Does seawall greening facilitate non-indigenous species?

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Declaration

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

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Abstract

Artificial structures such as seawalls, typically support less biodiversity than the natural habitats they replace and can harbour non-indigenous species (NIS). Greening projects enhance biodiversity by adding complexity and surface area. It is, however, unclear to what extent they facilitate NIS. In one of the largest attempts to green seawalls through retrofitting, two 12m stretches were fitted with habitat enhancing concrete panels of six designs – five complex and one flat. Sampling of whole panels and the microhabitats within these were assessed as to - (1) whether colonisation of NIS was enhanced on the complex panels when compared to the flat panel, (2) whether there were particular designs and microhabitats that promoted NIS, and (3) whether colonisation patterns differed among tidal elevations. At high and mid intertidal elevations, the contribution of NIS to total abundance and richness was generally very small on both complex and flat panels. At the low intertidal elevation by contrast, NIS contributed approximately 75% sessile cover, 50% richness and were in some instances 50% more abundant and diverse in growth on the complex rather than flat panels. Within the panels, NIS were particularly abundant in moist, shaded microhabitats. Knowledge of these factors that promoted NIS colonisation will assist in designing future greening interventions that do not facilitate NIS.

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1. Introduction

Urbanisation is rapidly occurring around the world due to population growth and increasing migration from rural areas to cities (Hammond, 1992). Growth has been particularly large in coastal regions where a majority of cities are located (Timmerman and White, 1997). Further estimates suggest that over 75% of the human population will live within 100km of the coast by 2025, placing significant pressure on the associated habitats (Agency, 2006, Benoit and Comeau, 2012). Population increase and urbanisation have been linked to a variety of different anthropogenic pressures, including hardening, chemical contamination, light and noise pollution, as well as the introduction of invasive species (reviewed by Bugnot et al., 2019). In marine and coastal environments, impacts on natural systems can include fragmentation of habitats, altered and polluted water flow, sediment contamination and disturbance, nutrient loading and the introduction of non-indigenous species (NIS) (Boudouresque et al., 2009, Bulleri, 2005a, Chapman, 2003, Dolbeth et al., 2007, Hedge et al., 2009)

Two pressures which occur simultaneously in urbanised marine habitats, and have been shown to interact, are hardening and colonisation by NIS (Glasby et al., 2007, Ruiz et al., 1997). Coastal hardening modifies or replaces natural shoreline habitats such as sand- and mud-flats, oyster reefs, mangrove forests, seagrass beds and saltmarshes, through the addition of infrastructure, such as breakwaters, jetties, groynes, pilings, and seawalls, that protect coastal properties or provide other services (Connell and Glasby, 1999, Davis et al., 2002, Reilly et al., 1996). Population growth is a major driver of coastal hardening, with the amount of hard defence structures predicted to increase to protect human assets from more frequent storm events and sea level rises associated with global warming (Bulleri and Chapman, 2010). Seawalls are a common form of coastal armouring. For example, in Sydney Harbour, Australia, over 50% of the foreshore has been modified with seawalls (Dafforn et al., 2015), and in Hong Kong, only 5% of the natural shoreline of Victoria Harbour remains, with the remaining 95% of shoreline dominated by seawall (Loke et al., 2017). The increase of coastal armouring is of concern because recent research has shown that while these structures provide substrate for some marine organisms to colonise, the communities differ greatly from those found in the sedimentary habitats they typically replace (Dugan et al., 2011), as well as natural hard substrate habitats such as rocky shores (Bulleri and Chapman, 2010, Chapman, 2003, Glasby et al., 2007, Miller and Etter, 2008, Moreira et al., 2007).

Community differences between seawalls and other hard substrates have been partly attributed to the physical characteristics of seawalls, which differ from rocky shores with respect to slope, orientation, and complexity (Chapman and Bulleri, 2003, Whorff et al., 1995). Rocky shores, the closest natural analogues of seawalls, often have a gently sloping horizontal platform that supports large areas of

intertidal and subtidal substrate (Chapman and Bulleri, 2003). In contrast, seawalls are vertically orientated or steeply sloped (i.e. angle of 30-90 degrees) so the area of substrate available for colonisation is reduced (Dafforn, 2017). Furthermore, seawalls often have less complexity and so provide fewer and different habitat niches compared to the pits, rockpools and crevices found on rocky shores (Chapman, 2003). Lower surface area and lower structural complexity have both been linked to reduced abundances and species diversity (Matias et al., 2011). These physical differences are also thought to influence community composition and whether native or non-indigenous (NIS) species recruit and persist on seawalls (Bulleri and Chapman, 2004, Bulleri, 2005b, Bulleri et al., 2005, Chapman, 2006, Megina et al., 2013, Tyrrell and Byers, 2007). Artificial structures in general have been found to support more NIS than natural habitats (Tyrrell and Byers, 2007). For example, Dafforn et al. (2013) found that pilings and pontoons were hotspots of NIS, and Mayer-Pinto et al. (2018) revealed that seawalls in Sydney Harbour had 50% more NIS than natural rocky shores.

 One potential mechanism for enhanced NIS recruitment on artificial structures relates to their close proximity to NIS transport vectors, recreational and commercial vessels (Clarke Murray et al., 2014, Dafforn et al., 2009, Dafforn et al., 2011, Davidson et al., 2010). New structures provide bare hard substrate that is initially free from native competitors and predators and is available for colonisation by NIS (Dafforn et al., 2009). Furthermore, the urban contaminants entering waterways create highly disturbed environments, which tend to favour opportunistic colonisers such as NIS (Crooks et al., 2011, Piola and Johnston, 2008). The long term use of antifouling paints and copper biocide has led to metallotolerant NIS that are transported via hull fouling and are able to establish and thrive in contaminated harbours (Piola et al., 2009). This has further led to the reduction of native species on hard substrates that are less adept at these altered conditions (Piola and Johnston, 2008). The substrates used to construct artificial structures can also influence whether native species or NIS recruit to the available space. For example, NIS recruit more to concrete surfaces than other natural materials such as sandstone (Glasby et al., 2007). Therefore, seawalls may facilitate establishment of NIS that have the potential to reduce native biodiversity (Dafforn et al., 2009, Holloway and Keough, 2002, Mack et al., 2000).

To address issues of biodiversity loss from coastal hardening, ecological or "eco" engineering aims to integrate ecological understanding into the design and engineering of artificial structures (Chapman and Underwood, 2011). This is especially important in areas where soft approaches that incorporate complex wetlands or shellfish reefs as "living shorelines" are not viable alternatives to armouring (Morris et al., 2019). Practical applications of eco-engineering have so far involved modifying the material composition of structures. These adaptions support greater biodiversity. Increasing the habitat complexity and microhabitat diversity of seawalls through the addition of complex panels and

water retaining features (Browne and Chapman, 2011, Chapman and Blockley, 2009, Evans et al., 2016, Firth et al., 2016a, Hall et al., 2019, Morris et al., 2018, Strain et al., 2018b, Strain et al., 2018a, Waltham and Sheaves, 2018) provide refuge from desiccation (Martins et al., 2007) as well as predation (Fairweather, 1988, Schonbeck and Norton, 1978) and provide additional microhabitats on otherwise uniform seawalls (Laure et al., 2009, Wai and Williams, 2006). Compared to flat panels, panels with protective ridge and crevice microhabitats can reduce fish predation on oysters by up to 50% (Strain et al., 2018a). Other approaches include direct modification of the substrate to increase the provision of microhabitats. Research from the UK found that drilling rock pools up to 12cm depth into a breakwall resulted in artificial pools that had the same species richness as nearby natural rockpools (Evans et al., 2016). Similarly, block removals from seawalls in Australia created cavities that increased the abundance of sessile and mobile species, in particular foliose algae (Chapman and Blockley, 2009).

To review and quantify ecological outcomes of manipulating complexity on urban structures, Strain et al. (2018b) conducted a systematic review and metanalysis on 109 projects. They found that while all manipulations increased either the abundance or richness of some groups of species relative to flat controls, effects varied with functional group (Strain et al., 2018b). While such experiments demonstrate the potential benefits to biodiversity of eco-engineering that adds complexity, such interventions are rarely applied at large scales, and few studies distinguish the proportion of the biodiversity that is made up of NIS versus native species. Eco-engineering may fail to produce net benefits if enhancements in biodiversity are driven by increased numbers of NIS that are known to be invasive or a pest species.

Knowledge of which eco-engineering interventions facilitate NIS is essential for designing management strategies that avoid maladaptive approaches and focus on those that enhance native recruitment over that of NIS (Dafforn, 2017, Miller and Etter, 2008, Morris et al., 2018, Strain et al., 2018b). Many NIS display broad environmental tolerances as they had to overcome significant environmental filtering during translocation from their home region (Dafforn, 2017). A large aspect of the translocation occurs during transport on vessel hulls, which selects for species tolerant to shaded conditions in the low intertidal and shallow subtidal (Dafforn et al., 2012, Minchin and Gollasch, 2003). Therefore, the provision by eco-engineering of shaded or water retaining microhabitats in lower tidal ranges of seawalls might therefore favour NIS.

In this study we tested how the addition of complexity to two seawalls, as part of large-scale eco-engineering interventions, influences the colonisation of native and non-indigenous species. We hypothesised that in addition to greater native species abundance and richness on complex panels rather than flat panels, that there would also be greater NIS abundance and richness on complex

panels compared to flat panels. We also expected that the number and type of native and NIS supported will vary with the type of complexity and microhabitats provided. Within the complex surfaces, we expected more NIS in shaded microhabitats. Furthermore, we anticipated that the abundance and richness of NIS would increase with decreasing tidal elevation, so that differing effects of complexity would be greater at low rather than higher intertidal elevations.

2. Material and Methods

2.1. Study sites and panel installation

Hypotheses were tested at two locations within Sydney Harbour, New South Wales, Australia: Sawmillers Reserve (-33.846085, 151.202020) and Milsons Point (-33.849849, 151.212870; Figure 1). At each site, vertical sandstone seawalls, extending from the shallow subtidal (~ 0.5 m below mean low water springs [MLWS]) to the supratidal, supported reclaimed park and public land. Sites were each approximately 7km from the mouth of the Sydney Harbour estuary, had salinities that averaged ~35 ppt and were subject to semi-diurnal tides with a mean range of ~1.5 m (PCTMSL, 2018).
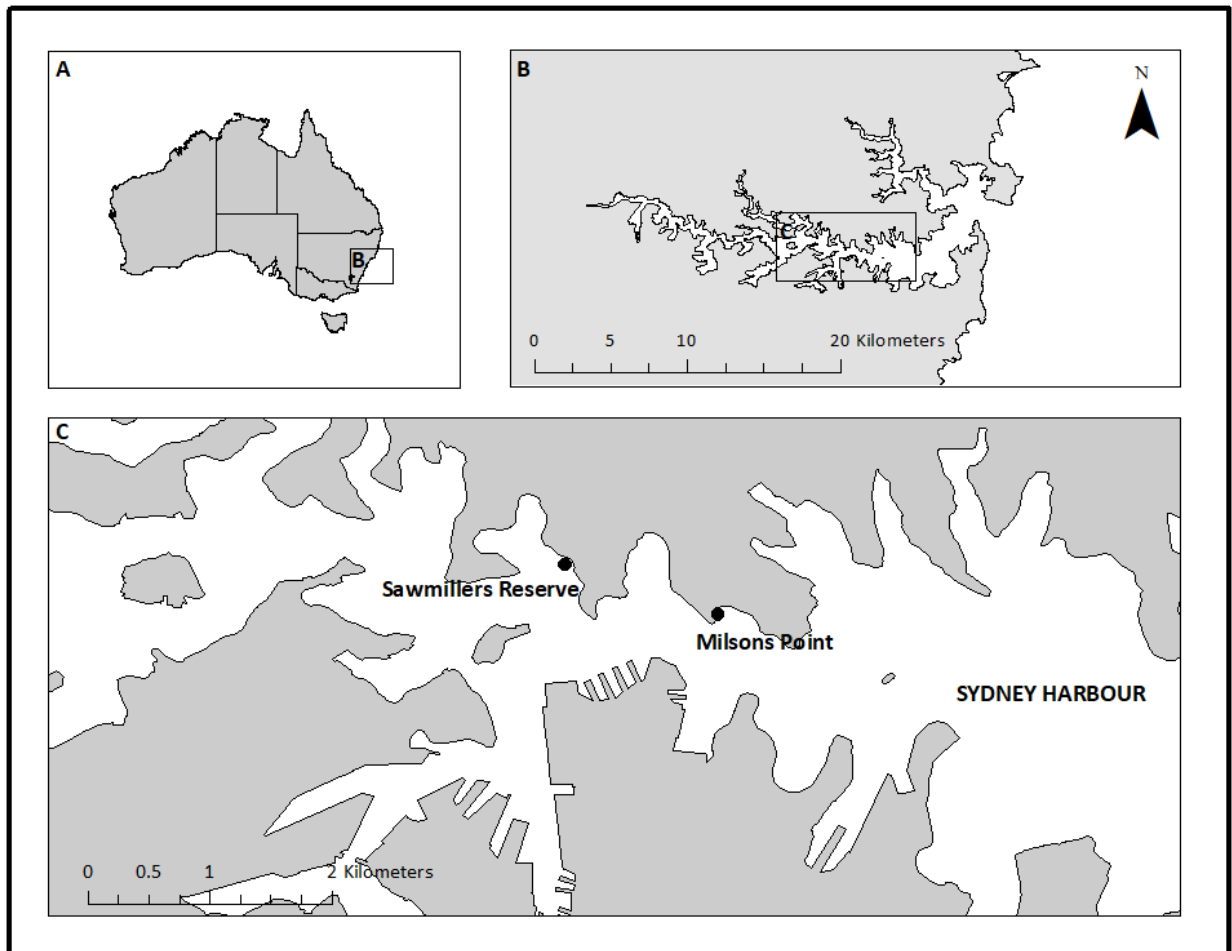
Figure 1. Map of Sydney Harbour showing the location of study sites.

