

The benefits of adding complexity to seawalls vary across environmental gradients

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A thesis for submission for the degree of Masters of Research

4 June 2020

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This thesis is written in the form of a journal article for 'Ecological Engineering'

Declaration

I would like to declare that this work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and beliefs, this thesis contains no material previously published or written by another person except for where due references are made in the thesis itself.

I wish to acknowledge the assistance of my supervisors Melanie Bishop and Katherine Dafforn in the research detailed in this report.

All other research described in this report is my own original work.

Gemma Clifton (42611989)

04/06/2020

Acknowledgements

I would like to acknowledge my wonderful supervisors Melanie Bishop and Katherine Dafforn, without the both of you none of this would have been possible. Especially for providing an excellent project, providing valuable feedback, and having the patience dealing with me having to work.

I would also like to make mention of the wonderful support from my lab group especially Maria Vozzo, Kate Dodds and Tegan Furchert who helped with identification of species and ibutton temperature loggers.

I would like to thank the people that provided the support I needed especially in tough times, my father, sister Melinda, and her daughter Chloe and my three wonderful children Aiden, Stephanie, and Nikolas who also assisted me in the field at times. My boss and work colleagues for understanding my needs and allowing me to take time off for to complete my research. The volunteers who gave up their time to come out and help prepare and install tiles.

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Abstract

Artificial structures such as seawalls are an increasingly dominant habitat of marine urban environments. As compared to natural habitats, seawalls are usually flat, featureless, vertical surfaces that support reduced biodiversity. Eco-engineering aims to mitigate negative ecological effects of seawalls by incorporating ecological principles into their design. One approach is to add complexity that increases microhabitat diversity and surface area. While initial tests have provided positive results, it is unclear the range of environmental conditions across which eco-engineering interventions provide ecological benefits. This study assessed how the effects of complexity on biodiversity vary across pollution and estuarine gradients. Colonisation of flat and complex (creviced / ridged) tiles, affixed to seawalls, was compared between sites close to and away from stormdrains, in inner and outer Sydney Harbour. Effects of complexity on the biodiversity colonising seawall tiles varied from neutral to highly positive. Whereas complexity effects were independent of proximity to stormdrain, having generally greater effects in the outer than inner harbour. This latter result may reflect the greater species pool of colonists in the outer harbour. These results suggest that eco-engineering interventions based on complexity will not have universally positive effects and are dependent on the species pool and the environmental conditions.

1. Introduction

Coastal ecosystems, such as estuaries provide essential services to humans such as nutrient cycling, as well as the provision of clean water, food, and coastline protection from wave inundation and erosion (Bouma et al. 2014, Clark et al. 2015, Perkol-Finkel et al. 2017). Estuaries are transitional zones in which ecological communities experience a range of physio-chemical conditions from the inner estuary to the mouth. Many estuaries are also impacted by human activities (Lotze et al. 2006), with urbanisation as a key driver of ecological changes (McKinney 2002). Urbanization exposes vulnerable coastal ecosystems to chemical (e.g. pollutants) and physical (e.g. habitat modification) stressors introduced through various activities including shipping, industry, stormwater discharge and habitat conversion (Rivero et al. 2013, Mayer-Pinto et al. 2015, Bugnot et al. 2019). As the human population continues to grow, there is an increasing need to understand how the ecological impacts of urbanisation in diverse estuarine ecosystems can be mitigated into the future (Perkol-Finkel et al. 2017).

Among the growing impacts of coastal urbanization, shoreline hardening has resulted in significant loss of habitat in order to stabilise reclaimed land and to protect assets from erosion and inundation. Natural shorelines in urban areas around the world have already been replaced by hundreds of kilometres of seawalls (Chapman et al. 2017, Perkol-Finkel et al. 2017). Seawall construction is likely to increase as cities expand, sea level rises, and more extreme and frequent storms threaten coastal assets (Airoidi et al. 2005, Chapman 2005, Bulleri and Chapman 2010, Morris et al. 2017, Morris et al. 2019).

Seawalls differ in orientation, complexity, surface area and material composition compared to the natural habitats they replace, as well as their closest natural analogue, rocky shores. Consequently, seawalls support distinct ecological communities, often of reduced biodiversity compared to natural habitats (Airoidi et al. 2005, Bulleri and Chapman 2010, Chapman et al. 2017). The vertical or steeply-sloping orientation of seawalls contrasts the largely horizontal, gradual slope of natural intertidal shorelines (Bulleri and Chapman 2010, Firth et al. 2014, Chapman et al. 2017). Whereas natural shorelines are topographically complex, with microhabitats such as rock pools, crevices and overhangs, seawalls are mainly vertical flat, and homogenous (Chapman and Bulleri 2003, Chapman 2005, Firth et al. 2014). These microhabitats of natural rocky shores act as refuges from predation and environmental

stressors such as high temperatures and desiccation (Helmuth and Hofmann 2001, Seabra et al. 2011, Bolton et al. 2018). The net outcome of the replacement of natural shoreline habitats with seawalls is the reduced intertidal area for organismal attachment, reduced niche spaces and fewer protective microhabitats (Bulleri and Chapman 2010). Consequently, organisms on seawalls may experience enhanced intraspecific competition, and be more susceptible to predation and environmental stressors than organisms inhabiting natural substrates (Bulleri and Chapman 2010). Seawalls often support less biodiversity than natural rocky shores (Bulleri and Chapman 2010), and demographic (e.g. growth rates, reproduction) and functional (e.g. filtration) processes may also differ (Moreira et al. 2006, Chapman and Underwood 2011).

As knowledge of the ecological impacts of coastal structures, such as seawalls has grown, so too has interest in developing mitigation strategies. In some instances, the construction of coastal structures may be avoided, for example through the use of nature-based solutions that stabilise the shoreline (Bilkovic et al. 2016, Morris et al. 2019). In other cases, coastal structures are necessary to protect property and infrastructure and strategies are instead needed for improving their ecological function (Morris et al. 2019). Ecological (“Eco-”) engineering aims to mitigate the negative effects of artificial structures such as seawalls and breakwaters by incorporating ecological principles into their design, while also preserving their original purpose (protection of assets) (Chapman and Underwood 2011, Chapman et al. 2017, Dennis et al. 2018).

While eco-engineering might be most effectively done during the design of new structures, strategies are also needed for improving the ecological value of existing structures (Chapman et al. 2017, Strain et al. 2018). This might be done by adding cracks, holes, and pools to structures, that increase structural complexity and surface area, either through drilling or attaching habitat panels (Browne and Chapman 2014, Firth et al. 2014, Evans et al. 2016). These features can be designed to mimic microhabitats found in natural habitats (Chapman and Underwood 2011, Morris et al. 2016, Dennis et al. 2018), and may target particular taxa (Morris et al. 2018), or alternatively, biodiversity more generally by enhancing microhabitat diversity and niche space (Mayer-Pinto et al. 2017, Strain et al. 2018). Enhancing species diversity is often a desirable goal because diverse ecosystems are overall more resilient to environmental change and provide more ecosystem services than less diverse ecosystems (Loreau et al. 2004, Srivastava and Vellend 2005, Tilman et al. 2006).

It is often assumed that the addition of microhabitats, and hence complexity, to seawalls will have universally positive effects on biodiversity, but eco-engineering studies are typically poorly replicated and biased towards high-biodiversity sites (reviewed by Chapman et al. 2018, but see Strain et al. in review for an exception). Where the effects of complexity are neutral or negative, eco-engineering strategies based on the addition of complexity would be a waste of money at best, or maladaptive at worst. Consequently, there is a need to understand the range of conditions across which interventions would be effective. In the broader ecological literature, there is growing evidence that the relationship between complexity and biodiversity is mediated by environmental factors (McAfee et al. 2016, Bateman and Bishop 2017, Bracewell et al. 2018).

Where complexity acts to facilitate species by providing protective microhabitats, its effects on biodiversity are predicted to and have been empirically demonstrated to increase across gradients of environmental and/or biotic (i.e. predation) stress (McAfee et al. 2016, Bracewell et al. 2018). Environmental conditions may also influence complexity-biodiversity interactions by influencing the species pool of colonists on which complexity can act. Stressors, such as contaminants may over-ride the effects of complexity where they create conditions that are inhibitory to the survival of most species (Mormul et al. 2011, Mayer-Pinto et al. 2016). Effects of complexity on seawall biodiversity therefore needs to be tested across a range of environmental conditions, to assess how ecological outcomes might vary across pollution, temperature and salinity gradients that determine environmental stress and/or the species pool of available colonists (Strain et al. in review).

Pollution is broadly regarded as a key determinant of biodiversity in urban estuaries (Mayer-Pinto et al. 2015). Estuaries are commonly contaminated by heavy metals, fertilisers, sewage, and synthetic compounds from human activities (Dafforn et al. 2012, Lee and Birch 2013, Clark et al. 2015, Johnston et al. 2017). Important sources of these contaminants are industrial activities and storm water discharge (Lee and Birch 2013). Untreated stormwater runoff from impervious surfaces such as roads, roofs and paths enters coastal ecosystems transporting an array of wastes including sediment, rubbish, organic matter, inorganic nutrients, metalloids and organic chemicals (Mayer-Pinto et al. 2015, Banks et al. 2016, Sutherland et al. 2017). Stormwater drains are often located in low flow embayments that trap

contaminants within them, resulting in hotspots of contaminants next to the point of discharge and decreasing concentrations with distance away (Sutherland et al. 2017). Contaminants can accumulate in soft sediments in pore-water or bind to sediment particles (Sutherland et al. 2017), remaining in the sediment from years to decades, with periodic resuspension by physical disturbances such as wind, shipping, dredging, boat generated waves or storms (Dafforn et al. 2012, Clark et al. 2015). When resuspended, these contaminants can be absorbed directly from the water column by sessile invertebrates or ingested during filter feeding (Clark et al. 2015). Contamination has been linked to shifts in community composition, where tolerant species dominate, and declines in diversity (Mayer-Pinto et al. 2015). Where contamination limits the survival of species, it may over-ride any effects of complexity (Mayer-Pinto et al. 2015).

Additionally, salinity and temperature gradients can be a key determinant of estuarine biodiversity. Within estuaries, species richness generally declines from the mouth of the estuary to the mid-reaches, where a biodiversity minimum occurs due to the physiological challenges imposed on organisms by variable salinities (Remane 1934, Telesh and Khlebovich 2010). Diurnal temperature ranges within estuaries can increase from the mouth, upstream, as the thermal buffering role of the ocean diminishes, and air temperatures play an increasingly important role in shaping water temperatures (Vaz and Dias 2008). Particularly in the intertidal zone, where many organisms live at or close to their thermal maximum (Stillman and Somero 2000), this may lead to spatial variation in the temperature stress that organisms experience. Microhabitats that provide protection from thermal stress may be expected to be more effective where this stress is greater.

The overall aim of this study was to investigate whether on seawalls, complex surfaces with crevices and ridges consistently support greater species richness and abundance of species compared to flat surfaces, irrespective of environmental settings. As compared to flat surfaces, complex surfaces with crevices and ridges increase the surface area of substrate to which organisms can attach, increasing the availability of shaded and moist habitat, and provide greater protection from predation by fish (Strain et al. 2020). Specifically, I assessed how differences in colonisation of complex and flat tiles, attached to seawalls, varies between sites close to and away from stormdrains, and between the inner and outer harbour in Sydney, Australia. I hypothesised that 1) metal contamination would be greater at sites close to than away from stormdrains; 2) environmental conditions, such as temperature and salinity, would

vary between the inner and outer Sydney Harbour; 3) consequently, the overall biodiversity would vary according to the interacting effects of proximity to stormdrains and position in harbour, being less close to stormdrains and in the inner harbour and 4) the effects of complexity on biodiversity would also vary spatially, being greater at outer harbour sites away from stormdrains and weakest at inner harbour sites close to stormdrains. Within the complex tiles, I expected that biodiversity would differ between crevices and ridges, supporting a role for the tiles in increasing not only surface area, but microhabitat diversity.

2. Methods

2.1. Study sites

The experiment was conducted in Sydney Harbour, New South Wales, Australia (33.8462° S, 151.2489° E). Sydney Harbour is a drowned river valley, containing a network of embayment's and inlets that are connected via a larger channel that flows into the Pacific Ocean (Sutherland et al. 2017). The circulation of Sydney Harbour is tidally controlled, with semidiurnal tides displaying a maximum range of 2.1m (Banks et al. 2016). The inner harbour and embayments (defined here as west of the Sydney Harbour Bridge) generally have muddy sediments, while the outer harbour (east of the Sydney Harbour Bridge) generally has sandy sediments (Banks et al. 2016). Further, the outer harbour has greater wave action, larger tidal influences, and more oceanic flushing than inner harbour sites (Dafforn et al. 2012). Boat wake can, however, produce significant wave action at some inner harbour sites (Bishop and Chapman 2004). Based on these observations, we considered inner and outer harbour sites separately.

Within the harbour, eight study sites with seawalls were selected (Fig 1): four within the inner harbour and four within the outer harbour. In each of the inner and outer harbour two of the sites, were within 50m of the point at which a stormwater drain empties into an embayment (hereafter 'stormdrain') and two of the sites were more than 1km away from drains (hereafter 'reference'), in a setting of similar wave exposure. Previous research from Sydney Harbour has found that between 0 – 200m from the point of discharge into the embayment the contamination levels are high but are minimal by 1000m away (Sutherland et al. 2017). The study sites generally had sloped seawall orientations, and were constructed of sandstone, though there were several exceptions where seawalls of these properties could not

be accessed in certain places in the harbour. (Table 1). There were no systematic differences in properties of seawalls between the inner and outer harbour or close to and away from stormdrains, such that they were not confounded with these spatial factors. Furthermore, within sites, flat and complex tiles were subject to the same set of ambient environmental conditions.

Table 1: Characteristics of seawalls on which experimental tiles were deployed.

Site	Zone	orientation	Slope ($^{\circ}$)	Height of seawall base as compared to mean low water(m)	Construction material
Stormdrain 1	Inner harbour	North	45	0.5	Concrete
Reference 1	Inner harbour	North	45	0.5	Sandstone
Stormdrain 2	Inner harbour	East	45	0.4	Sandstone
Reference 2	Inner harbour	North	45	0.4	Sandstone
Stormdrain 3	Outer harbour	South	45	0.4	Sandstone
Reference 3	Outer harbour	West	90	0	Sandstone
Stormdrain 4	Outer harbour	South	45	0.3	Sandstone
Reference 4	Outer harbour	West	90	0	Sandstone

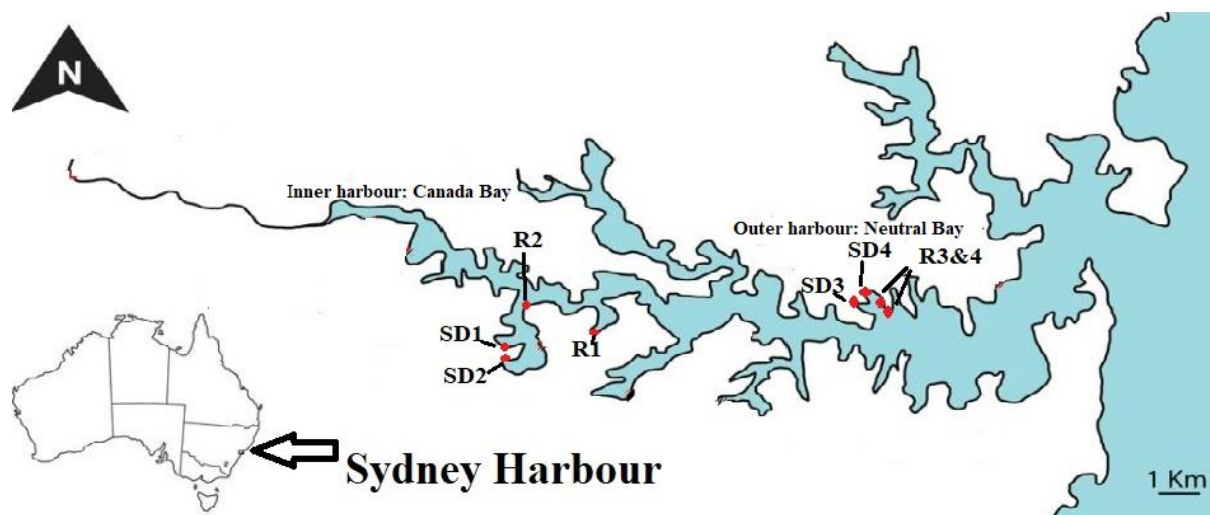


Fig 1: Map of study sites within Sydney Harbour, NSW, Australia. Two sites were selected close to stormdrains (SD) and two were far from stormdrains (R) within each of the inner and outer harbour.

