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Aim

Topographic complexity is widely accepted as a key driver of biodiversity, but at the patch-scale, complexity-biodiversity relationships may vary spatially and temporally according to the environmental stressors complexity mitigates, and the species richness and identity of potential colonists. Using a manipulative experiment, we assessed spatial variation in patch-scale effects of complexity on intertidal biodiversity.

Location

27 sites within 14 estuaries/bays distributed globally

Time period

2015-2017

Major taxa studied

Functional groups of algae, sessile and mobile invertebrates

Methods

Concrete tiles of differing complexity (flat; 2.5 cm or 5 cm complex) were affixed at low-high intertidal elevation on coastal defence structures, and the richness and abundance of the colonising taxa were quantified after 12 months.

Results

The patch-scale effects of complexity varied spatially and among functional groups. Complexity had neutral to positive effects on total, invertebrate and algal taxa richness, and invertebrate abundances. However, effects on the abundance of algae ranged from positive to negative, depending on location and functional group. The tidal elevation at which tiles were placed accounted for some variation. The total and invertebrate richness were greater at low or mid than at high intertidal elevations. Latitude was also an important source of spatial variation, with the effects of complexity on total richness and mobile mollusc abundance greatest at lower latitudes, whilst the cover of sessile invertebrates and sessile molluscs responded most strongly to complexity at higher latitudes.

Conclusions

After 12 months, patch-scale relationships between biodiversity and habitat complexity were not universally positive. Instead, the relationship varied among functional groups and according to local abiotic and biotic conditions. This result challenges the assumption that effects of complexity on biodiversity are universally positive. The variable effect of complexity has ramifications for community and applied ecology, including eco-engineering and restoration that seek to bolster biodiversity through the addition of complexity.

Introduction:

Habitat complexity the physical structure of environments, is a key driver of variability in the distribution of biodiversity (Huston, 1979; Kovalenko, Thomaz, & Warfe, 2012). In general, more complex habitats, with a greater density of spatial elements, support greater species richness and abundance, across a range of functional groups, than less complex habitats (McCoy & Bell, 1991; Stein, Gerstner, & Kreft, 2014). Habitat complexity may be derived from both topographic (e.g. undulations, depressions, and protrusions) or biogenic (e.g., trees, grasses, seaweeds, ants, corals and bivalves) structures. Complex habitats can influence the colonisation and subsequent survival of species by determining the area available for organisms to occupy (Connor & McCoy, 1979), which in turn can influence biotic interactions (Hixon & Beets, 1993; Holt, 1987). Complex habitats can also have area-independent effects on niche diversity (Johnson, Frost, Mosley, Roberts, & Hawkins, 2003), and consequently the availability of refuges from environmental stressors and predators (Strain, Cumbo, Morris, Steinberg, & Bishop, 2020). At land- and sea-scape scales complexity enhances biodiversity by increasing habitat heterogeneity and niche space

(Kovalenko, Thomaz, & Warfe, 2012). However, at smaller scales, biodiversity and habitat complexity relationships may vary depending on the type of complexity provided and how it interacts with the environmental and biological setting (Loke & Todd, 2016).

The environmental variation among sites at local and biogeographic scales may influence patch-scale habitat complexity (hereafter complexity) - biodiversity relationships by determining resource availability, environmental conditions, as well as the species pool on which complexity can act (Johnson et al., 2003); Bracewell et al., 2018). The stress gradient hypothesis (Bertness & Callaway, 1994) proposes that positive interactions among species (e.g. between habitat-forming and dependent taxa) will be most prevalent in environmentally stressful environments, where local habitat amelioration is critical to organismal survival (Bracewell, Clark, & Johnston, 2018; McAfee, Cole, & Bishop, 2016). Hence, microhabitats that ameliorate extreme temperatures and/or desiccation stressors could increase in importance with increasing tidal elevation (Bateman & Bishop, 2016) and decreasing latitude (Bracewell et al., 2018). Conversely, the patch-scale effects of complexity may be consistent across latitude if the local species are adapted to their local conditions or could have a greater influence in locations where there is a greater difference between the air and sea temperatures.

Additionally, complexity may be expected to have greatest patch-scale effects on biodiversity in environments where there is a diverse species pool on which it can act, whereby, the effects of complexity may vary across latitudinal gradients in species richness (Bracewell et al., 2018). At local scales, anthropogenic stressors such as contaminants may over-ride the effects of complexity where they create conditions that are inhibitory to the survival of most species (Mayer-Pinto, Matias, & Coleman, 2016). How species abundance and, hence, richness responds to complexity may also vary according to the dominant functional groups present at a given location (Strain, Olabarria, et al., 2018). Functional groups, defined here as groups of organisms displaying distinct life-forms, that differ in their niche requirements, tolerance to environmental stressors, and susceptibility to predation (Micheli & Halpern, 2005). While, overall, increasing complexity is expected to enhance microhabitat diversity and niche space, the availability of some microhabitat types will decline and others will increase with different types of complexity (Kelaher, 2003).

The taxa whose niche requirements are favoured by increasing complexity will benefit at the expense of other taxa whose niches match microhabitats that decline in abundance or area (Malumbres-Olarte, Vink, Ross, Cruickshank, & Paterson, 2013). For example, on intertidal rocky shores, algae can be among the dominant space occupants of well-lit yet wet microhabitats (e.g. rockpools), that prevent desiccation, and allow adequate light for photosynthesis (Wilson, James, Newman, & Myers, 1992). In contrast, mobile invertebrates, particularly sessile invertebrates benefit from microhabitats (e.g. crevices) that provide protection from predators, but are also sufficiently shaded that their algal competitors cannot survive (Glasby, 1999; Miller & Etter, 2008). Stress-sensitive taxa may benefit more than stress-tolerant taxa from microhabitats that ameliorate environmental stressors (Darling et al., 2017). Similarly, taxa that are more susceptible to predation (i.e. lack morphological or behavioural defences) or have body sizes that most closely match the size of the microhabitats may benefit most from complexity-mediated predator amelioration (Strain, Morris, et al., 2018). Experimental research on the effects of increasing complexity on different functional groups (i.e. algae, sessile invertebrates, and mobile invertebrates) is lacking (but see Strain et al. 2020).

Few studies have examined the effects of complexity at large spatial scales, across functional groups and the influence of varying environmental contexts, to test the generality of patch-scale complexity-biodiversity relationships. Understanding how complexity underpins richness and abundance of different taxa and functional groups across a range of environmental conditions is of particular importance, given accelerating habitat loss and homogenisation (Kovalenko et al., 2012). In urban marine environments, natural habitats are being replaced by artificial structures (e.g. seawalls, groynes, breakwaters and wharves) with reduced complexity (Airoldi, Connell, & Beck, 2009; Bulleri & Chapman, 2010). Such habitat homogenisation often occurs simultaneously with other anthropogenically-derived environmental changes, such as pollution and/or species invasions (McKinney, 2008). The smooth, relatively homogenous, surfaces of artificial structures typically support fewer native species and individuals (Chapman, 2003), but more non-native species (Airoldi & Bulleri, 2011) compared to the more complex natural habitats they replace.

There has been increasing interest in how complexity might be incorporated into the design of marine urban structures so as to enhance their ecological value (O'Shaughnessy et al., 2020). The addition of complexity to topographically homogenous marine urban structures has been proposed as a mechanism by which the overall richness and abundances of key functional groups might be enhanced (Strain et al. 2018). However, the manner in which complexity acts will be context dependent and researchers have recommended that latitudinal and biogeographic considerations are taken into account prior to design or construction (Mayer-Pinto, Dafforn, & Johnston, 2019).

Using standardised experiments on a global scale, we investigated how manipulating one form of complexity (crevices/ridges) on tiles affected the richness and abundance of colonising taxa at fourteen urban estuaries or bays spread across nine biogeographic realms. We predicted that patch-scale complexity would have a positive influence on the taxa richness and abundances of all sessile and mobile invertebrates functional groups but not algae, which have higher light requirements, because of greater shading in the crevices (Strain et al., 2020). Furthermore, we expected that the positive effects of increased complexity on richness and abundances of sessile and mobile invertebrates would increase with tidal elevation and with decreasing latitude, as desiccation stress and extreme high temperatures increase, respectively. Finally, we hypothesised that complexity would have a reduced effect on the richness and abundances of sessile and mobile invertebrates in highly polluted environments such as those located near marinas or ports, where the effects of pollution can over-ride the effects of complexity (Mayer-Pinto et al. 2018).

Materials and methods

Study sites

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

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

Experimental design

At each site, 0.25×0.25 m concrete tiles were affixed to the coastal defence structures (i.e. seawalls, or breakwaters). The tiles allowed manipulation of intertidal habitat complexity by provisioning crevices and ridges as well as associated increase in surface area. The tiles, designed and manufactured by Reef Design Lab (Melbourne, Australia), were flat (surface area = 0.0625 m^2), had 0.025 m high ridges separated by 0.015 to 0.05 m wide crevices (hereafter '2.5 cm complex'; surface area = 0.090 m^2) or had 0.05 m high ridges, each separated by 0.015 to 0.05 m wide crevices (hereafter '5 cm complex'; surface area = 0.136 m^2; Fig. 2). At each site, five tiles of each design were either directly attached to the structures, in the centre of 0.3×0.3 m patches cleared of pre-existing flora and fauna, or attached to wood backing boards that were suspended off the top of the structures using rope or nails. Tiles were attached to the structures, backing boards or steel frames using bolts that were placed through a drilled hole in two to four corners of the tiles. At each site, the tiles were deployed in a single horizontal row, from a low to high intertidal elevation, depending on the location. Tiles were deployed in random order with respect to the experimental treatments, with the complex tiles positioned so that the crevices and ridges were orientated vertically. In temperate locations, the tiles were deployed between early spring to late autumn during the period of greatest species recruitment and growth (Table S1).

