table S1).
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172 **Fig 2:** The three experimental treatments: a) flat, b) 2.5 cm complex, c) 5 cm complex.

173

174 **Colonising taxa**

175 After 12 months, all tiles were removed from the field, individually bagged and frozen until
176 analysis. On each tile, we recorded the identity and percentage cover (pooling across primary
177 and secondary growth) of all sessile algae and invertebrate taxa and removed all mobile
178 invertebrates ($> 500 \mu\text{m}$), using tweezers and by carefully rinsing the tile area with seawater
179 over a $500 \mu\text{m}$ sieve from the whole tile or two subsamples, depending on location
180 (Supplementary S1). At locations where subsampling was conducted, these were from one
181 pre-determined crevice (0.016 m^2) and one ridge (0.013 m^2) of each complex tile, that were
182 not adjacent to each other, but were pooled for the purposes of the analyses. On flat tiles, two
183 areas of similar size were subsampled and pooled. A pilot study conducted using Sydney data
184 revealed similar treatment effects on the richness and abundance of colonising taxa,
185 irrespective of whether a subsample or the full tile was sampled (Supplementary S2). All taxa
186 were identified to species or morphospecies using dissecting microscopes and then classified
187 into three coarser-level functional groups (hereafter ‘functional groups’) including algae,
188 sessile invertebrates and mobile invertebrates as well as nineteen finer-level functional
189 groups (Supplementary S2) based on the CATAMI classification guide (Althaus et al., 2015);
190 hereafter ‘CATAMI groups.

191

192 **Environmental parameters**

193 To test hypotheses about potential sources of variability in complexity effects, we estimated
194 the tidal elevation, temperature, and proximity to boating facilities of tiles at each study site.

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3 195 For tidal elevation we recorded the inundation period (proportion of time underwater) of the
4
5 196 tiles using a pressure logger. At each site, one pressure logger was attached to the top of a flat
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8 197 tile and programmed to record water depth every 20 min for a period of one-month.
9
10 198 Measurements were made using either a Sensus Ultra (Reefnet Pty Ltd; +/- 0.03 m accuracy),
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12 199 a Hobo Onset (Onsetcomp; +/- 0.02 m accuracy) or EasyTREK SP-300 (NIVELCO; +/-
13
14 200 0.05% of the measured range accuracy). Based on these measurements, the tidal elevation
15
16
17 201 was categorised as either high (inundated for <33% of the tidal cycle), mid (inundated for
18
19 202 >34 to 65% of the tidal cycle) or low (inundated for >66% of the tidal cycle; Supplementary
20
21 203 S1).
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25 204

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28 205 Throughout the 12-month experiment, we took measurements of temperature at 21 sites
29
30 206 (Supplementary S1). At each site, we deployed three DS1921G ThermoChron iButton data
31
32 207 loggers (Thermodata Pty. Ltd. Warrnambool, Australia) haphazardly on flat tiles. The
33
34
35 208 iButtons were waterproofed with Plastidip rubber coating (Plasti Dip International, Blaine,
36
37 209 Minnesota, USA). The iButtons were programmed to record temperatures at 20 min intervals,
38
39 210 across a one-month period, with 0.5°C accuracy. The iButtons were attached to the tiles using
40
41
42 211 cable ties so that they could easily be removed, downloaded, and replaced each month. Mean
43
44 212 (both aerial and in water), maximum (aerial) and minimum (aerial) temperature were
45
46 213 negatively correlated with absolute latitude at the 21 sites (Supplementary S4). Hence, to
47
48 214 avoid issues with collinearity between these two predictor variables, subsequent analyses
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51 215 were run only on latitude of study sites.
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56 217 At the end of the experiment, we measured the distance from the centre of each site to the
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58 218 nearest boating facility (port or marina) using satellite images in Google Earth. For 17 sites,
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3 219 we also obtained information on the concentration of copper from sediment sampling
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5 220 (Supplementary S1). Increasing distance of study sites to the nearest boating facility was
6
7 221 negatively correlated (but not significantly) with the amount of copper (historically used as
8
9 222 an antifouling agent; Dafforn et al. 2011) in sediment at the 17 sites for which both sets of
10
11 223 data were available (Supplementary S4). Hence, distance to the nearest boating facility,
12
13 224 which could be measured for all 27 sites, was used as a proxy for contamination.
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19 226 **Analyses**

21 227
22
23 228 We used multivariate generalised linear modelling to test the effects of complexity (fixed, 3
24
25 229 levels: flat, 2.5 cm or 5 cm), location (fixed, 14 levels) and site nested within location (fixed
26
27 230 1-2 levels) on the abundances of each of the 19 CATAMI groups. These data were modelled
28
29 231 using a negative binomial distribution due to overdispersion from the Poisson distribution.
30
31 232 Where multivariate analyses indicated a significant main effect of treatment, or an interaction
32
33 233 of treatment with location or site(location) univariate post hoc test statistics and p-values
34
35 234 were calculated for each group separately adjusting for multiple comparisons. For those
36
37 235 groups found to have significant effects of treatment (either occurring independently of or
38
39 236 interacting with spatial factors), pairwise differences between treatment levels, were assessed
40
41 237 using univariate linear models (LMs). Where both the treatment \times location and treatment \times
42
43 238 site (location) were significant, only the treatment \times location interaction was interpreted as its
44
45 239 significance demonstrates effects of location that are apparent over smaller site-scale
46
47 240 variability. Similarly, we used LMs or generalised linear models (GLMs) with the factors
48
49 241 complexity, location and site nested within location to compare the richness and abundances
50
51 242 (cover or counts) of total taxa, algae, sessile invertebrates and mobile invertebrates across
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53 243 treatments, at 12 months.
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6 245 To test hypotheses about whether the effects of complexity on the richness and abundances of
7
8 246 the key functional groups on the tiles, varied by tidal elevations, latitude and distance from
9
10 247 the nearest marina or port, we used analyses on the standard mean difference (SMD) between
11
12 248 the 5 cm and flat tile. The Hedge's G SMD was calculated at the scale of site, using the
13
14 249 average and standard deviation of the five tiles sampled within each site, for each treatment.
15
16
17 250 We chose the SMD effect size rather than the log response ratio because these data contained
18
19 251 many zeros (i.e. no species observed and/or no variance observed between replicates within
20
21 252 the same treatment) (Borenstein, Hedges, Higgins, & Rothstein, 2010). We tested the effects
22
23 253 of tidal zone, latitude and distance to the nearest marina or port using the Hedges random
24
25 254 effects estimator (Hedges, 1981) with the package metafor (Viechtbauer, 2010). For the
26
27 255 analyses testing the effects of tidal zone, we adjusted for the effects of location, by adding
28
29 256 location as a moderator in a multilevel random effects model.
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34
35 258 All statistical analyses were undertaken in R 3.5.0 (R Core Team, 2016). For all models we
36
37 259 offset the sample area (m²), to separate the effects of complexity from surface area.
38
39
40 260 Generalised linear models were undertaken in the package MASS and figures were produced
41
42 261 using the package ggplot 2 (Wickham, 2016). The multivariate analyses were undertaken
43
44 262 with the packages mvabund and boral (Hui, 2016). All models were checked for over-
45
46 263 dispersion and spatial and temporal autocorrelation with plots, and the residuals were visually
47
48 264 inspected for heteroscedasticity. Where appropriate, post hoc comparisons were undertaken
49
50 265 using the package emmeans (Lenth, Singmann, & Love, 2018) to identify sources of
51
52 266 treatment effects.
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56 267

58 268 **Results**

269 **Effect of complexity on richness**

270

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

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

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

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

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

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

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

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

279 1.1-2.4 times) than on the 2.5 cm complex tiles or the flat tiles at two locations, but displayed

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

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

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

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

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

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

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

287 Supplementary S5).

288

289

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

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

292 differences (at $\alpha = 0.05$) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are

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

294 **Table 1:** Overview of the posthoc tests for significant complexity by location interactions in
 295 the total richness and the richness and abundance of functional groups. 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.
 298 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

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3 3054
5 306 **Effect of complexity on abundances**6
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10 308 The effects of complexity varied among functional groups (algae, sessile and mobile
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12 309 invertebrates) and the 19 CATAMI groups, and within these groupings, according to location
13
14 310 and/or site (Table 1, Table 2, Supplementary S5-S6). The abundances (i.e. percentage cover
15
16 311 or counts) of algae, sessile and mobile invertebrates (Table 1, Supplementary S5) as well as
17
18 312 that of encrusting macroalgae, bryozoans, sessile and mobile crustaceans, sessile and mobile
19
20 313 molluscs and sessile worms each displayed significant positive effects of the 2.5 cm and/or
21
22 314 the 5 cm complex tiles relative to the flat tiles, at one or more locations, with non-significant
23
24 315 effects at the remaining (Table 2, Supplementary S5).

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29 316 The abundances of mobile crustaceans and mobile molluscs showed significant positive
30
31 317 effects of either the 2.5 cm and/or 5 cm tiles compared with the flat tiles, at some sites, but
32
33 318 these differences were not consistent between sites within locations (Tables 2, Supplementary
34
35 319 S6). The effects of complexity were, among locations, spatially variable in both occurrence
36
37 320 and direction for filamentous/filiform macroalgae cover and mobile worm abundances and
38
39 321 between sites for foliose macroalgae cover (Table 2, Supplementary S6). Although present on
40
41 322 tiles, globose saccate macroalgae, articulated calcareous macroalgae, ascidians, cnidarians,
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43 323 sponges, hexapods, arthropods and echinoderms displayed patterns in abundance that did not
44
45 324 respond to complexity, at any of the sites or locations (Table 2, Supplementary S6).

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327 **Table 2:** Overview of the posthoc tests for significant complexity by location or complexity by site(location) interactions in the abundance of
 328 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 '<',
 329 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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45 332 **Correlates of spatial variation in effects of complexity**6
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10 334 The standard mean difference (SMD) of total, sessile invertebrate and mobile invertebrate
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12 335 richness, the percentage cover of filamentous/filiform macroalgae, encrusting algae, sessile
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14 336 bivalves, sessile crustaceans, sessile worms and the abundances of mobile worms on the 5 cm
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17 337 compared to the flat tiles varied significantly among tidal zones (Fig. 4, Supplementary S7).
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19 338 Significant differences in the SMDs were found in the mid and low tidal zone for each of
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21 339 total and sessile and mobile invertebrate richness and in the high, mid and low tidal zone for
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23 340 the abundances of mobile molluscs (Fig. 4, Supplementary S7). In contrast, the difference in
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25 341 the SMD was only significant in the high tidal zone for the percentage cover of encrusting
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27 342 algae and in the mid and high tidal zones for the percentage cover of sessile worms and the
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29 343 abundances of mobile crustaceans. The percentage cover of sessile bivalves and sessile
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31 344 crustaceans and the abundances of mobile worms displayed differences in the SMDs that
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33 345 were only significant in the mid-tidal zone and in the low tidal zone for the percentage cover
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35 346 of filamentous algae (Fig. 4, Supplementary S7).
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42 348 The SMD in the richness of sessile invertebrate species between the 5 cm complex and flat
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44 349 tiles increased with distance from the nearest marina or port. However, the SMD for other
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46 350 groups was unaffected by this variable (Supplementary S7). The SMD of total taxa richness
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48 351 significantly decreased with latitude (Fig. 5), as did abundance of molluscs, while conversely,
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50 352 SMD of percentage cover of sessile bivalves increased with latitude (Supplementary S7). All
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52 353 other groups were unaffected by latitude (Supplementary S7).
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3 356 **Fig. 4:** Effects of tidal zones on the standard mean difference SMD (\pm CI) in a) richness of
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5 357 total taxa, algae, sessile invertebrates and mobile invertebrates and b) abundances (percentage
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7 358 cover or abundance) of key CATAMI groups between 5 cm complex and flat tiles (high $n = 5$
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9 359 sites, mid $n = 18$ sites, and low $n = 4$ sites). Effects are significant if the confidence intervals
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11 360 do not overlap zero (dashed line). Significant differences (at $\alpha = 0.05$) between high (H), and
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13 361 mid (M) or low (L) tidal zones are indicated by '>' or '<'.
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24 365 **Fig. 5:** Effects of absolute latitude on the standard mean differences SMD in total taxa
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26 366 between 5 cm complex and flat tiles ($n = 27$ sites), where the size of the circle varies
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28 367 according to the variance.
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35 370 **Discussion**