2.2. Experimental design

To investigate whether the effects of complexity provided by crevices and ridges varied with proximity to drains, and with position in the harbour, tiles of two designs were deployed on seawalls at each site in March 2019 and remained in place for twelve months in total. All tiles were 25 x 25cm in dimension and fabricated from concrete. Complex tiles (designed by Reef

Design Lab, Melbourne, Australia) contained five, 5cm ridges that were 2.5cm apart and separated by crevices (Fig 2. Strain et al. 2017). The complex tiles had a total surface area of 0.136m². Flat tiles lacked crevices and ridges and had a surface area of 0.0625m². Tiles of both designs had a fine scale microstructure of < 1mm deep contours created by the 3D printing process that was used to produce moulds.

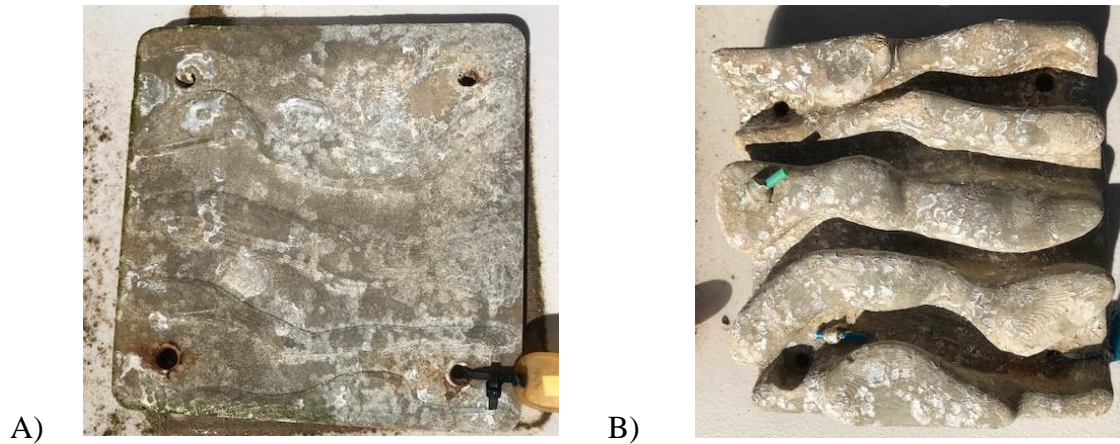


Fig 2: Images of (A) flat and (B) complex tiles.

At each site six initially bare tiles of each type were attached directly, in random order, at the mean low tide level of seawalls. The seawall surface to which tiles are attached had been cleared of existing organisms using hammer, chisel, and wire brush to an area of 900cm². Complex tiles were installed so that crevices and ridges ran horizontally. Tiles were attached at least 2.5m apart and affixed them to the seawall using four 8mm x 80mm dynabolts, one per corner of the tile.

2.3. Sampling

To compare potential contaminant exposure between stormdrain and reference sites, two sediment traps were secured to the seawall at each site in April 2019. Each comprised a vertically orientated 250mm length of 50mm diameter polyvinyl chloride pipe, capped and sealed at the bottom end, with the top end covered by mesh (2mm x 1.5mm) secured with a cable tie to allow sediment deposition into the pipe, but to keep out mobile fauna such as octopus and blennies (Larsson et al. 1986). Sediment traps were secured by brackets dynabolted vertically to the seawall. Upon retrieval, in January 2020, sediment traps were sealed and transported on ice back to the lab and left in a refrigerator to settle overnight, then transferred into cleaned specimen jars. Each sample was oven dried at 50⁰ C for seven days. Samples were separated by grain size and a small 0.5g sample of dried sediment was milled in Retsch MM 400 Ball Mill machine for 3 minutes 30 seconds at 20 revolutions per second.

Following milling samples were pressed into clear tubes and the metal concentrations analysed for copper, lead and zinc using X-Ray fluorescence (XRF, Olympus Delta Premium 50 kV with Au anode tube (serial # 161)). This study focused on concentrations of three contaminants that are typically associated with storm water discharge, copper, lead and zinc (Birch and Taylor 1999). Contaminant concentrations were compared against the ANZECC sediment quality guidelines, with concentrations above sediment quality guideline values (SQGVs) indicative of possible ecological toxicity effects, and while concentrations above SQVG – high guidelines indicative of a high probability of toxicity related effects (McCready et al. 2006, Simpson et al. 2013).

Differences in temperature among flat tiles and, crevice and ridge microhabitats of complex tiles were assessed using ibutton (Thermochron) temperature loggers that were waterproofed for deployment with clear Plasti Dip (Performix). Loggers were deployed on three randomly selected flat and three randomly selected complex tiles per site, with one logger per flat tile, and two per complex tile (one on a ridge and one in a crevice). Loggers were programmed using thermodata viewer (version 3.11.18) to record hourly for the duration of the experiment, with loggers interchanged every three months to maintain continuity of data collection. Loggers were attached to tiles by placing a small amount of epoxy (Ramset, Reo 502), to cable ties that were attached to each logger.

The salinity at each site was assessed at each sampling site using a digital refractometer (Serenity Aquatics). Measurements were taken at low tide 1,2 and 3 months after tile installation, from a 50ml sample of seawater, collected from immediately adjacent to each seawall. The refractometer output was converted to parts per thousand (ppt) from the salinity percentage.

Ecological communities of algae and invertebrates colonising tiles were monitored every month for the first three months, then every three months until twelve months. At each sampling time, the percentage cover of sessile species was estimated using a 25x 25cm quadrat strung evenly with 5 x 5 strings, to create 25 evenly spaced intersection points, under which the presence of sessile species was recorded. Sessile species present on tiles, but not under an intersection point were given a nominal 0.5 percentage cover. The number of mobile species (>0.1mm diameter) on each tile was counted *in situ* by species.

2.4. Statistical analysis

Metal concentrations could not be compared statistically because no suspended sediment was collected in traps at some sites as some replicates had no sediment and some were lost during the study period. Two sample t-tests were run in R (version 3.5.3) to assess differences in salinity measured between the inner and outer harbour at each site. The effects of complexity treatment or microhabitat on each of the minimum and maximum temperatures recorded on a tile during the study was assessed using separate generalized linear models (GLMs). Besides habitat complexity (flat vs complex) or microhabitat (crevice vs ridge), these had the factors: position in harbour (inner vs outer), distance from stormdrain (near (stormdrain) vs far (reference)). Site (within stormdrain x position in harbour) and tile (with site) were included as nested random factors.

Biological data was analysed using multivariate Permutational Analysis of Variance (PERMANOVAs: (Anderson 2001)), run on the community data sets for each of the sessile and mobile groups of taxa. Univariate GLMs that were run on the total richness, of each of the sessile and mobile groups, the total cover of sessile species, the total abundance of mobile species, and the abundance of key components of the community (algae, sessile invertebrates, non-limpet gastropods and limpets). The analyses had the factors: complexity treatment (flat vs complex), position in harbour, distance from stormdrain, site (2 levels, random, nested within harbour and proximity to drain) and sampling month (a repeated measure, with 1,2,3,6,9 and 12 months for mobile taxa and 2,3,6,9, and 12 months for sessile taxa which were rare at 1 month). Separate analyses compared the species richness and abundance of mobile species between crevices and ridges of the complex tiles. These had the factors: microhabitat (crevice vs ridge), position in harbour, distance from stormdrain, site and sampling month (as above), with tile identity nested within each site.

PERMANOVAs were run using Primer 7 on Bray Curtis dissimilarity matrices produced using untransformed data. PERMANOVA's do not have assumptions regarding the underlying distributions of data. As the assumption of sphericity for multivariate repeated measures tests could not be examined in PRIMER, treatment effects were only considered significant at $\alpha = 0.01$ to offset the enhanced probability of Type I error that occurs where sphericity is violated (Anderson et al. 2008). Where analyses detected significant treatment effects at $\alpha = 0.05$, these were followed by either *a posteriori* pairwise PERMANOVAs. SIMPER analysis identified taxa that were key contributors to multivariate differences among treatments (dissimilarity to standard deviation ratio >1.3). nMDS plots were used to visualise

data. BEST analyses were conducted separately on assemblages of mobile and sessile species to identify subsets of up to 5 taxa that were key drivers of dissimilarity between flat and complex treatments.

GLMs were run in R (version 3.5.3), using the packages ‘lme4’, ‘lmerTest’. Prior to each analysis, residual tests were run and confirmed that the data in all instances met assumptions of normality. Additionally, for repeated measures GLMs, sphericity of data was examined prior to each test using Mauchly’s test, and in no instances was sphericity violated. Where analyses detected significant (at $\alpha = 0.05$ for GLMs, as all assumptions were tested for and met) treatment differences between flat versus complex tiles that varied among months (i.e. Month x Treatment), distances from stormdrains (i.e. Distance x Treatment), position in harbour (i.e. Harbour x Treatment) and / or as a function of multiple spatial and temporal factors (e.g. Month x Treatment x Harbour), these were followed by either *a posteriori* pairwise comparisons of treatment means within levels of spatial and / or temporal factors using the package ‘emmeans’.

3. Results

3.1. Environmental conditions

Metal concentrations (copper, lead and zinc) in trap-collected suspended sediments from all stormdrain sites and one reference site were above the sediment quality guideline values (SQGV) at which ecological toxicity effects may be expected to occur (Simpson et al. 2013). At three of the stormdrain sites, concentrations of copper, lead and zinc were also above the SQGV-High, which indicates a high probability of ecological impacts (Table 2). Additionally, one reference site in the inner harbour had levels of zinc that exceeded the SQGV-High. Low levels of all three contaminants were observed at reference site 2 in the inner harbour, but at the two reference sites in the outer harbour, no sediment analysis was possible due to the paucity of suspended sediment collected in traps.

Table 2) Mean (\pm SE) of concentrations of copper, lead and zinc in sediment from traps deployed at each of the eight study sites. Sites were situated in the inner and outer zones of Sydney Harbour, near to stormdrains (SD) or at reference sites (R) far from stormdrains. Bold text indicates where contaminant concentrations exceeded the SQGVs and an * indicates the values that also exceeded the SQGV-High (Simpson et al. 2013). Where no standard error (SE) values are given, only one replicate was recovered and N/A indicates insufficient sediment available in the trap for analysis, n=1-2 traps per site.

Zone	Distance from stormdrain	Site	Copper (mg/kg)	Lead (mg/kg)	Zinc (mg/kg)
Inner	Near	SD1	152 \pm 9.8	206 \pm 19.7	478\pm23.7
Inner	Near	SD2	294\pm6.5	305\pm4.5	634\pm16
Inner	Far	R1	125 \pm 3	267\pm9.5	1015\pm0.5
Inner	Far	R2	9	27	48
Outer	Near	SD3	319\pm226	237\pm153	700\pm341
Outer	Near	SD4	310\pm3	352\pm1.5	618\pm18.5
Outer	Far	R3	N/A	N/A	N/A
Outer	Far	R4	N/A	N/A	N/A
Sediment Quality Guideline Values (SQGV)			65	50	200
SQGV-High			270	220	410

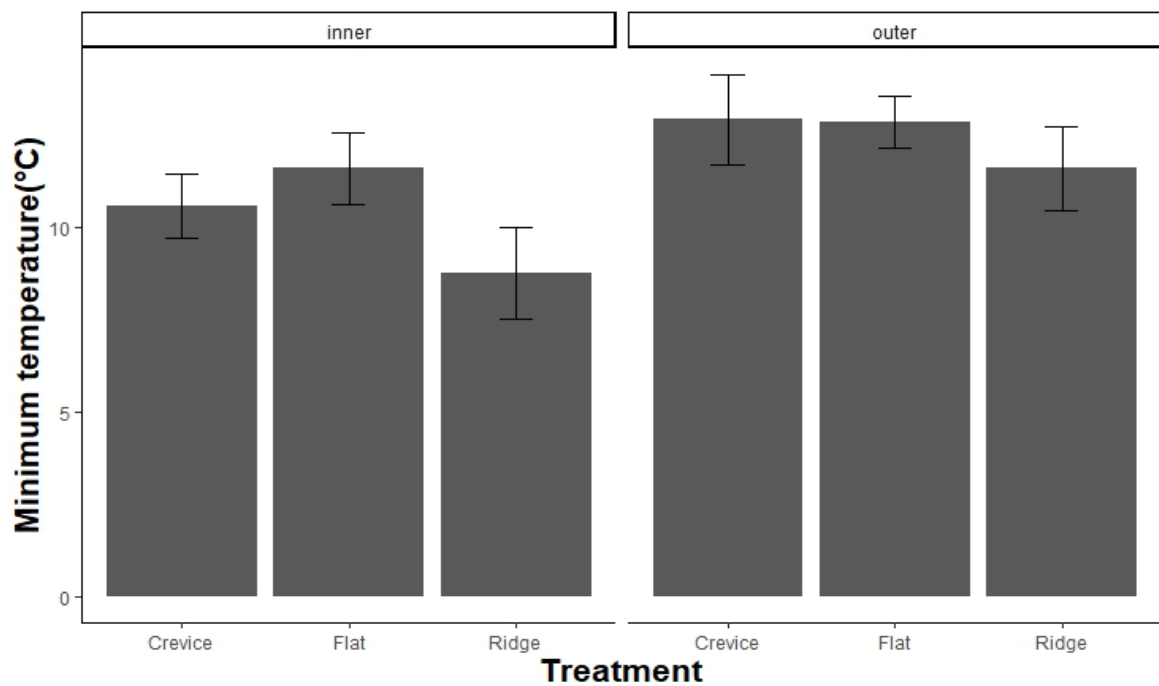
There was a non-significant trend ($p = 0.06$) for cooler minimum temperatures on the flat than complex tiles, and within the complex tiles on ridges than in crevices (Table 3, Fig. 3). Temperatures were generally higher in the inner compared to the outer harbour (Fig. 3), but this was not significant and there was no significant difference in maximum or minimum temperatures between stormdrain and reference sites (Table 3).

Table 3) Generalised linear mixed effects models testing the effects of A) treatment (Tr): flat vs complex and B) microhabitat (Ha: crevice vs ridge) on the maximum and minimum temperature recorded by loggers between April 2019 and February 2020. Tiles were deployed in the inner and outer zones of Sydney Harbour (Zone (Z)) at different distances from stormdrains (Distance (D)). Bold font indicates a significant result ($\alpha = 0.05$).