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

Colonising taxa

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

Environmental parameters

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

For tidal elevation we recorded the inundation period (proportion of time underwater) of the tiles using a pressure logger. At each site, one pressure logger was attached to the top of a flat tile and programmed to record water depth every 20 min for a period of one-month. Measurements were made using either a Sensus Ultra (Reefnet Pty Ltd; +/- 0.03 m accuracy), a Hobo Onset (Onsetcomp; +/- 0.02 m accuracy) or EasyTREK SP-300 (NIVELCO; +/- 0.05% of the measured range accuracy). Based on these measurements, the tidal elevation was categorised as either high (inundated for <33% of the tidal cycle), mid (inundated for >34 to 65% of the tidal cycle) or low (inundated for >66% of the tidal cycle; Supplementary S1).

Throughout the 12-month experiment, we took measurements of temperature at 21 sites (Supplementary S1). At each site, we deployed three DS1921G Themochron iButton data loggers (Thermodata Pty. Ltd. Warrnambool, Australia) haphazardly on flat tiles. The iButtons were waterproofed with Plastidip rubber coating (Plasti Dip International, Blaine, Minnesota, USA). The iButtons were programmed to record temperatures at 20 min intervals, across a one-month period, with 0.5ºC accuracy. The iButtons were attached to the tiles using cable ties so that they could easily be removed, downloaded, and replaced each month. Mean (both aerial and in water), maximum (aerial) and minimum (aerial) temperature were negatively correlated with absolute latitude at the 21 sites (Supplementary S4). Hence, to avoid issues with collinearity between these two predictor variables, subsequent analyses were run only on latitude of study sites.

At the end of the experiment, we measured the distance from the centre of each site to the nearest boating facility (port or marina) using satellite images in Google Earth. For 17 sites, we also obtained information on the concentration of copper from sediment sampling (Supplementary S1). Increasing distance of study sites to the nearest boating facility was negatively correlated (but not significantly) with the amount of copper (historically used as an antifouling agent; Dafforn et al. 2011) in sediment at the 17 sites for which both sets of data were available (Supplementary S4). Hence, distance to the nearest boating facility, which could be measured for all 27 sites, was used as a proxy for contamination.

Analyses

We used multivariate generalised linear modelling to test the effects of complexity (fixed, 3 levels: flat, 2.5 cm or 5 cm), location (fixed, 14 levels) and site nested within location (fixed 1-2 levels) on the abundances of each of the 19 CATAMI groups. These data were modelled using a negative binomial distribution due to overdispersion from the Poisson distribution. Where multivariate analyses indicated a significant main effect of treatment, or an interaction of treatment with location or site(location) univariate post hoc test statistics and p-values were calculated for each group separately adjusting for multiple comparisons. For those groups found to have significant effects of treatment (either occurring independently of or interacting with spatial factors), pairwise differences between treatment levels, were assessed using univariate linear models (LMs). Where both the treatment × location and treatment × site (location) were significant, only the treatment × location interaction was interpreted as its significance demonstrates effects of location that are apparent over smaller site-scale variability. Similarly, we used LMs or generalised linear models (GLMs) with the factors complexity, location and site nested within location to compare the richness and abundances (cover or counts) of total taxa, algae, sessile invertebrates and mobile invertebrates across treatments, at 12 months.

To test hypotheses about whether the effects of complexity on the richness and abundances of the key functional groups on the tiles, varied by tidal elevations, latitude and distance from the nearest marina or port, we used analyses on the standard mean difference (SMD) between the 5 cm and flat tile. The Hedge's G SMD was calculated at the scale of site, using the average and standard deviation of the five tiles sampled within each site, for each treatment. We chose the SMD effect size rather than the log response ratio because these data contained many zeros (i.e. no species observed and/or no variance observed between replicates within the same treatment) (Borenstein, Hedges, Higgins, & Rothstein, 2010). We tested the effects of tidal zone, latitude and distance to the nearest marina or port using the Hedges random effects estimator (Hedges, 1981) with the package metafor (Viechtbauer, 2010). For the analyses testing the effects of tidal zone, we adjusted for the effects of location, by adding location as a moderator in a multilevel random effects model.

All statistical analyses were undertaken in R 3.5.0 (R Core Team, 2016). For all models we offset the sample area (m^2), to separate the effects of complexity from surface area. Generalised linear models were undertaken in the package MASS and figures were produced using the package ggplot 2 (Wickham, 2016). The multivariate analyses were undertaken with the packages mvabund and boral (Hui, 2016). All models were checked for over-dispersion and spatial and temporal autocorrelation with plots, and the residuals were visually inspected for heteroscedasticity. Where appropriate, post hoc comparisons were undertaken using the package emmeans (Lenth, Singmann, & Love, 2018) to identify sources of treatment effects.

Results

Effect of complexity on richness

The effect of complexity on total taxa richness and the richness of each of the three coarse-level functional groups (algae, sessile invertebrates, and mobile invertebrates) varied among locations (Fig. 3, Table 1, Supplementary S5). Where significant effects were seen, the 2.5 cm and/or the 5 cm complex tiles (i.e. with cervices/ridges) supported greater taxa richness than the flat tiles (Table 1). Total taxa richness was greater on the 5 cm complex tiles than the flat tiles (by 0.8 – 2.7 times) at 10 of the 14 locations and on the 2.5 cm complex relative to the flat tiles at eight locations, with no effect of complexity on total richness at four locations (Fig. 3, Table 1, Supplementary S5). Algal richness was greater on 5 cm complex tiles (by 1.1-2.4 times) than on the 2.5 cm complex tiles or the flat tiles at two locations, but displayed no significant effect of complexity at the other 12 locations (Table 1, Supplementary S5). Sessile invertebrates were more speciose on the 5 cm complex tiles than on flat tiles at nine locations (by 1.0-1.8 times), and more speciose on the 2.5 cm complex than flat tiles at seven locations, but did not differ among treatments at the other five locations (Table 1, Supplementary S5). There were more mobile species on the 5 cm complex tiles compared with the flat tiles at eight locations (1.0-2.4 times), and on the 2.5 cm complex tiles relative to flat tiles at five locations, with no significant differences for the other nine locations (Table 1, Supplementary S5).

Fig 3: Effect of complexity (flat and 2.5 cm or 5 cm complex tiles) on the mean (+/-SE) total taxa richness at each of fourteen locations by realm (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 '>' or '<', with 'ns' or '=' denoting treatments that did not significantly differ.

Table 1: Overview of the posthoc tests for significant complexity by location interactions in the total richness and the richness and abundance of functional groups. Significant differences (at α = 0.05) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are indicated by '>' or '<', with 'ns' or '=' denoting treatments that did not significantly differ. Locations are ordered by realm. Details of these analyses are given in Appendices S4.

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

Effect of complexity on abundances

The effects of complexity varied among functional groups (algae, sessile and mobile invertebrates) and the 19 CATAMI groups, and within these groupings, according to location and/or site (Table 1, Table 2, Supplementary S5-S6). The abundances (i.e. percentage cover or counts) of algae, sessile and mobile invertebrates (Table 1, Supplementary S5) as well as that of encrusting macroalgae, bryozoans, sessile and mobile crustaceans, sessile and mobile molluscs and sessile worms each displayed significant positive effects of the 2.5 cm and/or the 5 cm complex tiles relative to the flat tiles, at one or more locations, with non-significant effects at the remaining (Table 2, Supplementary S5).

The abundances of mobile crustaceans and mobile molluscs showed significant positive effects of either the 2.5 cm and/or 5 cm tiles compared with the flat tiles, at some sites, but these differences were not consistent between sites within locations (Tables 2, Supplementary S6). The effects of complexity were, among locations, spatially variable in both occurrence and direction for filamentous/filiform macroalgae cover and mobile worm abundances and between sites for foliose macroalgae cover (Table 2, Supplementary S6). Although present on tiles, globose saccate macroalgae, articulated calcareous macroalgae, ascidians, cnidarians, sponges, hexapods, arthropods and echinoderms displayed patterns in abundance that did not respond to complexity, at any of the sites or locations (Table 2, Supplementary S6).