At each site, concrete habitat enhancing recruitment panels that were 550 x 520 x 100 mm in size were retrofitted to the intertidal section of the seawall. The panels were hexagonally shaped so that they could fit together in habitat mosaics that covered the seawall. The panels, designed by Reef Design Lab (Melbourne, Victoria), had complex surfaces that mimicked natural features of intertidal rocky and mangrove foreshores in Sydney Harbour. Across the two sites, there were six designs: 1) crevices, 2) rockpools, 3) honeycomb, 4) swimthrough, 5) mangrove roots, and 6) flat, control panels (Figure 2). Crevice panels had eight crevices (depth 170mm, height 45mm) and eight ridges to provide additional surface space for species to attach; rockpool panels had 15 pools ranging in volume from (44 cm^3 - 678cm^3) that retained water during low tide; honeycomb panels with pocks ranging in area from 0.9 cm^2 – 19cm^2 were moulded to resemble the natural weathering of intertidal sandstone reefs; swimthrough panels had a mosaic of elliptical holes ranging in area from 2cm^2 – 91cm^2 to allow small and juvenile fish to swim through during high tide; mangrove panels were designed to

resemble mangrove roots with interstitial spaces. These features were selected based on a meta-analysis by Strain et al. (2018), which showed that the addition of water retaining features, pits, and crevices to artificial structures is particularly effective at enhancing the biodiversity and richness of sessile species. (Dafforn et al., 2008)
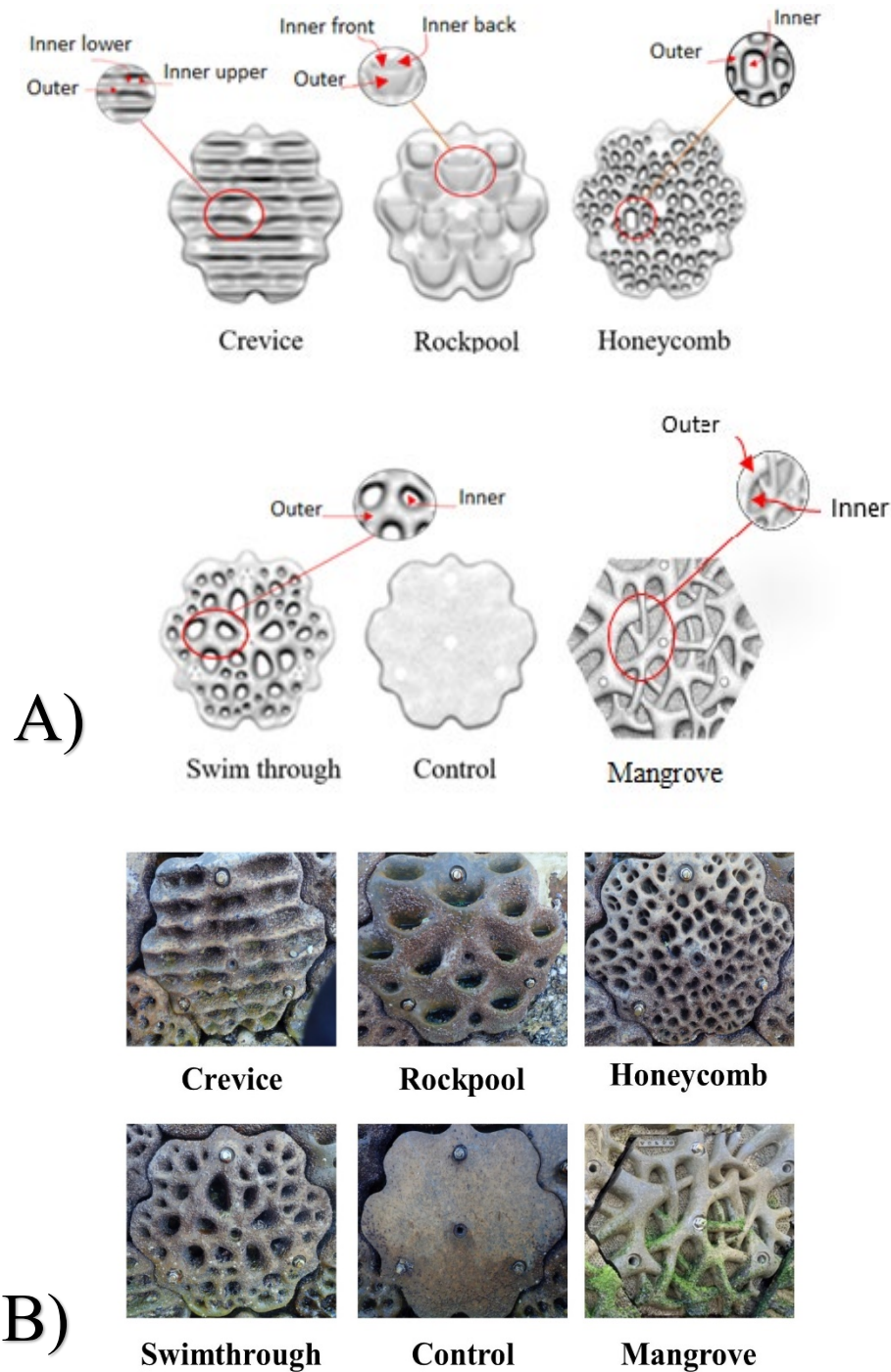
Figure 2. A) Habitat complexity panel designs, with defined microhabitats. B) Panels six months post deployment.

Panels were installed on seawalls in October (Milsons Point) and November (Sawmillers Reserve) 2018, during the Austral Spring. The panels were affixed to the low-to-high intertidal seawall (i.e. 0.25-1.2 m above MLWS) using 16mm stainless steel marine grade rods drilled into the seawall at three attachment points per panel. The rods held the panels 10cm out from the surface of the seawall, eliminating the need to clear the walls of existing marine growth. Panels were attached to walls, so they provided a continuous facade.

At Sawmillers Reserve, 72 panels representing a mixture of five designs (rockpools, honeycomb, swimthrough, crevices, control; Figure 2) were installed along a 12 m-long stretch of seawall (Figure 3a). At Milsons Point, 59 panels of two designs (mangrove roots, control; Figure 2) were installed along a 13m-long stretch of seawall (Figure 3b).
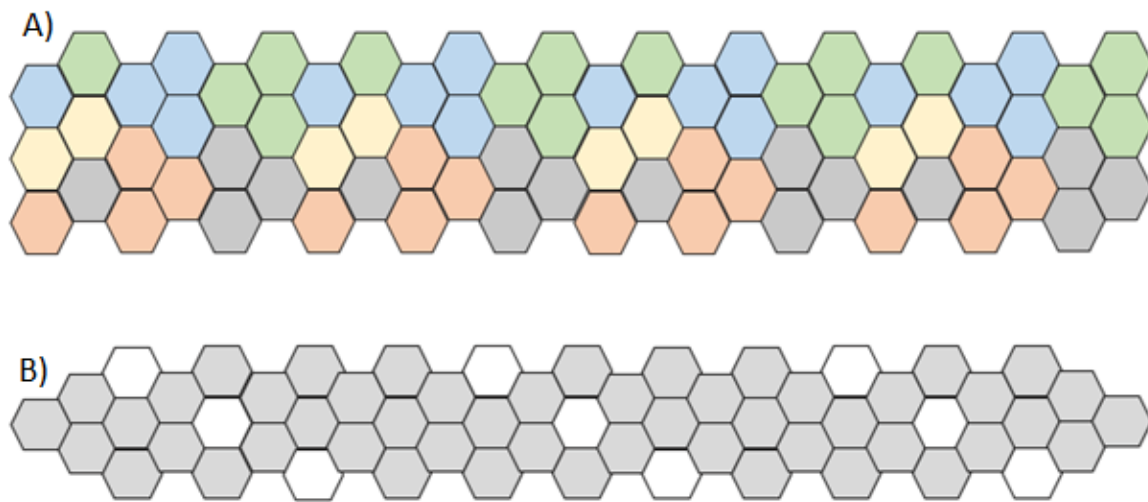
Figure 3. Panel configurations at (A) Sawmillers Reserve and (B) Milson's Point. Colours represent panel design. A) Crevice: pink; rockpool: green; honeycomb: blue; swimthrough: grey; control: yellow. B) Mangrove roots: grey; control: white.

2.2. Biodiversity sampling

To test hypotheses about how panel design and microhabitat identity influences colonisation of native and non-indigenous species, four replicate panels of each of five designs (rockpools, honeycomb, swim-through, crevices, control; Figure 2) were sampled at a mid-intertidal elevation at Sawmillers Reserve at 2, 4, 6 and 8 months following panel deployment. To test how effects of panel complexity and microhabitat vary with tidal elevation, at Milsons Point, three each of the mangrove and control panels were sampled at each of the low, mid and high intertidal elevations at 6, 8 and 10 months

following deployment. At each location, the replicate panels of a given treatment were spatially separated so as to maintain spatial independence. However, this necessitated that the same panels were sampled at each sampling time so were temporally non-independent. Panels were repeatedly sampled through time to assess whether NIS persisted or were replaced by native species.

Two different methods of non-destructive in-situ sampling were used to investigate the sessile and mobile biota (invertebrates and macroalgae) recruiting to panels. The first, which enabled a comparison among whole panels, documented the biodiversity of entire panels using a single 25 x 25 cm quadrat (strung with 5 x 5 evenly spaced strings to create 25 intersection points) placed at its centre. The second method used 4 x 4 cm quadrats (printed on clear vellum, with 3 x 3 evenly spaced lines, creating nine intersection points) to compare biota among microhabitats within panels. Two to three microhabitats were identified per panel (Figure 2), with six 4 x 4 cm quadrats sampled per microhabitat, per panel. For each of the honeycomb, swimthrough and mangrove panels, two microhabitats were defined: 1) 'outer' – which was the panel surface between depressions and 2) 'inner' - which were inside the depressions (Figure 2). For the rockpool panels, 'outer' was between rockpools and for crevices, it was on the ridges between crevices. The 'inner' microhabitats of rockpools were further divided into the front (outward facing) and back (inward facing) surfaces, and crevices into the upper and lower surfaces of the vertically orientated crevices (Figure 2).

For each of the methods, within each quadrat, percent covers of sessile biota were assessed using the point-intercept method and all mobile biota were counted to give abundance estimates. For each quadrat, both primary (i.e. attached directly to the substrate) and secondary (i.e. growing on the primary habitat-forming species) cover were recorded separately. Sessile taxa that were present within the quadrat but did not fall beneath a point intercept were given a percentage cover of 0.1% to note their presence. In order to present the full sessile community assemblage, the percent cover of primary and secondary species was summed; therefore, the total percent cover in some instances exceeded 100%. All species were identified to species level, or where this was not possible, morphospecies and classified as native (species indigenous to a particular region), non-indigenous (introduced to a region beyond its native range), invasive (a NIS that spreads rapidly, subsequently causing damage to the surrounding ecosystem), cryptogenic (origin is unknown) or cosmopolitan (home range cannot be defined as range extends across most of the world). Oysters present on the panels were not able to be identified as native (*Saccostrea glomerata)* or non-indigenous (*Magallana gigas*) without destructive sampling. Using previous data collected from two artificial substrates in Birchgrove Park (Scanes et al., 2016), it was estimated that *S. glomerata* are 12 times more abundant than *M. gigas* on artificial structures in the surrounding harbour. For this reason, oysters in this study were classified as the native *S. glomerata.* The dominant mussel in this thesis was visually identified

as *Mytilus galloprovincialis* by morphology, along with reports provided by Berents and Hutchings (2002), and Glasby et al. (2007) documenting its presence in the study area. The classification of *M. galloprovincialis* as an invasive species in Australia is a contentious issue due to its hybridization with the native mussel *Mytilus planulatus* (Hedge et al. 2014)*,* which has a history of being misidentified as *M. galloprovincialis*. While the dominant mussel is classified at the invasive *M. galloprovincialis* for the purposes of this thesis, genetic analysis will be conducted for molecular confirmation before publication occurs. Due to page restrictions in this master's thesis, graphs contain sessile percent cover, mobile abundance and species richness of native and non-indigenous species only.

2.3. Statistical analysis

Multivariate and univariate permutational analyses of variance PERMANOVA; (Anderson et al., 2008) were used to test hypotheses about how panel design elevation, and microhabitat identity influences colonisation of native and non-indigenous species. Sets of analyses were run on the percent covers of sessile species, the abundances of mobile species, and on the total species richness of sessile and mobile taxa summed together. For the percentage cover and abundances, separate analyses were run on each of the full multivariate data matrix, as well as the total cover/abundance of each of the native, non-indigenous, cryptogenic and cosmopolitan species categories, and the cover/abundance of key discriminating taxa responsible for multivariate differences between treatments.

For species richness, analyses were run on native, non-indigenous, cryptogenic and cosmopolitan species categories, with species lists for full panel analyses pooled across the whole panel and microhabitat sampling. Key discriminating taxa were those identified by similarity of percentages analysis SIMPER; (Clarke, 1993) to have a dissimilarity to standard deviation ratio of greater than 1.3. Multivariate analyses were run on Bray Curtis dissimilarity measures (Bray and Curtis, 1957), produced using untransformed data, while univariate analyses were run on Euclidean distances.

First, three-way analyses with time as a repeated measure (factors - month: 2, 4, 6, 8, fixed; panel design rockpools, honeycomb, swimthrough, crevices, control, fixed; panel number: 4 levels, random, nested in panel design) tested for differences in whole panel colonisation among panel designs at the mid intertidal elevation of Sawmillers Reserve. Second, four-way repeated measures analyses (factors – month, 6, 8, 10 fixed; tidal elevation; low, mid, high, fixed; panel design mangrove, control, fixed; panel number; 3 levels, random, nested in tidal elevation and panel design) assessed how effects of panel design influenced colonisation at the whole panel scale at each of the three tidal elevations at

Milsons Point. Third, three- (Sawmillers Reserve) or four- (Milsons Point) factor repeated measure analyses assessed how, within each panel design, colonisation varied among microhabitats. These analyses had the factors - month: fixed; microhabitat; fixed; panel number; random; and for Milsons Point, also the factor elevation (fixed), in which panel number was nested. Month was considered a repeated measure in analyses due to temporally non-independent sampling, necessitated by the spatial arrangement of panels on the seawalls. Where PERMANOVAs detected significant treatment effects at α=0.05, these were followed by pairwise *a posteriori* PERMANOVAs identifying sources of difference. For *a posteriori* tests where the number of possible permutations was below 100, p-values were calculated using Monte-Carlos simulations (Anderson et al., 2008). In all other instances, p-values were calculated via permutation.

3. Results

There were 95 taxa identified in this study (Table 1; Appendix 1). Of these; forty one taxa were identified as native to Australia; which were comprised of Plantae (algae; Chlorophyta (green), Phaeophyta (brown), Rhodophyta (red)), Isopoda (isopods), Sessila (barnacles), Ectoprocta (bryozoans), Bivalvia (oysters and mussels), Gastropoda (sea snails and limpets), Polychaeta (polychaetes) and Porifera (sponges). Seventeen taxa were identified as NIS; comprised of Phaeophyta, Rhodophyta, Isopoda, Sessila, Ectoprocta, Bivalvia, Polychaeta and Tunicata (ascidians and tunicates). Thirty four taxa were identified as cryptogenic; comprised of Phaeophyta, Rhodophyta, Amphipoda (amphipods), Isopoda, Cnidaria (hydroids), Polychaeta, Porifera and Tunicata, and three taxa we identified as cosmopolitan; comprised of Chlorophyta and Phaeophyta. Of the seventeen NIS taxa, only *Mytilus galloprovincialis* was considered invasive (Table 1; Appendix 1).

3.1. Sawmillers Reserve – effects of panel design on colonisation

3.1.1. Panel design

Multivariate analysis of the community assemblages (sessile and mobile) colonising the panels, highlighted differences among designs that varied through time (Table 1). Between deployment and 6 months, differences in assemblages among panel designs generally strengthened (Mo x Pa, Table 1). Swimthrough and crevice panels were the only ones that differed from control panels 2 months

after deployment, by 6 months all four complex panel designs had developed distinct communities to the flat control panels. Crevice and honeycomb panels also differed significantly from one another (*a posteriori* tests, p < 0.05). By 8 months, there was convergence between the assemblages of most panel designs, except rockpools, which maintained distinct assemblages to controls and crevices.

Table 1. *Results of multivariate three-factor repeated measures PERMANOVAs testing for the effects through time (4 levels; 2, 4, 6 and 8 month) of panel design (5 levels: crevice, honeycomb, swimthrough, rockpool, control) on the community assemblage. Panel no. = panel number (nested in panel design). Terms significant at α = 0.05 are in* **bold**.