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39 372 The incorporation of complexity into artificial structures is increasingly being advocated as a
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41 373 mechanism to maintain or enhance native biodiversity, but most studies to date have
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43 374 examined effects of complexity on marine built structures over a relatively narrow range of
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45 375 environmental conditions (reviewed by Strain et al. 2018). Our study, spanning 27 sites from
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47 376 14 locations across the globe, provided the first experimental test of how effects of patch-
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49 377 scale complexity on artificial structures vary across very large spatial scales. After 12
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51 378 months, complexity had positive effects on the richness and abundance of the colonising taxa
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53 379 at most (10 out of 14) of the locations tested. Nevertheless, the effects of complexity on the
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55 380 colonisation of individual functional groups, varied spatially according to tidal elevation and
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3 381 latitude. These results challenge the paradigm that environmental that complexity has
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5 382 universally positive effects on biodiversity (Huston, 1979) and instead support the growing
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7 383 assertion (Beck, 1998) that at the patch-scale effects of complexity on biodiversity can vary
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10 384 in magnitude and direction according to local abiotic and biotic stressors, niche requirements
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12 385 of the dominant taxa and the scale of complexity provided.
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18 387 The study, which manipulated a single type of habitat complexity (crevices/ridges), was not
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20 388 designed to disentangle complexity effects arising from enhancement of surface area and
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22 389 microhabitat diversity. The complex tiles not only had greater surface area but, in providing
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24 390 crevices and ridges, provided greater microhabitat diversity than the flat tiles that had only a
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26 391 single microhabitat type. These crevices and ridges have previously been demonstrated to
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28 392 differ in light, humidity, temperature, and predator access (Strain et al. 2018; 2020),
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30 393 supporting distinct communities of algae and invertebrates (Strain et al. 2020). The spatially
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32 394 variable effects of crevices and ridges on biodiversity suggest that differences between
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34 395 complex and flat treatments did not simply reflect the greater surface area of the former, but
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36 396 also modification of environmental conditions and biological interactions by the
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38 397 microhabitats. Further, whereas differences were consistently found between complex and
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40 398 flat tiles, differences between the two complex treatments, with 5 cm or 2.5 cm deep crevices,
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42 399 were often absent, suggesting a greater role of microhabitat identity and diversity than surface
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44 400 area in driving the patterns.
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54 402 Whereas effects of the complex tiles on the richness and abundance of invertebrate groups
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56 403 were, where present, positive, effects of the complex tiles on the richness and abundance of
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58 404 algae were highly variable, not only in occurrence, but also direction. The sessile invertebrate
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3 405 groups that responded most positively to the crevices and ridges provided by this study were
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5 406 taxa that are limited to shaded and moist low intertidal and subtidal shore (such as bryozoans)
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7 407 (Miller & Etter, 2008), and taxa commonly targeted by benthic predators (e.g. molluscs,
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9 408 crustaceans, worms) (Janssen, Sabelis, Magalhães, Montserrat, & Van der Hammen, 2007;
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11 409 Strain, Morris, et al., 2018). In contrast, the mobile invertebrates that responded positively
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13 410 were taxa that could rapidly colonise by migration from nearby habitats (e.g. mobile molluscs
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15 411 and crustaceans), (Martins, Thompson, Neto, Hawkins, & Jenkins, 2010). These taxa were
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17 412 predominantly found in the protective crevices of the complex tiles, suggesting that the
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19 413 provision of refugia could have played an important role (Strain et al., 2020). Filamentous
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21 414 and foliose macroalgae were negatively affected by complexity at some sites, despite the
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23 415 overall greater surface area of complex tiles. This may be because light in the crevices was
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25 416 insufficient to meet the needs of these taxa that have high light requirements (Markager &
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27 417 Sand-Jensen, 1992), or alternatively because of enhanced top-down control by the abundant
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29 418 grazer communities in the crevices. Encrusting algae, which have low light requirements
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31 419 (Markager & Sand-Jensen, 1992) and a tough thallus that deters grazers (Bertness, Yund, &
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33 420 Brown, 1983) were the only algal group to consistently respond positively to complexity.
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43 422 Thermal and desiccation stress have long been implicated in setting the upper distributional
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45 423 limits of organisms intertidally (Harley, 2003; Wolcott, 1973) while classically, the lower
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47 424 distributional limits are thought to be set by biological interactions such as competition and
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49 425 predation (Connell, 1961). Consistent with this thinking and previous within-site comparisons
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51 426 of complexity-biodiversity relationships among elevations (Cordell et al. 2017), we found the
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53 427 effects of added complexity on taxa richness and abundance of colonising organisms differed
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55 428 among tidal elevations, as well as among functional groups. Total taxa richness and the
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57 429 richness of sessile and mobile invertebrates responded most strongly to complexity in the low
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3 430 intertidal zone, but the richness and abundances of algae, and abundances of sessile
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5 431 invertebrates responded more strongly in the mid and high intertidal zones. In the low
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7 432 intertidal, the crevices on complex tiles may provide refuge to invertebrate taxa from large-
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10 433 bodied marine predators, such as fish, which can exert considerable top-down control on the
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12 434 communities of coastal structures (Connell & Anderson, 1999) and/or from wave exposure
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14 435 that can challenge the attachment strength of organisms and interfere with feeding behaviour
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17 436 (Bulleri & Chapman, 2010; Moschella et al., 2005). In the high and mid intertidal, on
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19 437 artificial coastal defences as on natural rocky shores, cool and shaded crevices could
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21 438 influence the richness and abundances of algae and the abundances of invertebrates by
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23 439 providing refuge from extreme temperatures and desiccation at low tide (Chapman &
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26 440 Blockley, 2009; Strain et al., 2020).

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30 442 Additionally, we found evidence for latitudinal variation in the effects of complexity on total
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32 443 taxa richness and the abundance of some invertebrate groups. Complexity had the greatest
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34 444 effects on the total richness of taxa and the abundances of mobile molluscs at low latitudes,
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36 445 where average temperatures, primary productivity as well as taxa richness and abundance are
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38 446 generally highest (Hillebrand, 2004). However, the cover of sessile molluscs displayed the
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40 447 reverse pattern of greater effects of complexity at higher latitudes, where average
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42 448 temperatures and the percentage cover of sessile invertebrates were lower. These results are
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44 449 consistent with other studies that have demonstrated positive effects of complexity on the
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46 450 richness or diversity of invertebrates at tropical latitudes in intertidal systems (Freestone &
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48 451 Osman, 2007; Menge & Lubchenco, 1981). Latitudinal variation in the effects of complexity
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50 452 likely reflects spatial variation in the local species pool, functional group identity and species
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52 453 recruitment, predation, and growth rates.
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3 455 Despite our hypothesis that pollutants would override the effects of complexity, proximity of
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5 456 sites to marinas and port facilities, which are commonly highly contaminated (Adamo et al.,
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7 457 2005; Rivero, Dafforn, Coleman, & Johnston, 2013), explained little of the variation in
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9 458 effects of complexity for most groups of algae and invertebrates. There was, however, a
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11 459 positive effect of the distance to the nearest port or marina on the relationship between
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13 460 complexity and richness of sessile invertebrates. Although our study did not document spatial
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15 461 variation in the size of the species pool of available colonists, the positive relationship
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17 462 between distance from boating facilities and effects of complexity on sessile invertebrates is
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19 463 consistent with the contaminants associated with boating facilities adversely impacting the
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21 464 native species pool on which complexity can act. Heavy metals, such as copper, either
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23 465 historically or presently used in antifouling paints, can negatively impact native biodiversity
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25 466 (Dafforn, Lewis, & Johnston, 2011; Kinsella & Crowe, 2016). Previous studies have
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27 467 demonstrated these contaminants can also enhance the richness and abundances of invasive
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29 468 species (Marraffini, Ashton, Brown, Chang, & Ruiz, 2017; Piola, Dafforn, & Johnston,
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31 469 2009); thus complexity could facilitate the increase of the non-endemic species pool. Studies
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33 470 directly manipulating contamination inside and outside harbours would be required to
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35 471 establish the importance of this factor as a moderator of complexity effects.
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44 473 Our results support previous suggestions that the addition of complexity to the homogenous,
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46 474 flat surfaces of coastal defence structures has the potential to improve ecological outcomes
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48 475 (O'Shaughnessy et al., 2020). As compared to the natural habitats they replace,
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50 476 topographically simple artificial structures commonly support reduced native biodiversity
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52 477 (Airoldi, Turon, Perkol-Finkel, & Rius, 2015). Eco-engineering complexity and missing
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54 478 microhabitats on these artificial structures to enhance the biodiversity and ecosystem
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56 479 functioning of their communities, is increasingly common. However, scientific studies
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3 480 providing the evidence base for this rapidly-growing field are often poorly replicated and
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5 481 carried out over small spatial and temporal scales (Chapman, Underwood, & Browne, 2018;
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7 482 Firth et al., 2020). Global integration of small-scale ecological experiments such as those
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9 483 conducted here can be useful in identifying appropriate eco-engineering approaches before
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11 484 they are scaled up. Our study provides the most geographically comprehensive test of the
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13 485 effects of complexity on the biodiversity of coastal defence structures across the globe. We
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15 486 clearly demonstrate that complexity can affect the richness and abundances of colonising
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17 487 taxa, and despite large biogeographic variation in the identity of taxa present, these effects are
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19 488 largely of a consistent and positive direction for particular functional groups, across the
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21 489 globe.
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28 491 Despite the generally positive effects of complexity, we found that the magnitude of these
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30 492 varied spatially from negligible to strongly positive (or in the case of some algae, negative).
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32 493 This is an important result as it suggests that economically costly eco-engineering
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34 494 interventions may have negligible benefit at some locations and may even negatively
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36 495 influence some functional groups if applied blindly. Effective eco-engineering requires
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38 496 understanding of the key environmental stressors that may be mitigated and the functional
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40 497 traits of taxa that are being targeted for enhancement (see also Morris et al. 2018). By
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42 498 designing microhabitats with the niches of target functional groups in mind, the benefits of
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44 499 complexity additions to structures may be maximised. Critically, the finding that the effect of
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46 500 complexity varied among locations, tidal zones and with latitude, highlights the importance
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48 501 of understanding how the effects of complexity are shaped by the local abiotic and biotic
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50 502 environments before implementing eco-engineering solutions – one size will not necessarily
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52 503 fit all. Manipulative experiments are now needed to confirm how specific environmental and
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54 504 biological factors mediate complexity-biodiversity relationships, within urbanised marine
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3 505 settings and whether the effects of complexity identified over a 12-month period here persist
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5 506 over longer time scales. Moreover, to fully assess the biodiversity benefits of eco-engineering
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7 507 interventions that add complexity, we would also need to compare the complex tiles to the
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9 508 surface of the coastal defence structure and adjacent natural rocky shores.
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14 510 Eco-engineering, like ecological restoration (Ewel, 1987) provides the ultimate test of
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16 511 ecological theory (Mitsch 1996), by reassembling ecosystems from first principles. A
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18 512 cornerstone of community ecology has been the positive relationship between complexity and
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20 513 diversity (Dean & Connell, 1987; Kovalenko et al., 2012). Our global study challenges this
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22 514 paradigm in demonstrating that at patch-scales complexity effects can range from positive to
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24 515 neutral to negative, depending upon location and functional group. General guidelines to
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26 516 enhance biodiversity in coastal constructions will benefit from a grounding in ecological
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28 517 theory that can help developers predict the influence of local environmental and biotic
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30 518 contexts (Mayer-Pinto et al 2019).
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42
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44
45 523 funding bodies (see Supplementary S9 for full details).
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49 524 **Data Availability**

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51 525 The data are available as Supporting Information
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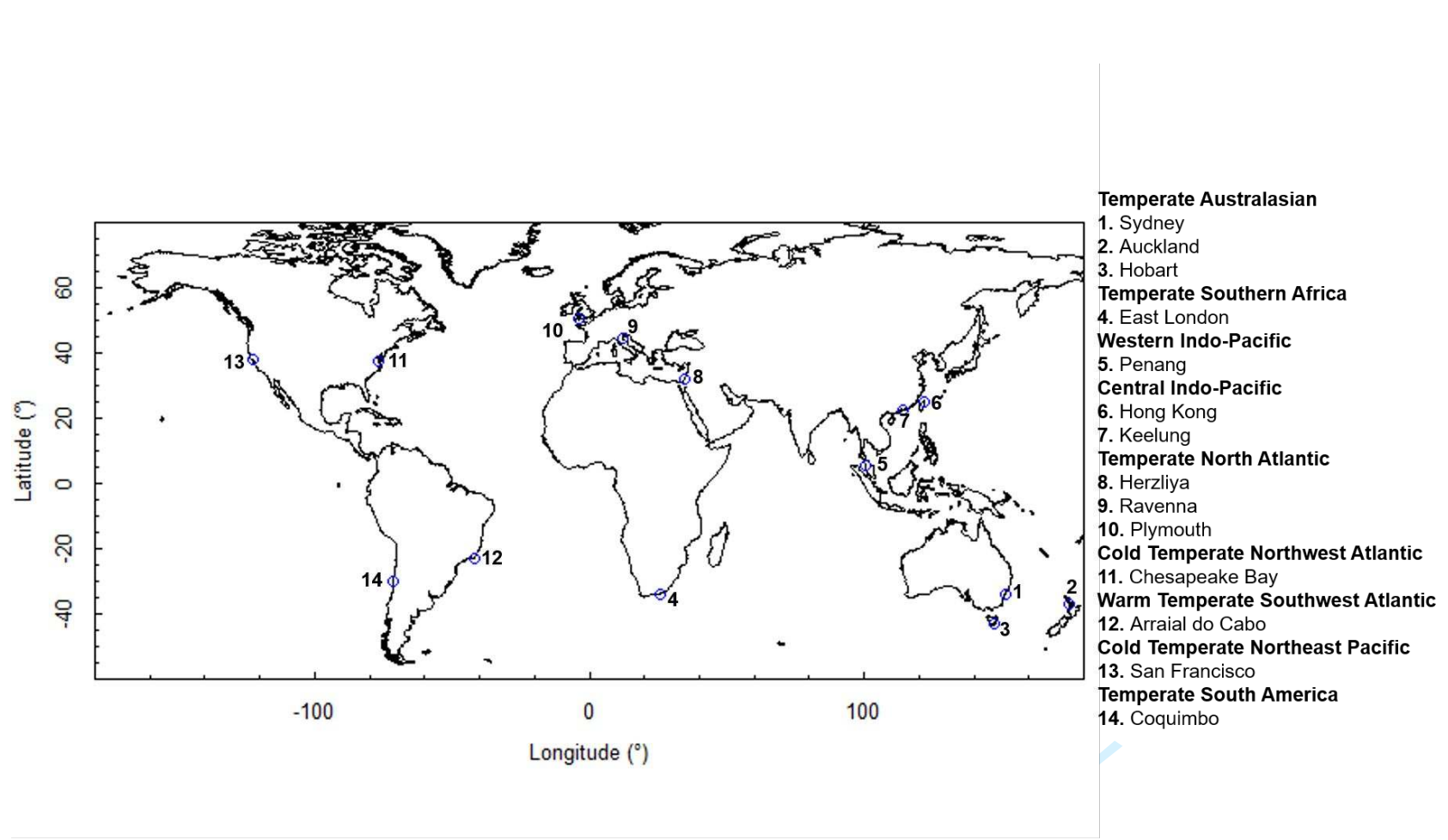


Fig 1: Map showing the experimental locations. Locations are ordered by biogeographic realm.