Table 2: Overview of the posthoc tests for significant complexity by location or complexity by site(location) interactions in the abundance of CATAMI groups. Significant differences (at α = 0.05) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are denoted with '>' or '<', 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

Correlates of spatial variation in effects of complexity

The standard mean difference (SMD) of total, sessile invertebrate and mobile invertebrate richness, the percentage cover of filamentous/filiform macroalgae, encrusting algae, sessile bivalves, sessile crustaceans, sessile worms and the abundances of mobile worms on the 5 cm compared to the flat tiles varied significantly among tidal zones (Fig. 4, Supplementary S7). Significant differences in the SMDs were found in the mid and low tidal zone for each of total and sessile and mobile invertebrate richness and in the high, mid and low tidal zone for the abundances of mobile molluscs (Fig. 4, Supplementary S7). In contrast, the difference in the SMD was only significant in the high tidal zone for the percentage cover of encrusting algae and in the mid and high tidal zones for the percentage cover of sessile worms and the abundances of mobile crustaceans. The percentage cover of sessile bivalves and sessile crustaceans and the abundances of mobile worms displayed differences in the SMDs that were only significant in the mid-tidal zone and in the low tidal zone for the percentage cover of filamentous algae (Fig. 4, Supplementary S7).

The SMD in the richness of sessile invertebrate species between the 5 cm complex and flat tiles increased with distance from the nearest marina or port. However, the SMD for other groups was unaffected by this variable (Supplementary S7). The SMD of total taxa richness significantly decreased with latitude (Fig. 5), as did abundance of molluscs, while conversely, SMD of percentage cover of sessile bivalves increased with latitude (Supplementary S7). All other groups were unaffected by latitude (Supplementary S7).

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

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

Discussion

The incorporation of complexity into artificial structures is increasingly being advocated as a mechanism to maintain or enhance native biodiversity, but most studies to date have examined effects of complexity on marine built structures over a relatively narrow range of environmental conditions (reviewed by Strain et al. 2018). Our study, spanning 27 sites from 14 locations across the globe, provided the first experimental test of how effects of patch-scale complexity on artificial structures vary across very large spatial scales. After 12 months, complexity had positive effects on the richness and abundance of the colonising taxa at most (10 out of 14) of the locations tested. Nevertheless, the effects of complexity on the colonisation of individual functional groups, varied spatially according to tidal elevation and latitude. These results challenge the paradigm that environmental that complexity has universally positive effects on biodiversity (Huston, 1979) and instead support the growing assertion (Beck, 1998) that at the patch-scale effects of complexity on biodiversity can vary in magnitude and direction according to local abiotic and biotic stressors, niche requirements of the dominant taxa and the scale of complexity provided.

The study, which manipulated a single type of habitat complexity (crevices/ridges), was not designed to disentangle complexity effects arising from enhancement of surface area and microhabitat diversity. The complex tiles not only had greater surface area but, in providing crevices and ridges, provided greater microhabitat diversity than the flat tiles that had only a single microhabitat type. These crevices and ridges have previously been demonstrated to differ in light, humidity, temperature, and predator access (Strain et al. 2018; 2020), supporting distinct communities of algae and invertebrates (Strain et al. 2020). The spatially variable effects of crevices and ridges on biodiversity suggest that differences between complex and flat treatments did not simply reflect the greater surface area of the former, but also modification of environmental conditions and biological interactions by the microhabitats. Further, whereas differences were consistently found between complex and flat tiles, differences between the two complex treatments, with 5 cm or 2.5 cm deep cervices, were often absent, suggesting a greater role of microhabitat identity and diversity than surface area in driving the patterns.

Whereas effects of the complex tiles on the richness and abundance of invertebrate groups were, where present, positive, effects of the complex tiles on the richness and abundance of algae were highly variable, not only in occurrence, but also direction. The sessile invertebrate groups that responded most positively to the cervices and ridges provided by this study were taxa that are limited to shaded and moist low intertidal and subtidal shore (such as bryozoans) (Miller & Etter, 2008), and taxa commonly targeted by benthic predators (e.g. molluscs, crustaceans, worms) (Janssen, Sabelis, Magalhães, Montserrat, & Van der Hammen, 2007; Strain, Morris, et al., 2018). In contrast, the mobile invertebrates that responded positively were taxa that could rapidly colonise by migration from nearby habitats (e.g. mobile molluscs and crustaceans), (Martins, Thompson, Neto, Hawkins, & Jenkins, 2010). These taxa were predominantly found in the protective crevices of the complex tiles, suggesting that the provision of refugia could have played an important role (Strain et al., 2020). Filamentous and foliose macroalgae were negatively affected by complexity at some sites, despite the overall greater surface area of complex tiles. This may be because light in the crevices was insufficient to meet the needs of these taxa that have high light requirements (Markager & Sand-Jensen, 1992), or alternatively because of enhanced top-down control by the abundant grazer communities in the crevices. Encrusting algae, which have low light requirements (Markager & Sand-Jensen, 1992) and a tough thallus that deters grazers (Bertness, Yund, & Brown, 1983) were the only algal group to consistently respond positively to complexity.

Thermal and desiccation stress have long been implicated in setting the upper distributional limits of organisms intertidally (Harley, 2003; Wolcott, 1973) while classically, the lower distributional limits are thought to be set by biological interactions such as competition and predation (Connell, 1961). Consistent with this thinking and previous within-site comparisons of complexity-biodiversity relationships among elevations (Cordell et al. 2017), we found the effects of added complexity on taxa richness and abundance of colonising organisms differed among tidal elevations, as well as among functional groups. Total taxa richness and the richness of sessile and mobile invertebrates responded most strongly to complexity in the low intertidal zone, but the richness and abundances of algae, and abundances of sessile invertebrates responded more strongly in the mid and high intertidal zones. In the low intertidal, the crevices on complex tiles may provide refuge to invertebrate taxa from large-bodied marine predators, such as fish, which can exert considerable top-down control on the communities of coastal structures (Connell & Anderson, 1999) and/or from wave exposure that can challenge the attachment strength of organisms and interfere with feeding behaviour (Bulleri & Chapman, 2010; Moschella et al., 2005). In the high and mid intertidal, on artificial coastal defences as on natural rocky shores, cool and shaded crevices could influence the richness and abundances of algae and the abundances of invertebrates by providing refuge from extreme temperatures and desiccation at low tide (Chapman & Blockley, 2009; Strain et al., 2020).

Additionally, we found evidence for latitudinal variation in the effects of complexity on total taxa richness and the abundance of some invertebrate groups. Complexity had the greatest effects on the total richness of taxa and the abundances of mobile molluscs at low latitudes, where average temperatures, primary productivity as well as taxa richness and abundance are generally highest (Hillebrand, 2004). However, the cover of sessile molluscs displayed the reverse pattern of greater effects of complexity at higher latitudes, where average temperatures and the percentage cover of sessile invertebrates were lower. These results are consistent with other studies that have demonstrated positive effects of complexity on the richness or diversity of invertebrates at tropical latitudes in intertidal systems (Freestone & Osman, 2007; Menge & Lubchenco, 1981). Latitudinal variation in the effects of complexity likely reflects spatial variation in the local species pool, functional group identity and species recruitment, predation, and growth rates.

Despite our hypothesis that pollutants would override the effects of complexity, proximity of sites to marinas and port facilities, which are commonly highly contaminated (Adamo et al., 2005; Rivero, Dafforn, Coleman, & Johnston, 2013), explained little of the variation in effects of complexity for most groups of algae and invertebrates. There was, however, a positive effect of the distance to the nearest port or marina on the relationship between complexity and richness of sessile invertebrates. Although our study did not document spatial variation in the size of the species pool of available colonists, the positive relationship between distance from boating facilities and effects of complexity on sessile invertebrates is consistent with the contaminants associated with boating facilities adversely impacting the native species pool on which complexity can act. Heavy metals, such as copper, either historically or presently used in antifouling paints, can negatively impact native biodiversity (Dafforn, Lewis, & Johnston, 2011; Kinsella & Crowe, 2016). Previous studies have demonstrated these contaminants can also enhance the richness and abundances of invasive species (Marraffini, Ashton, Brown, Chang, & Ruiz, 2017; Piola, Dafforn, & Johnston, 2009); thus complexity could facilitate the increase of the non-endemic species pool. Studies directly manipulating contamination inside and outside harbours would be required to establish the importance of this factor as a moderator of complexity effects.

Our results support previous suggestions that the addition of complexity to the homogenous, flat surfaces of coastal defence structures has the potential to improve ecological outcomes (O'Shaughnessy et al., 2020). As compared to the natural habitats they replace, topographically simple artificial structures commonly support reduced native biodiversity (Airoldi, Turon, Perkol-Finkel, & Rius, 2015). Eco-engineering complexity and missing microhabitats on these artificial structures to enhance the biodiversity and ecosystem functioning of their communities, is increasingly common. However, scientific studies providing the evidence base for this rapidly-growing field are often poorly replicated and carried out over small spatial and temporal scales (Chapman, Underwood, & Browne, 2018; Firth et al., 2020). Global integration of small-scale ecological experiments such as those conducted here can be useful in identifying appropriate eco-engineering approaches before they are scaled up. Our study provides the most geographically comprehensive test of the effects of complexity on the biodiversity of coastal defence structures across the globe. We clearly demonstrate that complexity can affect the richness and abundances of colonising taxa, and despite large biogeographic variation in the identity of taxa present, these effects are largely of a consistent and positive direction for particular functional groups, across the globe.