A) Flat versus Complex						
	Minimum			Maximum		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Treatment (Tr)	44	1.94	0.06	60	0.40	0.69
Distance (D)	5	-0.59	0.58	4	-0.10	0.92
Zone (Z)	5	1.53	0.19	4	-0.97	0.38
Tr x D	44	-0.98	0.33	60	-0.62	0.54
Tr x Z	44	-1.33	0.19	60	0.08	0.93
D x Z	5	-0.93	0.40	4	0.50	0.64
Tr x D x Z	44	1.09	0.28	60	0.75	0.45

B) Crevice versus Ridge						
	Minimum			Maximum		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Microhabitat (Ha)	20	-1.99	0.06	36	-1.63	0.11
Distance (D)	5	-0.66	0.54	5	-0.49	0.64
Zone (Z)	5	1.45	0.21	5	-1.08	0.33
Ha x D	20	1.03	0.31	36	0.79	0.44
Ha x Z	20	0.56	0.58	36	0.85	0.40
D x Z	5	-0.81	0.46	5	-0.74	0.49
Ha x D x Z	20	-0.60	0.56	36	0.23	0.82

A)



B)

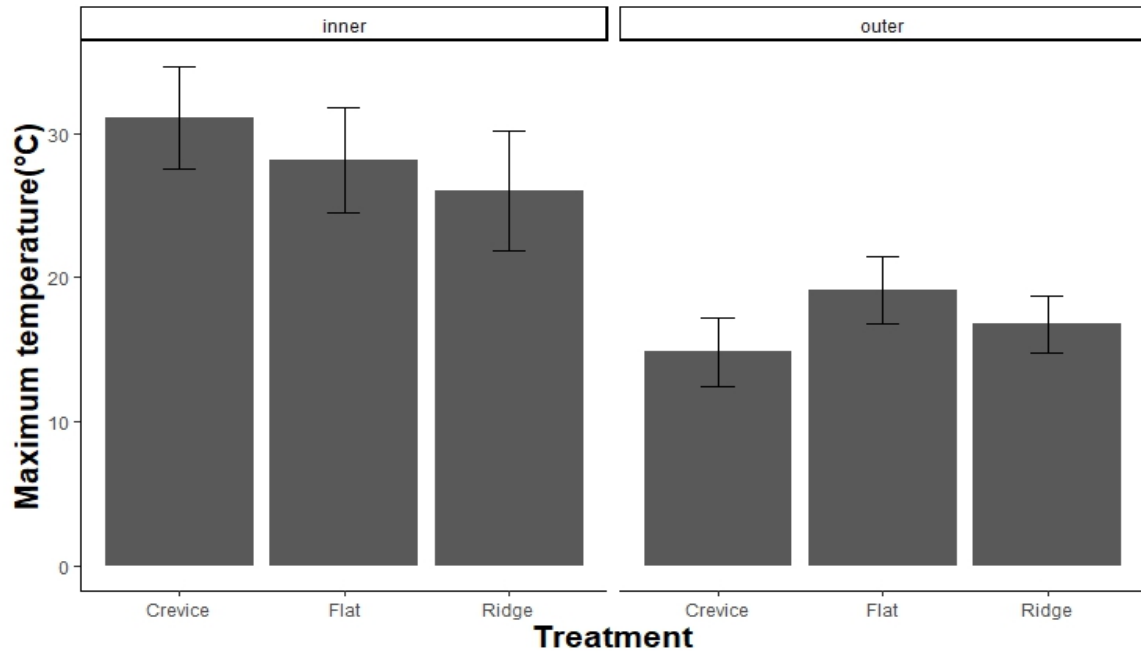


Fig 3) Mean and \pm SE of A) minimum and B) maximum temperatures recorded within each treatment type (Crevice, Flat and Ridge), at sites in the inner and outer Sydney Harbour, $n=12$.

As predicted, salinity was slightly lower in the inner than the outer harbour (Table 4), though this difference was not significant ($t=-0.99$, $df=22$, $p\text{-value}=0.33$).

Table 4) Mean \pm SE of salinity (parts per thousand (ppt)) measured at each of the eight study sites. Sites were situated in the inner and outer zones of Sydney Harbour, near to Stormdrains (SD) and Reference sites (R) far from stormdrains, $n=3$.

Zone	Distance from Stormdrain	Site	Salinity (ppt)
Inner	Near	SD1	29.2 \pm 0.85
Inner	Near	SD2	26.6 \pm 1.23
Inner	Far	R1	27.9 \pm 0.43
Inner	Far	R2	29.2 \pm 0.54
Outer	Near	SD3	31.8 \pm 1.59
Outer	Near	SD4	30.3 \pm 1.67
Outer	Far	R3	31.8 \pm 1.98
Outer	Far	R4	31.8 \pm 1.98

3.2. Biological communities

Across the eight study sites, a total of 83 species colonised the tiles, representing 41 mobile and 42 sessile taxa (Appendices Table S1, S2). These included 36 native, 3 cosmopolitan, 10 cryptogenic and 12 non-indigenous species.

Each of the mobile and sessile communities displayed differences in community structure between flat and complex tiles, that were dependent on site and sampling month, (sig. Treatment x Site x Month, (Table 5, Fig 4). Mobile species were absent from one of the eight sites, and among the remaining seven sites, significant differences in mobile species community structure between complex and flat tiles were only observed at two, each of which were situated in the inner harbour (*a posteriori* tests, sig. Treatment x Site x Month interaction, Table 6). At one of these sites, differences between complex and flat tiles were apparent from the first month of sampling, and at the other, from the third month (Table 5). Sessile species were detected at all eight sites, and their communities displayed significant effects of tile complexity at five (Table 5). Two of these five sites with significant effects of complexity were in the inner harbour, with the other three in the outer harbour. Effects of complexity on sessile communities generally took longer to establish than for mobile communities, with one site displaying significant differences from month 2, one from month 6, one from month 9 and the other two sites, not until month 12 (Table 7).

Within the complex tiles, mobile species similarly displayed site-specific effects of microhabitat (i.e. crevices vs ridge) that varied through time and were unrelated to position in harbour or proximity to drains (Table 7, Fig 5). By the end of the 12-month study, differences between microhabitats were apparent for mobile communities at four of the sites, two in each of the inner (apparent from month 1-2) and outer (apparent from month 6) harbour sites (Table 8).

Table 5: Multivariate PERMANOVAs testing for spatial variation in the effects of complexity Treatment (Tr; flat and complex) on communities of (A) mobile and (B) sessile species between positions in the Harbour (Z; inner and outer), and distances from Stormdrains (D; stormdrain and reference). Two sites were sampled within each zone and distance from stormdrain, to give a total of 8 Sites (S). Sampling of each of the Tiles (Ti) was repeated 1,2,3,6,9, and 12 months (M) following tile deployment) for mobile species and 2,3,6,9, and 12months for sessile species. Bold font indicates a significant result (at $\alpha = 0.05$).

Source	Mobile				Sessile			
	df	MS	Pseudo -F	P(perm)	df	MS	Pseudo -F	P(perm)
Treatment (Tr)	1	56519	2.93	0.16	1	14400	4.17	0.01
Zone (Z)	1	18815	0.86	0.40	1	2.99	4.63	0.11
Distance (D)	1	12494	0.57	0.53	1	2.9e+05	0.40	0.64
Month (M)	5	5807	4.16	0.001	4	8443	1.13	0.33
Tr x Z	1	16748	0.87	0.40	1	8461	2.45	0.06
Tr x D	1	2780	0.14	0.80	1	4932	1.43	0.27
Tr x M	5	3074	2.55	0.002	4	3118	2.70	0.002
Z x D	1	7447	0.34	0.66	1	40195	0.62	0.41
Z x M	5	2541	1.82	0.003	4	10405	1.39	0.15
D x M	5	2232	1.60	0.01	4	12101	1.61	0.08
Site (S)(Z x D)	4	24726	20.16	0.001	4	70880	47.55	0.001
Tr x Z x D	1	2843	0.15	0.80	1	26677	0.77	0.58
Tr x Z x M	5	1573	1.30	0.17	4	1901	1.64	0.05
T x D x M	5	1109	0.92	0.57	4	1657	1.43	0.11
Z x D x M	5	1899	1.36	0.05	4	15647	2.09	0.04
Tile (Ti)(S(Z x D)	40	1283	2.63	0.001	40	1537	2.36	0.001
Tr x S(Z x D)	4	22355	30.93	0.001	4	3714	4.33	0.001
S (Z x D) x M	20	1422	2.12	0.001	16	7824	9.84	0.001
Tr x Z x D x M	5	1158	0.96	0.48	4	1129	0.98	0.51
Tr x Ti (S (Z x D))	40	742	1.52	0.001	38	868.7	1.33	0.01
Ti (S(Z x D)) x M	195	674	1.38	0.001	155	800.2	1.33	0.01
Tr x S (Z x D) x M	20	1229	2.52	0.001	16	1178	1.81	0.001

Table 6: Summary of pairwise PERMANOVA tests for significant effects of Treatment (flat vs complex tiles) on each of sessile and mobile communities, at each of the eight study sites, and at each sampling time. Absent = Assemblage absent from study site; ns = non-significant (at $\alpha=0.05$) difference between treatments, * = significant treatment effect (at $\alpha = 0.05$).

Mobile								
Zone	Distance from stormdrain	Site	Month					
			1	2	3	6	9	12
Inner	Near	SD1	ns	absent	*	*	*	*
Inner	Near	SD2	absent	absent	absent	absent	absent	absent
Inner	Far	R1	*	*	*	*	*	*
Inner	Far	R2	absent	absent	ns	absent	ns	ns
Outer	Near	SD3	absent	ns	ns	ns	ns	ns
Outer	Near	SD4	absent	ns	ns	ns	ns	ns
Outer	Far	R1	absent	ns	ns	ns	ns	ns
Outer	Far	R2	absent	ns	ns	ns	ns	ns

Sessile							
Zone	Distance from stormdrain	Site	Month				
			2	3	6	9	12
Inner	Near	SD1	absent	ns	ns	ns	ns
Inner	Near	SD2	absent	ns	ns	*	*
Inner	Far	R1	absent	ns	ns	ns	*
Inner	Far	R2	absent	ns	ns	ns	ns
Outer	Near	SD3	*	*	*	*	*
Outer	Near	SD4	ns	ns	*	ns	*
Outer	Far	R3	ns	ns	ns	ns	ns
Outer	Far	R4	ns	ns	ns	ns	*

Table 7) Multivariate PERMANOVA testing for spatial variation in the effects of microhabitat (Ha, crevice and ridge) on communities of mobile species between positions in the harbour (Z; inner and outer) and distances from Stormdrain (D; stormdrain and reference). Two sites were sampled within each level of Harbour and Stormdrain, to give a total of eight sites (S). Sampling of each tile (Ti) was repeated 1,2,3,6,9, and 12 months (M) following deployment. Bold font indicates a significant result (at $\alpha = 0.05$).

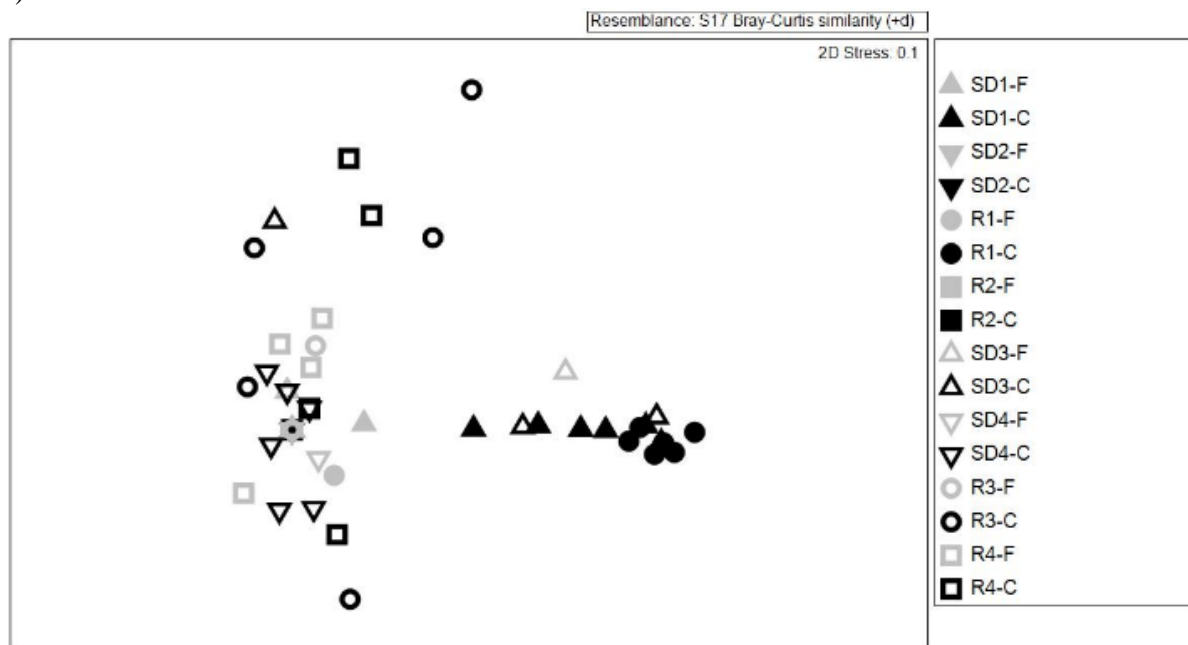
	Mobile			
Source	df	MS	Pseudo-F	P(perm)
Microhabitat (Ha)	1	75893	3.39	0.12
Zone (Z)	1	19919	0.78	0.41
Distance (D)	1	8644	0.36	0.66
Month (M)	5	4808	3.44	0.001
M x D	5	1778	1.27	0.14
M x Z	5	2162	1.55	0.02
M x Ha	5	3210	2.95	0.003
D x Z	1	4988	0.21	0.79
D x Ha	1	5209	0.23	0.71
Z x Ha	1	23419	1.05	0.37
S (D x Z)	4	24428	22.60	0.001
M x D x Z	5	1457	1.04	0.38
M x D x Ha	5	1010	0.93	0.55
M x Z x Ha	5	1360	1.25	0.24
D x Z x Ha	1	3238	0.14	0.81
Tile (Ti)(S (D x Z))	40	1088	2.48	0.001
M x S (D x Z)	20	1400	2.57	0.001
S (D x Z) x Ha	4	22518	30.42	0.001
M x D x Z x Ha	5	871	0.80	0.69
M x Ti (S (D x Z))	193	546	1.24	0.001
Ti (S (D x Z)) x Ha	40	744	1.70	0.001
M x S (D x Z) x Ha	20	1091	2.49	0.001

Table 8) Summary of pairwise comparisons testing effects of Microhabitat (crevice vs ridge) on mobile communities, at each of the eight study sites, and at each sampling time.

Absent=assemblages absent from study site: ns=non-significant (at $\alpha=0.05$) difference between treatments, *=significant treatment effects at $\alpha=0.05$. **=significant treatment effect at $\alpha=0.01$.