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

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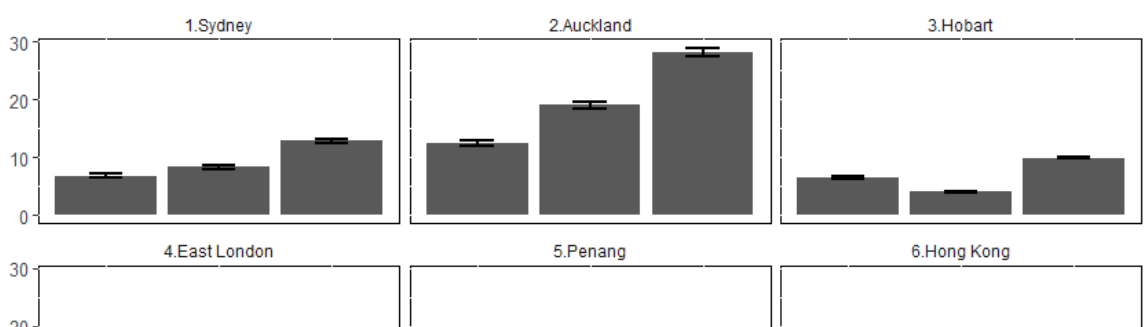
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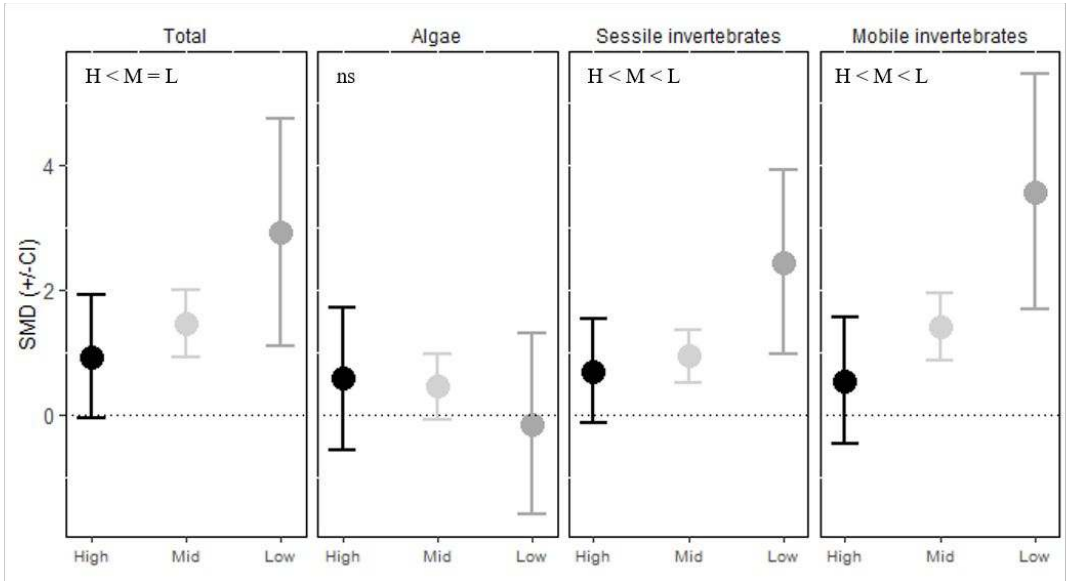


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5 **Fig 3:** Effect of complexity (flat and 2 cm or 5 cm complex tiles) on the mean (+/-SE) total taxa richness at each of fourteen locations by realm
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8 (n = 1 or 2 sites per location). Significant differences (at $\alpha = 0.05$) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are indicated by
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10 '>' or '<', with 'ns' or '=' denoting treatments that did not significantly differ.
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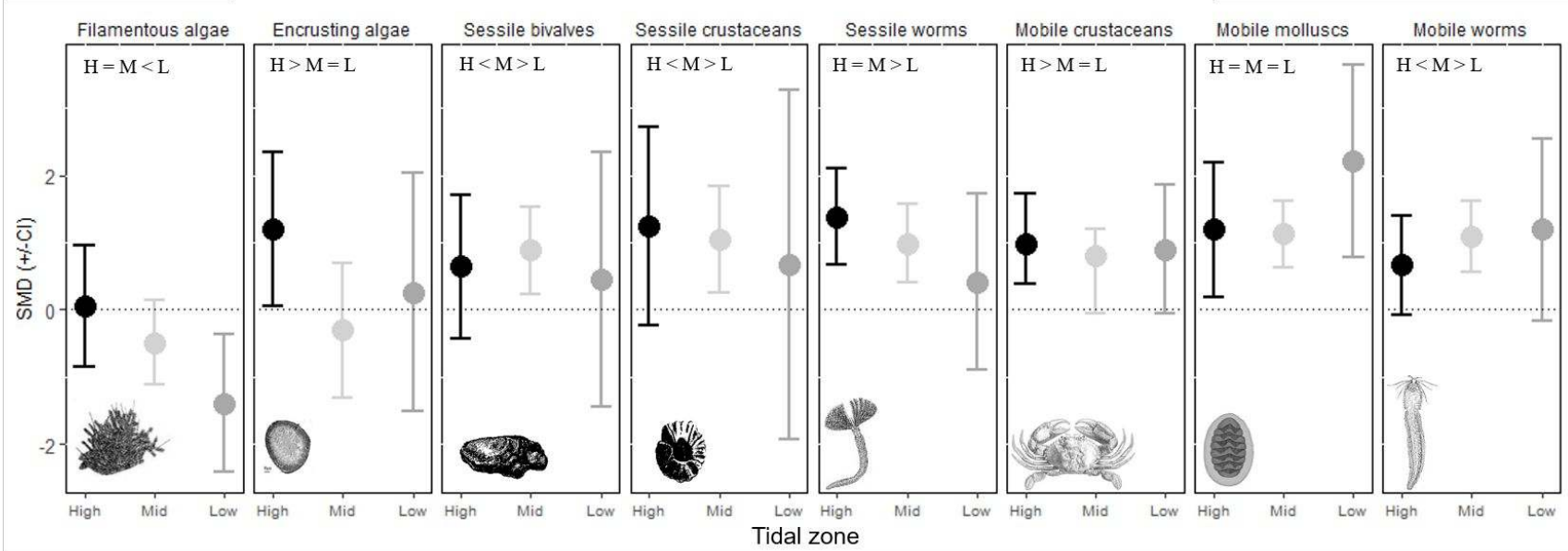
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a) Richness



b) Abundances

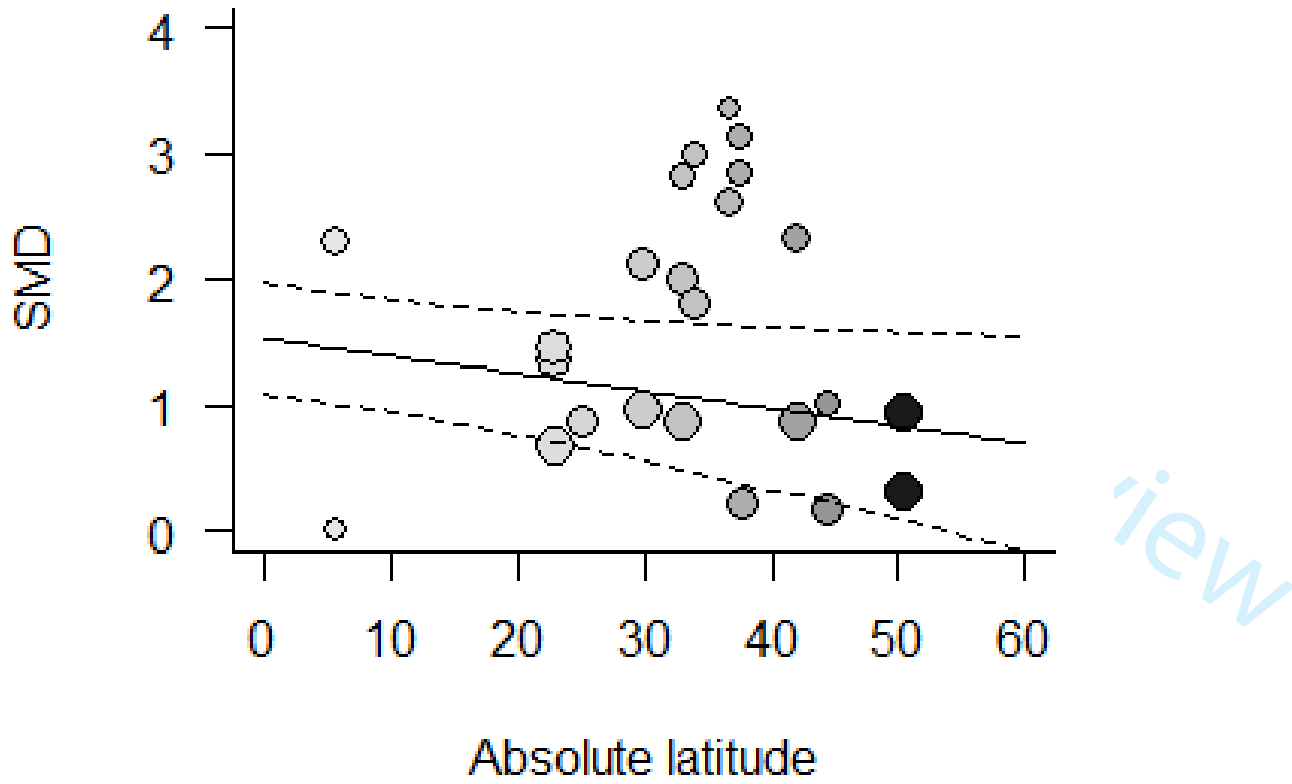


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5 **Fig. 4:** Effects of tidal zones on the standard mean difference SMD (+/-CI) in a) richness of total taxa, algae, sessiles invertebrates and mobile
6 invertebrates and b) abundances (percentage cover or abundances) of key CATAMI groups between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

Supplementary S1: Information on the experiment design, sampling and environmental parameters for each location and site.

Location	Season: month, and year of deployment	Sampling	Latitude	Average (Min - Max) Temperature (°C)	Tidal zone	Maximum tidal range (m)	Distance (km) to nearest port or marina	Reference	Source of heavy metals information
Sydney Harbour, Sydney Australia	Spring: November 2015	Sub sampling predefined area on complex and flat tiles	-33.85	Site 1: 19.66 (13.83 - 46.5) Site 2: 20.19 (13.66 - 43.16)	Mid	2.02	Site 1: 0.27 Site 2: 0.49	(Banks et al., 2016)	(Ling et al., 2018)
Waitemata Harbour, Auckland, New Zealand	Summer: January 2016	Full tiles	-36.84	NA	Low	3.53	Site 1: 0.5 Site 2: 0.28	(Aguirre et al., 2016)	(Council, 2012)
Keelung, Taiwan	Summer: April 2016	Full tiles	25.07	Site 1: 27.41 (19.83 - 49.77) Site 2: 27.47 (18.66 - 48.16)	Mid	1.5	Site 1: 1.5 Site 2: 0.05	NA	NA
Chesapeake Bay, USA	Summer: June 2016	Full tiles	37.37	Site 1: 18.91 (-9.00 - 42.00) Site 2: 18.91 (-8.50 - 45.00)	Mid	1.32	Site 1: 1.15 Site 2: 5.25	(O'Neil et al., 2020)	http://www.nerrsdata.org/
San Francisco Bay, USA	Summer; July 2016	Full tiles	37.81	Site 1: 15.70 (6.47 - 41.13) Site 2: 16.61 (10.55 - 23.83)	Low	3.01	Site 1: 0.34 Site 2: 3.00	NA	NA
Plymouth Estuary, UK	Summer; August 2016	Full tiles	50.37	Site 1: 16.56 (4.08 - 36.90) Site 2: 16.62 (3.51 - 35.60)	High	5.57	Site 1: 0 Site 2: 0.1	(Knights et al., 2016)	Environmental agency
Herzliya Marina, Israel	Summer; August 2016	Full tile - mobile invertebrates Sub sampling predefined areas on complex and	32.83	Site 1: 22.1 (7.50 - 35.50)	High	0.46	Site 1: 0	NA	Perkol-Finkel et al. unpublished data

		flat tiles – sessile invertebrates							
Ravenna Port, Italy	Summer; September 2016	Sub sampling predefined areas on complex and flat tiles	44.49	NA	Mid	0.89	Site 1: 0.5 Site 2: 0.5	(Airoidi, Ponti, & Abbiati, 2016)	NA
Penang Harbour, Malaysia	Dry, September 2016	Sub sampling predefined areas on complex and flat tiles	5.74	Site 1: 28.60 (17.64 - 48.75) Site 2: 30.17 (21.75 – 47.62)	Mid	2.35	Site 1: 0.05 Site 2: 0	NA	Chee et al. unpublished data
Arraial do Cabo Port, Brazil	Spring; September 2016	Sub sampling predefined areas on complex and flat tiles	-22.97	Site 1: 23.48 (16.00 – 46.00) Site 2: 27.41 (19.83 – 49.77)	Mid	1.26	Site 1: 0.1 Site 2: 0	(Soares-Gomes et al., 2016)	NA
Coquimbo, Chile	Spring; November 2016	Sub sampling predefined areas on complex and flat tiles	-29.79	Site 1: 16.22 (10.07 – 28.04) Site 2: 16.59 (8.59 – 35.44)	High	1.78	Site 1: 0.15 Site 2: 0	NA	Aguilera et al. unpublished data
East London Port, South Africa	Spring; November 2016	Sub sampling predefined areas on complex and flat tiles	-33.03	Site 1: 18.59 (9.72 – 37.61) Site 2: 17.40 (6.20 – 37.74)	Mid	2.03	Site 1: 0.61 Site 2: 0.65		NA
Derwent Estuary, Hobart, Australia	Spring; November 2016	Sub sampling predefined areas on complex and flat tiles	-50.00	Site 1: 17.53 (9.32 – 30.50) Site 2: 17.53 (10.32 – 30.50)	Mid	1.44	Site 1: 0.72 Site 2: 0.27	(Macleod & Coughanowr, 2019)	(Ling et al., 2018)
Hong Kong Bay, China	Spring; November 2016	Sub sampling predefined areas on complex and flat tiles	22.89	NA	Mid	2.54	Site 1: 1.9 Site 2: 5.5	(Lai et al., 2016)	(Birch et al., 2020)

Supplementary S2: Results of the pilot study testing the effects of topographic complexity and site nested within location on the sub-sample and full samples from Sydney.

Table S2a: Results of mixed effects models testing the effects of complexity (flat, 2.5 cm or 5 cm), and sites nested within location (2 levels) on the richness (total, algae, sessile invertebrates and mobile invertebrates) of the sub-samples or the full tile samples, sampled destructively at 12 months. The surface area of the tiles sampled (offset) was also included in the model. Details of significant post-hoc tests are shown.