Despite the generally positive effects of complexity, we found that the magnitude of these varied spatially from negligible to strongly positive (or in the case of some algae, negative). This is an important result as it suggests that economically costly eco-engineering interventions may have negligible benefit at some locations and may even negatively influence some functional groups if applied blindly. Effective eco-engineering requires understanding of the key environmental stressors that may be mitigated and the functional traits of taxa that are being targeted for enhancement (see also Morris et al. 2018). By designing microhabitats with the niches of target functional groups in mind, the benefits of complexity additions to structures may be maximised. Critically, the finding that the effect of complexity varied among locations, tidal zones and with latitude, highlights the importance of understanding how the effects of complexity are shaped by the local abiotic and biotic environments before implementing eco-engineering solutions – one size will not necessarily fit all. Manipulative experiments are now needed to confirm how specific environmental and biological factors mediate complexity-biodiversity relationships, within urbanised marine settings and whether the effects of complexity identified over a 12-month period here persist over longer time scales. Moreover, to fully assess the biodiversity benefits of eco-engineering interventions that add complexity, we would also need to compare the complex tiles to the surface of the coastal defence structure and adjacent natural rocky shores.

Eco-engineering, like ecological restoration (Ewel, 1987) provides the ultimate test of ecological theory (Mitsch 1996), by reassembling ecosystems from first principles. A cornerstone of community ecology has been the positive relationship between complexity and diversity (Dean & Connell, 1987; Kovalenko et al., 2012). Our global study challenges this paradigm in demonstrating that at patch-scales complexity effects can range from positive to neutral to negative, depending upon location and functional group. General guidelines to enhance biodiversity in coastal constructions will benefit from a grounding in ecological theory that can help developers predict the influence of local environmental and biotic contexts (Mayer-Pinto et al 2019).

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Data Availability

The data are available as Supporting Information

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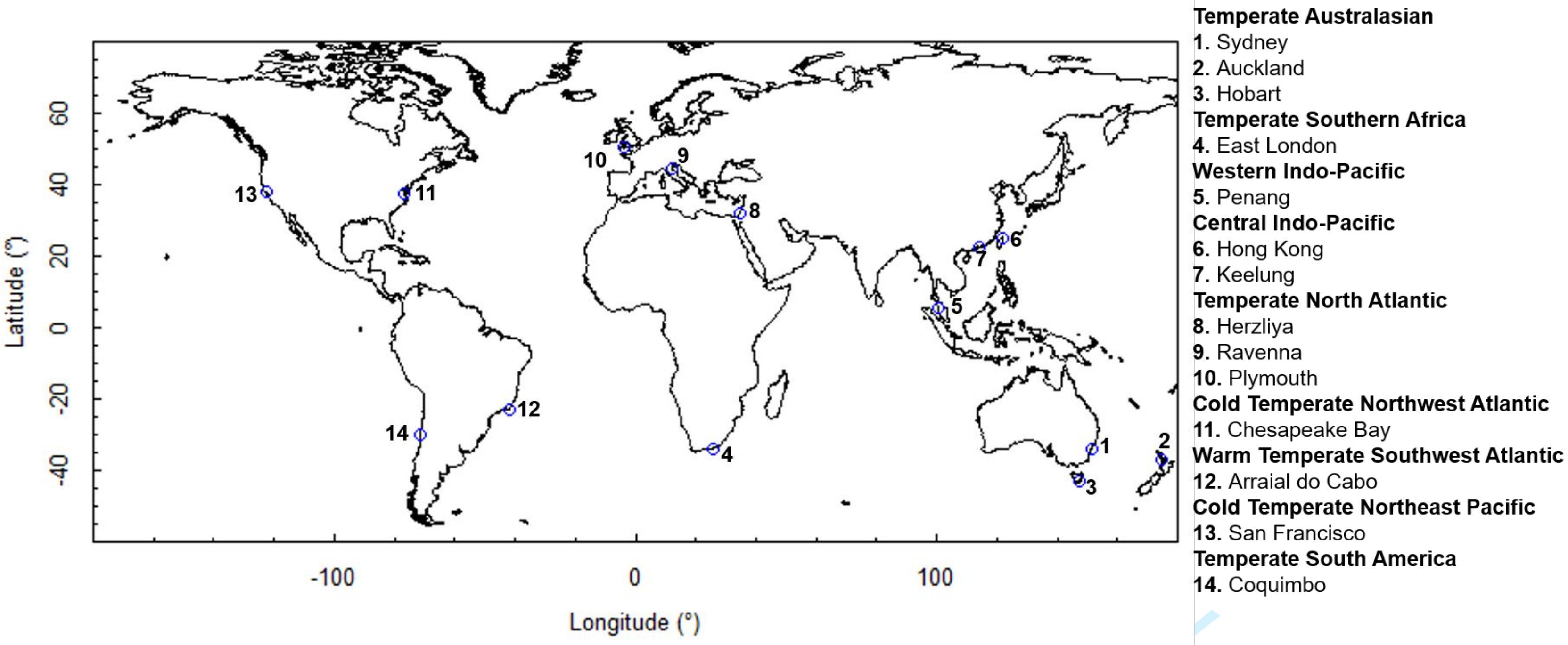

Fig 1: Map showing the experimental locations. Locations are ordered by biogeographic realm.

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

$F = 2.5 < 5$ $F < 2.5 < 5$ $F = 2.5 < 5$

$F = 2.5 < 5$ $F = 2.5 < 5$ $F < 2.5 < 5$

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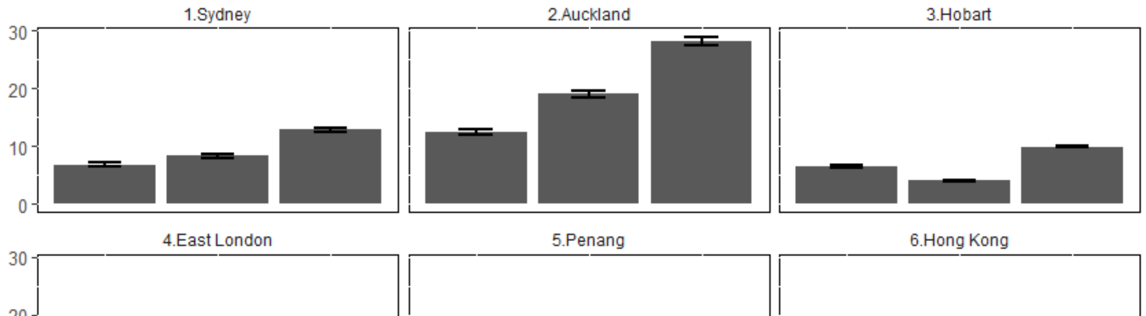
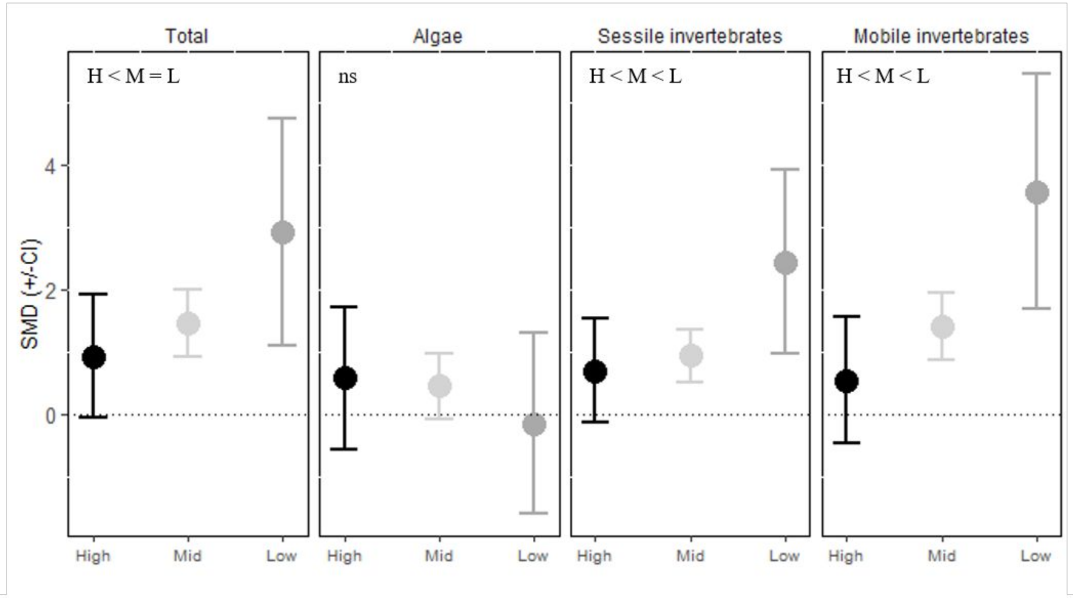