Mobile community structure in microhabitats								
Zone	Distance from stormdrain	Site	Month					
			1	2	3	6	9	12
Inner	Near	SD1	ns	*	*	**	**	**
Inner	Near	SD2	absent	absent	absent	absent	absent	absent
Inner	Far	R1	**	**	**	**	**	**
Inner	Far	R2	absent	absent	ns	absent	ns	absent
Outer	Near	SD3	absent	ns	ns	*	*	*
Outer	Near	SD4	absent	absent	ns	ns	ns	ns
Outer	Far	R3	absent	ns	ns	*	ns	*
Outer	Far	R4	absent	ns	ns	*	*	ns

A)



B)

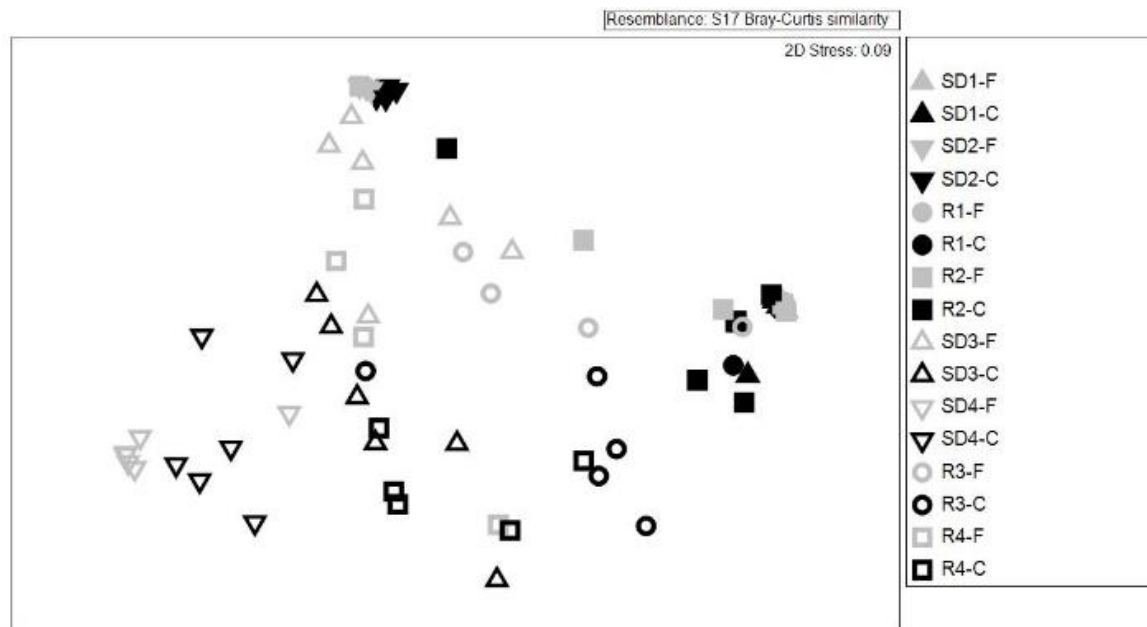


Fig 4) nMDS plots displaying differences in assemblages of A) mobile and B) sessile species between flat (grey symbols; F) and complex (black symbols; C) tiles. Tiles were deployed at eight sites in Sydney Harbour, four of which were situated in the inner harbour (SD1, SD2, R1 and R2, filled symbols) and four were situated in the outer harbour (SD3, SD4, R3 and R4, open symbols). Within each zone, two sites were situated close to stormdrains (SD) while the other two were reference sites (R), away from drains. Points represent communities on each tile at 12 months, the sampling time at which the effects of complexity on assemblages was generally the greatest (Table 6,8), $n=6$.

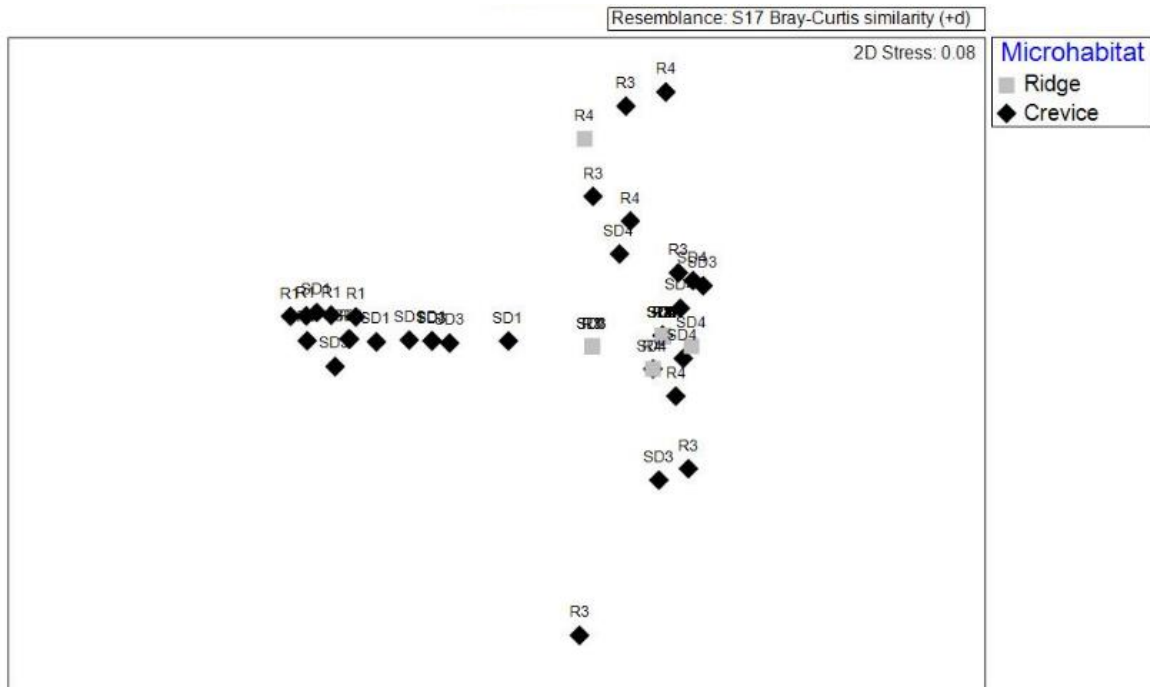


Fig 5) nMDS plots displaying differences in assemblages of mobile species between microhabitats (crevices: black triangles, ridges; grey squares) of the complex tiles. Tiles were deployed at eight sites, split between inner (SD1, SD2, R1 and R2) and outer (SD3, SD4, R3 and R4) Sydney Harbour, at stormdrain (SD) and reference (R) sites. Points represent microhabitats as sampled after 12 months, $n=6$.

BEST analysis of mobile species constrained to subgroups comprising a maximum of 5 species indicated that, collectively, the species *Bembicium auratum*, *Sypharochiton pellisperentis*, *Scutellastra champani*, *Onchidella patelloides* and *Bedevea paviae* accounted for most (88%) of the variation in sessile communities between complex and flat tiles. A subgroup containing *Ulva australis*, *Ulva compressa*, *Ralfsia verucosa*, *Spirobinae* and *Saccostrea glomerata* accounted for 98% of the variation between flat and complex tiles in sessile species.

3.3. Diversity, abundance, and percent covers of mobile and sessile species

Contrary to the hypotheses, total and sessile species richness displayed effects of complexity that were independent of position in harbour and proximity to stormdrains and varied only according to sampling month (Treatment x Month, Table 9). Whereas, initially there was no significant difference in these variables between complex and flat tiles, by 2 months complex tiles supported a significantly greater total and by 6 months a greater sessile species richness than flat tiles (Fig 6A and B). Mobile species richness, by contrast, displayed effects of complexity that varied according to the interacting effects of stormdrain and position in harbour, and among sampling months (Treatment x Month x Stormdrain x Harbour, Table 9,

10). Although, across all stormdrain and harbour treatments, a greater mobile richness was apparent on complex than flat tiles, by 9 months (Fig 7), this pattern was apparent from 3 months at the inner reference and outer stormdrain sites and from 6 months at outer reference sites (Table 10).

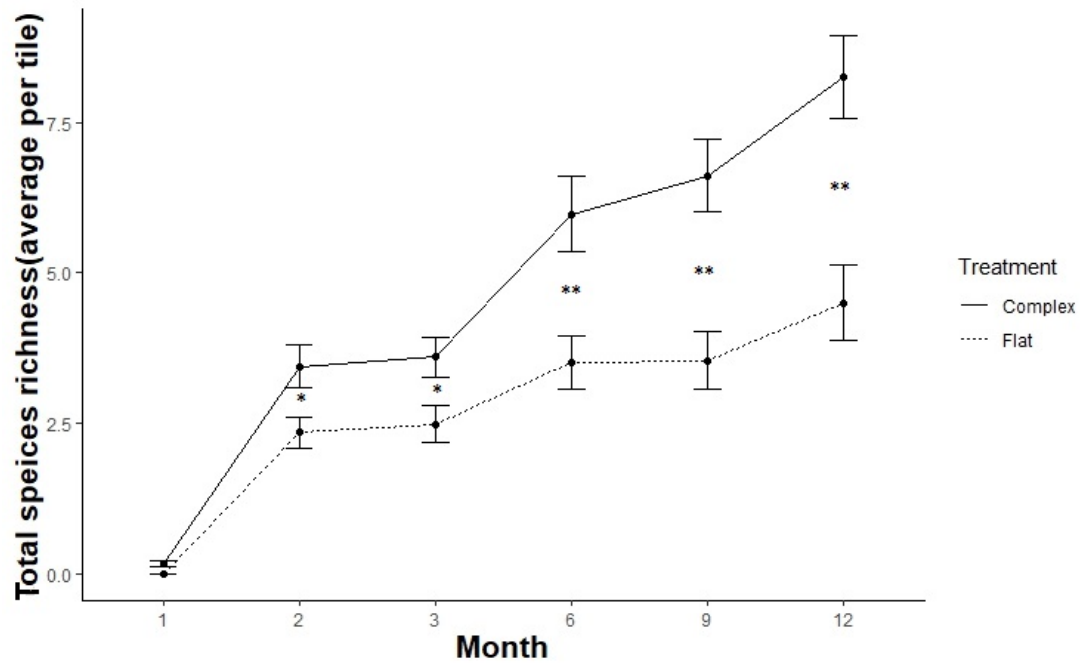
Though there was a general pattern of greater abundances of mobile species on complex than flat tiles, the magnitude of this effect depended on time of sampling (Treatment x Month, Table 9) and position in harbour (Treatment x Harbour, Table 9). As with total and sessile richness, mobile species abundance initially did not differ between complexity treatments, but over time became greater on complex than flat tiles (Fig 6C). Whereas in the inner harbour mobile species were significantly more abundant on complex than flat tiles, there was no significant effect of complexity treatment in the outer harbour (Fig 6D). For total sessile species cover, there was no effect of complexity at any of the sites or sampling months (Table 9).

Table 9) Generalized linear mixed models testing for effects of complexity treatment (Tr; complex, flat), position in harbour (Z; inner vs outer), distance from stormdrain (D; stormdrain vs reference) and month (M; repeated measure) on total species richness, mobile species richness, total mobile species abundance and the percent cover of sessile species. Site (within stormdrain x position in harbour) and tile (with site) were included as nested factors. Bold font indicates a significant result (at $\alpha = 0.05$).

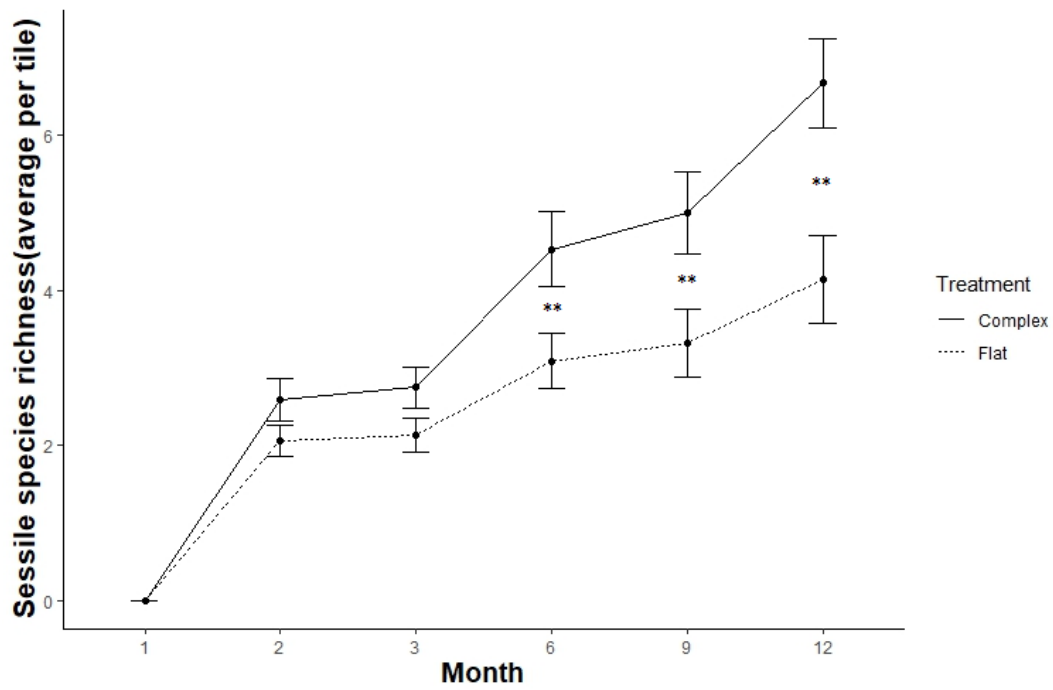
	Total richness			Mobile species richness			Sessile species richness		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Month (M)	450	7.30	1.29e-12	449	2.79	0.005	449	7.15	3.60e-12
Treatment (Tr)	310	0.36	0.72	197	-1.46	0.15	313	1.23	0.22
Distance (D)	8	0.13	0.89	8	-0.14	0.89	7	0.19	0.85
Zone (Z)	8	1.60	0.15	9	0.72	0.49	7	1.25	0.25
M x Tr	449	-3.90	0.0001	449	-1.78	0.08	449	-3.69	0.0003
M x D	449	-1.02	0.31	449	-0.68	0.450	449	-0.87	0.39
Tr x D	310	-0.14	0.88	197	0.15	0.88	313	-0.25	0.81
M x Z	461	8.79	<2e-16	457	6.60	1.12e-10	460	7.09	5.02e-12
Tr x Z	323	-0.59	0.56	206	1.33	0.18	326	-1.45	0.15
D x Z	8	0.01	0.99	8	-0.69	0.51	7	0.31	0.77
M x Tr x D	449	0.74	0.46	449	0.48	0.63	449	0.64	0.53
M x Tr x Z	466	-1.06	0.29	463	-4.28	2.29e-05	465	0.72	0.47
M x D x Z	455	-3.15	0.002	453	-3.19	0.002	455	-2.16	0.03
Tr x D x Z	317	-0.54	0.59	201	-0.88	0.38	320	0.11	0.91
M x Tr x D x Z	458	0.89	0.37	456	2.64	0.01	458	-0.16	0.87

	Sessile species percent cover			Mobile abundance		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Month (M)	533	-1.45	0.15	451	7.08	5.63e-12
Treatment (Tr)	533	-0.49	0.63	148	-3.22	0.002
Distance (D)	5	-1.66	0.16	5	-1.13	0.31
Zone (Z)	5	0.04	0.97	5	-1.16	0.29
M x Tr	533	0.22	0.82	451	-4.94	1.10e-06
M x D	533	5.33	1.44e-07	451	-1.64	0.10
Tr x D	533	0.43	0.67	148	-1.88	0.06
M x Z	533	4.39	1.38e-05	457	-1.61	0.11
Tr x Z	533	-0.09	0.93	154	2.40	0.01
D x Z	5	1.36	0.24	5	0.70	0.51
M x Tr x D	533	-0.11	0.91	451	1.14	0.25
M x Tr x Z	533	-0.45	0.66	462	1.15	0.25
M x D x Z	533	-2.79	0.01	454	0.11	0.91
Tr x D x Z	533	0.71	0.48	151	-1.56	0.12
M x Tr x D x Z	533	-0.35	0.73	457	0.15	0.88

A)



B)