Total taxa richness								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	9.5625	9.9514	0.002	Site 1 Flat vs. 5 cm	-0.429	-1.767	>0.05
Site (Location)	1	5.9187	4.0327	0.015	Site 2 Flat vs. 5 cm	-0.537	-2.629	0.0086
Complexity x Site (Location)	1	0.1153	3.9173	>0.05				
b) Sub sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	5.0906	10.2925	0.024	Site 1 Flat vs. 5 cm	-0.463	-1.494	>0.05
Site (Location)	1	5.9823	4.3101	0.015	Site 2 Flat vs. 5 cm	-0.405	-2.662	0.047
Complexity x Site (Location)	1	0.0210	4.2891	>0.05				
Algae richness								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	0.86639	6.0051	>0.05	NA			
Site (Location)	1	2.83976	3.1654	>0.05				
Complexity x Site (Location)	1	0.83192	2.3335	>0.05				
b) Sub sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	0.78644	6.0051	>0.05	NA			
Site (Location)	1	2.83976	3.1654	>0.05				
Complexity x Site (Location)	1	0.83192	2.3335	>0.05				
Sessile invertebrate richness								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value

Complexity	1	0.80781	5.0519	>0.05				
Site (Location)	1	2.52672	2.5251	>0.05				
Complexity x Site (Location)	1	0.06153	2.4636	>0.05				
b) Sub sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	0.80781	5.0519	>0.05				
Site (Location)	1	2.52672	2.5251	>0.05				
Complexity x Site (Location)	1	0.06153	2.4636	>0.05				
Mobile invertebrate richness								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	8.3126	5.0043	0.004	Flat vs. 5 cm	-0.525	-2.718	0.007
Site (Location)	1	1.4474	3.5568	>0.05				
Complexity x Site (Location)	1	1.2405	2.3163	>0.05				
b) Sub sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	2.78205	4.3121	0.046	Flat vs. 5 cm	-1.444	-2.619	0.011
Site (Location)	1	0.86182	3.4503	>0.05				
Complexity x Site (Location)	1	0.54766	2.9027	>0.05				

Table S2b: Results of mixed effects models testing the effects of complexity (flat, 2.5 cm or 5 cm), and sites nested within location (2 levels) on the abundances (cover of algae and sessile invertebrates and counts of mobile invertebrates) of the sub-samples or the full tile samples, sampled destructively at 12 months. The surface area of the tiles sampled (offset) was also included in the model. Details of significant post-hoc tests are shown.

log(Algae percentage cover)								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	1.5644	7.5826	0.014	Site 1 Flat vs. 5 cm	-1.702	4.086	<.0001
Site (Location)	1	2.6197	4.9628	0.002	Site 2 Flat vs. 5 cm	0.258	0.619	>0.05
Complexity x Site (Location)	1	2.8803	2.0825	0.001				
b) Sub sample								

Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	2.5313	5.5123	0.001	Site 1 Flat vs. 5 cm	-1.702	-4.131	<0.001
Site (Location)	1	1.6341	3.8782	0.011	Site 2 Flat vs. 5 cm	-0.135	-0.328	>0.05
Complexity x Site (Location)	1	1.8412	2.0370	0.007				
Sessile invertebrate cover								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	62.832	49.880	<0.001	Flat vs. 5 cm	-4.58	-5.799	<0.001
Site (Location)	1	28.135	21.745	<0.001				
Complexity x Site (Location)	1	6.799	14.945	>0.05				
b) Sub sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	59.708	58.793	<0.001	Flat vs. 5 cm	-4.46	-5.391	<0.001
Site (Location)	1	33.043	25.750	<0.001				
Complexity x Site (Location)	1	9.312	16.438	>0.05				
log(Mobile invertebrate abundances)								
a) Full sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	5.0962	1.6960	<0.001	Flat vs. 5 cm			
Site (Location)	1	0.4286	1.2673	>0.05				
Complexity x Site (Location)	1	0.1874	1.0800	>0.05				
b) Sub sample								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	1	2.33701	0.8732	<0.001	Flat vs. 5 cm	0.883	4.683	<0.001
Site (Location)	1	0.00214	0.8711	>0.05				
Complexity x Site (Location)	1	0.01873	0.8523	>0.05				

1 **Supplementary S3:** List of the functional groups, nineteen CATAMI groups and species/taxa on the experiment treatments, after 12 months.
 2 Species/morphospecies are classified as non-indigenous based on the published literature. Where species/morphospecies were observed at
 3 multiple locations, the location at which it is non-indigenous is indicated.
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Functional group	CATAMI classification	Taxon	Location	Non-indigenous
Algae	Algal mats	Algal mat morphospecies 1	Chesapeake	
		Algal mat morphospecies 2-4	Penang	
		Algal mat morphospecies 5-6	San Francisco	
	Macroalgae articulated calcareous	<i>Corallina officinalis</i>	Auckland, Sydney	
	Macroalgae encrusting	<i>Lithothamnium</i> sp.	Coquimbo	
		Encrusting coralline algae unknown	Arraial do Cabo	
		<i>Hildenbrandia</i> spp.	Coquimbo, East London, San Francisco	
		<i>Ralfsia verrucosa</i>	Sydney	
		<i>Ralfsia</i> sp.	Coquimbo	
		Encrusting macroalgae morphospecies 1 (black)	Keelung	
Encrusting macroalgae	Sydney			

		morphospecies 1 (green)		
	Macroalgae filamentous/filiform	Ectocarpaceae unknown	Coquimbo	
		Turf macroalgae morphospecies 1	Ravenna	
		Turf macroalgae morphospecies 2-4 (brown)	San Francisco, Sydney	
		Turf macroalgae morphospecies 5-6 (green)	Sydney, Keelung	
		Turf macroalgae morphospecies 7-8 (red)	San Francisco, Sydney	
	Macroalgae globose/saccate	<i>Colpomenia</i> sp.	Auckland	
	Macroalgae foliose	<i>Mastocarpus</i> morphospecies 1-2	San Francisco	
		<i>Gelidium</i> sp.	East London	
		<i>Gracilaria</i> sp.	Chesapeake	
		<i>Pterocladia capillacea</i>	Auckland	
		<i>Fucus</i> spp.	Plymouth, San Francisco	
		<i>Phyllospora comosa</i>	Hobart	
		<i>Mazzaella</i> sp. 1	San Francisco	
		<i>Mazzaella</i> sp. 2	San Francisco	
		<i>Pachymenia lusoria</i>	Auckland	
		<i>Porphyra</i> sp.	Hobart	

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		<i>Pyropia</i> sp.	San Francisco	
		<i>Ulva lactuca</i>	Auckland	
		<i>Ulva</i> spp. (8 morphospecies)	Chesapeake, Coquimbo, East London, Hobart, San Francisco, Sydney, Keelung	
		Sheet-like macroalgae morphospecies 1 (brown)	Sydney	
		Sheet-like macroalgae morphospecies 2 (red)	Sydney	
		Macroalgae unknown morphospecies 1 (brown)	Auckland	
		Macroalgae unknown morphospecies 2 (green)	Auckland	
		Macroalgae unknown morphospecies 3-6	Hobart	
Sessile invertebrates	Ascidians	<i>Corella eumyota</i>	Auckland	
		<i>Pyura</i> sp.	Hobart	
		Stalked ascidian morphospecies 1	Hobart	
		<i>Botrylloides niger</i>	Arraial do Cabo	(Granthom-Costa, Ferreira, & Dias, 2016)
		<i>Botryllus tabori</i>	Arraial do Cabo	
		Ascidian morphospecies 1	Auckland	

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		Membraniporidae sp.	San Francisco	(Bishop & Hutchings, 2011)	
		<i>Schizoporella errata</i>	Arraial do Cabo	(Almeida, Souza, Gordon, & Vieira, 2015)	
		<i>Schizoporella</i> sp.	Herzliya	www.marinespecies.org	
		<i>Watersipora cucullata</i>	Herzliya	www.marinespecies.org	
		<i>Watersipora subtorquata</i>	Hobart	(Bishop & Hutchings, 2011)	
		<i>Watersipora</i> spp.	Auckland, Sydney	(Bishop & Hutchings, 2011)	
	Bryozoans	Encrusting bryozoa morphospecies 1	Arraial do Cabo		
		Encrusting bryozoa morphospecies 2	Chesapeake		
		Encrusting bryozoa morphospecies 3	Herzliya		
		Encrusting bryozoa morphospecies 4-6	Hobart		
		Encrusting bryozoa morphospecies 7	Plymouth		
		<i>Bugula neritina</i>	Herzilya, Penang	www.marinespecies.org Herzilya (Tilbrook & Gordon, 2016) Penang	
		Bryozoan unknown	Auckland		
		Cnidarians	Hydroid morphospecies (rope)	Chesapeake	
			Anemone unknown	Auckland	

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24		<i>Amphibalanus</i>	Herzliya, Hong Kong, Penang,
25		<i>amphitrite</i>	Sydney
26			(Rainbow, 2000) Hong
27		<i>Amphibalanus</i>	Kong
28		<i>variegatus</i>	
29			
30		<i>Amphibalanus</i> spp.	East London, Keelung
31			
32		<i>Austrobalanus</i>	
33		<i>imperator</i>	Sydney
34			
35		<i>Austrominius</i>	
36		<i>modestus</i>	Auckland, Plymouth, Sydney
37			(Bracewell, Spencer,
38			Marrs, Iles, & Robinson,
39			2012) Plymouth
40		<i>Balanus</i> sp.	Chesapeake
41			
42		Balanidae unknown	Coquimbo
43			
44		<i>Chamaesipho</i>	
45		<i>tasmanica</i>	Hobart
46			
47		<i>Chthamalus</i>	
48		<i>antennatus</i>	Hobart, Sydney
49			
50		<i>Chthamalus</i> <i>stellatus</i>	Ravenna
51			
52		Chthamalidae	
53		unknown	Coquimbo
54			
55		<i>Hexaminius</i> sp.	Sydney
56			
57		<i>Striatobalanus tenuis</i>	Penang
58			
59		<i>Tetraclita japonica</i>	Hong Kong
60			
		<i>Tetraclita stalactifera</i>	Arraial do Cabo
		<i>Tetraclita</i> sp.	East London
		<i>Tetraclita squamosa</i>	Penang
		Barnacle unknown	
		recruits spp.	Arraial do Cabo, Hong Kong
		Barnacle unknown 1	Auckland
		Barnacle unknown 2	San Francisco

Crustaceans sessile

		<i>Capitulum mitella</i>	Hong Kong	
		<i>Barbatia virescens</i>	Hong Kong	
		<i>Brachidontes mutabilis</i>	Hong Kong	
		<i>Crassostrea gigas</i>	Plymouth	www.marinespecies.org/
			Hobart, Sydney	(Bishop and Hutchings 2011)
			Penang	
		<i>Crassostrea virginica</i>	Chesapeake	
		<i>Isognomon bicolor</i>	Arraial do Cabo	(López, Lavrado, & Coutinho, 2014)
		<i>Magallana angulata</i>	Penang	
		<i>Magallana ariakensis</i>	Penang	
		<i>Magallana bilineata</i>	Penang	
	Molluscs sessile	<i>Mytilus galloprovincialis</i>	Ravenna	
		<i>Mytilus</i> sp.	Hobart	
		<i>Perna canaliculus</i>	Auckland	
		<i>Perna viridis</i>	Penang	
		<i>Perumytilus purpuratus</i>	Coquimbo	
		<i>Pinctada imbricata radiata</i>	Herzliya	
		<i>Ostrea edulis</i>	Herzliya	
		<i>Ostreidae oyster recruit</i>	Ravenna	
		<i>Saccostrea cucullata</i>	Hong Kong, Penang, Keelung	
		<i>Saccostrea glomerata</i>	Sydney	

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		<i>Geukensia demissa</i>	Chesapeake	
		<i>Ischadium recurvum</i>	Chesapeake	
		Mussel unknown sp. 2	Keelung	
		Oyster unknown sp.	Auckland	
		Oyster recruit unknown sp.	Arraial do Cabo	
Sponge		<i>Chondrilla australiensis</i>	Penang	
		<i>Crambe crambe</i>	Herzliya	
		Sponge crust morphospecies 1 (gray)	Auckland	
		Sponge crust morphospecies 2 (orange)	Sydney	
Worms sessile		<i>Galeolaria caespitosa</i>	Hobart	
		Serpulidae spp.	Arraial do Cabo, Herzliya	
		<i>Spirobranchus cariniferus</i>	Auckland	
		Spirorbinae spp.	Herzliya, Sydney, Keelung	
		Tubeworm morphospecies 1	Auckland	
		Tubeworm morphospecies 2 (sand)	Auckland	
		Tubeworm morphospecies 3 (keel)	Penang	

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		<i>Parasabella microphthalma</i>	Chesapeake	
Mobile invertebrates	Arthropods	<i>Achelia assimilis</i>	Auckland	
		Chelicerates	Sydney	
		Spider unknown	Auckland	
		Uniramia unknown	Sydney	
	Crustaceans mobile	<i>Petrolisthes japonica</i>	Keelung	
		<i>Petrolisthes elongatus</i>	Auckland, Hobart	(Steger & Gardner, 2007) Hobart
		<i>Acanthocyclus gayi</i>	Coquimbo	
		<i>Armases cinereum</i>	Chesapeake	
		<i>Callinectes sapidus</i>	Chesapeake	
		<i>Cyclograpsus granulatus</i>	Hobart	
		<i>Cyclograpsus punctatus</i>	East London	
		<i>Eriphia ferox</i>	Keelung	
		<i>Eurypanopeus depressus</i>	Chesapeake	
		Grapsidae unknown	Herzliya	
		<i>Halicarcinus quoyi</i>	Hobart	(Sliwa, Migus, McEnnulty, & Hayes, 2009)
		Halicarcinus sp.	Auckland	
		Hemigrapsus sp.	Keelung	
		<i>Heteropanope glabra</i>	Hong Kong	
		<i>Nanosesarma minutum</i>	Hong Kong	

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	<i>Nasutoplax rostrate</i>	Hobart	
	Paragrapsus sp.	Sydney	
	<i>Parasesarma pictum</i>	Hong Kong	
	<i>Pilumnus</i> sp.	Sydney	
	<i>Pinnotheres hickmani</i>	Hobart	
	<i>Pinnotheres ostreum</i>	Chesapeake	
	<i>Pinnotheres</i> sp.	Hong Kong	
	Sesarma sp.	Sydney	
	Crab morphospecies 1-2	Auckland	
	<i>Alpheus</i> sp.	Hong Kong	
	<i>Americamysis bigelowi</i>	Chesapeake	
	<i>Palaemonetes pugio</i>	Chesapeake	
	Processidae unknown	Herzliya	
	<i>Amphitoe</i> sp.	Sydney	
	<i>Ampithoe valida</i>	Chesapeake	
	Amphipod morphospecies 1	Coquimbo	
	Amphipod morphospecies 2-3	Keelung	
	Amphipod morphospecies 4	Hong Kong	
	<i>Apocorophium lacustra</i>	Chesapeake	
	Bellorchestia sp. 1	Auckland	
	Bellorchestia sp. 2	Auckland	