Fig 3: Effect of complexity (flat and 2 cm or 5 cm complex tiles) on the mean (+/-SE) total taxa richness at each of fourteen locations by realm (n = 1 or 2 sites per location). Significant differences (at α = 0.05) between flat (F), and 2.5 cm (2.5) or 5 cm (5) complex tiles are indicated by '>' or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

a) Richness



b) Abundances

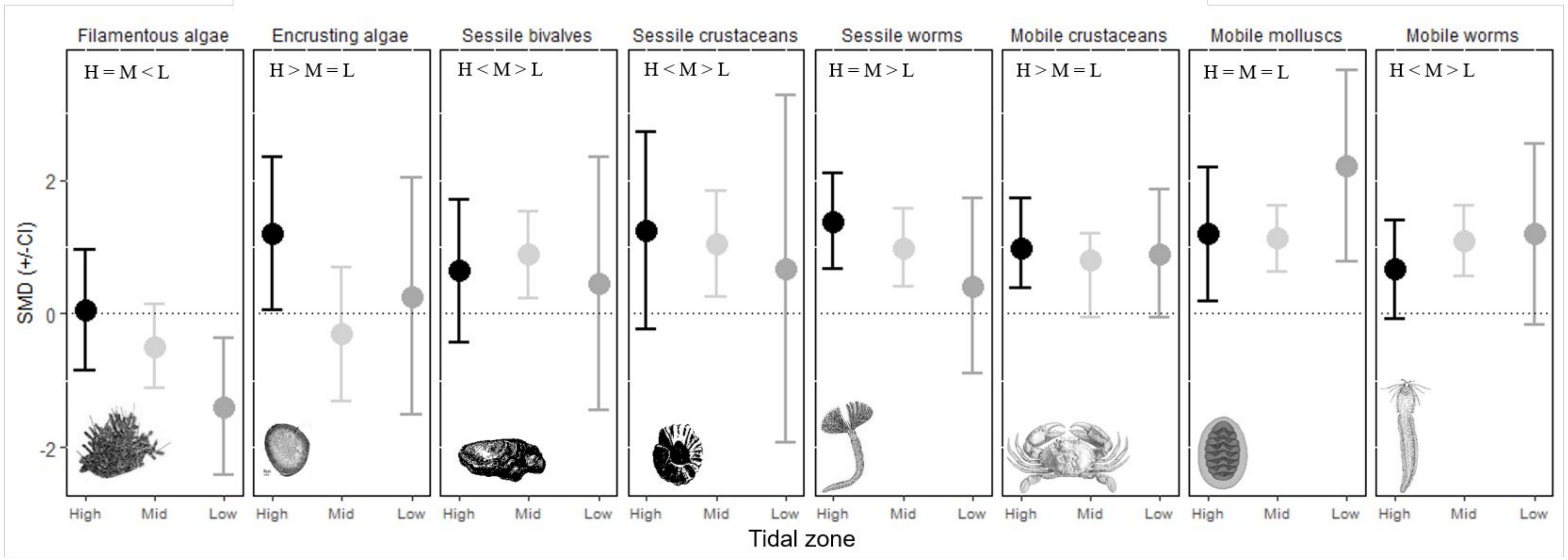
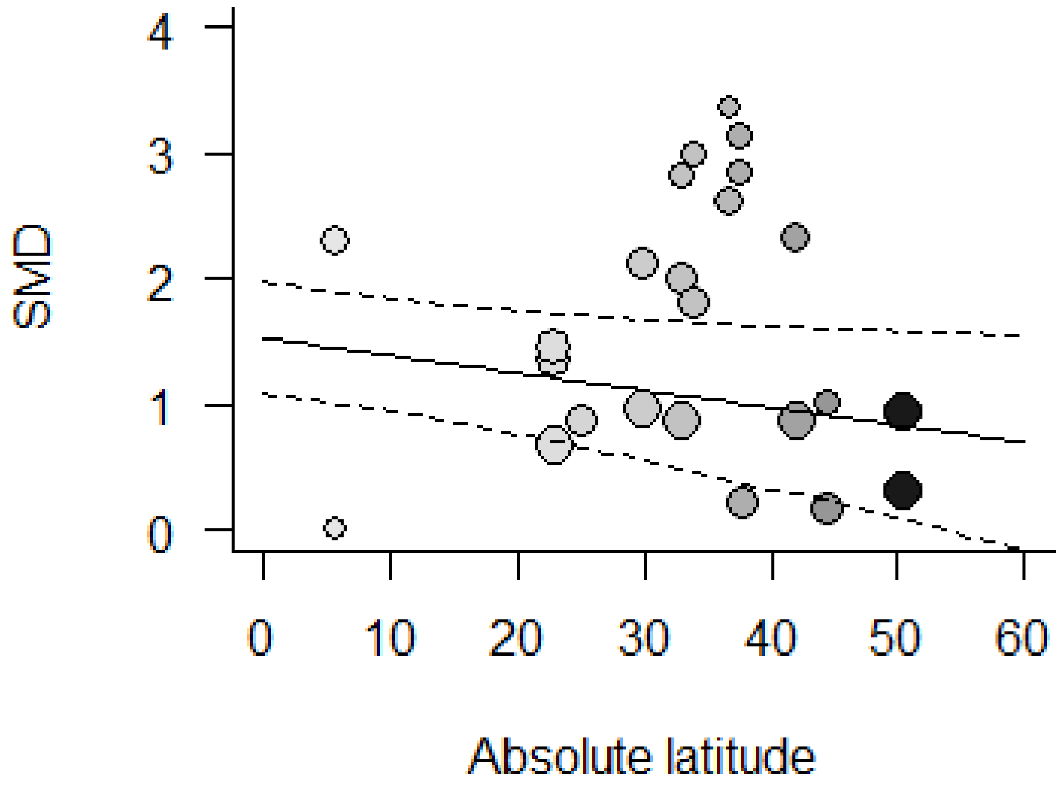


Fig. 4: Effects of tidal zones on the standard mean difference SMD (+/-CI) in a) richness of total taxa, algae, sessiles invertebrates and mobile invertebrates and b) abundances (percentage cover or abudances) of key CATAMI groups between 5 cm complex and flat tiles (high n = 5 sites, mid n = 18 sites,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


SMD
4
3
2
1
0
0
10
20
30
40
50
60
Absolute latitude

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	(Airoldi, 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	**<.0001**
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				

Supplementary S3: List of the functional groups, nineteen CATAMI groups and species/taxa on the experiment treatments, after 12 months. Species/morphospecies are classified as non-indigenous based on the published literature. Where species/morphospecies were observed at multiple locations, the location at which it is non-indigenous is indicated.

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	*Corallina officinalis*	Auckland, Sydney	
	Macroalgae encrusting	*Lithothamnium* sp.	Coquimbo	
		Encrusting coralline algae unknown	Arraial do Cabo	
		Hildenbrandia spp.	Coquimbo, East London, San Francisco	
		Ralfsia verrucosa	Sydney	
		Ralfsia 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	*Colpomenia* sp.	Auckland	
	Macroalgae foliose	Mastocarpus morphospecies 1-2	San Francisco	
		Gelidium sp.	East London	
		Gracilaria sp.	Chesapeake	
		Pterocladiella capillacea	Auckland	
		Fucus spp.	Plymouth, San Francisco	
		Phyllospora comosa	Hobart	
		Mazzaella sp. 1	San Francisco	
		Mazzaella sp. 2	San Francisco	
		Pachymenia lusoria	Auckland	
		Porphyra sp.	Hobart	

		Pyropia sp.	San Francisco	
		Ulva lactuca	Auckland	
		Ulva 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	*Corella eumyota*	Auckland	
		Pyura sp.	Hobart	
		Stalked ascidian morphospecies 1	Hobart	
		Botrylloides niger	Arraial do Cabo	(Granthom-Costa, Ferreira, & Dias, 2016)
		Botryllus tabori	Arraial do Cabo	
		Ascidian morphospecies 1	Auckland	

	Bryozoans	Membraniporidae sp.	San Francisco	(Bishop & Hutchings, 2011)
		Schizoporella errata	Arraial do Cabo	(Almeida, Souza, Gordon, & Vieira, 2015)
		Schizoporella sp.	Herzliya	www.marinespecies.org
		Watersipora cucullata	Herzliya	www.marinespecies.org
		Watersipora subtorquata	Hobart	(Bishop & Hutchings, 2011)
		Watersipora spp.	Auckland, Sydney	(Bishop & Hutchings, 2011)
		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	
		Bugula neritina	Herzilya, Penang	www.marinespecies.org Herzilya (Tilbrook & Gordon, 2016) Penang
		Bryozoan unknown	Auckland	
	Cnidarians	Hydroid morphospecies (rope)	Chesapeake	
		Anemone unknown	Auckland	

	Crustaceans sessile	*Amphibalanus amphitrite*	Herzliya, Hong Kong, Penang, Sydney	(Rainbow, 2000) Hong Kong
		Amphibalanus variegatus	Sydney	
		Amphibalanus spp.	East London, Keelung	
		Austrobalanus imperator	Sydney	
		Austrominius modestus	Auckland, Plymouth, Sydney	(Bracewell, Spencer, Marrs, Iles, & Robinson, 2012) Plymouth
		Balanus sp.	Chesapeake	
		Balanidae unknown	Coquimbo	
		Chamaesipho tasmanica	Hobart	
		Chthamalus antennatus	Hobart, Sydney	
		Chthamalus stellatus	Ravenna	
		Chthamalidae unknown	Coquimbo	
		Hexaminius sp.	Sydney	
		Striatobalanus tenuis	Penang	
		Tetraclita japonica	Hong Kong	
		Tetraclita stalactifera	Arraial do Cabo	
		Tetraclita sp.	East London	
		Tetraclita squamosa	Penang	
		Barnacle unknown recruits spp.	Arraial do Cabo, Hong Kong	
		Barnacle unknown 1	Auckland	
		Barnacle unknown 2	San Francisco	