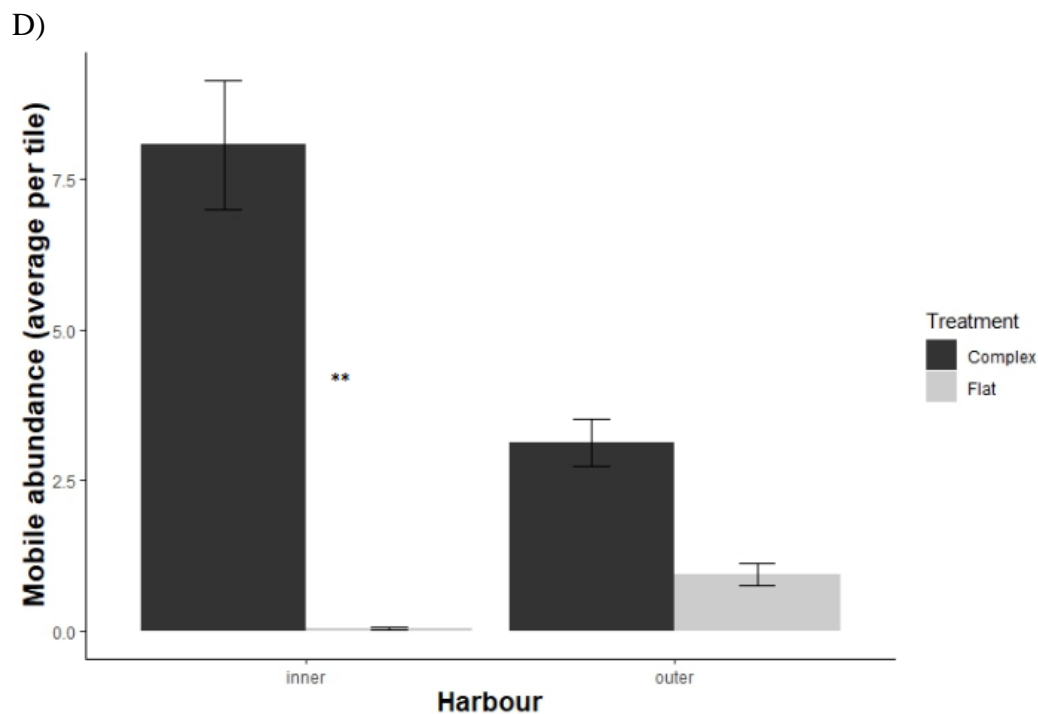
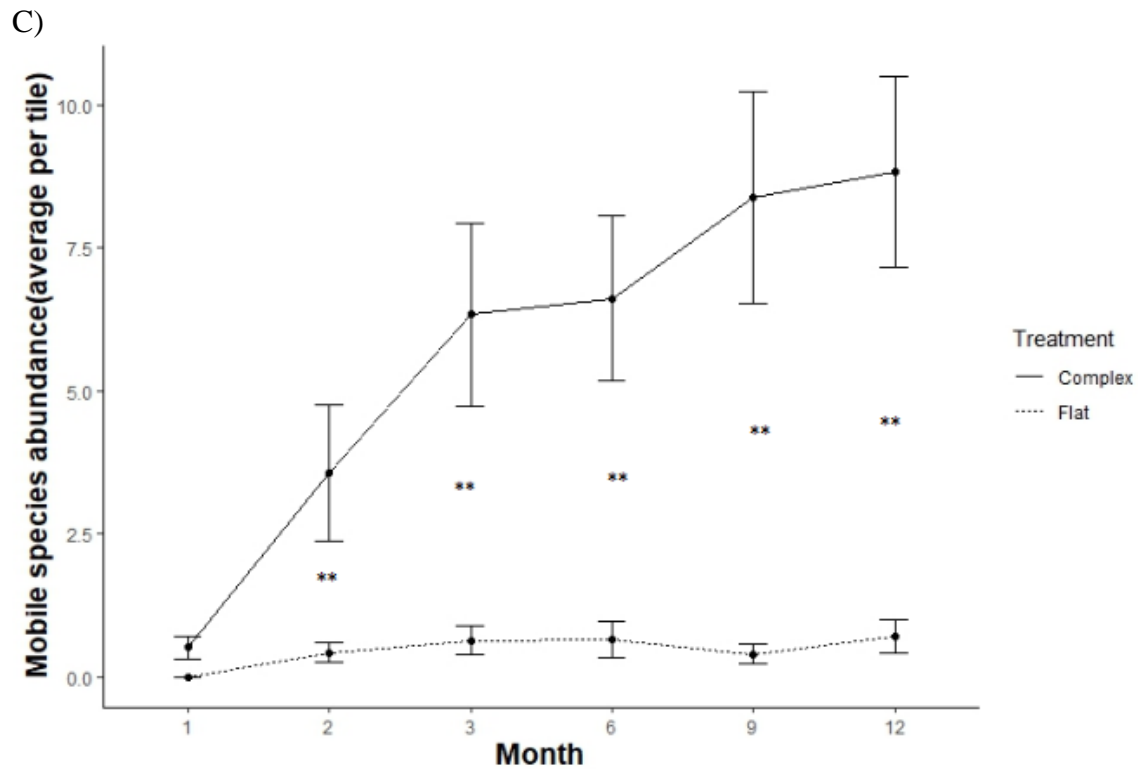


Fig 6) Mean \pm SE A) total species richness, B) sessile species richness, C) mobile species abundance on complex and flat tiles, at each sampling time. Values are averaged across eight study sites, as there was no effect of position in harbour or proximity to drain on effects of complexity, $n = 48$. D) Mobile species abundance also displayed an effect of complexity that was dependent on position in harbour that was independent of sampling time, $n=24$. Significant differences between complexity treatments at $\alpha = 0.05$ and $\alpha = 0.01$ are denoted with a * and **, respectively.

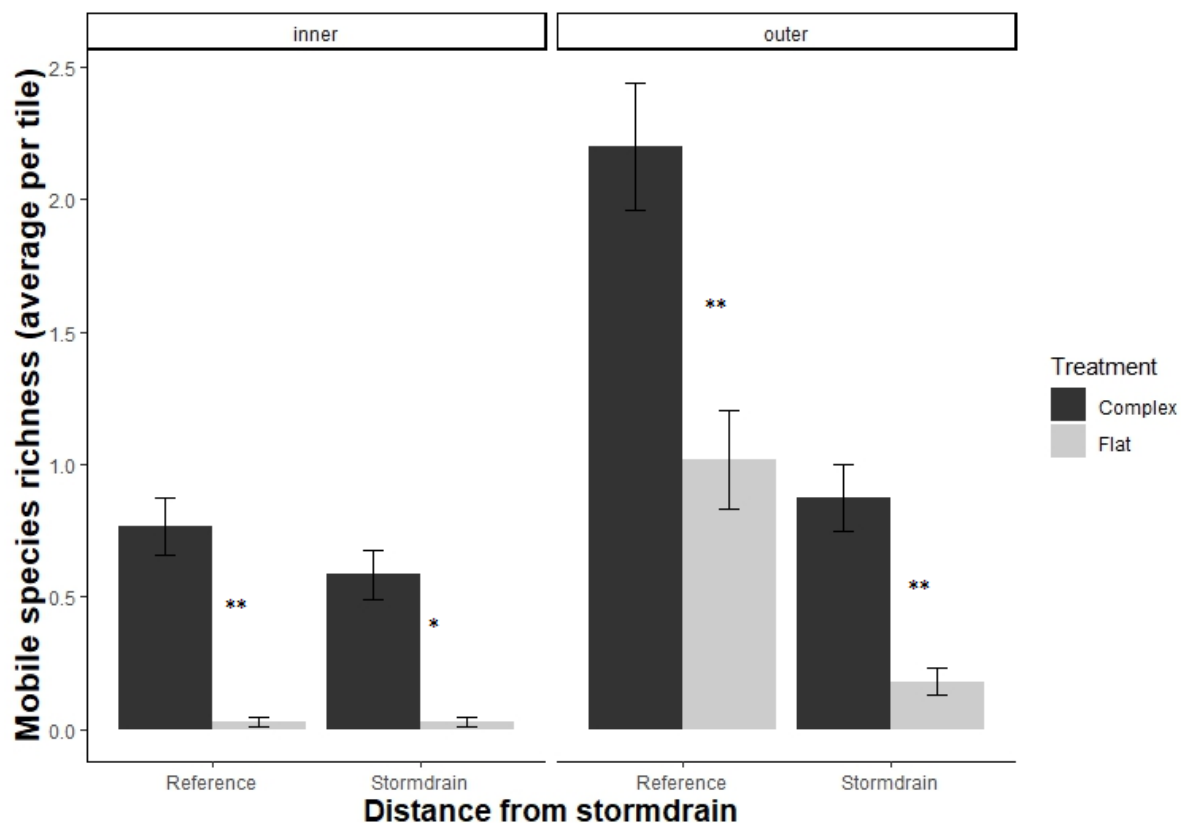


Fig 7) Mean and \pm SE of mobile species richness found on complex (black) and flat (grey) tiles, at Reference and Stormdrain sites, in inner and outer Sydney Harbour, averaged across the entire study period, $n=12$.

Table 10) Summary of pairwise comparisons testing the significant effects of Treatment (flat vs complex tiles) (crevice vs ridge) on mobile species richness, for stormdrain (SD) and reference (R) treatments in the inner (IN) and outer (OUT) harbour at each sampling time. ns=non-significant (at $\alpha=0.05$) difference between treatments, *=significant treatment effects at $\alpha=0.05$. **=significant treatment effect at $\alpha=0.01$.

Mobile species richness							
Zone	Distance from stormdrain	Month					
		1	2	3	6	9	12
Inner	Near (SD)	ns	ns	ns	ns	*	*
Inner	Far (R)	ns	ns	*	*	**	**
Outer	Near (SD)	ns	ns	*	**	*	**
Outer	Far (R)	ns	ns	ns	**	**	**

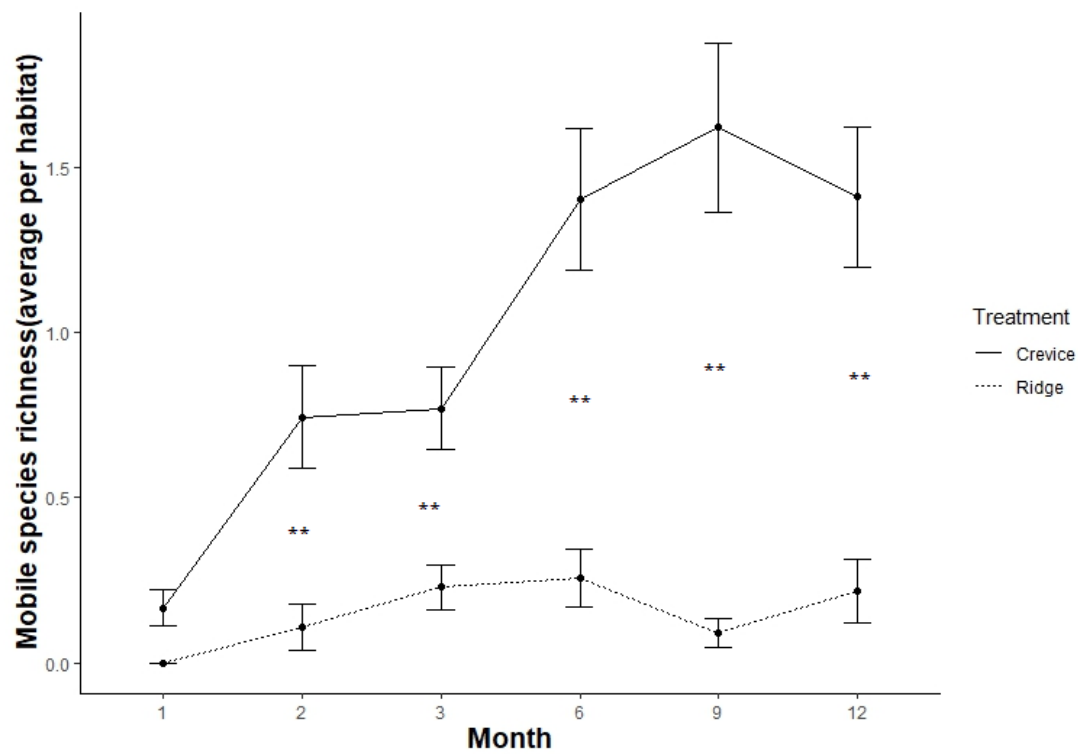
The species richness of mobile taxa varied between microhabitats of the complex tiles, though this effect was dependent on month and position in the harbour, but not proximity to stormdrains (sig. Month x Habitat x Zone, Table 11). By the second month of sampling, crevices supported more mobile species than ridges, with patterns taking longer to develop in the inner harbour (Table 11, Fig 8A). Similarly, effects of microhabitat on mobile abundance

were dependent on sampling month (sig. Habitat x Month, Table 11), and position in harbour (sig. Habitat x Zone, Table 11). Through time, crevices acquired greater abundances of mobile taxa than ridges, a pattern that was significant from month 2 (Fig 8B). This effect was larger in the inner than the outer harbour, though significant at both (Table 11, Fig 8B).

Table 11) Generalized linear mixed models testing for effects of microhabitat (Ha; crevice and ridge), position in harbour (Z; inner vs outer), distance from stormdrain (D; stormdrain vs reference) and month (M; repeated measure) on mobile species richness, mobile species abundance. Site (within stormdrain x position in harbour) and tile (with site) were included as nested factors. Bold font indicates a significant result (at $\alpha = 0.05$).

	Microhabitat mobile richness			Microhabitat mobile abundance		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Month (M)	5	3.21	0.001	442	7.02	8.48e-12
Microhabitat (Ha)	3	-1.45	0.15	179	3.45	0.0007
Distance (D)	8	0.00	0.99	7	-1.33	0.23
Zone (Z)	8	0.69	0.51	7	-1.97	0.09
M x Ha	5	-2.12	0.04	458	-4.56	6.62e-12
M x D	5	-0.86	0.39	456	-1.87	0.06
Ha x D	3	-0.13	0.90	224	1.67	0.10
M x Z	5	5.51	5.87e-08	450	-1.80	0.07
Ha x Z	4	-0.24	0.81	232	2.89	0.004
D x Z	8	-0.75	0.47	7	1.16	0.29
M x Ha x D	5	0.73	0.47	473	1.32	0.19
M x Ha x Z	5	-3.28	0.001	471	0.89	0.37
M x D x Z	5	-2.62	0.01	463	0.35	0.73
Ha x D x Z	4	0.79	0.43	277	-1.75	0.08
M x Ha x D x Z	5	1.29	1.20	482	-0.21	0.84

A)



B)

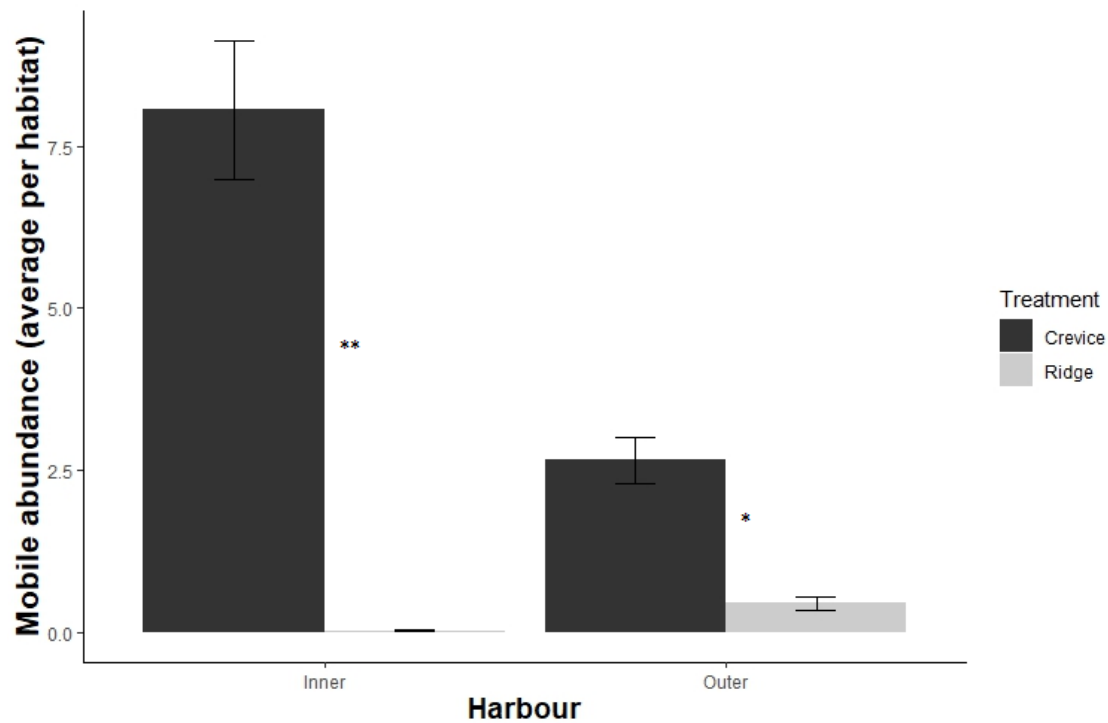


Fig 8) Mean and \pm SE of A) Total species richness through time and B) mobile species abundance between the inner and outer Sydney harbour, for each of the microhabitats (Crevices vs Ridges) of complex tiles *=0.05 significant and **=0.01 significant, n=6.