Multivariate				
Community composition				
Source	df	MS	Pseudo-*F*	P(perm)
Month(Mo)	3	2973.30	4.08	**0.001**
Panel design(Pa)	4	7223.00	7.93	**0.001**
Panel no.(Pn)	14	907.61	0.34	0.998
MoxPa	12	1185.60	1.64	**0.012**
Residual	46	2654.20		
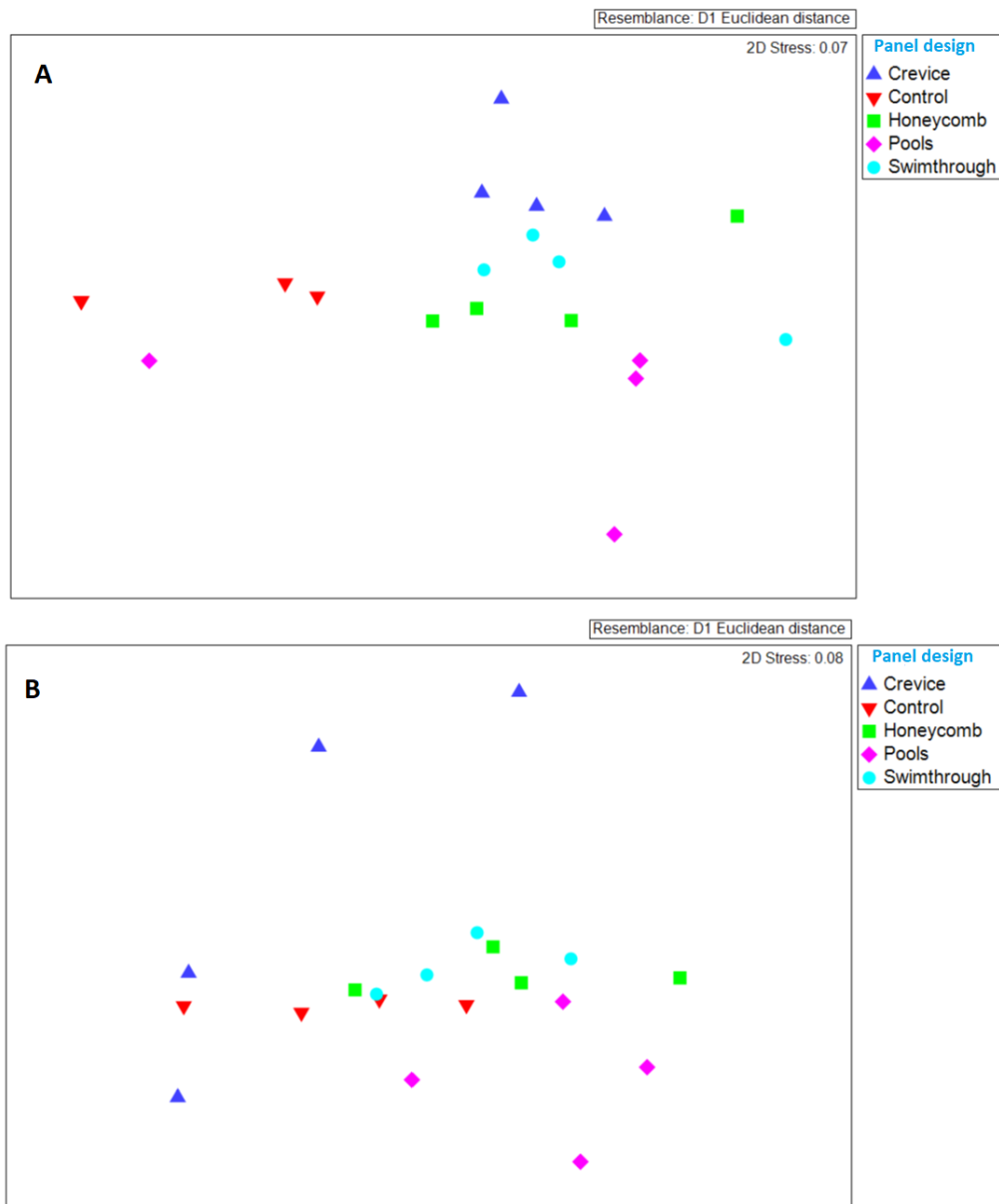
Figure 4. nMDS plot displaying differences in fouling communities among panel designs at Sawmillers Reserves at six months (A) and eight months (B) after panel deployment. Each point represents a panel, with colours denoting panel designs (crevice; blue, control: red, honeycomb: green, rockpools; pink, swimthrough; light blue), Appendix 1/ Table 2.

SIMPER analysis identified the native barnacle, *Hexaminius popeiana*, as the only sessile taxon to meet the criteria for a key discriminating taxon (dissimilarity to standard deviation of > 1.3) across multiple pair-wise comparisons of panel design. Independent of time, the cover of *H. popeiana* was significantly greater on each of the four complex panel designs than on the flat control panels, and among complex panels, greater on the swimthrough than the honeycomb panels, with no significant differences among the other designs (*a posteriori* tests, sig. Pa, Table 2, Figure 4). The mobile species that was the best discriminator among panel designs was the native limpet *Patellioda mimula*

(dissimilarity to standard deviation generally >0.9). This species was first detected on the panels at six months, and only on the rockpool panels, with the difference in abundance between rockpool and other designs only significant at 8 months (*a posteriori* tests, sig. Mo x Pa, Table 2).

*Table 2. Results of univariate three-factor repeated measures PERMANOVAs testing for the effects through time (4 levels; 2, 4, 6 and 8 month) of panel design (5 levels: crevice, honeycomb, swimthrough, rockpool, control) on the cover (Hexaminius popeiana) or abundance (Patelloida mimuli) of key discriminating taxa. Panel no. = panel number (nested in panel design). Terms significant at α = 0.05 are in **bold**.*

Source	df	*Hexaminius popeiana* MS	Pseudo-*F*	P(perm)	*Patelloida mimula* MS	Pseudo-*F*	P(perm)	*Ligia exotica* MS	Pseudo-*F*	P(perm)
Month(Mo)	3	1.07	0.07	0.971	7.19	8.41	**0.001**	4.82	7.57	**0.001**
Panel design(Pa)	4	253.50	14.80	**0.001**	18.28	52.24	**0.001**	1.43	2.77	0.073
Panel number(Pn)	14	17.05	0.36	0.944	0.34	0.00		0.51	0.00	
MoxPa	12	37.37	2.00	**0.055**	5.78	6.78	**0.001**	1.30	2.05	**0.035**
MoxTn	42	18.64	0.39	0.951	0.84	0.00		0.63	0.00	
Residual	4	47.12			-2.54			-1.43		

When the cover of sessile species was examined separately, the colonisation of native, but not of NIS, cryptogenic or cosmopolitan species varied significantly with panel design (Table 3, Fig. 4a). Cover of native species was significantly less on control panels than on complex panels (control "CO" vs crevice "CR": t=6.51, p=0.001; honeycomb "HC": t=5.01, p=0.001; rockpool "RP": t=7.60, p=0.002; and swimthrough "ST": t=6.64, p=0.001). Among the complex panels, the cover of sessile native species was significantly less on the honeycomb than on the other panel designs (HC vs RP: t=3.65, p=0.01; ST: t=2.73, p=0.03; CR: t=2.95, p=0.02; Figure 5). NIS were absent from control and honeycomb panels; cryptogenic species were absent from control and swimthrough panels and cosmopolitan species were absent from crevice and honeycomb panels across all sampling times. Among the remainder of panel designs, these three categories were rare, accounting for no more than 8% of cover on a panel at any sampling time.

*Table 3. Results of univariate three-factor repeated measures PERMANOVAs testing for the effects through time (4 levels; 2, 4, 6 and 8 month) of panel design (5 levels: crevice, honeycomb, swimthrough, rockpool, control) on cover of sessile species and the abundance of mobile species. Analyses were done separately on native, non-indigenous, cryptogenic and cosmopolitan groups of species. Panel no. = panel number (nested in panel design). Terms significant at α = 0.05 are in **bold**.*

Univariate										
Native		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	3	6.75	0.33	0.821	23.48	7.26	**0.001**	3.77	5.75	**0.001**
Panel design(Pa)	4	411.95	25.65	**0.001**	42.18	11.51	**0.004**	3.75	4.49	**0.022**
Panel no.(Pn)	14	15.99	0.79	0.669	3.65	1.13	0.314	0.84	1.28	0.245
MoxPa	12	35.56	1.75	0.087	12.14	3.75	**0.001**	3.42	5.22	**0.001**
Residual	46	20.28			3.23			0.66		
NIS		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	3	0.11	1.45	0.236	4.98	8.62	**0.001**	0.03	0.34	0.79
Panel design(Pa)	4	0.06	0.72	0.606	1.43	2.78	0.062	5.33	35.22	**0.003**
Panel no.(Pn)	14	0.08	1.10	0.399	0.51	0.89	0.555	0.15	1.55	0.103
MoxPa	12	0.11	1.45	0.146	1.31	2.27	**0.027**	0.19	1.92	**0.049**
Residual	46	0.08			0.58			0.10		
Cryptogenic		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	3	0.11	3.94	**0.017**	22.80	5.50	**0.002**	0.83	1.56	0.199
Panel design(Pa)	4	0.05	1.58	0.252	33.00	3.39	**0.036**	119.53	1785.40	**0.002**
Panel no.(Pn)	14	0.03	1.10	0.368	9.71	2.34	**0.031**	0.06	0.11	0.999
MoxPa	12	0.05	1.75	0.081	19.58	4.73	**0.002**	0.88	1.64	0.093
Residual	46	0.03			4.14			0.54		
Cosmopolitan		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	3	0.01	1.02	0.402				0.15	1.75	0.137
Panel design(Pa)	4	0.02	1.52	0.241				4.31	16.20	**0.005**
Panel no.(Pn)	14	0.01	1.10	0.386				0.27	3.17	**0.002**
MoxPa	12	0.01	1.02	0.464				0.19	2.23	**0.022**
Residual	46	0.01						0.08		
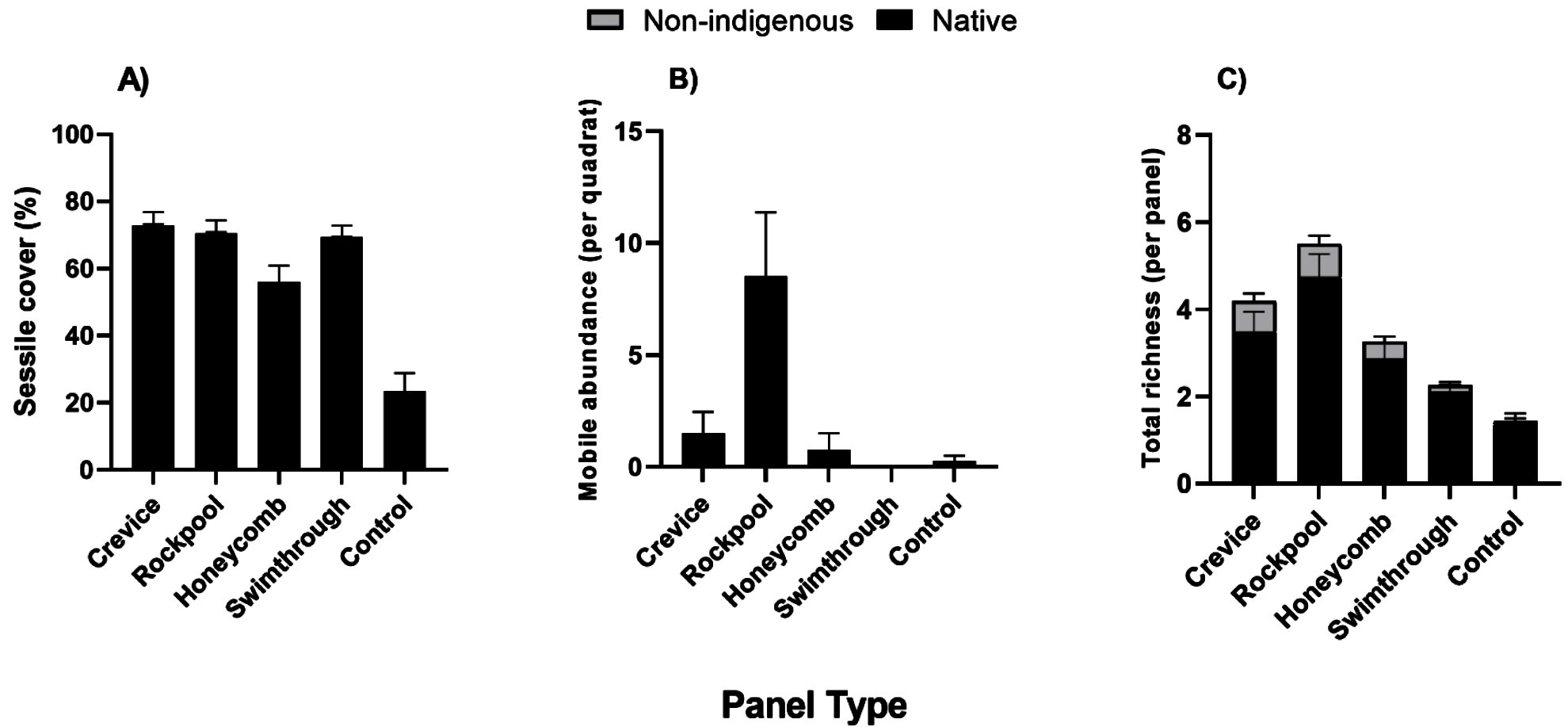
Figure 5. Mean (+ SE) of (A) percent cover of sessile species, (B) abundance of mobile species, and (C) total species richness, of NIS (grey) and native species (black), colonising each of five seawall panel designs, eight months following their deployment at a mid-intertidal elevation of Sawmillers Reserve seawall. Covers and counts are expressed per 0.25 x 0.25 m quadrat, centred over each panel design. Richnesses are derived from pooling species across both whole panel and microhabitat sampling of panels. n = 4.

Mobile species classified as native, non-indigenous and cryptogenic each differed in abundance among panel designs over time (Table 3). No mobile cosmopolitan species were detected on any of the panels, at any of the sampling times. At two months post installation, native and cryptogenic mobile species were absent from the panels and only the NIS *Ligia exotica* was observed in similar abundances on control and rockpool panels (*a posteriori* pairwise; p > 0.05, Table 2). After four months, *L. exotica* was significantly more abundant on the rockpool than the control or swimthrough panels, from which it was absent, with other differences non-significant (p > 0.05). Native and cryptogenic species were present at low abundances and did not differ among panel designs (p > 0.05). By six months, the NIS were more abundant on the honeycomb than the crevice panels (CR vs HC: t=2.44, p=0.045), but mobile native species (solely comprising gastropods) were more abundant on the rockpool than the control, swimthrough or crevice panels (RP vs CO: t= 4.91, p=0.004; ST: 5.54, p=0.001; CR: t=3.72, p=0.012). By the eighth month, the mobile NIS was no longer present on the panels (Figure 5). The native gastropods were however, significantly more abundant on the rockpool than on the honeycomb or swimthrough panels (RP vs HC t=2.61, p=0.055; ST: t=2.95, p=0.039). By this stage, there were also cryptogenic amphipods and isopods, which collectively were more abundant on the crevice than the honeycomb or swimthrough panels (CR vs HC: t=2.44, p=0.051; ST: t=2.44, p=0.049).