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<i>Cirolana harfordi</i>	Sydney	(Bugnot, Coleman, Figueira, & Marzinelli, 2014)
Corophiidae unknown	Herzliya	
Corophium spp.	Sydney, San Francisco	
<i>Cymodocella pustulata</i>	East London	
<i>Elasmopus levis</i>	Chesapeake	
Eusiridae unknown	Hobart	
<i>Gammarus mucronatus</i>	Chesapeake	
Gammaridae unknown	Herzliya	
Haylidae unknown	Hobart	
<i>Isocladus armatus</i>	Auckland	
Isopod morphospecies 1-4	Auckland	
Isopod morphospecies 5	Sydney	
Isopod morphospecies 6	Keelung	
<i>Jassa marmorata</i>	Hobart	
<i>Leucothoe spinicarpa</i>	East London	
Ligia (Megaligia) exotica	Chesapeake, Hong Kong, Keelung	
Ligia sp.	Herzliya	
<i>Melita nitida</i>	Chesapeake	
<i>Paracorophium</i> sp.	Hobart	
<i>Parhyale</i> sp.	Hong Kong	

	<i>Sphaeroma quadridentatum</i>	Chesapeake	
	Sphaeromatidae unknown	Hobart, San Francisco Bay	
Echinoderm	<i>Ophiomyxa brevirima</i>	Auckland	
	<i>Parvulastra exigua</i>	East London, Sydney	
	<i>Patiriella regularis</i>	Auckland	
Hexapods	Chironomid	Hobart	
	Chironomid larvae	Chesapeake	
	Insect unknown	Sydney	
	Collembola unknown	Sydney	
Molluscs mobile	<i>Eualetes tulipa</i>	Arraial do Cabo	
	<i>Brachidontes semistriatus</i>	East London	
	<i>Geukensia demissa</i>	Chesapeake	
	<i>Ischadium recurvum</i>	Chesapeake	
	<i>Lasaea adansoni</i>	East London	
	<i>Lasaea australis</i>	Sydney	
	<i>Mytilus galloprovincialis</i>	East London	
	<i>Mytilus sp.</i>	San Francisco	
	<i>Perna perna</i>	East London	
	<i>Tapes spp.</i>	Sydney	
	Mussel unknown	Keelung	
<i>Acanthopleura echinata</i>	Coquimbo		
<i>Acanthopleura gaimardi</i>	Sydney		

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<i>Acanthochitona garnoti</i>	East London	
<i>Acanthochitona zelandica</i>	Auckland	
<i>Chiton glaucus</i>	Auckland	
<i>Liolophura japonica</i>	Hong Kong	
<i>Sypharochiton pelliserpentis</i>	Auckland, Hobart, Sydney	
<i>Ascorhis tasmanica</i>	Hobart	
<i>Austrocochlea porcata</i>	Sydney	
<i>Austrolittorina araucana</i>	Coquimbo	
<i>Austrolittorina unifasciata</i>	Hobart	
<i>Austrolittorina sp.</i>	Auckland	
<i>Bedevea paivae</i>	Sydney	
<i>Bembicium auratum</i>	Sydney	
<i>Bembicium nanum</i>	Sydney	
<i>Bittium alternatum</i>	Chesapeake	
<i>Cellana grata</i>	Hong Kong, Keelung	
<i>Cellana toreuma</i>	Hong Kong, Keelung	
<i>Cellana tramoserica</i>	Sydney	
<i>Cellana spp.</i>	Auckland, Penang	
Columbellidae unknown	Sydney	
<i>Cryptassiminea buccinoide</i>	Sydney	
<i>Cymbula oculus</i>	East London	

<i>Dicathais orbita</i>	Auckland	
<i>Diloma concameratum</i>	Sydney	
<i>Diloma subrostratum</i>	Auckland	
<i>Echinolittorina radiata</i>	Hong Kong	
<i>Echinolittorina vidua</i>	Hong Kong	
<i>Fissurella</i> spp.	Arraial do Cabo, Coquimbo	
<i>Haustrum scobina</i>	Auckland	
<i>Helcion concolor</i>	East London	
<i>Littoraria articulata</i>	Hong Kong	
<i>Littoraria irrorata</i>	Chesapeake	
<i>Littoraria luteola</i>	Sydney	
<i>Littorina littorea</i>	Plymouth	
<i>Littorina obtusata</i>	Plymouth	
<i>Littorina saxatilis</i>	Plymouth	
<i>Lottia luchuana</i>	Hong Kong, Keelung	
<i>Lottia</i> sp.	Arraial do Cabo	
<i>Lunella smaragda</i>	Auckland	
<i>Mitrella</i> spp.	Coquimbo	
<i>Nipponacmea concinna</i>	Hong Kong	
<i>Notoacmea flammea</i>	Hobart, Sydney	
<i>Notoacmea petterdi</i>	Sydney	
<i>Onchidella nigricans</i>	Auckland	
<i>Oxystele sinensis</i>	East London	
<i>Oxystele tabularis</i>	East London	

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<i>Oxystele tigrina</i>	East London	
<i>Patella caerulea</i>	Ravenna	
<i>Patella depressa</i>	Plymouth	
<i>Patella vulgata</i>	Plymouth	
<i>Patelloida latistrigata</i>	Sydney	
<i>Patelloida mimuli</i>	Sydney	
<i>Patelloida ryukyuensis</i>	Hong Kong	
<i>Patelloida saccharina</i>	Hong Kong, Sydney	
<i>Reishia clavigera</i>	Hong Kong	
<i>Scurria araucana</i>	Coquimbo	
<i>Scurria ceciliana</i>	Coquimbo	
<i>Scurria variabilis</i>	Coquimbo	
<i>Scurria</i> spp.	Coquimbo	
<i>Scutellastra argenvillei</i>	East London	
<i>Scutellastra granularis</i>	East London	
<i>Scutellastra laticostata</i>	Hobart	
<i>Scutellastra longicosta</i>	East London	
<i>Sigapatella novaezealandiae</i>	Auckland	
<i>Siphonaria australis</i>	Auckland	
<i>Siphonaria capensis</i>	East London	
<i>Siphonaria concinna</i>	East London	

		<i>Siphonaria denticulata</i>	Sydney	
		<i>Siphonaria diemenensis</i>	Hobart	
		<i>Siphonaria funiculata</i>	Hobart	
		<i>Siphonaria japonica</i>	Hong Kong, Keelung	
		<i>Siphonaria laciniosa</i>	Hong Kong, Keelung	
		<i>Siphonaria serrata</i>	East London	
		<i>Siphonaria</i> spp.	Coquimbo, Sydney	
		<i>Siphonaria</i> sp. unknown juvenile	Hong Kong	
		Snail unknown	Auckland	
		Snail, screwshell unknown	Sydney	
		<i>Steromphala umbilicalis</i>	Plymouth	
		<i>Tenguella marginalba</i>	Sydney	
	Worms mobile	<i>Coronadena mutabilis</i>	Chesapeake	
		Platyhelminthes unknown	Hobart	
		<i>Stylochus ellipticus</i>	Chesapeake	
		Nemertean spp. Unknown	Chesapeake	
		Nemertean unknown	Hobart	
		<i>Alitta succinea</i>	Chesapeake	
		Capitellidae unknown	Chesapeake	
		<i>Eulalia microphylla</i>	Auckland	
		Hesionidae unknown	Herzliya	

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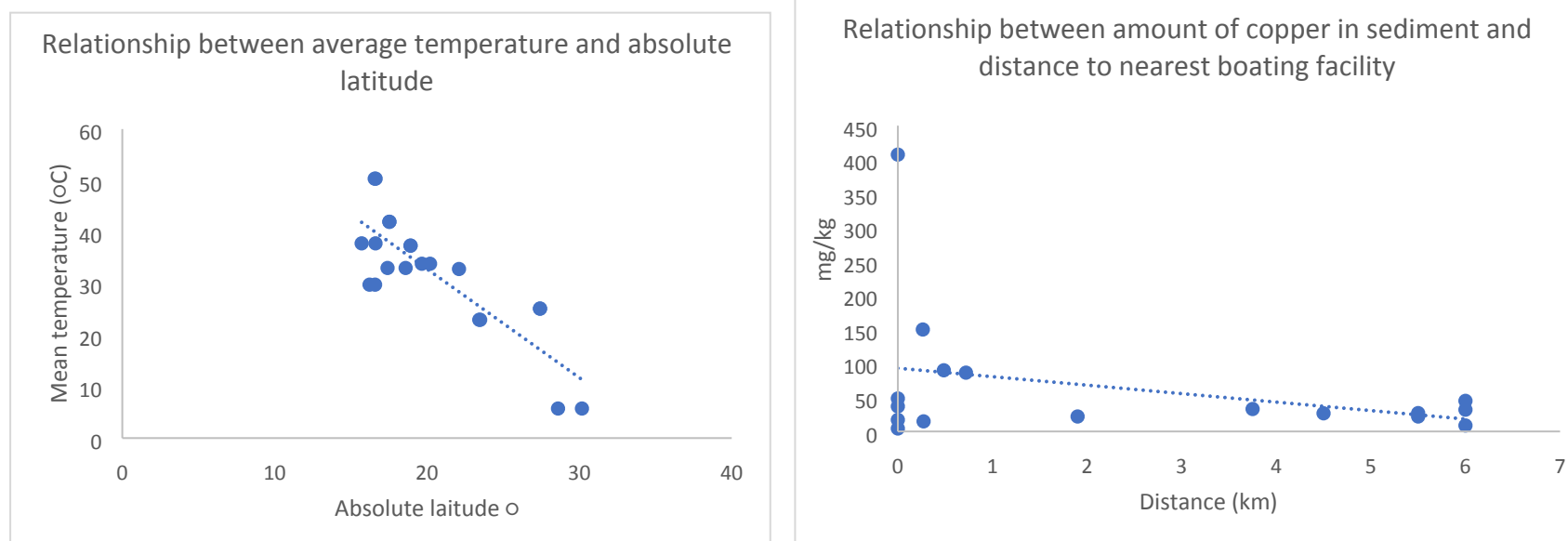
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	<i>Hypereteone heteropoda</i>	Chesapeake	
	<i>Loimia medusa</i>	Chesapeake	
	<i>Neanthes vaalii</i>	Hobart	
	Nereididae spp.	East London, Herzliya, Hong Kong, Sydney	
	Phyllodocidae sp. 1	Auckland	
	<i>Polydora websteri</i>	Chesapeake	
	Polynoidae unknown	Sydney	
	Phyllodocidae unknown	Sydney	
	Spionidae unknown	Sydney	
	Syllidae unknown	Sydney	
	Polychaete morphospecies 1	Auckland	
	Polychaete morphospecies 2	Coquimbo	
	Polychaete morphospecies 3-7	Keelung	
	<i>Sipuncula</i> spp.	East London, Penang, Sydney	

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18 **Supplementary S4:** The relationships between the environmental parameters and sites.



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20 **Fig S4a:** The relationship between a) mean temperature and absolute latitude (significant) and b) amount of copper in sediment (mg/kg) and
21 distance to nearest marina by sites (non-significant). The measurements of temperature were taken at twenty-one sites, within eleven locations
22 throughout the experiment and the measurements of heavy metals were taken at eighteen sites, within nine locations, across the globe.

26 **Table S4b:** Results of linear models testing the relationship between a) average temperature and absolute latitude and b) amount of copper in
27 sediment and distance to the nearest boating facility

Factor	Estimate	Standard error	T-value	P-value
Average temperature	-2.112	0.322	-6.568	<0.001
Average maximum temperature	-0.9032	0.2510	-3.598	0.00192
Average minimum temperature	-0.8729	0.2824	-3.091	0.00602
Distance to boating facility	-0.038	0.020	-1.894	>0.05

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34 **Supplementary S5: Effects of adding topographic complexity on the total taxa richness**
35 **and the richness and abundances of algae, sessile invertebrates and mobile**
36 **invertebrates**

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38 Total taxa richness was greater on the 5 cm complex tiles than the flat tiles at eleven locations
39 (Arraial do Cabo, Auckland, Chesapeake Bay, Coquimbo, East London, Herzliya, Hobart,
40 Hong Kong, Keelung, Penang, and Sydney); and on the 2.5 cm complex relative to the flat
41 tiles at eight locations (Arraial do Cabo, Auckland, Chesapeake Bay, Coquimbo, Herzliya,
42 Hong Kong, Keelung and Penang). Algal richness was greater on 5 cm complex tiles than on
43 the 2.5 cm complex tiles or the flat tiles at two of the fourteen locations (Arraial do Cabo and
44 Sydney), whereas the 2.5 cm complex tiles and the flat tiles did not significantly differ . At
45 the other twelve locations, there were no significant differences in algal richness among
46 treatments. Sessile invertebrates were more speciose on the 2.5 cm and 5 cm complex tiles
47 than on flat tiles at seven locations (Arraial do Cabo, Auckland, Chesapeake Bay, Herzliya,
48 Hong Kong, Penang and Ravenna), more speciose on the 5 cm complex than the 2.5 cm and
49 flat tiles at two locations (Hobart and Sydney), but did not differ among treatments at the
50 other five locations. There were more mobile species on the 2.5 and 5 cm complex tile
51 compared with the flat tiles at six locations (Auckland, Coquimbo, Hong Kong, Hobart,
52 Keelung, Sydney) and on the 5 cm complex tiles relative to the 2.5 cm and flat tiles at two
53 locations (Chesapeake Bay and East London), with no significant differences for the other six
54 locations.

Table S5a: Results of mixed effects models testing the effects of complexity (flat, 2.5 cm or 5 cm), locations (14 levels) and sites nested within location (1-2 levels) on the richness (total, algae, sessile invertebrates and mobile invertebrates) sampled destructively at 12 months. The surface area of the tiles sampled (offset) was also included in the model. Details of significant post-hoc tests are shown.