3.4. Key components of the community

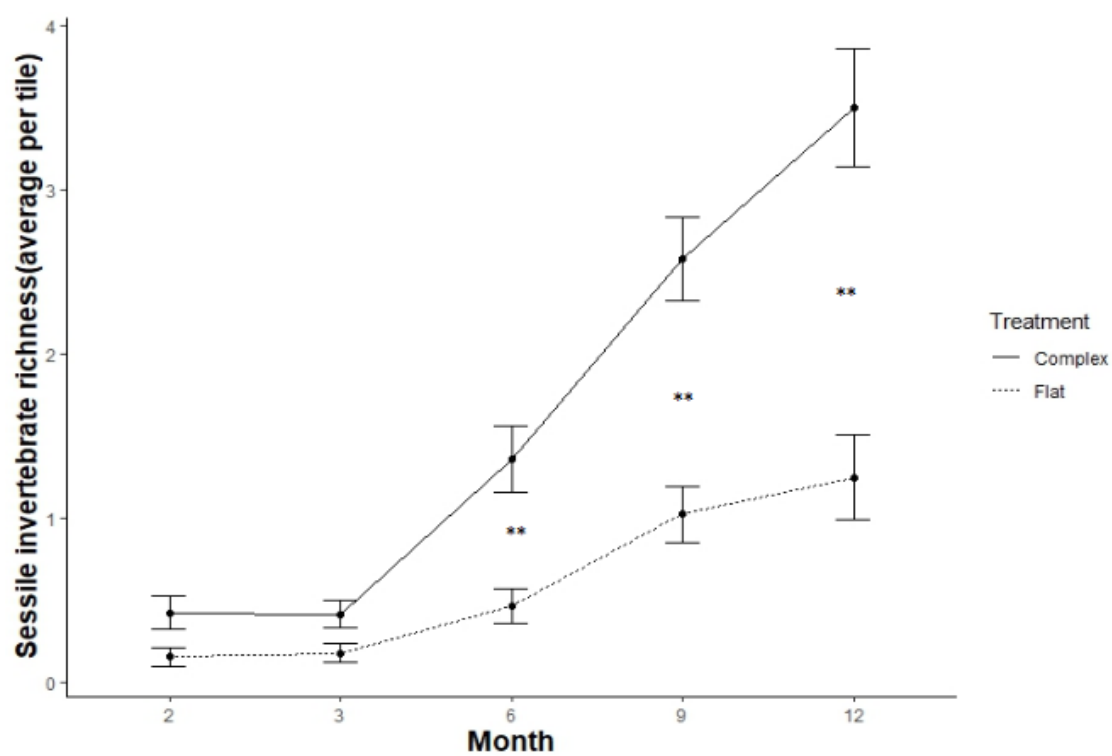
For algal taxa richness and abundance there were no significant effects of complexity, but both measures varied between zone, distance from stormdrain and month of sampling (Table 11). Sessile invertebrate richness and abundance each displayed a positive effect of complexity, that was apparent for all stormdrain and harbour treatments, but varied in the timing of development (Table 12, 13, fig 9). Similarly, non-limpet gastropod and limpet species richness and abundance displayed a positive effect of complexity regardless of proximity to stormdrain or position harbour with spatial variation in the time required for this pattern to develop (Table 13, Fig 9). By contrast non-limpet gastropod abundance, displayed stronger positive effects of complexity in the inner than outer harbour, and in the outer harbour stormdrain than reference sites, with the latter not displaying a significant effect (Fig 9). Limpet richness and abundance only displayed a significant positive effect of complexity at the inner harbour reference sites, with no significant effect in other places (Table 13, Fig 9).

Table 12) Generalized linear mixed models testing for effects of complexity treatment (Tr; complex, flat), position in harbour (Z; inner vs outer), distance from stormdrain (D; stormdrain vs reference) and month (M; repeated measure) on each of algal species, sessile invertebrate, gastropod and limpet species richness and abundance. Site (within stormdrain x position in harbour) and tile (with site) were included as nested factors. Bold font indicates a significant result (at $\alpha = 0.05$).

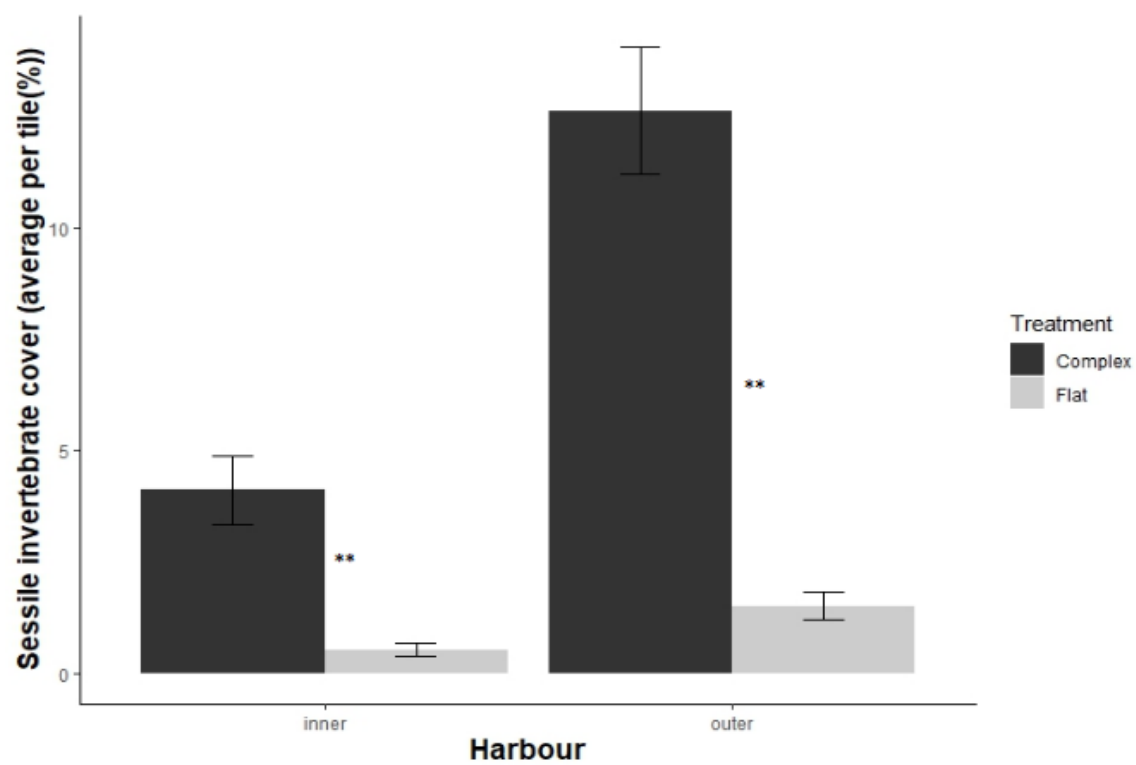
	Algae species richness			Algae percentage cover			Sessile invertebrate richness			Sessile invertebrate cover		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Month (M)	354	0.71	0.48	5	-6.47	2.58e-10	353	9.69	<2e-16	349	5.18	3.68e-07
Treatment (Tr)	396	0.30	0.77	436	-0.85	0.40	339	1.89	0.06	523	1.26	0.21
Distance (D)	5	-0.58	0.59	436	-2.42	0.07	11	-0.02	0.99	17	0.12	0.91
Zone (Z)	5	2.01	0.10	5	0.34	0.75	12	0.37	0.72	17	0.70	0.49
M x Tr	366	-0.92	0.36	5	1.41	0.16	363	-5.38	1.32e-07	359	-3.47	0.001
M x D	367	0.56	0.58	436	8.86	2e-16	363	-0.02	0.99	359	-0.36	0.72
Tr x D	399	-0.28	0.78	436	0.62	0.54	357	0.09	0.93	366	0.04	0.97
M x Z	363	2.63	0.01	436	1.87	0.06	360	7.41	9.06e-13	356	7.63	2.12e-13
Tr x Z	406	-0.99	0.32	436	-0.07	0.95	374	-1.30	0.19	381	0.82	0.41
D x Z	5	0.25	0.81	5	2.07	0.10	11	1.48	0.17	17	0.42	0.68
M x Tr x D	376	0.64	0.52	436	-0.43	0.67	371	0.19	0.85	368	0.24	0.81
M x Tr x Z	383	1.83	0.07	436	0.74	0.46	375	-1.10	0.27	373	-4.92	1.30e-06
M x D x Z	370	1.92	0.06	436	-4.78	2.40e-06	367	-7.21	3.20e-12	363	-2.85	0.01
Tr x D x Z	405	-0.03	0.98	436	0.47	0.64	374	-0.50	0.62	380	-0.33	0.74
M x Tr x D x Z	385	-1.83	0.07	436	-0.76	0.45	379	2.37	0.02	377	1.66	0.10

	Non-limpet gastropod richness			Non-limpet gastropod abundance			Limpet richness			Limpet abundance		
	df	t-value	Pr(> t)	df	t-value	Pr(> t)	df	t-value	Pr(> t)	df	t-value	Pr(> t)
Month (M)	441	2.52	0.01	435	6.61	1.16e-10	445	2.84	0.01	448	1.76	0.08
Treatment (Tr)	327	-1.66	0.85	184	-3.44	0.001	319	0.20	0.10	342	0.05	0.96
Distance (D)	8	-0.27	0.99	7	-1.32	0.23	9	0.01	0.79	14	-0.03	0.98
Zone (Z)	8	0.14	0.50	7	-1.87	0.11	9	0.71	0.89	14	0.64	0.53
M x Tr	459	-1.54	0.08	451	-4.24	2.75e-05	462	-1.77	0.13	465	-1.04	0.30
M x D	459	-0.29	0.44	449	-1.64	0.10	462	-0.78	0.77	465	-0.46	0.65
Tr x D	350	0.34	0.92	230	1.78	0.08	344	0.10	0.73	363	0.10	0.92
M x Z	453	6.59	4.77e-05	443	-1.42	0.16	455	4.11	1.20e-10	458	3.84	0.0001
Tr x Z	359	2.14	0.39	246	3.12	0.002	355	0.87	0.03	372	0.48	0.63
D x Z	8	-0.11	0.83	7	1.17	0.28	9	0.22	0.92	14	0.61	0.55
M x Tr x D	477	0.22	0.70	466	1.11	0.27	479	0.39	0.83	482	0.19	0.85
M x Tr x Z	486	-4.43	0.02	470	0.47	0.64	486	-2.30	1.16e-05	490	-2.01	0.05
M x D x Z	465	-3.92	0.0001	456	0.00	0.99	467	-3.91	0.0001	470	-3.85	0.0001
Tr x D x Z	366	-1.72	0.11	286	-2.1	0.03	363	-1.58	0.09	377	-1.44	0.15
M x Tr x D x Z	493	3.13	0.01	478	0.43	0.67	494	2.79	0.002	496	2.61	0.01

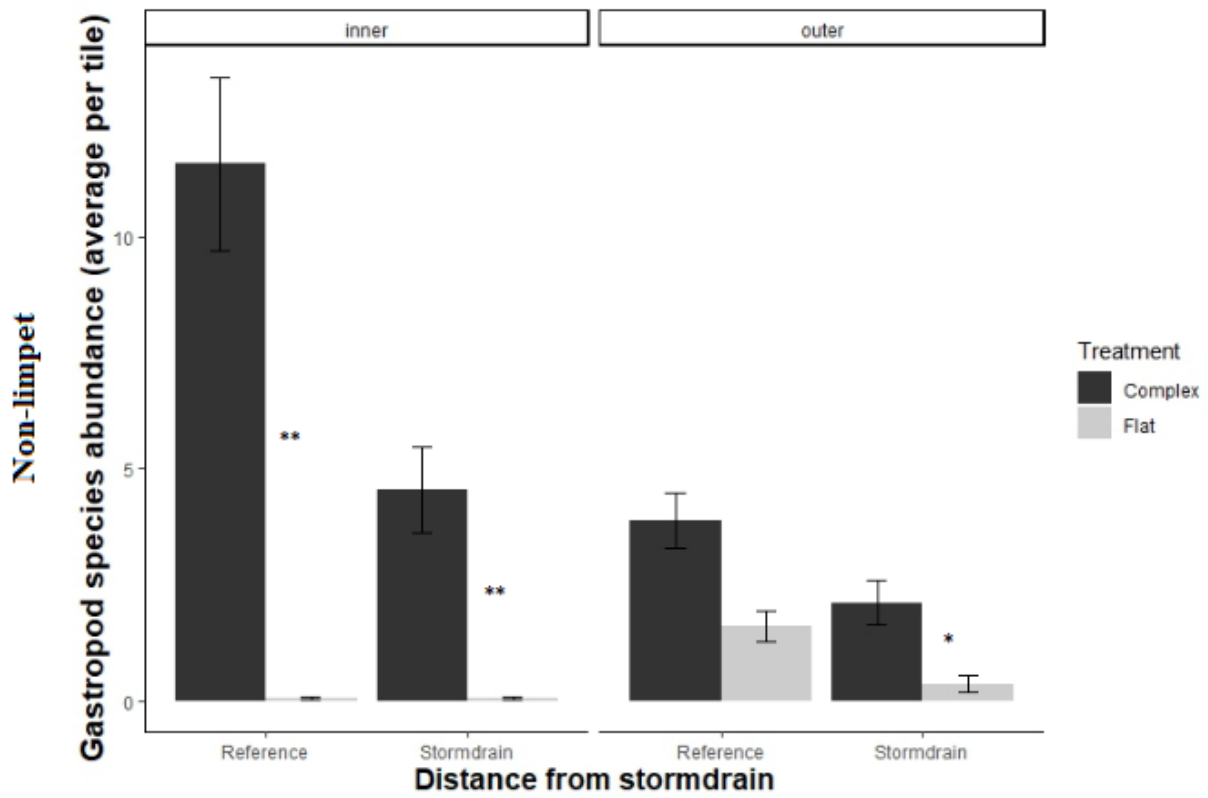
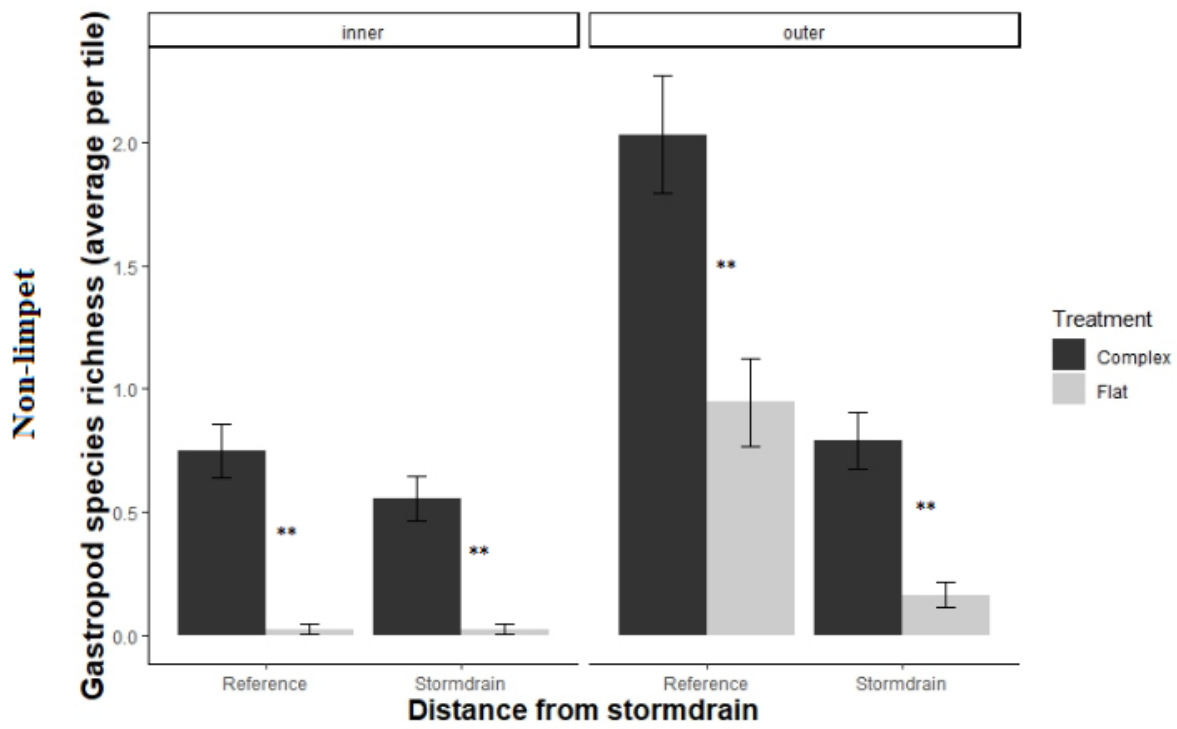
A)