Each of native, non-indigenous, and cryptogenic species richness displayed a temporally consistent effect of panel design (Table 3). At two months post installation only native species differed between panels which were more abundant on the swimthrough panel than all others (ST vs CR: t=3, p=0.018; HC: t=3, p=0.041; CO: t=2.67, p=0.045). At months four and six post installation, both native and non-indigenous species differed between panels with rockpool panels having higher richness than all other panels (*a posteriori* tests, sig. Mo x Pa, Table 3). By month eight native, non-indigenous and cryptogenic species varied between panels with the crevice panels having the highest species richness (*a posteriori* tests, sig. Mo x Pa,).

3.1.2. Microhabitats within panels

On rockpool panels, the relative abundance and richness of native, non-indigenous, cryptogenic and cosmopolitan groups differed among microhabitats and this varied in magnitude through time (Table 4). Independent of time, the cover of both Spirorbinae and *H. popeiana* differed greatly among microhabitats. *H. popeiana* was significantly greater on the outer rather than the inner microhabitats, while Spirorbinae occurred in greater densities on the inner back microhabitat rather than the inner

front microhabitat (*a posteriori* tests, sig. Mo x Mi). At most time points, species covers were greater on the front surface of the inside rather than the outside of the rockpools, while the outside of the rockpools had greater cover than the inside back surface of the rockpools (Outside < Inner Front; Outside < Inner Back; *a posteriori* tests, sig. Mo x Mi and Mi effects, Table 4). Within the rockpools, the native and cosmopolitan groups were the only ones to differentially utilise the front and back surfaces, and only at months 2 and 8 when covers were greater on the front than back surfaces (*a posteriori* tests, sig. Mo x Mi and Mi effects, Table 4, Fig. 6). Analyses of mobile species, by contrast, revealed that only the cryptogenic group varied with microhabitat (Table 4), and only in months 2 and 4 at which time abundance was significantly greater on the inside front rather than the inside back surface, and the internal microhabitats were more speciose than the outside of the rockpools (*a posteriori* tests, sig. Mo x Mi and Mi effects, Table 4). Each of non-indigenous, cryptogenic and cosmopolitan species richness displayed a temporally consistent effect of microhabitat (Table 4). NIS and cryptogenic groups were each significantly less speciose on the outside than the inside front or back of rockpools, with the latter two microhabitats not significantly differing (*a posteriori* tests, sig. Mi, Table 4).

On honeycomb panels, only the species richness of natives displayed an effect of microhabitat, with sessile species cover and mobile species abundance not differing between microhabitats, irrespective of species origin (Table 4, Figure 6). Independent of time, the cover of *H. popeiana* was significantly greater on the internal depressions rather than the outer microhabitat (*a posteriori* tests, sig. Mi, Table 4).The effect of microhabitat on native species richness was temporally variable, with a weak, though non-significant trend for greater richness inside than outside of depressions (Table 4).

On swimthrough panels, non-indigenous, cryptogenic and cosmopolitan species were in low abundance, and did not significantly differ in sessile covers, mobile abundances or total richness among microhabitats (Table 4). There were no dominant species that explained the differences, although cover of native species was generally greater inside than outside of depressions, but this pattern was only significant in months 2, 4, and 6 (*a posteriori* tests, sig. Mo x Mi, Table 4, Fig. 6). Native species displayed a weak, though non-significant trend for greater richness on the inner than outer surface of the panels (Table 4, Fig. 6).
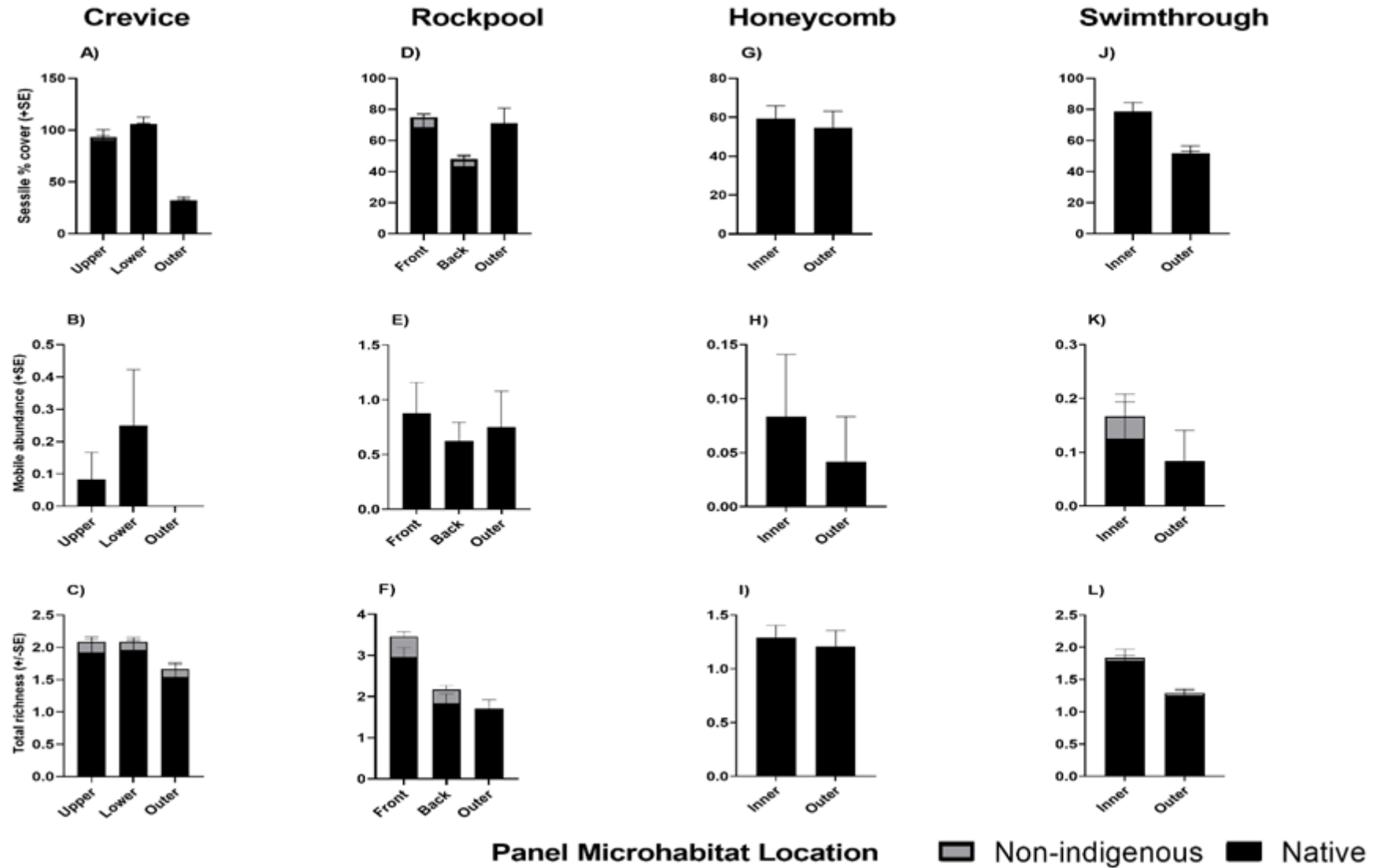
Figure 6. Mean (+SE) (A) percent cover of sessile species, (B) abundance of mobile species and (C) total species richness of all taxa colonising inner and outer microhabitats of mangrove panels 10 months following their installation across three elevations. Numbers are expressed per 0.04 x 0.04 m quadrat (n = 18).

*Table 4. Results of three-factor repeated measures PERMANOVAs testing for differences of microhabitat (crevice: 3 levels; inner upper vs inner lower vs outer; rockpool: 3 levels; inner front vs inner back vs outer; honeycomb + swimthrough: 2 levels; inner vs outer) on the combined cover of sessile species and mobile abundance for multivariate analysis, and on cover of sessile species, the abundance of mobile species for univariate analysis among microhabitats within panel designs through time (Month: 4 levels; 2, 4, 6, 8 months). Microhabitats are as defined in Figure 2. Each panel design was analysed separately. Terms significant at α = 0.05 are in **bold**.*

Crevice panel										
Multivariate										
Community composition										
Source	df	MS	Pseudo-F	P(perm)						
Month(Mo)	3	6865.8	7.89	**0.001**						
Microhabitat(Mi)	2	53418	119.88	**0.001**						
Panel no.(Pn)	3	993.63	1.13	0.319						
MoxMi	6	1219.5	1.5	0.171						
MoxPn	9	869.44	1.05	0.389						
MixPn	6	445.61	0.54	0.957						
Residual	267	821.46								
Univariate										
Native		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	38.44	7.62	**0.001**	0.2	2.05	0.194	2.56	4.99	**0.002**
Microhabitat(Mi)	2	864.67	788.89	**0.001**	0.13	2.36	0.192	16.9	56.81	**0.001**
Panel no.(Pn)	3	7.06	1.4	0.245	0.13	1.68	0.091	0.46	0.89	0.459
MoxMi	6	22.51	4.46	**0.001**	0.09	1.14	0.323	2.33	4.54	**0.001**
MoxPn	9	1.09	0.22	0.88	0.1	1.21	0.218	0.88	1.78	0.065
MixPn	6	1.1	0.22	0.969	0.05	0.68	0.773	0.3	0.58	0.74
Residual	267	5.05			0.08			0.51		

Table 4 cont.

NIS

Source	df	Sessile % cover MS	Pseudo-F	P(perm)	Mobile abundance MS	Pseudo-F	P(perm)	Species richness MS	Pseudo-F	P(perm)
Month(Mo)	3	0.44	6.41	**0.001**				0.32	6.77	**0.001**
Microhabitat(Mi)	2	0.06	1.33	0.332				0.01	0.31	0.759
Panel no.(Pn)	3	0.19	2.81	**0.029**				0.15	3.23	**0.021**
MoxMi	6	0.06	0.8	0.57				0.01	0.12	0.989
MoxPn	9	0.08	1.25	0.278				0.07	1.63	0.109
MixPn	6	0.04	0.6	0.746				0.03	0.71	0.663
Residual	267	0.07						0.05		

Cryptogenic

Source	df	Sessile % cover MS	Pseudo-F	P(perm)	Mobile abundance MS	Pseudo-F	P(perm)	Species richness MS	Pseudo-F	P(perm)
Month(Mo)	3	7.35	4.02	**0.002**	0.09	1.74	0.221	0.68	11.3	**0.004**
Microhabitat(Mi)	2	1.92	1.2	0.396	0.05	0.71	0.567	0.09	0.1	0.398
Panel no.(Pn)	3	1.83	1.86	0.114	0.05	0.84	0.468	0.06	1.05	0.41
MoxMi	6	1.92	1.95	**0.047**	0.05	0.76	0.618	0.09	1.1	0.365
MoxPn	9	1.83	1.86	**0.046**	0.05	0.84	0.596	0.6	1.05	0.358
MixPn	6	1.6	1.62	0.131	0.06	1.07	0.37	0.08	1.54	0.142
Residual	267	0.98			0.06			0.05		

Cosmopolitan

Source	df	Sessile % cover MS	Pseudo-F	P(perm)	Mobile abundance MS	Pseudo-F	P(perm)	Species richness MS	Pseudo-F	P(perm)
Month(Mo)	3	1.13	8.38	**0.011**				0.05	6	**0.024**
Microhabitat(Mi)	2	0.38	0.98	0.426				0.02	1.23	0.351
Panel no.(Pn)	3	0.13	0.4	0.817				0	0.74	0.563
MoxMi	6	0.38	1.12	0.304				0.02	1.23	0.34
MoxPn	9	0.13	0.4	0.991				0	0.74	0.692
MixPn	6	0.38	1.15	0.272				0.01	1.57	0.153
Residual	267	0.34						0.01		

Table 4 cont.

				Rockpool panel					
				Multivariate					
Community composition									
Source	df	MS	Pseudo-F	P(perm)					
Month(Mo)	3	12558	5.85	**0.001**					
Microhabitat(Mi)	2	1.94	68.22	**0.004**					
Panel no.(Pn)	3	1900.2	1.16	0.267					
MoxMi	6	4252.5	2.98	**0.011**					
MoxPn	9	2145.1	1.31	0.082					
MixPn	6	2190.1	1.34	**0.09**					
Residual	267	1629.4							
				Univariate					
Native			**Sessile % cover**			**Mobile abundance**		**Species richness**	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	72.67	8.47	**0.001**	6.74	45.41	**0.001**	12.45	14.95	**0.001**
Microhabitat(Mi)	2	392.39	244.25	**0.001**	1.07	2.39	0.164	3.51	6.31	0.058
Panel no.(Pn)	3	4.65	0.54	0.641	0.11	0.17	0.915	1.69	2.03	0.109
MoxMi	6	30.24	3.53	**0.003**	0.47	0.77	0.6	5.32	6.38	**0.001**
MoxPn	9	12.02	1.48	0.13	0.15	0.24	0.985	1.01	1.22	0.26
MixPn	6	1.61	0.19	0.978	0.45	0.73	0.65	0.56	0.67	0.668
Residual	267	8.58			0.61			0.83		

Table 4 cont.

NIS			Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	0.87	2.76	**0.042**	0.19	2.86	**0.035**	0.26	1.18	0.315
Microhabitat(Mi)	2	4.22	13.41	**0.006**	0.11	2.51	0.168	4.14	20.19	**0.004**
Panel no.(Pn)	3	0.47	1.49	0.225	0.09	1.97	0.101	0.43	1.93	0.143
MoxMi	6	0.49	1.57	0.138	0.03	0.75	0.644	0.45	2.04	0.066
MoxPn	9	0.24	0.78	0.63	0.07	1.48	0.117	0.39	1.89	0.065
MixPn	6	0.31	1	0.427	0.04	0.96	0.485	0.2	0.92	0.5
Residual	267	0.31			0.04			0.22		

Cryptogenic			Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	57.31	7.98	**0.012**	104.03	4.94	**0.027**	2.95	2.54	0.117
Microhabitat(Mi)	2	930.14	55.6	**0.006**	208.51	19.72	**0.005**	128.38	840.27	**0.001**
Panel no.(Pn)	3	11.73	2.03	0.112	4.81	0.37	0.795	0.14	0.18	0.925
MoxMi	6	28.61	4.94	**0.001**	37.94	2.9	**0.009**	0.21	1.58	0.218
MoxPn	9	7.18	1.24	0.276	21.07	1.61	0.118	1.16	1.5	0.157
MixPn	6	16.73	2.89	**0.016**	10.58	0.81	0.583	0.15	0.19	0.976
Residual	267	5.79			13.07			0.77		

Cosmopolitan			Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	6.76	5.07	**0.024**				0.72	5.58	**0.009**
Microhabitat(Mi)	2	28.55	77.31	**0.005**				7.07	21.9	**0.003**
Panel no.(Pn)	3	0.61	0.51	0.696				1.05	5.06	**0.004**
MoxMi	6	5.55	4.64	**0.001**				0.46	2.11	0.104
MoxPn	9	1.33	1.11	0.345				0.13	0.62	0.78
MixPn	6	0.37	0.31	0.937				0.32	1.54	0.172
Residual	267	1.2						0.2		0.428

Table 4
cont.