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

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

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

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

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

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

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

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

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

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

		Hypereteone heteropoda	Chesapeake	
		Loimia medusa	Chesapeake	
		Neanthes vaalii	Hobart	
		Nereididae spp.	East London, Herzliya, Hong Kong, Sydney	
		Phyllodocidae sp. 1	Auckland	
		Polydora websteri	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	
		*Sipuncul*a spp.	East London, Penang, Sydney	

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

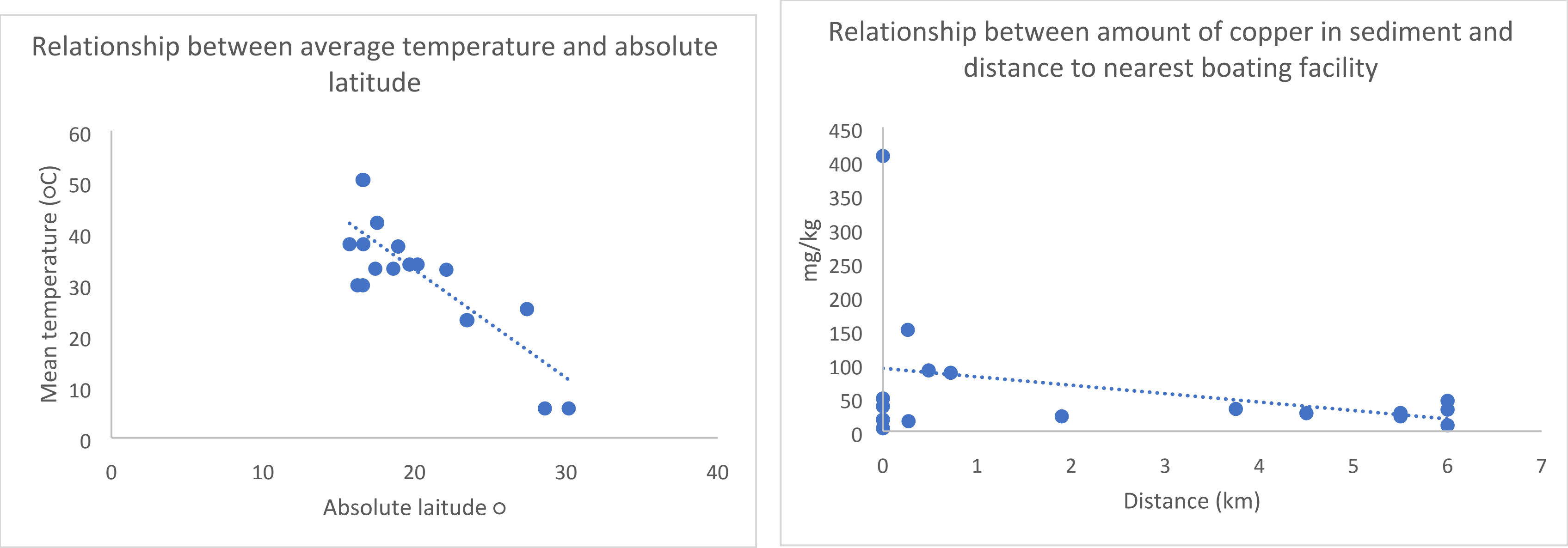

Fig S4a: The relationship between a) mean temperature and absolute latitude (significant) and b) amount of copper in sediment (mg/kg) and distance to nearest marina by sites (non-significant). The measurements of temperature were taken at twenty-one sites, within eleven locations throughout the experiment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

Table S4b: Results of linear models testing the relationship between a) average temperature and absolute latitude and b) amount of copper in 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

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

Total taxa richness was greater on the 5 cm complex tiles than the flat tiles at eleven locations (Arraial do Cabo, Auckland, Chesapeake Bay, Coquimbo, East London, Herzliya, Hobart, Hong Kong, Keelung, Penang, and Sydney); and on the 2.5 cm complex relative to the flat tiles at eight locations (Arraial do Cabo, Auckland, Chesapeake Bay, Coquimbo, Herzliya, Hong Kong, Keelung and Penang). Algal richness was greater on 5 cm complex tiles than on the 2.5 cm complex tiles or the flat tiles at two of the fourteen locations (Arraial do Cabo and Sydney), whereas the 2.5 cm complex tiles and the flat tiles did not significantly differ . At the other twelve locations, there were no significant differences in algal richness among treatments. Sessile invertebrates were more speciose on the 2.5 cm and 5 cm complex tiles than on flat tiles at seven locations (Arraial do Cabo, Auckland, Chesapeake Bay, Herzliya, Hong Kong, Penang and Ravenna), more speciose on the 5 cm complex than the 2.5 cm and flat tiles at two locations (Hobart and Sydney), but did not differ among treatments at the other five locations. There were more mobile species on the 2.5 and 5 cm complex tile compared with the flat tiles at six locations (Auckland, Coquimbo, Hong Kong, Hobart, Keelung, Sydney) and on the 5 cm complex tiles relative to the 2.5 cm and flat tiles at two locations (Chesapeake Bay and East London), with no significant differences for the other six 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 Hobart 2.5cm vs. 5 cm	-0.438 -0.943	-3.081 -5.605	**0.006** **<0.001**
					Hong Kong Flat vs. 2.5 cm, Hong Kong Flat vs. 5 cm Hong Kong 2.5cm vs. 5 cm	-0.622 -0.626 -0.003	-1.644 -1.650 -0.026	**0.023** **0.023** >0.05
					Keelung Flat vs. 2.5 cm, Keelung Flat vs. 5 cm Keelung 2.5cm vs. 5 cm	-0.511 -0.502 0.009	-2.491 -2.461 0.052	**0.034** **0.037** >0.05
					Penang Flat vs. 2.5 cm, Penang Flat vs. 5 cm Penang 2.5cm vs. 5 cm	-0.557 -0.589 -0.032	-2.213 -2.438 -0.146	>0.05 **0.039** >0.05
					Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	-0.145 -0.577 -0.432	-1.003 -4.502 -3.530	>0.05 **<0.001** **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 Arraial do Cabo Flat vs. 5 cm Arraial do Cabo 2.5 cm vs. 5 cm	-1.725 -4.443 -2.718	-1.900 -4.893 -3.076	>0.05 **<0.001** **0.007**
Location	13	206.173	52.829	**<0.001**	Sydney Flat vs. 2.5 cm Sydney Flat vs. 5 cm Sydney 2.5 cm vs. 5 cm	0.769 -3.175 -3.943	0.869 -3.593 -4.463	>0.05 **0.001** **<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	-1.218	-1.366	**0.036**
					Arraial do Cabo Flat vs. 5 cm	-1.178	-1.112	**0.041**
					Arraial do Cabo 2.5 cm vs. 5 cm	0.041	0.261	>0.05
Location	13	11.024	91.257	**<0.001**	Auckland Flat vs. 2.5 cm	-0.391	-2.513	**0.033**
					Auckland Flat vs. 5 cm	-1.027	-6.428	**<0.001**
					Auckland 2.5 cm vs. 5 cm	-0.631	-3.982	**0.001**
Site (Location)	1	1.207	9.988	**0.002**	Chesapeake Bay Flat vs. 2.5 cm	-0.616	-3.959	**0.001**
					Chesapeake Bay Flat vs. 5 cm	-0.674	-4.333	**0.001**
					Chesapeake Bay 2.5 cm vs. 5 cm	-0.058	-0.374	>0.05
Complexity x Location	26	0.404	3.346	**<0.001**	Herzliya Flat vs. 2.5 cm,	-0.493	-2.193	**0.044**
					Herzliya Flat vs. 5 cm	-0.522	-2.326	**0.034**
					Herzliya 2.5cm vs. 5 cm	-0.030	-0.133	>0.05
Complexity x Site (Location)	2	0.065	0.538	>0.05	Hobart Flat vs. 2.5 cm,	0.318	2.042	>0.05
					Hobart Flat vs. 5 cm	-0.456	-2.933	**0.010**
					Hobart 2.5cm vs. 5 cm	-0.774	-4.975	**<0.001**
Residual	329	0.121			Hong Kong Flat vs. 2.5 cm,	-0.464	-1.051	**0.005**
					Hong Kong Flat vs. 5 cm	-0.465	-1.030	**0.046**
					Hong Kong 2.5cm vs. 5 cm	-0.001	-0.007	>0.05
					Penang Flat vs. 2.5 cm,	-1.360	-1.845	**0.016**
					Penang Flat vs. 5 cm	-1.375	-2.004	**0.001**
					Penang 2.5cm vs. 5 cm	-0.015	-0.075	>0.05
					Ravenna Flat vs. 2.5 cm,	-0.856	-4.225	**0.001**
					Ravenna Flat vs. 5 cm	-0.490	-2.436	**0.041**
					Ravenna 2.5cm vs. 5 cm	0.366	1.822	>0.05
					Sydney Flat vs. 2.5 cm,	0.031	0.197	>0.05
					Sydney Flat vs. 5 cm	-0.418	-2.686	**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	-1.959	-6.186	**<0.001**
					Auckland Flat vs. 5 cm	-2.745	-8.473	**<0.001**
					Auckland 2.5 cm vs. 5 cm	-0.791	-2.483	**0.035**
Site (Location)	1	13.370	510.850	**<0.001**	Coquimbo Flat vs. 2.5cm	-1.395	-3.662	**0.001**
					Coquimbo Flat vs. 5 cm	-1.502	-3.964	**0.002**
					Coquimbo 2.5cm vs. 5 cm	-0.108	-0.318	>0.05
Complexity x Location	26	97.330	413.520	**<0.001**	East London Flat vs. 2.5cm	-0.781	-2.161	>0.05
					East London Flat vs. 5 cm	-1.516	-4.295	**0.001**
					East London 2.5cm vs. 5 cm	-0.735	-2.203	>0.05
Complexity x Site (Location)	2	4.560	408.960	>0.05	Hobart Flat vs. 2.5 cm,	1.609	4.847	**<0.001**
					Hobart Flat vs. 5 cm	-0.862	-2.743	**0.017**
					Hobart 2.5cm vs. 5 cm	-2.470	-7.491	**<0.001**
					Hong Kong Flat vs. 2.5 cm,	-0.936	-2.622	**0.023**
					Hong Kong Flat vs. 5 cm	-1.402	-3.890	**0.001**
					Hong Kong 2.5cm vs. 5 cm	-0.466	-1.368	>0.05
					Keelung Flat vs. 2.5 cm,	-1.202	-3.273	**0.003**
					Keelung Flat vs. 5 cm	-1.446	-3.966	**0.001**
					Keelung 2.5cm vs. 5 cm	-0.244	-0.712	>0.05
					Sydney Flat vs. 2.5 cm,	-0.654	-1.958	>0.05
					Sydney Flat vs. 5 cm	-1.011	-3.053	**0.007**
					Sydney 2.5cm vs. 5 cm	-0.358	-1.105	>0.05