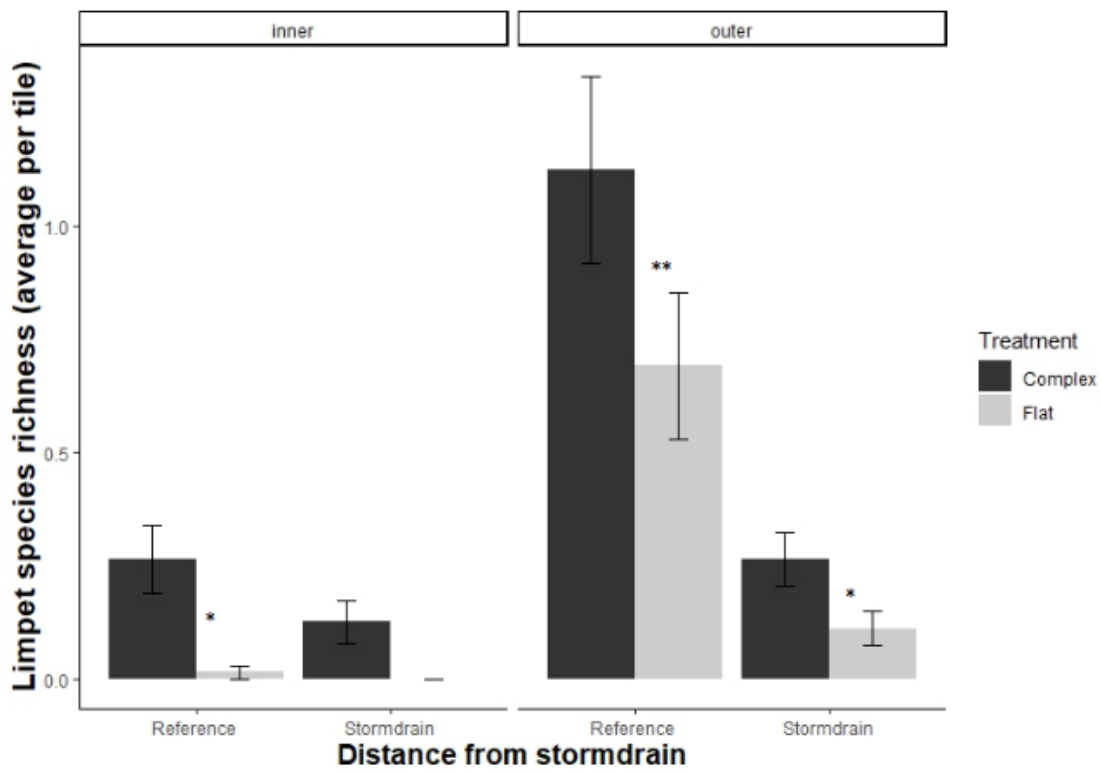
B)



C)



E)



F)

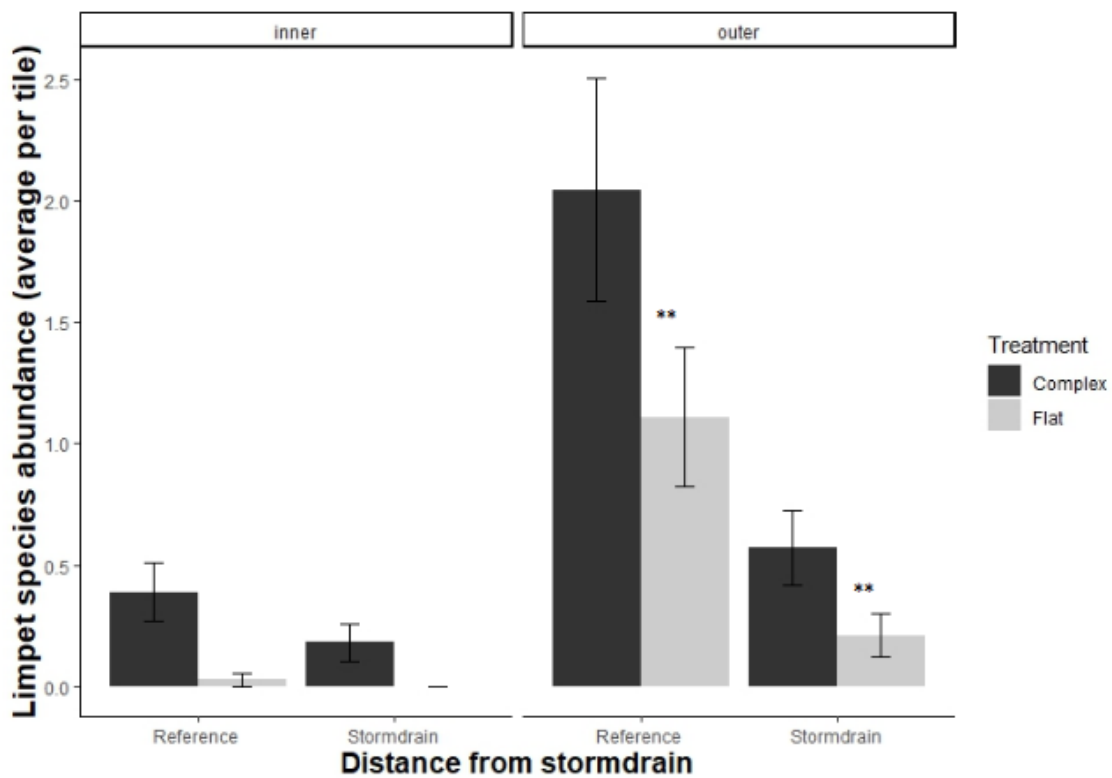


Fig 9) The mean \pm SE species richness and abundance of key functional groups on complex (black bars) and flat (grey bars) tiles. A) Sessile invertebrate richness over time, B) sessile

invertebrate cover, in the inner and outer harbour C) gastropod species richness found on tiles at stormdrain and reference sites in inner and outer Sydney Harbour, D) non-limpet gastropod species abundance found on tiles at stormdrain and reference sites in inner and outer Sydney Harbour, E) limpet species richness found on tiles at stormdrain and reference sites in inner and outer Sydney Harbour and F) limpet abundance found on tiles at stormdrain and reference site in inner and outer Sydney Harbour. For panels B-F, data are averaged across all sampling times. *=0.05 significance and **=0.01 significance n=6.

Tables 13) Summary of pairwise comparisons using emmeans testing the significant effects of Treatment (flat vs complex tiles) (crevice vs ridge) on A) sessile invertebrate richness B) sessile invertebrate percent cover, C) non-limpet gastropod species richness, D) limpet species richness and E) limpet species abundance averaged across each of the eight study sites, and at each sampling time (sessile species were only examined from month 2). ns=non-significant (at $\alpha=0.05$) difference between treatments, *=significant treatment effects at $\alpha=0.05$. **=significant treatment effect at $\alpha=0.01$. IN=inner harbour; OUT=outer harbour sites; SD=stormdrain site; R=reference site

A) Sessile invertebrate richness						
Zone	Distance from stormdrain	Month				
		2	3	6	9	12
Inner	Near (SD)	ns	ns	ns	**	**
Inner	Far(R)	ns	ns	ns	**	**
Far	Near (SD)	ns	ns	**	*	**
Far	Far (R)	*	ns	**	**	**

B) Sessile invertebrate species percent cover					
	Month				
	2	3	6	9	12
Inner	ns	ns	ns	**	**
Outer	ns	ns	**	**	*

C) Non-limpet gastropod species richness							
Zone	Distance from stormdrain	Month					
		1	2	3	6	9	12
Inner	Near (SD)	ns	ns	ns	ns	*	*
Inner	Far(R)	ns	ns	*	*	**	**
Far	Near (SD)	ns	ns	*	**	**	*
Far	Far (R)	ns	ns	ns	**	**	**

D) Limpet species richness							
Zone	Distance from stormdrain	Month					
		1	2	3	6	9	12
Inner	Near (SD)	ns	ns	ns	ns	ns	ns
Inner	Far(R)	ns	ns	ns	ns	*	ns
Far	Near (SD)	ns	ns	*	ns	ns	ns
Far	Far (R)	ns	ns	ns	ns	**	**

E) Limpet species abundance							
Zone	Distance from stormdrain	Month					
		1	2	3	6	9	12
Inner	Near (SD)	ns	ns	ns	ns	ns	ns
Inner	Far(R)	ns	ns	ns	ns	ns	ns
Far	Near (SD)	ns	ns	**	ns	ns	ns
Far	Far (R)	ns	ns	ns	*	**	**

Discussion

A cornerstone of community ecology has been the positive relationship between complexity and diversity (Huston 1979). Consequently, eco-engineering interventions often assume that adding complexity to structurally simplified, degraded habitats will be of universal benefit. However, I found that complexity manipulations on tiles affixed to seawalls, achieved through the addition of crevices and ridges, had spatially variable effects on the biodiversity of colonists. Even after 12 months of community development, effects of crevices and ridges ranged from neutral to positive, across all eight study sites. Whether a site was close to or far from stormdrains generally had little influence on the magnitude and direction of complexity effects. Instead, effects of complexity varied between the outer and inner harbour, with effects on sessile species generally greater for the outer harbour and on mobile species generally greater for the inner harbour. The site dependent effects of complexity have implications for the application of eco-engineering interventions based on the enhancement of complexity, but are typically blindly applied across sites without consideration of their suitability (Strain et al. 2018).

Complexity may enhance species richness by enhancing surface area (Connor and McCoy 1979), and by increasing the diversity and availability of microhabitats and hence the range of species niches supported (Johnson et al. 2003, Willis et al. 2004, Strain et al. 2018). The present study did not attempt to disentangle the effects of surface area and microhabitat diversity on biodiversity. In a previous study (Strain et al. 2020) utilizing the same complex tiles, with crevices and ridges, found that surface area alone could not explain differences in

species abundance and richness between flat and complex tiles. Instead, greater protection of colonists from fin-fish predators and from desiccation and heat stress in crevices than on ridges or flat tiles, appeared to be in part responsible for the greater abundances and richness on complex tiles (Strain et al. 2018b, 2020). The distinct ecological communities in crevices and ridges suggest that the complex tiles enhance species richness and abundance at least, in part, by enhancing niche diversity.

Variation in the strength of complexity effects between the inner and outer harbour likely reflected biological and environmental differences between these areas that affected the species pool of available colonists and the stressors which organisms were exposed to. Effects of complexity are predicted to be greatest where there is a diverse species pool of colonists on which complexity can act (Strain et al. in review). In estuaries, the species pool of available colonists generally decreases from the mouth to the mid reaches of estuaries (Remane 1934, Whitfield et al. 2012). Here, despite the similar salinities of outer and inner harbour sites, we found a total of 69 species colonising tiles in the outer and 17 species colonising tiles in the inner harbour sites. In particular, more species of algae were present in the outer than inner harbour. In urbanised harbours, increases in water retention time with distance upstream (Das et al. 2000) can contribute to greater contaminant concentrations in upstream embayments (Birch and Taylor 1999), and hence decreased biodiversity (Piló et al. 2015). Additionally, differences in the identity, area and connectivity of source habitats may play a role in determining the identity and richness of colonists. Whereas the natural shorelines of the outer harbour were predominantly comprised of rocky shore and sandy beaches, unmodified inner harbour shorelines were dominated by mangrove forests and sedimentary habitats, with smaller pockets of rocky shore.

Positive effects of complexity, arising from stressor amelioration, are most prevalent in environments where local habitat amelioration is critical to organismal survival (McAfee et al. 2016, Bracewell et al. 2018). Thermal stress is broadly regarded as one of the key determinants of intertidal species distributions with many species living at or close to their thermal maxima (Stillman and Somero 2000). The crevices of the complex tiles offer a protective microhabitat from predation and temperature extremes (Strain et al. 2018, Strain et al. 2020). The more strongly positive response of mobile species to complexity in the inner harbour may be in response to the greater thermal ranges in minimum and maximum temperatures experienced there than the outer harbour, although these were not significant. Surprisingly, and in contrast to previous studies (Strain et al. 2020), our study did not detect

thermal differences within crevices. Instead it is possible that there is a greater top-down control from predators on mobile species in the inner harbour, that lead to greater effects of complexity there.

Anthropogenic stressors such as contaminants have been demonstrated to over-ride the effects of complexity where they create conditions that are inhibitory to the survival of most species (Mormul et al. 2011, Mayer-Pinto et al. 2016). Despite predictions that proximity to stormdrains would create a contaminant gradient that would modulate the effects of complexity, this was not the case here. This may either reflect an insufficiently strong effect of stormdrains on contamination during our study, or alternatively adaption of species to the levels of contaminants that occur at these sites. Contaminants are transported into the harbour via stormwater drains following rainfall events (Beck and Birch 2012). However, during the study period, Sydney experienced a dryer than normal period with lower than average rainfall (BOM 2020). Nevertheless, sediment data showed that there was contamination at all sites from which sediments were collected in traps, with most stormdrain sites having elevated levels well above the high SQGV. Unfortunately, at the two outer harbour reference sites, no sediment was collected from traps, perhaps because sandy sediments require greater energy to re-suspend and there was a lack of storms and rainfall that are usually responsible for suspending sediments (Dafforn et al. 2012, Clark et al. 2015). Additionally, a reference site in the inner harbour had concentrations of lead and zinc well above the SQGV limit.