Honeycomb panel									
Multivariate									
Community composition									
Source	df	MS	Pseudo-F	P(perm)					
Month(Mo)	3	1810.2	2.99	**0.004**					
Microhabitat(Mi)	1	6704.5	7.64	**0.023**					
Panel no.(Pn)	3	873.49	0.8	0.566					
MoxMi	3	1254.4	1.3	0.266					
MoxPn	9	605.3	0.55	0.945					
MixPn	3	877.07	0.8	0.55					
Residual	178	1085.4							
Univariate									
Native		**Sessile % cover**			**Mobile abundance**			**Species richness**	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	6.85	0.71	0.543	0.01	0.33	0.78	0.42	0.97	0.405
Microhabitat(Mi)	1	48	7.11	0.073	0.19	9	0.053	1.69	11.57	**0.044**
Panel no.(Pn)	3	3.06	0.32	0.798	0.03	0.68	0.609	0.37	0.85	0.469
MoxMi	3	4.54	0.47	0.714	0.01	0.17	0.932	1.2	2.76	**0.045**
MoxPn	9	4.07	0.4	0.93	0.04	1.02	0.447	0.19	0.18	0.34
MixPn	3	6.75	0.7	0.552	0.02	0.51	0.691	0.15	0.34	0.778
Residual	178	9.62			0.04			0.43		

Table 4 cont.

NIS		Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3				0.02	1	**0.045**	0.02	2.17	0.087
Microhabitat(Mi)	1				0.02	1	0.383	0.02	1	0.401
Panel no.(Pn)	3				0.02	2.32	0.068	0.02	2.17	0.085
MoxMi	3				0.02	2.32	0.067	0.02	2.17	0.083
MoxPn					0.02	2.32	**0.024**	0.02	2.5	**0.008**
MixPn	3				0.02	2.32	0.082	0.02	2.17	0.092
Residual	178				0.01			0.01		
Cryptogenic		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	0.01	1	0.442	0.01	1	0.424	0	0.6	0.651
Microhabitat(Mi)	1	0.01	1	0.38	0.01	1	0.411	0.02	3	0.191
Panel no.(Pn)	3	0.01	1	0.386	0.01	1	0.411	0	0.66	0.569
MoxMi	3	0.01	1	0.37	0.01	1	0.411	0	0.6	0.626
MoxPn	9	0.01	1	0.451	0.01	1	0.433	0.01	1.11	0.35
MixPn	3	0.01	1	0.414	0.01	1	0.399	0	0.66	0.549
Residual	178	0.01			0.01			0.01		

Table 4 cont.

Swimthrough Panel									
Multivariate									
Community composition									
Source	df	MS	Pseudo-F	P(perm)					
Month(Mo)	3	7412.5	10.02	**0.001**					
Microhabitat(Mi)	2	9193	10.93	**0.005**					
Panel no.(Pn)	3	1517.5	2.23	**0.015**					
MoxMi	6	2107.3	3.43	**0.008**					
MoxPn	9	739.5	1.08	0.33					
MixPn	6	840.84	1.23	0.262					
Residual	267	679.75							
Univariate									
Native		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	19.06	4.83	**0.002**	0.12	2.48	0.137	0.65	1.63	0.17
Microhabitat(Mi)	1	170.63	19.4	**0.035**	0.01	0.27	0.645	3.52	8.59	0.059
Panel no.(Pn)	3	9.77	2.47	0.06	0.02	0.56	0.543	0.83	2.08	0.118
MoxMi	3	9.56	2.42	0.07	0.03	0.97	0.378	0.48	1.2	0.322
MoxPn	9	5.32	1.46	0.167	0.05	1.38	0.17	0.43	1.09	0.381
MixPn	3	8.8	2.23	0.101	0.02	0.56	0.547	0.41	1.02	0.393
Residual	178	3.95			0.03			0.4		

Table 4 cont.

NIS		Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	0.03	0.56	0.735	0.01	1	0.438	0.02	0.74	0.479
Microhabitat(Mi)	1	0	0	1	0.01	1	0.388	0.05	1.42	0.302
Panel no.(Pn)	3	0.03	0.56	0.632	0.01	1	0.396	0.01	0.2	0.896
MoxMi	3	0.1	1.57	0.204	0.01	1	0.383	0.02	0.74	0.531
MoxPn	9	0.24	0.78	0.645	0.01	1	0.438	0.02	0.91	0.601
MixPn	3	0.1	1.57	0.199	0.01	1	0.416	0.03	1.28	0.294
Residual	178	0.06			0.01			0.03		

Cryptogenic		Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	0.63	3.16	0.076	0.01	1	0.452	0.13	9.94	**0.04**
Microhabitat(Mi)	1	0.26	0.95	0.389	0.01	1	0.376	0	0.27	0.631
Panel no.(Pn)	3	0.2	0.7	0.695	0.01	1	0.359	0.03	1.37	0.269
MoxMi	3	0.26	0.89	0.601	0.01	1	0.425	0	0.27	0.831
MoxPn	9	0.2	0.7	0.976	0.01	1	0.448	0.03	1.37	0.194
MixPn	3	0.27	0.94	0.535	0.01	1	0.401	0.01	0.79	0.51
Residual	178	0.29			0.01			0.02		

Cosmopolitan		Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	3	0.05	1	0.457				0	1	0.517
Microhabitat(Mi)	1	0.05	1	0.385				0	1	0.387
Panel no.(Pn)	3	0.05	1	0.388				0	1	0.38
MoxMi	3	0.05	1	0.403				0	1	0.428
MoxPn	9	0.05	1	0.46				0	1	0.437
MixPn	3	0.05	1	0.396				0	1	0.374
Residual	178	0.05						0		

3.2. Milsons Point - Effects of tidal elevation on colonisation of panels

3.2.1. Panel design

At each of the intertidal elevations, the assemblages colonising mangrove and control panels differed (*a posteriori* tests, sig. Pa x Te, Table 6). SIMPER analysis (Table 7, Figure 7) and revealed that two native algal species, C*orallina officinalis and Ralfsia verrucosa,* a non-indigenous alga *Dictyota dichotoma,* a non-indigenous bryozoan, *Tricellaria inopinata* and a cryptogenic alga *Gelidium pusillum* were the taxa contributing the most (standard deviation to dissimilarity ratio generally > 1.3) to differences in community structure among elevations and panel designs. Of these, only *R. verrucosa* (t=6.27, p=0.004) and *T. inopinata* (t=2.97, p=0.049) displayed an effect of panel design (Table 7), and only at the low elevation, with differences at mid and high elevations non-significant. All five taxa differed in abundances among elevations at some sampling times. *G. pusillum* differed significantly among elevations, whereby it was more abundant at low than mid or high elevations (a pattern similarly displayed by *C. officinalis* (t=10.04, p=0.01), and *D. dichotoma* (t=6.07, p=0.003) although the magnitude of this effect varied among sampling times (sig. Te x Pa interaction, Table 7).

*Table 5. Results of four-factor repeated-measure PERMANOVAs testing for effects through time (3 levels: 6, 8 and 10 months) of panel design (2 levels: mangrove, control) and tidal elevation (3 levels: low, mid, high intertidal) for differences in the combined cover of sessile species and mobile abundance for multivariate analysis, among panel designs through time. For each elevation and panel design, three panels were repeatedly sampled through time. Panel no. = panel number (nested in panel design and elevation). Terms significant at α = 0.05 are in **bold**.*

Multivariate				
Community composition				
Source	df	MS	Pseudo-*F*	P(perm)
Month(Mo)	2	3956.4	2.31	**0.008**
Tidal elevation(Te)	2	25544	15.58	**0.001**
Panel design(Pa)	1	16081	9.81	**0.001**
MoxTe	4	2893.2	1.69	**0.019**
MoxPa	2	2535.2	1.48	0.115
TexPa	2	7104	4.33	**0.001**
Panel no.(Pn)	12	1638.7	0.95	0.574
MoxTexPa	4	2039.5	1.19	0.238
Residual	24	1711.3		
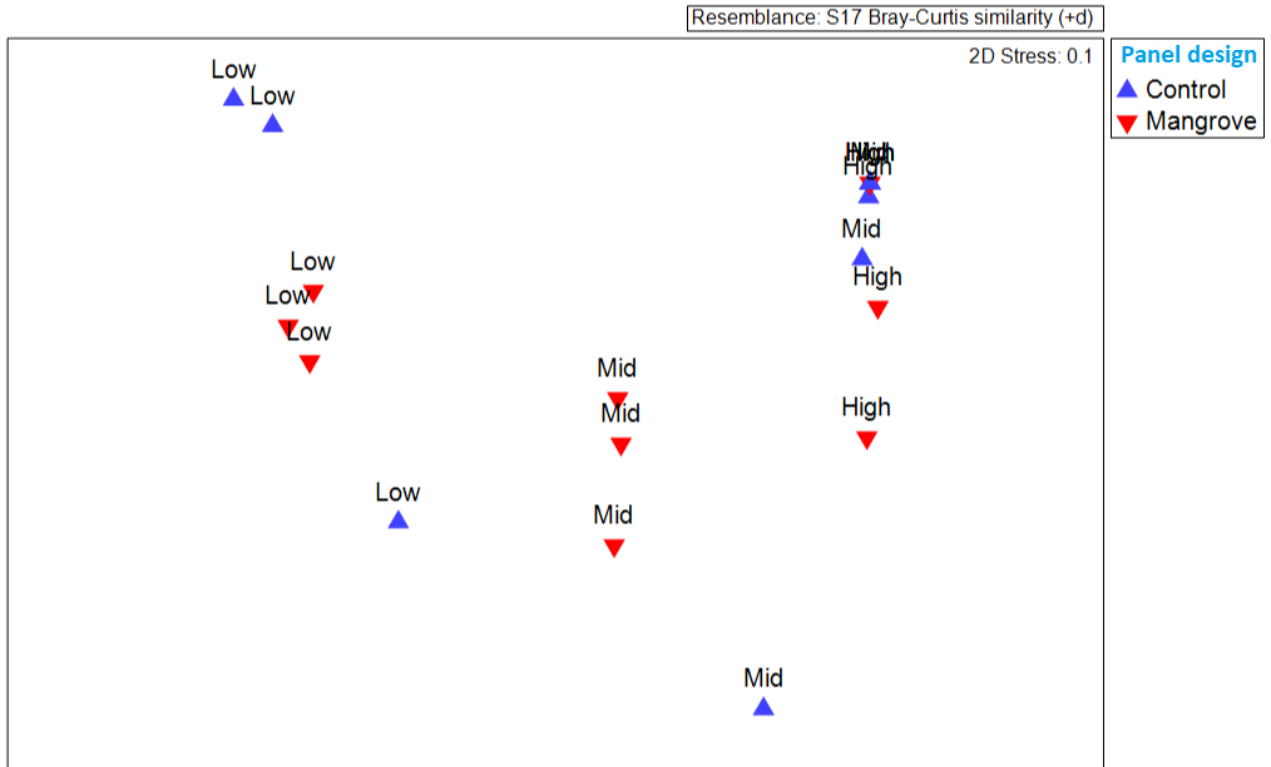
Figure 7. nMDS plot for Milsons point showing the species composition of communities on mangrove (blue) and control (red) panels, 10 months after deployment, at each of the tidal elevations; high, mid and low. Points represent individual panels, Appendix 1/ Table 2.

Analyses of the total cover of sessile species recruiting to whole panels revealed that those classified as native or non-indigenous differed among panel design at different elevations, those classified as cryptogenic displayed a time-dependent effect of elevation while those classified as cosmopolitan did not differ among elevations or panel designs (Table 6, Fig. 7). The cover of native sessile species did not differ between mangrove and control panels at either the high (t=0.69, p=0.589) or mid (t=2.15, p=0.119) intertidal elevations, but at the low elevation, where cover was greatest, cover was significantly greater on control than mangrove panels (t=3.94, p=0.017). Sessile NIS were present only at the mid and low intertidal elevations and like native species, did not differ in cover between panel designs at the mid intertidal elevation (t=4.56, p=0.43), but at the low elevation had greater cover on mangrove panels (t=10.09, p=0.013). Sessile species of cryptogenic origin were more abundant at the low than the mid or high intertidal elevations, 6 (Low [L] vs Mid [M]: t= 1.41, p=0.205; L vs High [H]: t=1.41, p=0.189) and 10 months (L vs M: t=3.42, p=0.013; L vs H: t=3.77, p=0.005; M vs H: t=1, p= 0.376) following panel deployment, but this difference was not significant at 8 months (L vs M: t=1.56, p=0.138, L vs H: t=1.83, p=0.107; M vs H: t=2.00, p=0.082).
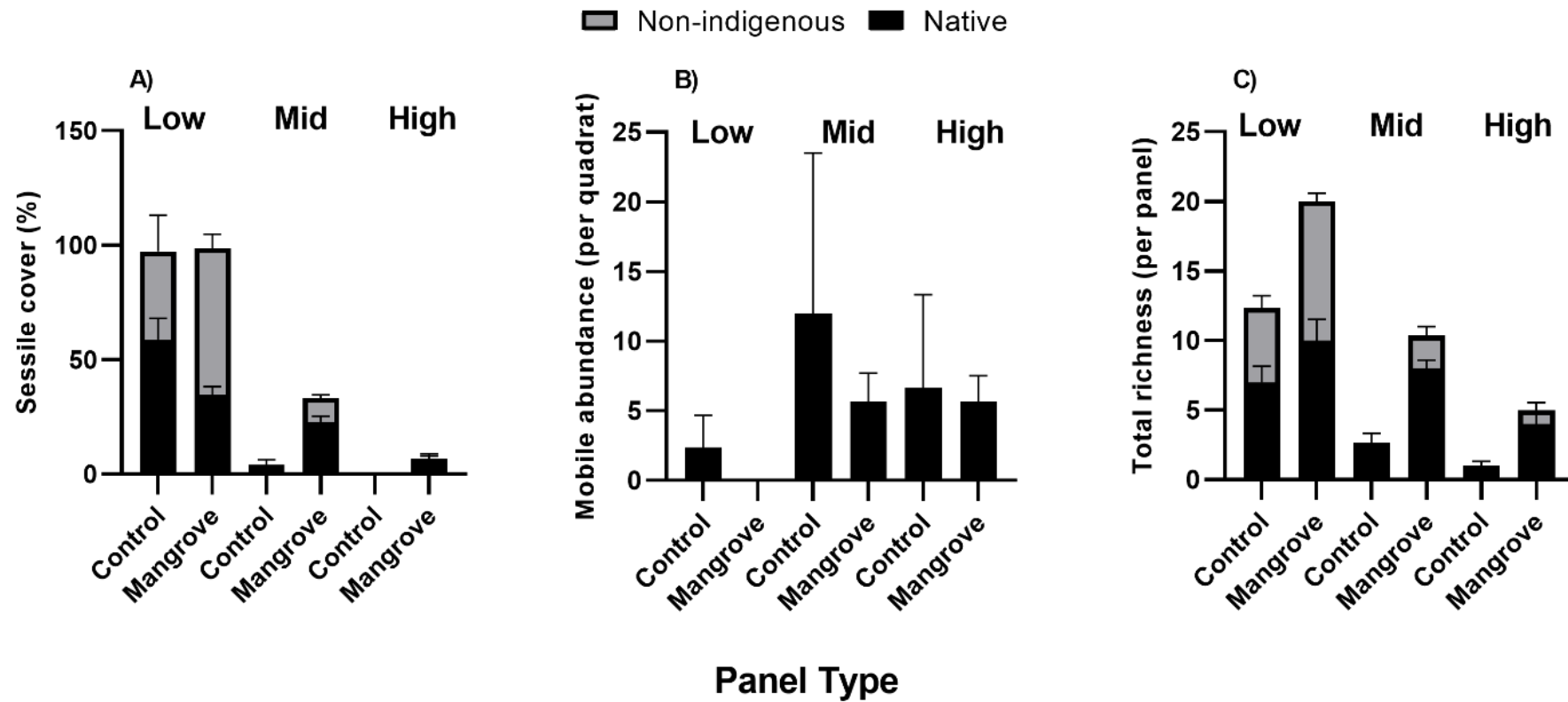
Figure 8. Mean (+SE) (A) percent cover of sessile species, (B) abundance of mobile species and (C) total species richness of all taxa colonising mangrove and control panels 10 months following their installation across three intertidal elevations (low, mid and high) at Milson's Point. Numbers are expressed per 0.25 x 0.25 m quadrat, centred over each panel design (n = 3).