Supplementary S6: Effects of adding topographic complexity (Flat, 2.5 cm or 5 cm) on the abundances of the nineteen CATAMI groups

Filamentous/filiform macroalgae percentage cover was less on the 5cm and 2.5 cm complex tiles than on the flat tiles at two locations (Coquimbo and Keelung), but greater on the 5 cm complex tiles than the flat tiles at one location (Sydney). Foliose macroalgae percentage cover 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 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 site (East London 2). Encrusting macroalgae displayed location-specific positive effects of habitat structure, displaying greater percentage cover 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 an additional two locations (East London and Sydney).

Bryozoans, sessile molluscs and sessile worms each displayed greater percentage cover on 5 cm complex, and in some instances, also 2.5 cm complex than flat tiles, at a subset of sites or locations. For bryozoans, such patterns were significant for three locations (Herzliya, Plymouth and Sydney), for sessile molluscs they were significant for seven locations (Auckland, Chesapeake Bay, Hobart, Hong Kong, Plymouth, Ravenna and Sydney) and for sessile worms, for five locations (Arraial do Cabo, Auckland, Herzliya, Keelung and Sydney). Additionally, sessile 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, Coquimbo, Herzliya, Hobart, Hong Kong, Plymouth and Ravenna), while sessile crustacean cover was lower on the flat tiles than the 5 cm and 2.5 cm complex tiles at two locations (San Francisco and Sydney).

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, 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 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 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 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, 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 (San Francisco). Mobile worms similarly displayed greater abundances on 5 cm complex than the flat tiles at four locations (Auckland, Chesapeake Bay and Sydney).

Table S6a: Results of multivariate and univariate mixed effects models testing the effects of complexity (flat, 2.5 cm or 5 cm) location (14 levels) and sites nested within location (1-2 levels) on the abundances of the nineteen CATAMI groups, sampled destructively at 12 months. The 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 Coquimbo Flat vs. 5 cm Coquimbo 2.5cm vs. 5 cm	0.482 0.173 -0.309	5.530 2.191 -3.480	**<0.001** **0.048** **0.002**
Complexity			0.14	>0.05	Keelung Flat vs. 2.5cm Keelung Flat vs. 5 cm Keelung 2.5cm vs. 5 cm	0.673 0.745 0.837	9.047 9.927 0.680	**<0.001** **<0.001** >0.05
Location			372.211	**0.001**	Sydney Flat vs. 2.5cm Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	1.617 -2.564 -2.181	0.010 5.527 -0.011	>0.05 **<0.001** >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, Auckland site 1 Flat vs. 5 cm Auckland site 1 2.5cm vs. 5 cm	1.521 2.488 0.967	1.607 4.014 1.560	**0.025** **0.002** >0.05
Complexity			0.37	>0.05	Coquimbo site 1 Flat vs. 2.5 cm, Coquimbo site 1 Flat vs. 5 cm Coquimbo site 1 2.5cm vs. 5 cm	1.332 1.459 0.128	2.279 2.497 0.217	**0.049** **0.034** >0.05
Location			336.885	**0.001**	East London site 1 Flat vs. 2.5 cm, East London site 1 Flat vs. 5 cm East London site 1 2.5cm vs. 5 cm East London site 2 Flat vs. 2.5 cm, East London site 2 Flat vs. 5 cm East London site 2 2.5cm vs. 5 cm	1.335 1.607 0.272 0.377 -1.903 -2.280	2.285 2.750 0.465 0.645 -3.256 -3.901	**0.048** **0.017** >0.05 >0.05 **0.003** **0.001**
Site (Location)			104.858	**0.001**	Hobart site 1 Flat vs. 2.5 cm, Hobart site 1 Flat vs. 5 cm Hobart site 1 2.5cm vs. 5 cm	-1.190 0.378 0.568	-1.325 0.647 0.971	**0.001** >0.05 >0.05
Complexity x Location			27.377	0.080	Plymouth site 1 Flat vs. 2.5 cm, Plymouth site 1 Flat vs. 5 cm Plymouth site 1 2.5cm vs. 5 cm	-1.491 -1.032 0.459	-2.552 -1.766 0.786	**0.029** >0.05 >0.05
Complexity x Site (Location)			42.402	**0.012**	Sydney site 1 Flat vs. 2.5 cm, Sydney site 1 Flat vs. 5 cm Sydney site 1 2.5cm vs. 5 cm	-1.673 -1.235 0.439	-2.862 -2.112 0.750	**0.012** >0.05 >0.05
Macroalgae encrusting								
Complexity			0.557	>0.05	Arraial do Cabo Flat vs. 2.5 cm, Arraial do Cabo Flat vs. 5 cm Arraial do Cabo 2.5cm vs. 5 cm	-0.756 -1.675 -0.920	-3.029 -6.713 -3.789	**0.007** **<0.001** 0.008
Location			212.209	**0.001**	East London Flat vs. 2.5 cm, East London Flat vs. 5 cm	0.006 -0.703	0.247 -2.895	>0.05 **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, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	0.395 -0.625 -1.020	1.628 -2.574 -4.203	>0.05 **0.027** **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, Herzliya Flat vs. 5 cm Herzliya 2.5cm vs. 5 cm	-0.849 -0.978 -0.129	-4.583 -5.280 -0.697	**<0.001** **<0.001** >0.05
Location			61.313	**0.001**	Plymouth Flat vs. 2.5 cm, Plymouth Flat vs. 5 cm Plymouth 2.5cm vs. 5 cm	-0.389 0.074 0.462	-2.965 0.561 3.527	**0.009** >0.05 **0.001**
Site (Location)			12.594	>0.05	Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	0.008 -0.302 -0.309	0.060 -2.301 -2.362	>0.05 **0.049** **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 Arraial do Cabo Flat vs. 5 cm Arraial do Cabo 2.5 cm vs. 5 cm	-1.414 -1.295 0.119	-6.182 -5.628 0.880	**<0.001** **<0.001** >0.05
Complexity			6.447	>0.05	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-1.394 -1.385 0.009	-4.681 -4.667 0.048	**<0.001** **<0.001** >0.05
Location			423.608	**0.001**	Coquimbo Flat vs. 2.5 cm Coquimbo Flat vs. 5 cm Coquimbo 2.5 cm vs. 5 cm	-1.034 -0.962 0.073	-12.915 -11.965 1.258	**<0.001** <0.001 >0.05
Site (Location)			137.372	**0.001**	Herzliya Flat vs. 2.5 cm, Herzliya Flat vs. 5 cm Herzliya 2.5cm vs. 5 cm	-0.710 -0.896 -0.186	-1.937 -2.530 -0.665	>0.05 **0.031** >0.05
Complexity x Location			78.89	**0.001**	Hobart Flat vs. 2.5 cm, Hobart Flat vs. 5 cm Hobart 2.5cm vs. 5 cm	-0.749 -0.550 0.200	-11.586 -8.237 3.663	**<0.001** **<0.001** **0.007**
Complexity x Site (Location)			73.151	**0.001**	Hong Kong Flat vs. 2.5 cm, Hong Kong Flat vs. 5 cm Hong Kong 2.5cm vs. 5 cm	-1.646 -2.115 -0.470	-13.422 -17.759 -7.515	**<0.001** **<0.001** **<0.001**
					Plymouth Flat vs. 2.5 cm, Plymouth Flat vs. 5 cm Plymouth 2.5cm vs. 5 cm	-0.639 -0.455 0.185	-13.497 -9.369 4.562	**<0.001** **<0.001** **<0.001**