Total taxa richness								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	115.650	1568.950	<0.001	Arraial do Cabo Flat vs. 2.5 cm Arraial do Cabo Flat vs. 5 cm Arraial do Cabo 2.5 cm vs. 5 cm	-0.603 -0.607 -0.005	-1.394 -1.437 -0.031	0.035 0.032 >0.05
Location	13	1093.780	475.170	<0.001	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-0.384 -7.993 -0.382	-3.784 -7.993 -4.529	0.001 <0.001 <0.001
Site (Location)	1	9.100	466.070	<0.001	Chesapeake Bay Flat vs. 2.5 cm Chesapeake Bay Flat vs. 5 cm Chesapeake Bay 2.5 cm vs. 5 cm	-0.457 -0.546 -0.090	-3.694 -4.527 -0.853	0.001 <0.001 >0.05
Complexity x Location	26	80.230	385.840	<0.001	Coquimbo Flat vs. 2.5cm Coquimbo Flat vs. 5 cm Coquimbo 2.5cm vs. 5 cm	-0.602 -0.606 -0.004	-1.706 -1.747 -0.026	0.021 0.019 >0.05
Complexity x Site (Location)	2	4.800	381.040	<0.001	East London Flat vs. 2.5cm East London Flat vs. 5 cm East London 2.5cm vs. 5 cm	-0.185 -0.680 -0.496	-0.810 -3.315 -2.585	>0.05 0.003 0.027
					Herzliya Flat vs. 2.5 cm, Herzliya Flat vs. 5 cm Herzliya 2.5cm vs. 5 cm	-0.612 -0.633 -0.021	-2.697 -2.842 -0.108	0.019 0.013 >0.05
					Hobart Flat vs. 2.5 cm,	0.505	0.787	>0.05

					Hobart Flat vs. 5 cm	-0.438	-3.081	0.006
					Hobart 2.5cm vs. 5 cm	-0.943	-5.605	<0.001
					Hong Kong Flat vs. 2.5 cm,	-0.622	-1.644	0.023
					Hong Kong Flat vs. 5 cm	-0.626	-1.650	0.023
					Hong Kong 2.5cm vs. 5 cm	-0.003	-0.026	>0.05
					Keelung Flat vs. 2.5 cm,	-0.511	-2.491	0.034
					Keelung Flat vs. 5 cm	-0.502	-2.461	0.037
					Keelung 2.5cm vs. 5 cm	0.009	0.052	>0.05
					Penang Flat vs. 2.5 cm,	-0.557	-2.213	>0.05
					Penang Flat vs. 5 cm	-0.589	-2.438	0.039
					Penang 2.5cm vs. 5 cm	-0.032	-0.146	>0.05
					Sydney Flat vs. 2.5 cm,	-0.145	-1.003	>0.05
					Sydney Flat vs. 5 cm	-0.577	-4.502	<0.001
					Sydney 2.5cm vs. 5 cm	-0.432	-3.530	0.001
Log(Algae richness)								
Factor	df	Mean square	F-value	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	28.759	7.369	<0.001	Arraial do Cabo Flat vs. 2.5 cm	-1.725	-1.900	>0.05
					Arraial do Cabo Flat vs. 5 cm	-4.443	-4.893	<0.001
					Arraial do Cabo 2.5 cm vs. 5 cm	-2.718	-3.076	0.007
Location	13	206.173	52.829	<0.001	Sydney Flat vs. 2.5 cm	0.769	0.869	>0.05
					Sydney Flat vs. 5 cm	-3.175	-3.593	0.001
					Sydney 2.5 cm vs. 5 cm	-3.943	-4.463	<0.001
Site (Location)	1	88.029	22.556	<0.001				
Complexity x Location	26	8.346	2.139	0.001				
Complexity x Site (Location)	2	9.921	2.542	>0.05				
Residual	329	3.903						
Sqrt(Sessile invertebrate richness)								

Factor	df	Mean square	F-value	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	2.903	24.028	<0.001	Arraial do Cabo Flat vs. 2.5 cm Arraial do Cabo Flat vs. 5 cm Arraial do Cabo 2.5 cm vs. 5 cm	-1.218 -1.178 0.041	-1.366 -1.112 0.261	0.036 0.041 >0.05
Location	13	11.024	91.257	<0.001	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-0.391 -1.027 -0.631	-2.513 -6.428 -3.982	0.033 <0.001 0.001
Site (Location)	1	1.207	9.988	0.002	Chesapeake Bay Flat vs. 2.5 cm Chesapeake Bay Flat vs. 5 cm Chesapeake Bay 2.5 cm vs. 5 cm	-0.616 -0.674 -0.058	-3.959 -4.333 -0.374	0.001 0.001 >0.05
Complexity x Location	26	0.404	3.346	<0.001	Herzliya Flat vs. 2.5 cm, Herzliya Flat vs. 5 cm Herzliya 2.5cm vs. 5 cm	-0.493 -0.522 -0.030	-2.193 -2.326 -0.133	0.044 0.034 >0.05
Complexity x Site (Location)	2	0.065	0.538	>0.05	Hobart Flat vs. 2.5 cm, Hobart Flat vs. 5 cm Hobart 2.5cm vs. 5 cm	0.318 -0.456 -0.774	2.042 -2.933 -4.975	>0.05 0.010 <0.001
Residual	329	0.121			Hong Kong Flat vs. 2.5 cm, Hong Kong Flat vs. 5 cm Hong Kong 2.5cm vs. 5 cm	-0.464 -0.465 -0.001	-1.051 -1.030 -0.007	0.005 0.046 >0.05
					Penang Flat vs. 2.5 cm, Penang Flat vs. 5 cm Penang 2.5cm vs. 5 cm	-1.360 -1.375 -0.015	-1.845 -2.004 -0.075	0.016 0.001 >0.05
					Ravenna Flat vs. 2.5 cm, Ravenna Flat vs. 5 cm Ravenna 2.5cm vs. 5 cm	-0.856 -0.490 0.366	-4.225 -2.436 1.822	0.001 0.041 >0.05
					Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm	0.031 -0.418	0.197 -2.686	>0.05 0.021

					Sydney 2.5cm vs. 5 cm	-0.449	-2.883	0.012
Mobile invertebrate richness								
Factor	df	Mean square	F-value	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	150.123	50.5677	<0.001	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-5.873 -10.677 -4.804	-8.133 -14.346 -6.455	<0.001 <0.001 <0.001
Location	13	146.015	49.1840	<0.001	Chesapeake Bay Flat vs. 2.5 cm Chesapeake Bay Flat vs. 5 cm Chesapeake Bay 2.5 cm vs. 5 cm	-0.873 -2.627 -1.754	-1.208 -3.638 -2.429	>0.05 0.001 0.042
Site (Location)	1	10.006	3.3706	>0.05	Coquimbo Flat vs. 2.5cm Coquimbo Flat vs. 5 cm Coquimbo 2.5cm vs. 5 cm	-1.578 -2.227 -0.654	-2.178 -3.084 -0.906	0.045 0.007 >0.05
Complexity x Location	26	19.559	6.5882	<0.001	East London Flat vs. 2.5 cm, East London Flat vs. 5 cm East London 2.5cm vs. 5 cm	-0.573 -3.037 -2.454	-0.793 4.192 -3.399	>0.05 0.001 0.002
Complexity x Site (Location)	2	1.138	0.3832	>0.05	Hobart Flat vs. 2.5 cm, Hobart Flat vs. 5 cm Hobart 2.5cm vs. 5 cm	1.008 -2.184 -3.192	1.396 -3.024 -4.420	>0.05 0.008 <0.001
Residual	329	2.969			Hong Kong Flat vs. 2.5 cm, Hong Kong Flat vs. 5 cm Hong Kong 2.5cm vs. 5 cm	-1.273 -1.677 -0.404	-1.762 -2.253 -0.543	0.019 0.015 >0.05
					Keelung Flat vs. 2.5 cm, Keelung Flat vs. 5 cm Keelung 2.5cm vs. 5 cm	-3.148 -2.752 0.396	-4.110 -3.593 0.517	<0.001 0.001 >0.05
					Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	-1.792 -3.284 -1.492	-2.482 -4.548 -2.066	0.036 <0.001 >0.05

Algal percentage cover was greater on the 2.5 cm and 5 cm complex tiles than the flat tiles at one location (Chesapeake Bay), with no effect of complexity at the other fourteen locations. Sessile invertebrate percentage cover was greater on the 2.5 cm and 5 cm complex tiles than the flat tiles at seven locations (Auckland, Coquimbo, Chesapeake Bay, Hobart, Herzliya, Hong Kong, and Plymouth) and on only the 5 cm complex tiles than the flat tiles at one location (Sydney), with no effects of complexity at the other six locations. Mobile invertebrate abundances were greater on the 2.5 cm and the 5 cm complex tiles than the flat tiles at six locations (Auckland, Chesapeake Bay, Coquimbo, East London, Hong Kong, Keelung and Sydney) and on the 5 cm complex tiles compared with the flat tiles at two locations (East London and Hobart).

Table S5b: Results of mixed effects models testing the effects of complexity (flat, 2.5 cm or 5 cm), locations (14 levels) and sites nested within location (1-2 levels) on the abundances (cover of algae, cover of sessile invertebrates and abundances of mobile invertebrates) sampled destructively at 12 months. The surface area of the tiles sampled (offset) was also included in the model. Details of significant post-hoc tests are shown.

Algae percentage cover								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	29.7	28811.3	>0.05	Chesapeake Bay Flat vs. 2.5 cm Chesapeake Bay Flat vs. 5 cm Chesapeake Bay 2.5 cm vs. 5 cm	-0.726 -0.699 0.027	-3.859 -3.725 0.180	0.003 0.006 >0.05
Location	13	19915.6	8895.7	<0.001	Coquimbo Flat vs. 2.5cm Coquimbo Flat vs. 5 cm Coquimbo 2.5cm vs. 5 cm	-1.043 -0.985 0.059	-3.953 -3.719 0.307	0.002 0.006 >0.05
Site (Location)	1	60.3	8835.4	>0.05				

Complexity x Location	26	1049.1	7786.2	0.002				
Complexity x Site (Location)	2	70.1	7716.2	>0.05				
Sessile invertebrate percentage cover								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	974.700	18339.700	<0.001	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-1.722 -2.055 -0.326	-2.142 -2.600 0.176	0.042 0.026 >0.05
Location	13	13156.000	5183.700	<0.001	Herzliya Flat vs. 2.5 cm, Herzliya Flat vs. 5 cm Herzliya 2.5cm vs. 5 cm	-0.983 -1.524 0.533	-1.242 -2.025 -1.014	0.043 0.011 >0.05
Site (Location)	1	253.900	4929.900	<0.001	Hobart Flat vs. 2.5 cm, Hobart Flat vs. 5 cm Hobart 2.5cm vs. 5 cm	-0.696 -0.596 0.100	-3.335 -2.806 0.572	0.003 0.014 >0.05
Complexity x Location	26	1069.500	3860.400	<0.001	Hong Kong Flat vs. 2.5 cm, Hong Kong Flat vs. 5 cm Hong Kong 2.5cm vs. 5 cm	-1.461 -1.845 -0.384	-4.274 -5.537 -1.982	0.001 <0.001 >0.05
Complexity x Site (Location)	2	113.800	3746.600	0.005	Plymouth Flat vs. 2.5 cm, Plymouth Flat vs. 5 cm Plymouth 2.5cm vs. 5 cm	-0.648 -0.503 0.145	-4.161 -3.170 1.099	0.001 0.005 >0.05
					Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	-0.137 -0.966 -0.830	-0.671 -5.507 -4.969	>0.05 <0.001 <0.001
Mobile invertebrate abundance								
Factor	df	Deviance Residual	Deviance	P-value	Post-hoc tests	Estimate	Z-value	P-value
Complexity	2	1112.26	1418.120	<0.001	Arraial do Cabo Flat vs. 2.5 cm Arraial do Cabo Flat vs. 5 cm Arraial do Cabo 2.5 cm vs. 5 cm	-0.399 -1.632 -0.233	-1.185 -1.886 -0.723	>0.05 0.015 >0.05

Location	13	893.910	524.220	<0.001	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-1.959 -2.745 -0.791	-6.186 -8.473 -2.483	<0.001 <0.001 0.035
Site (Location)	1	13.370	510.850	<0.001	Coquimbo Flat vs. 2.5cm Coquimbo Flat vs. 5 cm Coquimbo 2.5cm vs. 5 cm	-1.395 -1.502 -0.108	-3.662 -3.964 -0.318	0.001 0.002 >0.05
Complexity x Location	26	97.330	413.520	<0.001	East London Flat vs. 2.5cm East London Flat vs. 5 cm East London 2.5cm vs. 5 cm	-0.781 -1.516 -0.735	-2.161 -4.295 -2.203	>0.05 0.001 >0.05
Complexity x Site (Location)	2	4.560	408.960	>0.05	Hobart Flat vs. 2.5 cm, Hobart Flat vs. 5 cm Hobart 2.5cm vs. 5 cm	1.609 -0.862 -2.470	4.847 -2.743 -7.491	<0.001 0.017 <0.001
					Hong Kong Flat vs. 2.5 cm, Hong Kong Flat vs. 5 cm Hong Kong 2.5cm vs. 5 cm	-0.936 -1.402 -0.466	-2.622 -3.890 -1.368	0.023 0.001 >0.05
					Keelung Flat vs. 2.5 cm, Keelung Flat vs. 5 cm Keelung 2.5cm vs. 5 cm	-1.202 -1.446 -0.244	-3.273 -3.966 -0.712	0.003 0.001 >0.05
					Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	-0.654 -1.011 -0.358	-1.958 -3.053 -1.105	>0.05 0.007 >0.05

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3 **Supplementary S6: Effects of adding topographic complexity (Flat, 2.5 cm or 5 cm) on the abundances of the nineteen CATAMI groups**
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7 Filamentous/filiform macroalgae percentage cover was less on the 5cm and 2.5 cm complex tiles than on the flat tiles at two locations
8 (Coquimbo and Keelung), but greater on the 5 cm complex tiles than the flat tiles at one location (Sydney). Foliose macroalgae percentage cover
9 was less on the 5 and 2.5 cm complex tiles than on the flat tiles at three sites (Auckland 1, Coquimbo 1, East London 1), but greater on the 2.5
10 cm complex than flat tiles at three sites (Hobart 1, Plymouth 1 and Sydney 1) and on the 5 cm complex tiles compared with the flat tiles at one
11 site (East London 2). Encrusting macroalgae displayed location-specific positive effects of habitat structure, displaying greater percentage cover
12 on the 2.5 cm and 5 cm complex tiles than the flat tiles at one location (Arraial do Cabo) and on the 5 cm complex tiles relative to the flat tiles at
13 an additional two locations (East London and Sydney).
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25 Bryozoans, sessile molluscs and sessile worms each displayed greater percentage cover on 5 cm complex, and in some instances, also 2.5 cm
26 complex than flat tiles, at a subset of sites or locations. For bryozoans, such patterns were significant for three locations (Herzliya, Plymouth and
27 Sydney), for sessile molluscs they were significant for seven locations (Auckland, Chesapeake Bay, Hobart, Hong Kong, Plymouth, Ravenna
28 and Sydney) and for sessile worms, for five locations (Arraial do Cabo, Auckland, Herzliya, Keelung and Sydney). Additionally, sessile
29 crustacean percentage cover was greater on the 5 cm and 2.5 cm complex tiles than the flat tiles at eight locations (Arraial do Cabo, Auckland,
30 Coquimbo, Herzliya, Hobart, Hong Kong, Plymouth and Ravenna), while sessile crustacean cover was lower on the flat tiles than the 5 cm and
31 2.5 cm complex tiles at two locations (San Francisco and Sydney).
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5 Mobile crustacean abundance was greater on the 2.5 cm and 5 cm complex tiles than the flat tiles at nine sites (Auckland 1, Auckland 2,
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7 Chesapeake Bay 1, Chesapeake Bay 2, Hong Kong 1, Hong Kong 2, Keelung 2, Sydney 1 and Sydney 2). At two sites (Chesapeake Bay 1 and
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9 Sydney 1) the mobile crustacean abundance was greater on the 5 cm tiles than the 2.5 cm and flat tiles. Finally, at two sites mobile crustacean
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11 abundance was lower either the 2.5 cm or 5 cm than the flat tiles (Hobart 1 and San Francisco 1, Supplementary S6). Mobile mollusc abundance
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13 was greater on the 2.5 cm and 5 cm complex tiles than the flat tiles at eight locations (Arraial do Cabo, Auckland, Coquimbo, East London,
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15 Hobart, Hong Kong, Keelung, and Sydney), but there were fewer mobile molluscs on the 2.5 cm and 5 cm than the flat tile stiles at one location
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17 (San Francisco). Mobile worms similarly displayed greater abundances on 5 cm complex than the flat tiles at four locations (Auckland,
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19 Chesapeake Bay and Sydney).
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27 **Table S6a:** Results of multivariate and univariate mixed effects models testing the effects of complexity (flat, 2.5 cm or 5 cm) location (14
28 levels) and sites nested within location (1-2 levels) on the abundances of the nineteen CATAMI groups, sampled destructively at 12 months. The
29 surface area of the tiles sampled (offset) was also included in the model. Detail of significant post-hoc tests are shown.