Mobile species, irrespective of whether they were native, non-indigenous or cryptogenic, did not vary in abundance with respect to either tidal elevation or panel design. There were no cosmopolitan mobile species observed on any panel, at any time (Table 6).

Native and cryptogenic species richnesses displayed effects of panel design that varied with elevation, whereas NIS displayed temporally variable effects of each of panel design and elevation, and cosmopolitan species displayed a main effect of elevation (Table 6, Figure 8). Native species richness was significantly greater on mangrove than control panels at mid (t=4.43, p=0.011), and high (t=5.81, p=0.003) elevations, but did not significantly differ between panel designs at the low elevation (t=1.88, p=0.138), where richness was greatest. Cryptogenic species richness displayed no effect of panel design at high (t=1.00, p=0.405) or mid elevations (t=2.23, p=0.09) but at the low elevation was greater on mangrove than control panels (t=6.92, p=0.001). NIS richness did not differ between panel designs at 6 months (t=1.61, p=0.143), but at 8 (t=6, p=0.001) and 10 (t=5.42, p=0.001) months, NIS richness was greater on the mangrove than control panels. NIS richness was also significantly greater at low than mid (6 mo: t=3.28, p=0.012, 8 mo: t=9.54, p=0.001; 10 mo: t=10.42, p=0.0018) or high (6 mo: t=5.36, p=0.003, 8 mo: t=11.66, p=0.001; 10 mo: t=11.22, p=0.001) elevations at all sampling times, and was greater at mid than low elevation at months 8 and 10 only (8 mo: t=4.24, p=0.002; 10 mo: t=9.07, p=0.001). Cosmopolitan species displayed a similar, though non-significant, pattern of greater richness at low than mid or high elevation, with a slight, but non-significant, preference for mangrove rather than control panels (Table 6).

*Table 6. Results of four-factor repeated-measure PERMANOVAs testing for effects through time (3 levels: 6, 8 and 10 months) of panel design (2 levels: mangrove, control) and tidal elevation (3 levels: low, mid, high intertidal) for differences on cover of sessile species, the abundance of mobile species for univariate analysis for each tidal elevation and panel designs through time. For each elevation and panel design, three panels were repeatedly sampled through time. Panel no. = panel number (nested in panel design and elevation). Terms significant at α = 0.05 are in **bold**.*

Univariate										
Native		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	2	3.91	0.63	0.523	115.46	3.47	**0.016**	15.13	4.30	**0.028**
Tidal elevation(Te)	2	700.69	69.43	**0.001**	58.39	1.79	0.2	80.30	43.36	**0.001**
Panel design(Pa)	1	0.17	0.02	0.897	0.02	0.00	0.983	85.63	46.24	**0.001**
MoxTe	4	8.60	1.38	0.283	19.71	0.59	0.74	7.32	2.08	0.127
MoxPa	2	6.17	0.99	0.387	37.24	1.12	0.361	8.69	2.47	0.102
TexPa	2	102.39	10.15	**0.007**	2.63	0.08	0.934	7.19	3.88	0.056
Panel no.(Pn)	12	10.09	1.62	0.171	32.62	0.98	0.49	1.85	0.53	0.872
MoxTexPa	4	1.47	0.24	0.935	6.92	0.21	0.962	2.82	0.80	0.514
Residual	24	6.23			33.29			3.52		
NIS		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	2	13.56	1.85	0.172	0.07	2.00	0.161	8.17	14.00	**0.001**
Tidal elevation(Te)	2	732.72	288.81	**0.001**	0.02	0.50	0.617	158.17	76.95	**0.001**
Panel design(Pa)	1	66.67	26.28	**0.002**	0.00	0.00	1	46.30	22.52	**0.002**
MoxTe	4	5.53	0.75	0.567	0.02	0.50	0.73	5.42	9.29	**0.001**
MoxPa	2	3.56	0.48	0.63	0.00	0.00	1	2.80	4.79	**0.013**
TexPa	2	17.39	6.85	**0.011**	0.06	1.50	0.304	8.69	4.23	**0.041**
Panel no.(Pn)	12	2.54	0.35	0.979	0.04	1.00	0.48	2.06	3.52	**0.005**
MoxTexPa	4	9.03	1.23	0.296	0.06	1.50	0.221	0.77	1.32	0.315
Residual	24	7.34			0.04			0.58		

Table 6. cont

Cryptogenic		Sessile % cover			Mobile abundance			Species richness		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	2	12.52	9.52	**0.001**	0.35	1.46	0.222	3.91	9.38	**0.004**
Tidal elevation(Te)	2	36.07	8.05	**0.005**	0.02	0.08	0.921	26.24	157.44	**0.001**
Panel design(Pa)	1	4.74	1.06	0.39	0.02	0.08	0.791	6.00	36.00	**0.001**
MoxTe	4	10.30	7.83	**0.002**	0.30	1.23	0.322	4.41	10.58	**0.001**
MoxPa	2	1.41	1.07	0.364	0.13	0.54	0.578	0.50	1.20	0.321
TexPa	2	9.19	2.05	0.153	0.24	1.00	0.361	1.72	10.33	**0.005**
Panel no.(Pn)	12	4.48	3.41	**0.012**	0.24	1.00	0.46	0.17	0.40	0.959
MoxTexPa	4	2.52	1.92	0.124	0.19	0.77	0.617	0.89	2.13	0.111
Residual	24	1.31			0.24			0.42		
Cosmopolitan		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	2	6.50	2.83	**0.047**				0.57	1.59	0.208
Tidal elevation(Te)	2	6.89	3.07	0.082				6.13	8.49	**0.005**
Panel design(Pa)	1	2.67	1.19	0.297				0.30	0.41	0.54
MoxTe	4	2.47	1.08	0.388				0.55	1.51	0.219
MoxPa	2	2.72	1.19	0.306				0.24	0.67	0.563
TexPa	2	0.67	0.30	0.766				0.35	0.49	0.6
Panel no.(Pn)	12	2.24	0.98	0.493				0.72	2.00	0.09
MoxTexPa	4	0.97	0.42	0.885				0.55	1.51	0.224
Residual	24	2.30						0.36		

*Table 7. Results of four-factor repeated-measure PERMANOVAs testing for spatial variation in dominant mobile and sessile species through time (3 levels: 6, 8 and 10 months), between panel designs (2 levels: mangrove, control) and tidal elevation (3 levels: low, mid, high intertidal). For each elevation and panel design, three panels were repeatedly sampled through time. Panel no. = panel number (nested in panel design and elevation). Terms significant at α = 0.05 are in **bold**.*

		Corallina officinalis			*Ralfsia verrucosa*			*Dictyota dichotoma*		
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)
Month(Mo)	2	3.12	15.36	**0.001**	0.40	0.44	0.74	1.10	6.07	**0.008**
Tidal elevation (Te)	2	29.01	38.22	**0.001**	6.51	63.81	**0.001**	3.68	26.83	**0.001**
Panel design (Pa)	1	2.66	3.51	0.082	3.94	38.68	**0.008**	0.08	0.59	0.439
Panel no.(Pn)	12	9.11	3.72	**0.004**	0.10	0.11	0.999	0.13	0.75	0.718
MoxTe	4	2.04	10.04	**0.001**	0.33	0.36	0.895	1.10	6.07	**0.003**
MoxPa	2	0.38	1.90	0.179	0.79	0.87	0.480	0.01	0.82	0.928
TexPa	2	1.16	1.53	0.262	4.02	39.48	**0.006**	0.08	0.59	0.565
MoxTexPa	4	0.47	2.31	0.090	0.82	0.91	0.529	0.01	0.08	0.984
Residual	24	0.20								

		Tricellaria inopinata			*Gelidium pusillum*					
Source	df	MS	Pseudo-*F*	P(perm)	MS	Pseudo-*F*	P(perm)			
Month(Mo)	2	0.31	0.09	0.904	3.73	9.06	**0.001**			
Tidal elevation (Te)	2	93.35	123.71	**0.001**	3.73	9.06	**0.003**			
Panel design (Pa)	1	6.68	8.85	**0.016**	0.62	1.51	0.272			
Panel no.(Pn)	12	0.75	0.23	0.993	0.41	1.00	0.466			
MoxTe	4	0.31	0.09	0.985	3.73	9.06	**0.002**			
MoxPa	2	3.14	0.96	0.387	0.62	1.51	0.224			
TexPa	2	6.68	8.85	**0.009**	0.62	1.51	0.263			
MoxTexPa	4	3.14	0.96	0.459	0.62	1.51	0.185			
Residual	24	3.25			4.11					

3.2.2. Microhabitats within mangrove panels

Sessile species cover and total species richness varied between microhabitats of the mangrove panels at one or more intertidal elevations, but there was no effect of microhabitat on mobile species abundance (Table 9). SIMPER analysis revealed that three native algae species *Corallina officinalis*, *Gracilariopsis longissima, Griffithsia monilis* and the invasive mussel *Mytilus galloprovincialis* contributed to the dissimilarities between the microhabitats (Table 8). The three algal species varied between the inner and outer microhabitats on the low tidal elevation (*C. officinalis: t=5.68, p=0.031;* G. *longissimi:* t=4.16, p=0.057*; G. monilis*: t=3.34, p=0.08), while *M. galloprovincialis* varied between the inner and outer microhabitats at the mid and low intertidal elevations (M: t=13.22, p=0.008; L: t=11.10, p=0.01). The three algal species predominantly favoured the outer microhabitat, while *M. galloprovincialis* favoured the inner microhabitat.

*Table 8. Results of a four- factor repeated measures PERMANOVAs testing for the treatment effects of mangrove panel microhabitat (inner vs outer) and tidal elevation (high, mid, low intertidal) through time (6, 8 and 10 months) on four species identified as contributing most to differences among assemblages. For each elevation and microhabitat type, n=3 panels were repeatedly sampled through time. Panel no. = panel number (nested in elevation). Terms significant at α = 0.05 are in **bold**.*

Source	df	*Corallina officinalis* MS	Pseudo-*F*	P(perm)	*Gracilariopsis longissimi* MS	Pseudo-*F*	P(perm)	*Griffithsia monilis* MS	Pseudo-*F*	P(perm)	*Mytilus galloprovincialis* MS	Pseudo-*F*	P(perm)
Month(Mo)	1	0.00	0.00	0.97	3.73	8.29	**0.003**	0.43	1.02	0.312	9.25	3.47	0.068
Tidal elevation (Te)	1	8.44	14.49	**0.009**	8.96	24.98	**0.005**	15.09	34.21	**0.001**	213.21	76.29	**0.002**
Microhabitat(Mi)	0												
Panel no.(Pn)	8	0.44	1.05	0.383	0.27	0.67	0.719	0.33	0.78	0.613	0.21	0.79	0.641
MoxTe	3	0.94	2.22	0.086	2.13	5.26	**0.001**	0.32	0.76	0.517	2.39	0.89	0.42
MoxMi	1	0.26	0.61	0.412	3.37	8.29	**0.002**	0.05	0.13	0.708	8.44	3.17	0.077
TexMi	1	16.94	19.64	**0.002**	8.96	24.98	**0.001**	6.44	17.14	**0.003**	208.86	69.92	**0.001**
MixPn (Te)	8	0.65	1.54	0.144	0.27	0.67	0.735	0.28	0.67	0.716	2.24	0.84	0.582
MoxTexMi	3	0.21	0.50	0.681	2.13	5.26	**0.001**	0.33	0.79	0.524	1.78	0.67	0.582
Res	290	0.42			0.40			0.42			2.66		

The cover of each of native, non-indigenous, cryptogenic and cosmopolitan species displayed differences among microhabitats that were dependent on elevation (Table 9, Fig. 9). Native species had greater cover in outer than inner microhabitats at high (t=2.21, p=0.034) and low (t=9.09, p=0.001) elevations, as did cryptogenic species at the mid elevation (t=1.934, p=0.045), and cosmopolitan species at the low elevation (t=4.81, p=0.001), with differences at other elevations non-significant. NIS displayed the reverse pattern of greater cover in the inner than the outer microhabitat at each of the tidal elevations, although the magnitude of the effect varied among these (H: t=2.14, p=0.003; M: t=6.01, p=0.001; L: t=10.11, p=0.001). Native and NIS also displayed differences in richness between mangrove panel microhabitats that varied with elevation, but cryptogenic and cosmopolitan species richness did not respond to microhabitat or its interaction with any other factor (Table 9). Native species had greater richness on the inner microhabitat at low elevation (t=5.19, p=0.04) and the same pattern occurred with NIS, however only during month 8 (t=11, p=0.011).
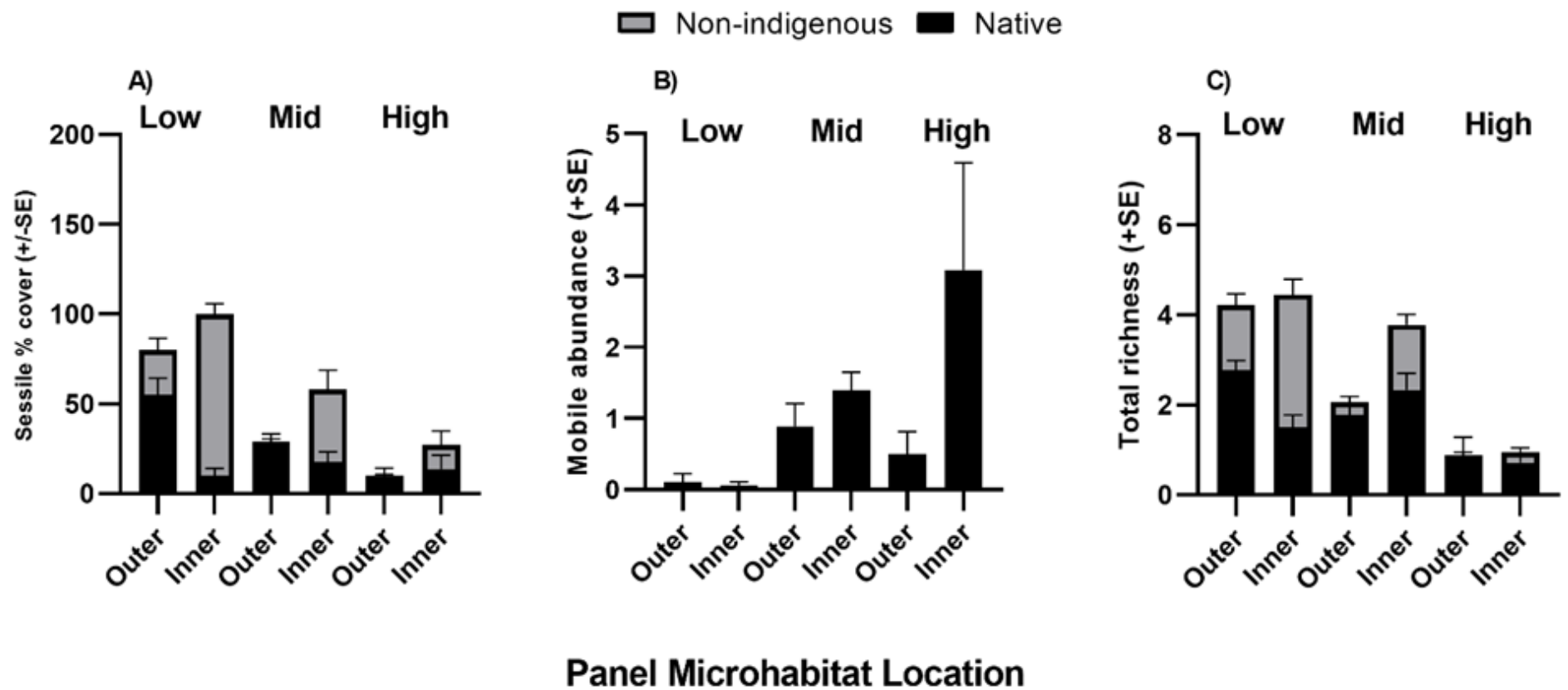
Figure 9. Mean (+SE) (A) percent cover of sessile species, (B) abundance of mobile species and (C) total species richness of all taxa colonising inner and outer microhabitats of mangrove panels 10 months following their installation across three elevations. Numbers are expressed per 0.04 x 0.04 m quadrat (n = 18).