					Ravenna Flat vs. 2.5 cm,	-1.251	-3.085	**0.006**
					Ravenna Flat vs. 5 cm	0.107	0.206	>0.05
					Ravenna 2.5cm vs. 5 cm	1.359	3.203	**0.004**
					San Francisco Flat vs. 2.5 cm,	0.708	8.869	**<0.001**
					San Francisco Flat vs. 5 cm	0.251	3.505	**0.002**
					San Francisco 2.5cm vs. 5 cm	-0.458	-5.274	**0.001**
					Sydney Flat vs. 2.5 cm,	0.432	5.385	**<0.001**
					Sydney Flat vs. 5 cm	0.152	2.061	>0.05
					Sydney 2.5cm vs. 5 cm	-0.280	-3.390	**0.002**
Sessile molluscs					Chesapeake Bay Flat vs. 2.5 cm	-0.704	-5.843	**<0.001**
					Chesapeake Bay Flat vs. 5 cm	-1.278	-11.503	**<0.001**
					Chesapeake Bay 2.5 cm vs. 5 cm	-0.574	-6.736	**<0.001**
Complexity			22.979	**0.001**	Hobart Flat vs. 2.5 cm	2.450	3.324	**0.003**
					Hobart Flat vs. 5 cm	-0.800	-3.192	**0.004**
					Hobart 2.5 cm vs. 5 cm	-3.249	-4.510	**<0.001**
Location			295.64	**0.001**	Hong Kong Flat vs. 2.5 cm	-0.799	-3.943	**0.002**
					Hong Kong Flat vs. 5 cm	0.430	1.621	>0.05
					Hong Kong 2.5 cm vs. 5 cm	1.229	5.279	**<0.001**
Site (Location)			66.54	**0.001**	Plymouth Flat vs. 2.5 cm	17.820	0.010	>0.05
					Plymouth Flat vs. 5 cm	-1.824	-4.165	**0.001**
					Plymouth 2.5 cm vs. 5 cm	-19.643	-0.011	>0.05
Complexity x Location			74.838	**0.001**	Ravenna Flat vs. 2.5 cm	-0.867	-2.510	**0.033**
					Ravenna Flat vs. 5 cm	-1.252	-3.810	**0.004**
					Ravenna 2.5 cm vs. 5 cm	-0.386	-1.604	>0.05
Complexity x Site (Location)			31.997	>0.05	Sydney Flat vs. 2.5 cm	-1.161	-9.724	**<0.001**
					Sydney Flat vs. 5 cm	-2.245	-20.482	**<0.001**
					Sydney 2.5 cm vs. 5 cm	-1.084	-16.128	**<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 Arraial do Cabo 2.5 cm vs. 5 cm	-2.548 0.096	-4.653 0.180	**<0.001** >0.05
Complexity			11.016	>0.05	Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5 cm vs. 5 cm	-0.896 -1.792 -0.897	-1.682 -3.272 -1.637	>0.05 **0.003** >0.05
Location			217.597	**0.001**	Herzliya Flat vs. 2.5 cm, Herzliya Flat vs. 5 cm Herzliya 2.5cm vs. 5 cm	-0.293 -2.927 -1.372	-0.389 -3.439 -1.822	>0.05 **0.002** >0.05
Site (Location)			34.825	**0.001**	Keelung Flat vs. 2.5 cm, Keelung Flat vs. 5 cm Keelung 2.5cm vs. 5 cm	-0.084 -1.695 -0.612	-0.132 -1.091 -0.960	>0.05 **0.049** >0.05
Complexity x Location			19.225	**0.049**	Sydney Flat vs. 2.5 cm, Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	-0.692 -3.184 -2.492	-1.150 -5.290 -4.140	>0.05 **<0.001** **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, Auckland site 1 Flat vs. 5 cm Auckland site 1 2.5cm vs. 5 cm Auckland site 2 Flat vs. 2.5 cm, Auckland site 2 Flat vs. 5 cm Auckland site 2 2.5cm vs. 5 cm	-0.846 -1.091 -0.246 -3.254 -4.018 -0.765	-6.883 -8.973 -2.652 -7.142 -8.909 -7.331	**<0.001** **<0.001** **0.0218** **<0.001** **<0.001** **<0.001**
Complexity			3.460	>0.05	Chesapeake Bay site 1 Flat vs. 2.5 cm Chesapeake Bay site 1 Flat vs. 5 cm	-0.828 -1.184 -0.355 -0.062 -0.428	-5.721 -8.611 -3.478 -0.727 -5.534	**<0.001** **<0.001** **0.001** >0.05 **<0.001**

					Chesapeake Bay site 1 2.5 cm vs. 5 cm Chesapeake Bay site 2 Flat vs. 2.5 cm Chesapeake Bay site 2 Flat vs. 5 cm Chesapeake Bay site 2 2.5 cm vs. 5 cm	-0.366	-4.871	**<0.001**
Location			335.469	**0.001**	Hong Kong site 1 Flat vs. 2.5 cm Hong Kong site 1 Flat vs. 5 cm Hong Kong site 1 2.5 cm vs. 5 cm Hong Kong site 2 Flat vs. 2.5 cm Hong Kong site 2 Flat vs. 5 cm Hong Kong site 2 2.5 cm vs. 5 cm	-1.819 -2.047 -0.229 -1.477 -2.260 -0.783	-2.927 -3.350 -0.751 -2.671 -4.268 -2.673	**0.010** **0.002** >0.05 **0.021** **0.001** **0.021**
Site (Location)			53.262	**0.001**	Hobart site 1 Flat vs. 2.5 cm Hobart site 1 Flat vs. 5 cm Hobart site 1 2.5 cm vs. 5 cm	4.928 -0.206 -5.133	4.910 -1.791 -5.118	**<0.001** >0.05 **<0.001**
Complexity x Location			30.203	>0.05	Keelung site 2 Flat vs. 2.5 cm Keelung site 2 Flat vs. 5 cm Keelung site 2 2.5 cm vs. 5 cm	-1.582 -1.556 0.026	-4.085 -4.091 0.124	**0.001** **0.001** >0.05
Complexity x Site (Location)			43.316	**0.012**	San Francisco site 1 Flat vs. 2.5 cm San Francisco site 1 Flat vs. 5 cm San Francisco site 1 2.5 cm vs. 5 cm	0.585 1.573 0.989	5.064 9.644 5.684	**<0.001** **<0.001** >0.05
					Sydney site 1 Flat vs. 2.5 cm Sydney site 1 Flat vs. 5 cm Sydney site 1 2.5 cm vs. 5 cm Sydney site 2 Flat vs. 2.5 cm Sydney site 2 Flat vs. 5 cm Sydney site 2 2.5 cm vs. 5 cm	-0.685 -1.403 -0.718 -2.854 -2.124 0.731	-2.167 -4.875 -3.226 -3.926 -2.841 2.471	>0.05 **<0.001** **0.0036** **0.001** **0.0125** **0.0359**
Mobile hexapods								

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

					Keelung Flat vs. 2.5 cm Keelung Flat vs. 5 cm Keelung 2.5 cm vs. 5 cm	-1.378 -1.652 -0.274	-6.296 -7.761 -2.149	**<0.001** **<0.001** >0.05
					San Francisco Flat vs. 2.5 cm San Francisco Flat vs. 5 cm San Francisco 2.5 cm vs. 5 cm	0.597 0.912 0.316	4.370 5.830 1.805	**<0.001** **<0.001** >0.05
					Sydney Flat vs. 2.5 cm Sydney Flat vs. 5 cm Sydney 2.5 cm vs. 5 cm	-0.485 -0.894 -0.410	-3.101 -6.132 -3.303	**0.006** **<0.001** **0.003**
Mobile worms					Auckland Flat vs. 2.5 cm Auckland Flat vs. 5 cm Auckland 2.5cm vs. 5 cm	-0.889 -2.399 -1.510	-1.840 -5.619 -1.510	>0.05 **<0.001** **<0.001**
Complexity			4.329	>0.05	Chesapeake Bay Flat vs. 2.5 cm Chesapeake Bay Flat vs. 5 cm Chesapeake Bay 2.5cm vs. 5 cm	-0.748 -1.142 -0.394	-8.064 -13.071 -5.904	**<0.001** **<0.001** **<0.001**
Location			247.461	**0.001**	Hobart Flat vs. 2.5 cm Hobart Flat vs. 5 cm Hobart 2.5cm vs. 5 cm	1.892 -0.647 -2.539	8.986 -6.875 -12.465	**<0.001** **<0.001** **<0.001**
Site (Location)			100.516	**0.001**	Sydney Flat vs. 2.5 cm Sydney Flat vs. 5 cm Sydney 2.5cm vs. 5 cm	16.008 -2.623 -18.631	0.009 -2.534 -0.010	>0.05 **0.031** >0.05
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	**<.0001**	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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