Alternatively, the lack of an effect of stormdrains may reflect the adaptation of the fauna of Sydney Harbour to contaminants. During the study 36 native, 3 cosmopolitan, 10 cryptogenic and 12 non-indigenous species were identified. Previous studies have shown that non-indigenous species that are introduced into harbours following transport on ship hulls and in ballast tanks that are painted with antifouling paints, display a greater tolerance of heavy metals than native species (Dafforn et al. 2008, 2009, Clark et al. 2015, Johnston et al. 2017). Additionally, many fouling species can build up some resistance to toxicants by being exposed to sub-lethal doses and therefore evolve genetically through natural selection (Dafforn et al. 2009). Therefore, their presence may not be affected by proximity to drains even where drains are associated with locally enhanced metal contamination.

This study attempted to match several seawall attributes (i.e. slope, construction material type) across sites. Seawalls, nevertheless, varied in factors such as aspect, age, height, length and connectivity to natural habitats. Each of these factors may have contributed to spatial

variation in community assemblage, and hence effects of complexity, either by influencing environmental conditions, or the proximity of source populations for colonisation.

The time available for community development, predictably, had a strong influence on the magnitude of complexity effects. As the months progressed, more and more species were found on tiles, and effects of complexity strengthened. Although the effects of complexity on mobile and sessile species took time to develop, effects were generally apparent earlier on for mobile than sessile species. Sessile species are dependent on settlement of propagules / larvae from the water column onto substrate and are therefore much slower to colonise than mobile species that can migrate in from adjacent habitats. The ability of species to colonise new areas can be strongly influenced by the distance of the most proximate source populations (Mormul et al. 2011). This could explain the reasons why some species remained completely absent from several of the inner harbour sites throughout the study.

Functional groups analysis indicated that the effects of complexity varied among these groups. In particular sessile invertebrates, limpets and gastropods displayed positive effects of complexity in some sites, macroalgae as whole did not respond well to complexity anywhere. Macroalgal species often display vertical limits on rocky shores that are limited by the amount of moisture as well as grazing pressure (Underwood 1980). The benefits of crevices in providing moisture retention, might be offset by their limited light availability reducing photosynthesis and enhanced grazing by limpets and gastropods that are able to use crevices as a refuge from environmental stressors, such as desiccation and predation. Gastropods displayed a strong positive response to complexity everywhere, and limpets displayed strong positive responses in the outer harbour, where they were most abundant.

The mobile species to respond most strongly to complexity were the gastropod *Bembicium auratum*, the chiton *Sypharochiton pellisperentis*, the limpet *Scutellastra champani*, the onchidium *Onchidella patelloides* and the oyster drill *Bedevelia paivae*. Sessile species to respond strongly were the algae, *Ulva australis*, *U. compressa*, *Ralfsia verucosa*, the tube worm Spirobinae and the oyster *Saccostrea glomerata*. Studies in intertidal mangrove forests have demonstrated that the availability of suitable hard substrate for grazing can limit the growth and survival of *Bembicium auratum* (Branch and Branch 1980), such that this species likely benefited from enhanced surface area and crevices of complex tiles. However, the almost exclusive occupation of crevices indicates that it may have benefited from the protective microhabitats provided by complex tiles, preventing the predation by birds and

larger crabs. Previous studies on outer harbour seawalls have found that oyster survival and recruitment is enhanced by the crevice of complex tiles which reduce rates of fish predation on juveniles (Strain et al. 2018), and may reduce thermal stress that occurs during summer afternoon low-tides (Strain et al. 2020). *Bedevelia paivae* are in turn a predator of oysters, so are likely indirectly benefiting from complexity as a result of the enhanced oyster abundance. The algae that responded to complexity, despite the overarching neutral effect within the functional group, were either opportunists that can rapidly colonise free space, or adapted to low light and frequent grazing pressure (Dethier and Steneck 2001).

The strongly site-dependent effects of complexity on species richness and abundance has implications for eco-engineering. Seawalls and other built structures are an increasingly common feature of urban marine seascapes (Dafforn et al. 2015). As compared to the natural habitats they replace, topographically simple artificial structures commonly support reduced biodiversity (Airoldi et al. 2015). Eco-engineering complexity and missing microhabitats on these artificial structures to enhance biodiversity and ecosystem functioning of these communities, is increasingly becoming more common (Strain et al. 2018). Such approaches are often blindly applied across sites without consideration of whether the type of complexity being manipulated will be of ecological benefit at that site. The scientific studies providing the evidence base for this rapidly growing field are often poorly replicated and carried out over small spatial scales (Chapman et al. 2018).

Together, with a recent study documenting spatially variable effects of complexity in harbour environments at biogeographic scales (Strain et al. in review), this study shows that effects of complexity are not universally positive, and can vary in magnitude between sites separated by as little as tens of kilometres. Hence, costly eco-engineering interventions aimed at enhancing biodiversity through the addition of complexity may be ineffective at some locations.

Experiments disentangling the role that the species pool plays, and the environmental stressors that modulate the effects of complexity will assist in identifying those areas in which the incorporation of complexity into marine built structures will produce the largest benefit to cost ratio. Careful considerations of environmental conditions and further testing needs to occur before implementing any kind of eco-engineering intervention that increases the complexity of a site. Studies that test eco-engineering interventions in a variety of environmental contexts are therefore needed to provide guidance to managers and stakeholders about where and when eco-engineering projects will provide the best overall outcomes.

Conclusion

This study has clearly shown that even within a very narrow geographic area, the complexity provided by crevices and ridges can have spatially variable effects on biodiversity among sites and functional groups, ranging from positive to neutral. These results challenge the assumption that adding complexity to degraded urban habitats will have universally positive effects and, instead supports a growing number of studies in suggesting that effects of complexity will be dependent on the size and identity of species pool of available colonists and the prevailing environmental conditions. Consequently, whether enhancing the complexity of urban structures represents a viable and value for money approach to mitigate the negative effects on biodiversity requires site by site consideration. Attempts to rehabilitate and/or repair degraded habitats through the addition of complexity require knowledge of target species, and local environmental conditions for them to work adequately so as to improve habitats.

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Appendices

Table S1. List of taxa colonising experimental tiles during the 12 months experiment

Kingdom/ Phylum	Order	Family	Species
<u>Plantae</u> / Chlorophyta	Ulvales	Ulvacea	<i>Ulva australis</i>
			<i>Ulva compressa</i>
			<i>Ulva intestinalis</i>
Phaeophyta	Scytosiphonales	Scytosiphonaceae	<i>Petalonia binghamiae</i>
	Dictyotales	Dictyotaceae	<i>Dictyota dichotoma</i>
	Ectocarpales	Scytosiphonaceae	<i>Colpomenia peregrina</i>
	Ralfsiales	Ralfsiaceae	<i>Ralfsia verrucosa</i>
Rhodophyta	Corallinales	Corallinaceae	<i>Corallina officinalis</i>
		Corallinaceae	<i>Amphiroa anceps</i>
	Ceramiales	Wrangeliaceae	<i>Griffithsia monalis</i>
	Gelidales	Gelidiaceae	<i>Gelidium corneum</i>
		Gelidiaceae	<i>Gelidium pusillum</i>
	Gracilariales	Gracilariaceae	<i>Gracilaria arcuata</i>
		Gracilariaceae	<i>Gracilaria howensis</i>
	Bangiales	Bangiaceae	<i>Pyropia pulchella</i>
<u>Animalia</u> / Arthropoda	Amphipoda		Unidentified amphipod 1
	Isopoda		Unidentified isopod 3
			Unidentified isopod 2
	Sessilia	Austrobalanidae	<i>Austrominius covertus</i>
		Austrobalanidae	<i>Hexaminius popeiana</i>
		Balanidae	<i>Amphibalanus amphitrite</i>
		Tetracitidae	<i>Tesseropora rosea</i>
		Tetracitidae	<i>Tetracitella purpurascen</i>
Crustacea	Decapoda		Unidentified crab 1
Annelida	Sabellida	Serpulidae	<i>Salmacina australis</i>
		Serpulidae	<i>Galeolaria caespitosa</i>
		Serpulidae	<i>Ficopomatus enigmaticus</i>

Cnidaria			Unidentified hydroid 1
<u>Bryozoa/</u> Gymnolaemata	Cheilostomata	Bugulidae	<i>Bugula neritina</i>
		Cryptosulidae	<i>Cryptosula pallasiana</i>
	Cheilostomatida	Lepraliellidae	<i>Celleporaria nodulosa</i>
		Candidae	<i>Tricellaria inopinata</i>
		Watersiporidae	<i>Watersipora arcuata</i>
		Watersiporidae	<i>Watersipora subtoquata</i>
<u>Mollusca/</u> Bivalvia	Mytilida	Mytilidae	<i>Mytilus galloprovincialis</i>
		Mytilidae	<i>Trichomya hirsuta</i>
	Ostreida	Osteidae	<i>Saccostrea glomerata</i>
Gastropoda	Patellogastropoda	Patellidae	<i>Cellana tramoserica</i>
		Patellidae	<i>Scutellastra chapmani</i>
		Patellidae	<i>Scutellastra peronii</i>
	Subclass: Orthogastropoda: Superorder: Vetigastropoda	Fissurellidae	<i>Montfortula rugosa</i>
	Superorder: Caenogastropoda: Infraorder: Littorinimorpha	Littorinidae	<i>Afrolittorina acutispira</i>
		Littorinidae	<i>Littoraria luteola</i>
		Littorinidae	<i>Bembicium auratum</i>
		Littorinidae	<i>Bembicium nanum</i>
	Subclass: Patellogastropoda	Littiidae	<i>Patelloida mimula</i>
		Littiidae	<i>Patelloida mufria</i>
		Littiidae	<i>Patelloida latistrigata</i>
		Littiidae	<i>Notoamea flammea</i>
		Littiidae	<i>Notuacmia petterdi</i>
	Trochida	Trochoidae	<i>Austrocochlea porcata</i>
		Trochoidae	<i>Austrocochlea concomerata</i>
		Trochoidae	<i>Austrocochlea constricta</i>
	Superorder: Caenogastropoda: Infraorder: Neogastropoda	Muricidae	<i>Bedeva paivae</i>
		Muricidae	<i>Tenguella marginalba</i>
	Systellommatophor a	Onchidiidae	<i>Onchidella patelloides</i>
		Onchidiidae	<i>Onchidium dameli</i>
	Siphonariida	Siphonariidae	<i>Siphonaria denticulata</i>
		Siphonariidae	<i>Siphonaria funiculata</i>
	Chitonida	Chitonidae	<i>Sypharochiton pelliserpentis</i>
		Chitonidae	<i>Acanthopleura gaimardi</i>

		Acanthochitonidae	<i>Acanthochitona pilsbryi</i>
	Neoloricata	Chitonidae	<i>Onithochiton quercinus</i>
Polychaeta	Canalipalpata	Serpulidae	<i>Galeolaria caespitosa</i>
		Serpulidae	<i>Hydroides</i> sp
		Serpulidae	Spirorbinae
Porifera	Leucosolenida		Unidentified encrusting sponge 1
			Unidentified sycon sponge 1
Tunicata	Stolidobranchia	Botrylloides	<i>Botrylloides leachii</i>
	Aplousobranchia	Aplousobranchia	<i>Didemnum</i> sp.

Table S2. Occurrence of species on each of the habitat treatments (F=flat tiles; C=complex tiles), at stormdrain (SD1 and 2) and reference (R1 and 2) sites in inner and outer Sydney Harbour, x=species present.

Species	Inner								Outer							
	SD1		SD2		R1		R2		SD3		SD4		R3		R4	
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C
<i>Ulva australis</i>							x	x	x	x	x	x	x	x	x	x
<i>Ulva compressa</i>			x	x			x	x	x	x	x	x	x	x	x	x
<i>Ulva intestinalis</i>												x	x	x	x	x
<i>Petalonia binghamiae</i>										x		x			x	x
<i>Dictyota dichotoma</i>														x		
<i>Colpomenia peregrina</i>							x			x	x	x		x	x	x
<i>Ralfsia verrucosa</i>					x	x		x	x	x	x	x	x	x	x	x
<i>Corallina officinalis</i>									x	x	x	x	x	x	x	x
<i>Amphiroa anceps</i>										x	x	x		x	x	x
<i>Griffithsia monalis</i>											x	x		x		x
<i>Gelidium corneum</i>															x	
<i>Gelidium pusillum</i>											x	x		x	x	x
<i>Gracilaria arcuata</i>									x	x	x	x	x	x	x	x
<i>Gracilaria howensis</i>									x	x	x	x	x	x	x	x
<i>Pyropia pulchella</i>													x	x	x	x
Unidentified amphipod															x	
Unidentified isopod 3										x						
Unidentified isopod 2											x	x		x	x	x
<i>Austrominius covertus</i>					x	x							x	x	x	x
<i>Hexaminius popeiana</i>	x	x	x	x	x	x	x	x					x	x		x
<i>Amphibalanus amphitrite</i>	x	x	x	x	x	x		x		x				x	x	x
<i>Tesseropora rosea</i>													x	x	x	x
<i>Tetraclitella purpurascens</i>													x	x	x	x
crab								x		x				x		
<i>Salmacina australis</i>																x
<i>Galeolaria caespitosa</i>														x		

<i>Ficopomatus enigmaticus</i>														X		
Unidentified hydroid 1								X		X	X		X			X
<i>Bugula neritina</i>																X
<i>Cryptosula pallasiana</i>								X	X				X			
<i>Celleporaria nodulosa</i>													X			
<i>Tricellaria inopinata</i>											X		X			X
<i>Watersipora arcuata</i>									X	X	X		X	X	X	X
<i>Watersipora subtoquata</i>											X		X			
<i>Mytilus galloprovincialis</i>		X		X			X						X			X
<i>Trichomya hirsuta</i>		X		X			X						X			X
<i>Saccostrea glomerata</i>		X		X	X	X	X		X		X	X	X	X	X	X
<i>Cellana tramoserica</i>												X	X	X	X	X
<i>Scutellastra chapmani</i>												X	X	X	X	X
<i>Scutellastra peronii</i>															X	X
<i>Notoacmea petterdi</i>		X			X	X				X	X		X			X
<i>Montfortula rugosa</i>												X	X			X
<i>Afrolittorina acutispira</i>													X			
<i>Littoraria luteola</i>													X			
<i>Bembicium auratum</i>	X	X			X	X		X	X		X		X			
<i>Bembicium nanum</i>												X	X			
<i>Patelloida mimula</i>		X			X		X		X			X	X	X	X	X
<i>Patelloida mufria</i>					X			X	X	X	X	X	X			X
<i>Patelloida latistrigata</i>		X			X							X				X
<i>Notoamea flammea</i>		X			X							X	X	X	X	X
<i>Notuacmia petterdi</i>		X			X	X				X	X		X			X
<i>Austrocochlea porcata</i>											X	X	X			
<i>Austrocochlea concomerata</i>									X				X			
<i>Austrocochlea constricta</i>									X							
<i>Bedevea paivae</i>									X		X		X			X
<i>Tenguella marginalba</i>									X		X		X			X
<i>Onchidella patelloides</i>												X	X	X	X	X
<i>Onchidium dameli</i>								X	X							
<i>Siphonaria denticulata</i>												X	X	X	X	X
<i>Siphonaria funiculata</i>									X				X	X	X	X
<i>Sypharochiton pelliserpentis</i>											X		X	X	X	X
<i>Acanthopleura gaimardi</i>															X	X
<i>Acanthochitona pilsbryi</i>										X						
<i>Onithochiton quercinus</i>													X			
<i>Galeolaria caespitosa</i>													X			
<i>Spirorbinae</i>								X	X	X	X	X	X	X	X	X

Unidentified encrusting sponge											X		X	X	X	X
Unidentified sycon sponge												X				
<i>Botrylloides leachii</i>														X		X
<i>Didemnum sp</i>														X	X	X