*Table 9. Results of a four- factor repeated measures PERMANOVAs testing for effects through time (3 levels: 6, 8 and 10 months) of mangrove panel microhabitat (2 levels: inner vs outer) and tidal elevation (3 levels: low, mid, high intertidal) on differences in the combined richness of sessile and mobile species for multivariate analysis, and on the cover of sessile species and the abundance of mobile species for univariate analysis among microhabitats. For each elevation and microhabitat type, three panels were repeatedly sampled through time. Panel no. = panel number (nested in elevation). Terms significant at α = 0.05 are in **bold**.*

Multivariate

Community composition									
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	1	13429.00	7.58	**0.001**						
Tidal elevation(Te)	1	74998.00	10.52	**0.006**						
Microhabitat(Mi)										
Panel no.(Pn)	8	5384.80	3.04	**0.001**						
MoxTe	3	8221.00	4.64	**0.001**						
MoxMi	1	4310.90	2.43	**0.009**						
TexMi	1	40227.00	11.13	**0.001**						
MixPn(Te)	8	2749.90	1.15	**0.002**						
MoxTexMi	3	2928.90	1.65	**0.026**						
Residual	290	1769.50								

Univariate

Native		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	1	54.00	9.53	**0.004**	7.78	4.01	**0.042**	-1.45	0.00	
Tidal elevation(Te)	1	2.04	0.12	0.716	23.14	4.62	0.081	0.23	0.22	0.638
Microhabitat(Mi)										
Panel no.(Pn)	8	23.91	4.22	**0.001**	3.86	1.99	**0.055**	1.94	1.84	0.077

Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
MoxTe	3	7.07	1.25	0.298	1.94	1.00	0.389	7.20	6.84	**0.001**
MoxMi	1	8.17	1.44	0.241	0.38	0.19	0.693	1.85	1.76	0.193
TexMi	1	238.56	25.81	**0.001**	6.24	1.88	0.2	86.89	59.14	**0.001**
MixPn(Te)	8	6.99	1.23	0.275	2.75	1.42	0.197	1.11	1.05	0.385
MoxTexMi	3	1.95	0.34	0.776	0.35	0.18	0.919	2.61	2.48	0.067
Residual	290	5.67			1.94			1.05		
NIS		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	1	0.07	0.02	0.879	0.00	1.51	0.212	0.67	0.90	0.355
Tidal elevation(Te)	1	848.07	134.97	**0.003**	0.00	0.22	1	74.67	39.70	**0.003**
Microhabitat(Mi)										
Panel no.(Pn)	8	4.72	1.03	0.421	0.00	1.13	0.318	1.42	1.90	0.054
MoxTe	3	9.21	2.00	0.121	0.00	1.01	0.411	0.53	0.71	0.552
MoxMi	1	34.24	7.44	**0.007**	0.00	1.51	0.205	0.02	0.02	0.884
TexMi	1	50.07	6.77	**0.026**	0.00	0.22	1	3.38	2.98	0.131
MixPn(Te)	8	5.71	1.24	0.293	0.00	1.13	0.313	0.91	1.22	0.275
MoxTexMi	3	1.91	0.42	0.768	0.00	1.01	0.381	2.23	3.00	**0.035**
Residual	290	4.61			0.00			0.74		
Cryptogenic		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	1	9.80	9.19	**0.003**				3.38	15.81	**0.001**
Tidal elevation(Te)	1	28.89	25.14	**0.006**	0.00	0.87	0.474	12.52	11.71	**0.01**
Microhabitat(Mi)										
Panel no.(Pn)	8	0.87	0.82	0.584	0.01	0.93	0.491	0.81	3.78	**0.002**

Source	df	Sessile % cover MS	Pseudo-F	P(perm)	Mobile abundance MS	Pseudo-F	P(perm)	Species richness MS	Pseudo-F	P(perm)
MoxTe	3	7.49	7.03	**0.001**	0.01	1.62	0.195	3.80	17.79	**0.001**
MoxMi	1	4.74	4.45	**0.046**				0.12	0.54	0.456
TexMi	1	7.04	1.36	2.272	0.00	0.87	0.427	0.67	0.92	0.372
MixPn(Te)	8	4.07	3.82	**0.002**	0.01	0.93	0.477	0.60	2.80	**0.003**
MoxTexMi	3	2.35	2.21	0.088	0.01	1.62	0.176	0.50	2.36	0.075
Residual	290	1.07								

Cosmopolitan		**Sessile % cover**			**Mobile abundance**			**Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Month(Mo)	1	0.12	0.32	0.592				0.07	0.57	0.437
Tidal elevation(Te)	1	7.41	11.19	**0.008**				3.63	19.51	**0.006**
Microhabitat(Mi)										
Panel no.(Pn)	8	0.50	1.39	0.204				0.14	1.08	0.399
MoxTe	3	0.56	1.54	0.202				0.07	0.54	0.666
MoxMi	1	0.78	2.16	0.136				0.91	6.92	**0.004**
TexMi	1	12.52	16.00	**0.005**				3.13	14.08	**0.005**
MixPn(Te)	8	0.59	1.63	0.109				0.17	1.29	0.261
MoxTexMi	3	0.19	0.52	0.695				0.27	2.02	0.108
Residual	290	0.36						0.13		

4. Discussion

Urbanisation is occurring at a rapid pace along coastal foreshores, with built infrastructure such as seawalls replacing natural marine habitats and supporting different and often depauperate assemblages (Bulleri and Chapman, 2010, Chapman and Bulleri, 2003, Dugan et al., 2011). Eco-engineering research is developing strategies to mitigate this habitat loss and enhance the biodiversity of built infrastructure (Chapman and Blockley, 2009, Firth et al., 2016b, Strain et al., 2018b), but few studies have considered the potential for such practices to be maladaptive by facilitating non-indigenous species (NIS). Artificial structures, such as seawalls, often support a higher richness and abundance of NIS compared to natural habitats (Dafforn et al., 2013, Tyrrell and Byers, 2007). NIS have been shown to have 50% higher cover on seawalls in Sydney Harbour, compared to the natural rocky shores (Mayer-Pinto et al., 2018). This study compared colonisation by NIS and native species among five types of complex, habitat-enhancing panels, that are part of an eco-engineering strategy, and on flat, control panels that were retrofitted to intertidal seawalls. At mid and high intertidal elevations, colonisation of NIS was similarly low across both complex and flat control panels, on average contributing less than 0.5% of total biological cover. By contrast, at low intertidal elevations, NIS contributed a third of the sessile cover, half of the species present and were in some instances 50% more abundant and diverse on the complex rather than the control panels. Within complex panels, NIS were particularly abundant within the protective microhabitats provided by rockpools, depressions and crevices.

Overall, across all panel designs, the cover of NIS on whole panels was eight times greater at the low, than at mid or high intertidal elevations. The observation by this and previous studies that NIS abundance and richness increased with decreasing tidal elevation (Bando, 2006, Cohen et al., 1998, Russell, 1992, Strayer and Smith, 2000) may reflect the mechanism by which many NIS are introduced, on vessel hulls or in ballast (Carlton, 1996). This transport mechanism selects for species that can rapidly colonise permanently submerged substrates, which may display low tolerance to desiccation stress (Drake et al., 2005, Gollasch, 2002, Hayes and Sliwa, 2003, Wyatt et al., 2005). The dominant mussel in this thesis may have a competitive advantage over native species at low elevations, at high elevations significant mortality and low rates of growth of NIS can prevent them from dominating (Krassoi et al., 2008).

Among panel designs, there was significant variation in the species assemblage, and number of NIS supported. Of the 95 species identified on the habitat panels, only four utilised all six panel designs

across the two sites. As predicted, given their greater surface area and microhabitat diversity (Strain et al., 2018b), complex panels supported greater abundances and richnesses of fouling organisms, compared to flat panels. At high and mid intertidal elevations, where NIS were rare and desiccation stress limits species abundance and diversity, the greater abundance and richness of species on complex panels was attributable to native species, with NIS displaying no significant response to complexity at the whole panel scale. At the low intertidal elevation, however, where NIS contributed to over 50% of cover and richness, both NIS and native species contributed to the pattern of greater richness on complex than flat panels, and NIS abundance responded positively to complexity, whereas native species cover was reduced on complex panels.

Among complex panel designs, variation in assemblages was also seen, supporting the hypothesis that different function groups respond to different microhabitat features (Mercurio et al., 1985, Schaal et al., 2011, Strain et al., 2018b). At the mid intertidal elevation of Sawmillers Reserve, honeycomb and rockpool panels showed the highest percent cover of native sessile species, while rockpools also had the highest abundance of mobile species, and overall richness. Water-retaining features are missing from seawalls (Bulleri, 2005a, Chapman and Blockley, 2009, Morris, 2016) and our results support previous research (Chapman and Blockley, 2009) in suggesting that their addition to seawalls can increase native biodiversity. Although not tested here, the facilitation of more diverse communities by complex panels may provide some biotic resistance to colonisation of NIS in the longer-term (Stachowicz et al., 1999). Here, however, mid intertidal rockpool, swimthrough and crevice panels supported NIS such as *Amphibalanus amphitrite,* and *Watersipora subtorquata* that were otherwise generally limited to subtidal areas (Ho et al., 2009, Parry et al., 1997). Dark and shaded microhabitats may allow species that are more typical of low intertidal and subtidal environments to extend their distributions vertically to elevations that would otherwise be too dry (Dafforn et al., 2012). Overall, among the complex designs, rockpool panels supported the most, while crevice and swimthrough panels the least NIS. The latter contained no more than 2% cover of NIS. Although barnacles (mostly native) were found across all panels, honeycomb panels supported the highest density, suggesting that the addition of pitting on artificial structures increases the colonisation of cyprids, that prefer to settle in depressions (Crisp and Barnes, 1954).

Temporal trends in NIS abundance and cover were in many instances consistent with the paradigm that they are opportunists that colonise early, but have inferior competitive abilities (Dafforn et al., 2009). Among mobile species, the NIS isopod *Ligia exotica* was the first to colonise panels, displaying strong patterns of difference among panel designs at 2 and 4 months, but had disappeared from panels by 8 months post panel installation. This result may be explained by the ability of the isopod to rapidly capitalise on newly available resources (Christofoletti et al., 2011),

such as algal biofilms growing on recently deployed panels and the availability of colonists (Lopes et al., 2006). Conversely, the native gastropod *Afrolittorina acutispira* was absent during the early months but colonised all panels during the later months of the study.

On the complex panels, we found that protective, internal microhabitats contained more NIS than external, exposed microhabitats across all tidal elevations. At the high and mid intertidal elevations, where these internal microhabitats also facilitated far more native species than the external microhabitats, the proportionate contribution of NIS to their total abundance and richness was small (<2%). At the low intertidal elevation however, NIS were 2 times more abundant than native species within the internal microhabitat, while native species were 11 times more abundant than NIS on the external microhabitat. The shaded and moist environment of internal microhabitats may have facilitated biodiversity by reducing temperature and desiccation stress (Brawley and Johnson, 1991, Chapperon and Seuront, 2011, Gedan et al., 2011) and/or provided refuge from predation (Brawley and Johnson, 1991) and hydrodynamic forces (Jackson et al., 2013). As compared to natural habitats, sessile organisms on seawalls can experience enhanced rates of predation and hydrodynamic forces from wave reflection (Firth et al., 2016c). High wave exposure can reduce recruitment of algae (Trowbridge, 1996) and sessile invertebrates such as barnacles (Guiler, 1960), ascidians and hydroids (Evans et al., 2016), all of which were found within the internal microhabitats. In a previous study at our study site, oysters suffered decreased predation inside versus outside of crevices on complex panels (Strain et al., 2018a). Here, the invasive mussel, *M. galloprovincialis,* which dominated internal microhabitats of the mangrove panels on the low shore, may have experienced a similar release from predation. In addition, this species has very particular settling preferences, preferring textures surfaces such as the small pock marks (Carl et al., 2012) found on the mangrove panel. While there was minimal settlement of other species in and around *M. galloprovincialis* by the tenth month post instillation, the nature of mussels as bioengineers, has the potential to increase biodiversity through the provision of cooler, protected environments between and underneath mussel shells (Cole, 2010).

On other types of artificial structure, NIS are particularly abundant on shaded substrates, such as vertical surfaces, or the underside of pontoons (Dafforn et al., 2009, Dafforn et al., 2012, Glasby et al., 2007, Kim and Micheli, 2013). This has been attributed to reduced competition for space between invertebrates and algae, the latter of which cannot photosynthesise and survive in poorly lit environments (Littler and Arnold, 1980). Our observation that, compared to external surfaces, protective internal microhabitats had higher abundances of NIS invertebrates such as *A. amphitrite, Botrylloides leachii, M. galloprovincialis*, *Styela plicata, and W. subtorquata* and lower abundance of native algae such as *Ulva australis, Corallina officinalis, Gracilaria mammillaris and Griffithsia*

monilis in microhabitats, suggests that shading may have contributed to spatial patterns in NIS in the internal microhabitats. Consistent with this hypothesis of shading reducing NIS from competition with native algae, inside the artificial pools of the rockpool panels, the shaded surface of the front wall supported a higher abundance and richness of NIS than the back wall, which could receive direct sunlight. Within horizontally orientated crevices, the shaded upper internal surface supported lower densities of native sessile and mobile species.