Fixed	Residual df	df diff	Dev	P- value	Post-hoc tests			
Multivariate								
Intercept	373.000							
Complexity	371.000	2	145.000	0.001				
Location	358.000	13	3510.000	0.001				
Site (Location)	333.000	25	868.000	0.001				
Complexity x Location	307.000	26	478.000	0.001				

Complexity x Site (Location)	293.000	50	354.000	0.001				
Univariate								
Algal mats								
Complexity			0.602	>0.05				
Location			225.091	>0.05				
Site (Location)			13.929	>0.05				
Complexity x Location			2.455	>0.05				
Complexity x Site (Location)			14.066	>0.05				
Macroalgae articulated calcareous								
Complexity			6.958	>0.05				
Location			81.927	0.001				
Site (Location)			31.469	0.001				
Complexity x Location			0.001	>0.05				
Complexity x Site (Location)			0.568	>0.05				
Macroalgae filamentous/filiform					Coquimbo Flat vs. 2.5cm	0.482	5.530	<0.001
					Coquimbo Flat vs. 5 cm	0.173	2.191	0.048
					Coquimbo 2.5cm vs. 5 cm	-0.309	-3.480	0.002
Complexity			0.14	>0.05	Keelung Flat vs. 2.5cm	0.673	9.047	<0.001
					Keelung Flat vs. 5 cm	0.745	9.927	<0.001
					Keelung 2.5cm vs. 5 cm	0.837	0.680	>0.05
Location			372.211	0.001	Sydney Flat vs. 2.5cm	1.617	0.010	>0.05
					Sydney Flat vs. 5 cm	-2.564	5.527	<0.001
					Sydney 2.5cm vs. 5 cm	-2.181	-0.011	>0.05
Site (Location)			38.877	0.001				
Complexity x Location			37.63	0.011				
Complexity x Site (Location)			34.375	0.034				
Macroalgae globose saccate								
Complexity			4.4	>0.05				
Location			10.029	>0.05				
Site (Location)			0.001	>0.05				

Complexity x Location			0.004	>0.05				
Complexity x Site (Location)			0.001	>0.05				
Macroalgae foliose					Auckland site 1 Flat vs. 2.5 cm,	1.521	1.607	0.025
					Auckland site 1 Flat vs. 5 cm	2.488	4.014	0.002
					Auckland site 1 2.5cm vs. 5 cm	0.967	1.560	>0.05
Complexity			0.37	>0.05	Coquimbo site 1 Flat vs. 2.5 cm,	1.332	2.279	0.049
					Coquimbo site 1 Flat vs. 5 cm	1.459	2.497	0.034
					Coquimbo site 1 2.5cm vs. 5 cm	0.128	0.217	>0.05
Location			336.885	0.001	East London site 1 Flat vs. 2.5 cm,	1.335	2.285	0.048
					cm,	1.607	2.750	0.017
					East London site 1 Flat vs. 5 cm	0.272	0.465	>0.05
					East London site 1 2.5cm vs. 5 cm	0.377	0.645	>0.05
					East London site 2 Flat vs. 2.5 cm,	-1.903	-3.256	0.003
					cm,	-2.280	-3.901	0.001
					East London site 2 Flat vs. 5 cm			
					East London site 2 2.5cm vs. 5 cm			
Site (Location)			104.858	0.001	Hobart site 1 Flat vs. 2.5 cm,	-1.190	-1.325	0.001
					Hobart site 1 Flat vs. 5 cm	0.378	0.647	>0.05
					Hobart site 1 2.5cm vs. 5 cm	0.568	0.971	>0.05
Complexity x Location			27.377	0.080	Plymouth site 1 Flat vs. 2.5 cm,	-1.491	-2.552	0.029
					Plymouth site 1 Flat vs. 5 cm	-1.032	-1.766	>0.05
					Plymouth site 1 2.5cm vs. 5 cm	0.459	0.786	>0.05
Complexity x Site (Location)			42.402	0.012	Sydney site 1 Flat vs. 2.5 cm,	-1.673	-2.862	0.012
					Sydney site 1 Flat vs. 5 cm	-1.235	-2.112	>0.05
					Sydney site 1 2.5cm vs. 5 cm	0.439	0.750	>0.05
Macroalgae encrusting								
Complexity			0.557	>0.05	Arraial do Cabo Flat vs. 2.5 cm,	-0.756	-3.029	0.007
					Arraial do Cabo Flat vs. 5 cm	-1.675	-6.713	<0.001
					Arraial do Cabo 2.5cm vs. 5 cm	-0.920	-3.789	0.008
Location			212.209	0.001	East London Flat vs. 2.5 cm,	0.006	0.247	>0.05
					East London Flat vs. 5 cm	-0.703	-2.895	0.011

				East London 2.5cm vs. 5 cm	-0.763	-3.142	0.005
Site (Location)		64.698	0.001	Sydney Flat vs. 2.5 cm,	0.395	1.628	>0.05
				Sydney Flat vs. 5 cm	-0.625	-2.574	0.027
				Sydney 2.5cm vs. 5 cm	-1.020	-4.203	0.001
Complexity x Location		33.57	0.039				
Complexity x Site (Location)		24.096	>0.05				
Ascidians							
Complexity		5.859	>0.05				
Location		24.142	0.003				
Site (Location)		11.016	>0.05				
Complexity x Location		1.006	>0.05				
Complexity x Site (Location)		0.001	>0.05				
Bryozoans							
Complexity		6.948	>0.05	Herzliya Flat vs. 2.5 cm,	-0.849	-4.583	<0.001
				Herzliya Flat vs. 5 cm	-0.978	-5.280	<0.001
				Herzliya 2.5cm vs. 5 cm	-0.129	-0.697	>0.05
Location		61.313	0.001	Plymouth Flat vs. 2.5 cm,	-0.389	-2.965	0.009
				Plymouth Flat vs. 5 cm	0.074	0.561	>0.05
				Plymouth 2.5cm vs. 5 cm	0.462	3.527	0.001
Site (Location)		12.594	>0.05	Sydney Flat vs. 2.5 cm,	0.008	0.060	>0.05
				Sydney Flat vs. 5 cm	-0.302	-2.301	0.049
				Sydney 2.5cm vs. 5 cm	-0.309	-2.362	0.048
Complexity x Location		33.31	0.042				
Complexity x Site (Location)		0.001	>0.05				
Cnidarians							
Complexity		2.912	>0.05				
Location		15.64	>0.05				
Site (Location)		0.001	>0.05				
Complexity x Location		0.003	>0.05				
Complexity x Site (Location)		2.716	>0.05				
Sponges							

Complexity			6.795	>0.05				
Location			32.15	0.001				
Site (Location)			4.568	>0.05				
Complexity x Location			9.376	>0.05				
Complexity x Site (Location)			5.986	>0.05				
Sessile crustaceans					Arraial do Cabo Flat vs. 2.5 cm	-1.414	-6.182	<0.001
					Arraial do Cabo Flat vs. 5 cm	-1.295	-5.628	<0.001
					Arraial do Cabo 2.5 cm vs. 5 cm	0.119	0.880	>0.05
Complexity			6.447	>0.05	Auckland Flat vs. 2.5 cm	-1.394	-4.681	<0.001
					Auckland Flat vs. 5 cm	-1.385	-4.667	<0.001
					Auckland 2.5 cm vs. 5 cm	0.009	0.048	>0.05
Location			423.608	0.001	Coquimbo Flat vs. 2.5 cm	-1.034	-	<0.001
					Coquimbo Flat vs. 5 cm	-0.962	12.915	<0.001
					Coquimbo 2.5 cm vs. 5 cm	0.073	-	>0.05
							11.965	
							1.258	
Site (Location)			137.372	0.001	Herzliya Flat vs. 2.5 cm,	-0.710	-1.937	>0.05
					Herzliya Flat vs. 5 cm	-0.896	-2.530	0.031
					Herzliya 2.5cm vs. 5 cm	-0.186	-0.665	>0.05
Complexity x Location			78.89	0.001	Hobart Flat vs. 2.5 cm,	-0.749	-	<0.001
					Hobart Flat vs. 5 cm	-0.550	11.586	<0.001
					Hobart 2.5cm vs. 5 cm	0.200	-8.237	0.007
							3.663	
Complexity x Site (Location)			73.151	0.001	Hong Kong Flat vs. 2.5 cm,	-1.646	-	<0.001
					Hong Kong Flat vs. 5 cm	-2.115	13.422	<0.001
					Hong Kong 2.5cm vs. 5 cm	-0.470	-	<0.001
							17.759	
							-7.515	
					Plymouth Flat vs. 2.5 cm,	-0.639	-	<0.001
					Plymouth Flat vs. 5 cm	-0.455	13.497	<0.001
					Plymouth 2.5cm vs. 5 cm	0.185	-9.369	<0.001
							4.562	

					Ravenna Flat vs. 2.5 cm, Ravenna Flat vs. 5 cm Ravenna 2.5cm vs. 5 cm	-1.251 0.107 1.359	-3.085 0.206 3.203	0.006 >0.05 0.004
					San Francisco Flat vs. 2.5 cm, San Francisco Flat vs. 5 cm San Francisco 2.5cm vs. 5 cm	0.708 0.251 -0.458	8.869 3.505 -5.274	<0.001 0.002 0.001
					Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	0.432 0.152 -0.280	5.385 2.061 -3.390	<0.001 >0.05 0.002
Sessile molluscs					Chesapeake Bay Flat vs. 2.5 cm Chesapeake Bay Flat vs. 5 cm Chesapeake Bay 2.5 cm vs. 5 cm	-0.704 -1.278 -0.574	-5.843 - 11.503 -6.736	<0.001 <0.001 <0.001
Complexity			22.979	0.001	Hobart Flat vs. 2.5 cm Hobart Flat vs. 5 cm Hobart 2.5 cm vs. 5 cm	2.450 -0.800 -3.249	3.324 -3.192 -4.510	0.003 0.004 <0.001
Location			295.64	0.001	Hong Kong Flat vs. 2.5 cm Hong Kong Flat vs. 5 cm Hong Kong 2.5 cm vs. 5 cm	-0.799 0.430 1.229	-3.943 1.621 5.279	0.002 >0.05 <0.001
Site (Location)			66.54	0.001	Plymouth Flat vs. 2.5 cm Plymouth Flat vs. 5 cm Plymouth 2.5 cm vs. 5 cm	17.820 -1.824 - 19.643	0.010 -4.165 -0.011	>0.05 0.001 >0.05
Complexity x Location			74.838	0.001	Ravenna Flat vs. 2.5 cm Ravenna Flat vs. 5 cm Ravenna 2.5 cm vs. 5 cm	-0.867 -1.252 -0.386	-2.510 -3.810 -1.604	0.033 0.004 >0.05
Complexity x Site (Location)			31.997	>0.05	Sydney Flat vs. 2.5 cm Sydney Flat vs. 5 cm Sydney 2.5 cm vs. 5 cm	-1.161 -2.245 -1.084	-9.724 - 20.482 - 16.128	<0.001 <0.001 <0.001
Sessile worms					Arraial do Cabo Flat vs. 2.5 cm	-2.644	-4.828	<0.001

					Arraial do Cabo Flat vs. 5 cm	-2.548	-4.653	<0.001
					Arraial do Cabo 2.5 cm vs. 5 cm	0.096	0.180	>0.05
Complexity		11.016	>0.05		Auckland Flat vs. 2.5 cm	-0.896	-1.682	>0.05
					Auckland Flat vs. 5 cm	-1.792	-3.272	0.003
					Auckland 2.5 cm vs. 5 cm	-0.897	-1.637	>0.05
Location		217.597	0.001		Herzliya Flat vs. 2.5 cm,	-0.293	-0.389	>0.05
					Herzliya Flat vs. 5 cm	-2.927	-3.439	0.002
					Herzliya 2.5cm vs. 5 cm	-1.372	-1.822	>0.05
Site (Location)		34.825	0.001		Keelung Flat vs. 2.5 cm,	-0.084	-0.132	>0.05
					Keelung Flat vs. 5 cm	-1.695	-1.091	0.049
					Keelung 2.5cm vs. 5 cm	-0.612	-0.960	>0.05
Complexity x Location		19.225	0.049		Sydney Flat vs. 2.5 cm,	-0.692	-1.150	>0.05
					Sydney Flat vs. 5 cm	-3.184	-5.290	<0.001
					Sydney 2.5cm vs. 5 cm	-2.492	-4.140	0.001
Complexity x Site (Location)		1.077	>0.05					
Mobile arthropods								
Complexity		4.388	>0.05					
Location		10.98	>0.05					
Site (Location)		3.005	>0.05					
Complexity x Location		0.004	>0.05					
Complexity x Site (Location)		0.001	>0.05					
Mobile crustaceans					Auckland site 1 Flat vs. 2.5 cm,	-0.846	-6.883	<0.001
					Auckland site 1 Flat vs. 5 cm	-1.091	-8.973	<0.001
					Auckland site 1 2.5cm vs. 5 cm	-0.246	-2.652	0.0218
					Auckland site 2 Flat vs. 2.5 cm,	-3.254	-7.142	<0.001
					Auckland site 2 Flat vs. 5 cm	-4.018	-8.909	<0.001
					Auckland site 2 2.5cm vs. 5 cm	-0.765	-7.331	<0.001
Complexity		3.460	>0.05		Chesapeake Bay site 1 Flat vs. 2.5	-0.828	-5.721	<0.001
					cm	-1.184	-8.611	<0.001
					Chesapeake Bay site 1 Flat vs. 5	-0.355	-3.478	0.001
					cm	-0.062	-0.727	>0.05
						-0.428	-5.534	<0.001

Complexity			4.572	>0.05				
Location			185.739	0.001				
Site (Location)			8.262	>0.05				
Complexity x Location			27.15	>0.05				
Complexity x Site (Location)			10.646	>0.05				
Mobile echinoderms								
Complexity			9.872	>0.05				
Location			49.061	0.001				
Site (Location)			14.939	0.045				
Complexity x Location			1.203	>0.05				
Complexity x Site (Location)			0.485	>0.05				
Mobile molluscs								
					Arraial do Cabo Flat vs. 2.5 cm	-0.411	-3.501	0.002
					Arraial do Cabo Flat vs. 5 cm	-0.629	-5.611	<0.001
					Arraial do Cabo 2.5cm vs. 5 cm	-0.219	-2.315	>0.05
Complexity			42.557	0.001	Auckland Flat vs. 2.5 cm	-2.405	-	<0.001
					Auckland Flat vs. 5 cm	-3.275	23.513	<0.001
					Auckland 2.5cm vs. 5 cm	-0.870	-	<0.001
							32.762	
							-	
							24.904	
Location			372.919	0.001	Coquimbo Flat vs. 2.5 cm	-1.870	-6.752	<0.001
					Coquimbo Flat vs. 5 cm	-1.901	-6.897	<0.001
					Coquimbo 2.5 cm vs. 5 cm	-0.031	-0.223	>0.05
Site (Location)			167.937	0.001	East London Flat vs. 2.5 cm	-0.758	-3.498	0.002
					East London Flat vs. 5 cm	-1.691	-8.700	<0.001
					East London 2.5 cm vs. 5 cm	-0.933	-6.559	<0.001
Complexity x Location			62.217	0.001	Hobart Flat vs. 2.5 cm	-2.072	-4.367	<0.001
					Hobart Flat vs. 5 cm	-2.088	-4.407	<0.001
					Hobart 2.5 cm vs. 5 cm	-0.016	-0.073	>0.05
Complexity x Site (Location)			62.142	0.001	Hong Kong Flat vs. 2.5 cm	-0.919	-3.978	0.002
					Hong Kong Flat vs. 5 cm	-1.428	-6.518	<0.001
					Hong Kong 2.5 cm vs. 5 cm	-0.509	-3.253	0.004

					Keelung Flat vs. 2.5 cm	-1.378	-6.296	<0.001
					Keelung Flat vs. 5 cm	-1.652	-7.761	<0.001
					Keelung 2.5 cm vs. 5 cm	-0.274	-2.149	>0.05
					San Francisco Flat vs. 2.5 cm	0.597	4.370	<0.001
					San Francisco Flat vs. 5 cm	0.912	5.830	<0.001
					San Francisco 2.5 cm vs. 5 cm	0.316	1.805	>0.05
					Sydney Flat vs. 2.5 cm	-0.485	-3.101	0.006
					Sydney Flat vs. 5 cm	-0.894	-6.132	<0.001
					Sydney 2.5 cm vs. 5 cm	-0.410	-3.303	0.003
Mobile worms					Auckland Flat vs. 2.5 cm	-0.889	-1.840	>0.05
					Auckland Flat vs. 5 cm	-2.399	-5.619	<0.001
					Auckland 2.5cm vs. 5 cm	-1.510	-1.510	<0.001
Complexity			4.329	>0.05	Chesapeake Bay Flat vs. 2.5 cm	-0.748	-8.064	<0.001
					Chesapeake Bay Flat vs. 5 cm	-1.142	-	<0.001
					Chesapeake Bay 2.5cm vs. 5 cm	-0.394	13.071	<0.001
							-5.904	
Location			247.461	0.001	Hobart Flat vs. 2.5 cm	1.892	8.986	<0.001
					Hobart Flat vs. 5 cm	-0.647	-6.875	<0.001
					Hobart 2.5cm vs. 5 cm	-2.539	-	<0.001
							12.465	
Site (Location)			100.516	0.001	Sydney Flat vs. 2.5 cm	16.008	0.009	>0.05
					Sydney Flat vs. 5 cm	-2.623	-2.534	0.031
					Sydney 2.5cm vs. 5 cm	-	-0.010	>0.05
						18.631		
Complexity x Location			42.496	0.005				
Complexity x Site (Location)			8.138	>0.05				

Supplementary S7: Correlates of spatial variation in effects of topographic complexity

Table S7a: Effects of tidal zone (high, mid or low) on the SMD of taxa richness (total, sessile invertebrate and mobile invertebrate) and the abundances of CATAMI groups between the 5 cm complex tile relative to flat tiles. Effects are significant if confidence intervals do not overlap zero. The overall estimates are based on the destructive sampling at 12 months. ns >0.05, * <0.05, **<0.01, ***<0.001. Details of significant post-hoc tests are shown.

Factor	Estimate	SE	Z-value	P-value	Lower CI	Upper CI	Post-hoc tests	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Total richness													
High	0.9226	0.5013	1.8405	>0.05	-0.0599	1.9052	Mid vs. Low	1.4521	1.0311	1.4083	>0.05	-0.5688	3.4729
Mid	1.4528	0.2693	5.3939	<0.001	0.9249	1.9807							
Low	2.9121	0.9256	3.1451	0.017	1.0979	4.7263							
Algal richness													
High	0.5699	0.5824	0.9784	>0.05	-0.5717	1.7114	NA						
Mid	0.4412	0.2703	1.6319	>0.05	-0.0887	0.9711							
Low	-0.1523	0.7412	-0.2055	>0.05	-1.6050	1.3003							
Sessile invertebrate richness													
High	0.6952	0.4255	1.6337	>0.05	-0.1388	1.5292	Mid vs. Low	1.5013	0.7704	1.9488	0.0413	0.009	3.0112
Mid	0.9344	0.2181	4.2842	<0.001	0.5069	1.3619							
Low	2.4343	0.7573	3.2144	0.0013	0.9599	3.9185							
Mobile invertebrate richness													
High	0.5387	0.5166	1.0428	>0.05	-0.4737	1.5511	Mid vs. Low	2.1599	1.0393	2.0781	0.0377	0.1228	4.1970
Mid	1.3963	0.2716	5.1414	<0.001	0.8640	1.9286							

Low	3.5630	0.9623	3.7026	0.0002	1.6769	5.4491							
Filamentous algae cover													
High	0.0509	0.4647	0.1095	>0.05	-0.8599	0.9617	NA						
Mid	-0.4937	0.3211	-1.5378	>0.05	-1.1230	0.1355							
Low	-1.3929	0.5227	-2.6648	0.0077	-2.4173	-0.3684							
Foliose algae cover													
High	0.5611	0.5140	1.0917	>0.05	-0.4462	1.5684	NA						
Mid	-0.2180	0.2120	-1.0279	>0.05	-0.6336	0.1976							
Encrusting algae cover													
High	1.2050	0.5840	2.0633	0.0391	0.0603	2.3496	NA						
Mid	-0.3078	0.5155	0.5972	>0.05	-1.3181	0.7025							
Low	0.2582	0.9018	0.2864	>0.05	-1.5093	2.0258							
Sessile bryozoans cover													
High	0.5317	0.3825	1.3899	>0.05	-0.2181	1.2815	NA						
Mid	0.5862	0.3935	1.4898	>0.05	-0.1850	1.3574							
Sessile bivalves cover													
High	0.6455	0.5450	1.1842	>0.05	-0.4228	1.7137	NA						
Mid	0.8845	0.3289	2.6892	0.0072	0.2399	1.5291							
Low	0.4539	0.9639	0.4710	>0.05	-1.4352	2.3431							
Sessile crustaceans cover													
High	1.2446	0.7538	1.6512	>0.05	-0.2327	2.7220	NA						
Mid	1.0458	0.4014	2.6056	0.0092	0.2591	1.8326							
Low	0.6784	1.3261	0.5116	>0.05	-1.9208	3.2775							
Sessile worms cover													

High	1.3851	0.3618	3.8290	0.001	0.6761	2.0942	Mid vs. High	-0.4009	0.4684	-0.8559	>0.05	-1.3189	0.5171
Mid	0.9843	0.2975	3.3084	0.009	0.4012	1.5674							
Low	0.4168	0.6660	0.6259	>0.05	-0.8884	1.7221							
Mobile crustaceans abundance													
High	0.9771	0.3880	2.5182	0.0118	0.2166	1.7376	Mid vs. High	0.1071	0.5265	0.2034	>0.05	-0.9249	1.1391
Mid	0.7937	0.2048	3.8757	<0.001	0.3923	1.1951							
Low	0.9008	0.4851	1.8571	>0.05	-0.0499	1.8515							
Mobile molluscs abundance													
High	1.1896	0.5121	2.3232	0.0202	0.1860	2.1932	Mid vs. High	-0.0604	0.5708	-1.058	>0.05	-1.1792	1.0585
Mid	1.1292	0.2523	4.4754	<0.001	0.6347	1.6237	Mid vs. Low	1.0775	0.7709	1.3978	>0.05	-0.4334	2.5884
Low	2.2068	0.7298	3.0237	0.0025	0.7764	3.6372	High vs. Low	1.0135	0.9041	1.1210	>0.05	-0.7585	2.7855
Mobile worms abundance													
High	0.6601	0.3776	1.7482	>0.05	-0.0800	1.4002	NA						
Mid	1.0911	0.2726	4.0032	<0.001	0.5569	1.6253							
Low	1.1885	0.6860	1.7324	>0.05	-0.1561	2.5330							

Table S7b: Effects of distance from the nearest boating facility or marina (km) on the SMD of taxa richness (total, sessile invertebrate and mobile invertebrate) and the abundances of the CATAMI groups between the 5 cm complex tile relative to flat tiles. Effects are significant if confidence intervals do not overlap zero. The overall estimates are based on the destructive sampling at 12 months. ns >0.05, * <0.05, **<0.01, ***<0.001.

Factor	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Total richness						
Distance	0.0177	0.163	0.1080	>0.05	-0.3029	0.3383

Algal richness						
Distance	-0.1303	0.1249	-1.0431	>0.05	-0.3751	0.1145
Sessile invertebrate richness						
Distance	0.2444	0.1221	2.0015	0.0453	0.0051	0.4838
Mobile invertebrate richness						
Distance	-0.0882	0.6634	-0.6281	>0.05	-1.7170	0.8836
Filamentous algae cover						
Distance	-0.4167	0.5215	0.1011	>0.05	-0.9694	1.0748
Foliose algae cover						
Distance	-0.3182	0.1885	-1.6878	>0.05	-0.6877	0.0513
Encrusting algae cover						
Distance	-0.7614	0.7544	-1.0092	>0.05	-2.2400	0.7173
Sessile bryozoans cover						
Distance	0.0390	0.1265	0.3083	>0.05	-0.2089	0.2869
Sessile bivalves cover						
Distance	0.1886	0.1759	1.0723	>0.05	-0.1561	0.5334
Sessile crustaceans cover						
Distance	1.0636	-0.2457	-1.1955	>0.05	-0.6486	0.1571
Sessile worms cover						
Distance	0.0691	0.1212	0.5702	>0.05	-0.1685	0.3068
Mobile crustaceans abundance						
Distance	0.0416	0.1241	0.3348	>0.05	-0.2017	0.2849
Mobile molluscs abundance						
Distance	0.0697	0.1649	0.4226	>0.05	-0.2535	0.3928
Mobile worms abundance						
Distance	0.1488	0.1373	1.0844	>0.05	-0.1202	0.4179

Table S7c: Effects of absolute latitude on the SMD of taxa richness (total, algae, sessile invertebrate and mobile invertebrate) and the abundances of the CATAMI groups between the 5 cm complex tile relative to flat tiles. Effects are significant if confidence intervals do not overlap zero. The overall estimates are based on the destructive sampling at 12 months. ns >0.05, * <0.05, **<0.01, ***<0.001.

Factor	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Total richness						
Absolute latitude	-0.0139	0.0066	-2.1242	0.0336	-0.0268	-0.0011
Algal richness						
Absolute latitude	-0.0079	0.0211	-0.3756	>0.05	-0.0492	0.0334
Sessile invertebrate richness						
Absolute latitude	-0.0148	0.0336	0.5437	>0.05	-0.0476	0.0841
Mobile invertebrate richness						
Absolute latitude	0.0183	0.6634	-0.6281	>0.05	-1.7170	0.8836
Filamentous algae cover						
Absolute latitude	0.0032	0.0350	0.0925	>0.05	-0.0653	0.0718
Foliose algae cover						
Absolute latitude	0.0562	2.1948	0.0256	>0.005	-0.0060	0.1063
Encrusting algae cover						
Absolute latitude	-0.0320	0.0223	-1.4341	>0.05	-0.0757	0.0117
Sessile bryozoans cover						
Absolute latitude	0.0257	0.0159	1.6207	>0.05	-0.0054	0.0568
Sessile bivalves cover						
Absolute latitude	0.0411	0.0225	1.8217	0.0485	0.0031	0.0852
Sessile crustaceans cover						
Absolute latitude	-0.0448	0.0284	-1.5750	>0.05	-0.1005	0.0109
Sessile worms cover						
Absolute latitude	0.0185	0.0171	1.0834	>0.05	-0.0149	0.0519
Mobile crustaceans abundance						
Absolute latitude	-0.0048	0.0188	-0.2556	>0.05	-0.0417	0.0321
Mobile molluscs abundance						
Absolute latitude	-0.0402	0.0215	-1.8664	0.0420	-0.0823	0.0020
Mobile worms abundance						
Absolute latitude	-0.0272	0.0208	-1.3062	>0.05	-0.0680	0.0136

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