In addition to influencing the community assembly of NIS, microhabitat identity also influenced native species assemblages. Grazing gastropods such as *Austrocochlea porcata, Bembicium nanum, Cellana tramoserica* and *Nerita atramentosa* were found in highest abundance in the rockpool microhabitats. Rockpools may not only provide them with protection from predation and environmental stressors, but also enhance foraging and grazing opportunities by providing the shaded and moist conditions that promote the growth and development of biofilms (Jackson et al., 2013). Although, overall, the internal microhabitats supported more species than the external microhabitats, barnacles dominated by *H. popeiana,* were to the contrary, more abundant on the external surfaces of complex panels. On surfaces more prone to desiccation, they may experience less competition with species prone to desiccation stress.

The results of this research suggest that, while greening of marine infrastructure at high and mid intertidal elevations is unlikely to facilitate NIS settlement and growth, at low intertidal elevations the distribution and abundance of NIS may be enhanced. In sites with high densities of *M. galloprovincialis*, the ecological strategies of this species should be considered, before complex greening structures are placed in low tidal elevations. This may include avoidance of small pits that enhance settlement. In order to minimise NIS recruitment, greening interventions should avoid the use of moist, texturized and shaded microhabitats, particularly in the low intertidal zone.

In minimising NIS colonisation of greening interventions, timing of substrate introduction is also a key consideration. In the present study, panels were strategically installed during the Austral summer of November and December. During this time there are many native propagules in the water column, promoting native species colonisation on the panels (Price, 1989, Wilson and Hodgkin, 1967). The most prevalent across all panels and time points, were two species of native barnacles *Austrominius covertus* and *H. popeiana,* which likely occurred because the species settle during the spring and summer months (Ross, 2001), when the tiles were initially deployed. Installation during the Austral winter may have resulted in differing patterns of native and NIS recruitment (Price, 1989, Wilson and Hodgkin, 1967). Furthermore, it will be important to follow changes in the communities on the panels for a longer period of time, to investigate whether further successional changes occur, or if the patterns in native and NIS apparent by the end of this study remain constant.

5. Conclusion

This ten-month study, has shown that complex panel designs support some NIS, however, when compared to native species, NIS have reduced abundance and richness. This finding suggests that the inclusion of complex tiles on seawalls could increase the abundance and richness of native species in Sydney Harbour, though further long-term monitoring is needed to understand seasonal differences and successional change in the communities. Many studies that have assessed the efficacy of marine greening interventions, have utilised a morphospecies approach that does not necessarily discriminate between native and NIS (Browne and Chapman, 2014, Chapman and Blockley, 2009, Firth et al., 2013, Waltham and Sheaves, 2018). Therefore, reports of increased biodiversity from seawall greening, may reflect increases in both native and non-indigenous species. This study has highlighted that greening interventions may have unintended negative consequences, through NIS facilitation at low intertidal elevations. Results from this study will help inform management decisions to aid in the increased abundance and diversity of native species in Sydney Harbour. To ensure that seawall greening interventions have targeted ecological outcomes, it is essential that monitoring and evaluation programs utilise rigorous surveys with species-level resolution so that NIS recruitment preferences can be identified. Non-indigenous species that become invasive are a leading cause of biodiversity and economic loss (Bax et al., 2003, Charles and Dukes, 2008, Floerl and Coutts, 2009, Katsanevakis et al., 2014, Vitousek et al., 1997), and factors that lead to their proliferation and spread need to be identified, prevented and managed accordingly (Lehtiniemi et al., 2015). Investigating the native and non-indigenous species recruiting to seawall greening interventions will allow designs with unintended negative consequences to be identified, and installations modified to ensure that attempts to green seawalls result in diverse native assemblages.

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7. Appendix

Appendix 1/ Table 1. List of species found throughout this study and their classification status (N) native, (NIS) non-indigenous, (COS) cosmopolitan, (C) cryptogenic.

Kingdom/Phylum/Order	Family	Species	Status (N/NIS/COS/I/C)	Reference
PLANTAE				
Chlorophyta				
Order: Ulvales				
	Ulvaceae	*Ulva australis*	N	(Burke et al., 2011)
	Ulvaceae	*Ulva compressa*	COS	(Hewitt et al., 2004)
	Ulvaceae	*Ulva intestinalis*	COS	(Hewitt et al., 2004)
Phaeophyta				
Order: Scytosiphonales				
	Scytosiphonaceae	*Petalonia binghamiae*	COS	(Kitayama and Lin, 2012)
	Scytosiphonaceae	*Colpomenia peregrina*	C	(Dafforn et al., 2008, Glasby et al., 2007, Hewitt et al., 2004)
Order: Dictyotales				
	Dictyotaceae	*Dictyota dichotoma*	NIS	(Dafforn et al., 2008, Glasby et al., 2007, Hewitt et al., 2004)
Order: Laminariales				
	Lessoniaceae	*Ecklonia radiata*	N	(Dafforn et al., 2008, Glasby et al., 2007)
Order: Ectocarpales				
	Ectocarpaceae	*Ectocarpus siliculosus*	C	(Charrier et al., 2008, Peters et al., 2004)
Order: Dictyotales				

Appendix 1/ Table 1 cont.

	Dictyotaceae	*Padina fraseri*	N	(Glasby et al., 2007)
Order: Ralfsiales				
	Ralfsiaceae	*Ralfsia verrucosa*	N	(Glasby et al., 2007)
Order: Fucales				
	Sargassaceae	*Sargassum sp*	N	(Glasby et al., 2007)
Rhodophyta				
Order: Hildenbrandiales				
	Hildenbrandiaceae	*Hildenbrandia rubra*	C	(Glasby et al., 2007, Hewitt et al., 2004)
Order: Corallinales				
	Corallinaceae	*Corallina officinalis*	N	(Glasby et al., 2007)
	Corallinaceae	crustose coralline algae sp.	N	(Harvey et al., 2009)
Order: Ceramiales				
	Wrangeliaceae	*Griffithsia monilis*	N	(Millar and Kraft, 1993)
Order: Gelidiales				
	Gelidiaceae	*Gelidium corneum*	NIS	(Moore, 2008)
	Gelidiaceae	*Gelidium pusillum*	C	(Hewitt et al., 2004)
Order: Gracilariales				
	Gracilariaceae	*Gracilaria arcuata*	N	(Witherell et al., 1994)
	Gracilariaceae	*Gracilaria mammillaris*	N	(Witherell et al., 1994)
	Gracilariaceae	*Hydropuntia preissiana*	N	(Witherell et al., 1994)
	Gracilariaceae	*Gracilaria secundata*	N	(Nelson, 1987)
	Gracilariaceae	*Gracilariopsis longissima*	N	(Witherell et al., 1994)
Order: Bangiales				
	Bangiaceae	*Pyropia pulchella*	N	(Ackland et al., 2006)

Appendix 1/ Table 1 cont.

ANIMALIA				
Arthropoda				
Order: Amphipoda				
		Amphipod 1	C	
		Amphipod 2	C	
		Amphipod 3	C	
		Amphipod 4	C	
		Amphipod 5	C	
	Caprellidae	Caprellid	C	
Order: Isopoda				
		Isopod 1	C	
		Isopod 2	C	
		Isopod 3	C	
		Isopod 4	C	
		Isopod 5	C	
		Isopod 6	C	
		Isopod 7	C	
		Isopod 8	C	
		Isopod 9	C	
		Isopod 10	C	
		Isopod 11	C	
		Isopod 12	C	
		Isopod 13	C	
		Ligia australiansis	N	
		Ligia exotica	NIS	
Order: Sessilia				
	Austrobalanidae	*Austrominius covertus*	N	(Ross, 1996)
	Austrobalanidae	*Hexaminius popeiana*	N	(Ross, 1996)
	Balanidae	*Amphibalanus amphitrite*	NIS	(Dafforn et al., 2009, Piola and Johnston, 2008)

Appendix 1/ Table 1 cont.

	Balanidae	*Amphibalanus variegatus*	N	(Dafforn et al., 2009, Piola and Johnston, 2008)
	Balanidae	*Megabalanus coccopoma*	NIS	(Dafforn et al., 2009)
	Catophragmidae	*Catomerus polymerus*	N	(York et al., 2008)
	Chthamalidae	*Chthamalus antennatus*	N	(Wisely and Blick, 1964)
	Tetraclitidae	*Tesseropora rosea*	N	(Glasby et al., 2007)
	Tetraclitidae	*Tetraclitella purpurascens*	N	(Glasby et al., 2007, Piola and Johnston, 2008)
Cnidaria				
		Hydroid 1	C	
		Hydroid 2	C	
Ectoprocta				
Order: Cheilostomata			NIS	
	Bugulidae	*Bugula neritina*		(Berents and Hutchings, 2002, Dafforn et al., 2009, Hewitt et al., 2004, Pollard and Pethebridge, 2002)
Order: Cheilostomatida				
	Lepraliellidae	*Celleporaria nodulosa*	N	(Dafforn et al., 2008, Dafforn et al., 2009, Glasby et al., 2007, Piola and Johnston, 2008)

Appendix 1/ Table 1 cont.

Cryptosulidae	*Cryptosula pallasiana*	NIS	(Berents and Hutchings, 2002, Dafforn et al., 2009, Hewitt et al., 2004, Pollard and Pethebridge, 2002)
Schizoporellidae	*Schizoporella errata*	NIS	(Dafforn et al., 2008, Dafforn et al., 2009, Glasby et al., 2007, Piola and Johnston, 2008)
Candidae	*Tricellaria inopinata*	NIS	(Dafforn et al., 2008, Dafforn et al., 2009, Glasby et al., 2007, Piola and Johnston, 2008)
Watersiporidae	*Watersipora arcuata*	NIS	(Berents and Hutchings, 2002, Dafforn et al., 2009, Hewitt et al., 2004, Pollard and Pethebridge, 2002)
Watersiporidae	*Watersipora subtorquata*	NIS	(Berents and Hutchings, 2002, Dafforn et al., 2008, Dafforn et al., 2009, Glasby et al., 2007, Hewitt et al., 2004, Piola and Johnston, 2008, Pollard and Pethebridge, 2002)

Mollusca
Bivalvia
Order: Mytilida

	Mytilidae	*Mytilus galloprovincialis*	I	(Berents and Hutchings, 2002, Glasby et al., 2007, Hedge et al., 2014)
	Mytilidae	*Trichomya hirsuta*	N	(Lopez et al., 2014)

Order: Ostreida

	Ostreidae	*Saccostrea glomerata*	N	(Scanes et al., 2016)

GASTROPODA
Order: Pattellogastropoda

	Patellidae	*Cellana tramoserica*	N	(Endean et al., 1956, Benkendorff and Przeslawski, 2008)
	Acmaeidae	Notoacmea petterdi	N	(Endean et al., 1956, Benkendorff and Przeslawski, 2008)
	Patellidae	Scutellastra chapmani	N	(Benkendorff and Przeslawski, 2008)

SUBCLASS: ORTHOGASTROPODA; Superorder: Vetigastropoda

	Fissurellidae	Montfortula rugosa	N	(Benkendorff and Przeslawski, 2008)

Superorder: Caenogastropoda; Infraorder: Littorinimorpha

	Littorinidae	Afrolittorina **acutispira**	N	(Endean et al., 1956, Benkendorff and Przeslawski, 2008)
	Littorinidae	Austrolittorina unifasciata	N	(Endean et al., 1956, Benkendorff and Przeslawski, 2008)

Appendix 1/ Table 1 cont.

	Littorinidae	*Bembicium auratum*	N	(Beechey, 2009)
	Littorinidae	Bembicium nanum	N	(Ayre et al., 2009, Benkendorff and Przeslawski, 2008)
	Littorinidae	Patelloida mimula	N	(Endean et al., 1956)
Superorder: Caenogastropoda; Infraorder: Neogastropoda				
	Muricidae	Bedeva paivae	N	(Benkendorff and Przeslawski, 2008)
	Muricidae	Tenguella marginalba	N	(Benkendorff and Przeslawski, 2008, Endean et al., 1956)
Pulmonata				
	Siphonariidae	Siphonaria denticulata	N	(Benkendorff and Przeslawski, 2008)
CLASS: POLYPLACOPHORA				
	Chitonidae	*sypharochiton pelliserpentis*	N	(Benkendorff and Przeslawski, 2008)
Polychaeta				
Order: Canalipalpata				
		Ficopomatus enigmaticus	NIS	(Berents and Hutchings, 2002, Hewitt et al., 2004)
	Serpulidae	*Galeolaria caespitosa*	N	(Dafforn et al., 2009)
	Serpulidae	*Hydroides sp (elegans & ezoensis)*	NIS	(Berents and Hutchings, 2002, Hedge et al., 2014, Piola and Johnston, 2008)
	Serpulidae	*Salmacina australis*	N	(Dafforn et al., 2008, Dafforn et al., 2009, Piola and Johnston, 2008)
	Serpulidae	*Spirorbinae*	C	(Dafforn et al., 2009, Piola and Johnston, 2008)
	Serpulidae	*Spirobranchus taeniatus*	N	(Piola and Johnston, 2008)

Appendix 1/ Table 1 cont.

Porifera
Order: Pleurogona

	Pyuridae	*Pyura praeputialis*	N	(Piola and Johnston, 2008)

Order: Leucosolenida

		Encrusting Sponge 1	C	
	Sycettidae	*Sycon sponge 1*	C	
	Sycettidae	*Sycon sponge 2*	C	
	Sycettidae	*Sycon sponge 3*	C	
	Sycettidae	*Sycon sponge 4*	C	
	Sycettidae	*Sycon sponge 5*	C	

Tunicata
Order: Stolidobranchia

	Botrylloides	*Botrylloides leachii*	NIS	(Berents and Hutchings, 2002, Dafforn et al., 2008, Dafforn et al., 2009, Hedge et al., 2014, Hewitt et al., 2004, Piola and Johnston, 2008)
	Botrylloides	*Botryllus schlosseri*	NIS	(Berents and Hutchings, 2002, Dafforn et al., 2009, Hewitt et al., 2004, Pollard and Pethebridge, 2002)

Order: Stolidobranchia

	Styelidae	*Styela plicata*	NIS	(Berents and Hutchings, 2002, Dafforn et al., 2008, Dafforn et al., 2009, Hedge et al., 2014, Hewitt, 2002, Hewitt et al., 2004, Pollard and Pethebridge, 2002)
		Unknown Ascidian 1	C	
		Unknown Ascidian 2	C	

Appendix 1/ Table 2. Species present on each panel design at the Sawmillers Reserve and Milsons Point sites (RP: rockpool; HC: honeycomb; ST: swimthrough; CR: crevice; MR: mangrove; and CO: control). + represents presence.

Taxa	Panel design						
	Sawmillers Reserve					Milsons point	
	RP	HC	ST	CR	CO	MR	CO
Phylum: Chlorophyta							
Family: Ulvaceae							
Ulva australis	+		+	+		+	+
Ulva compressa	+		+			+	+
Ulva intestinalis	+			+		+	+
Phylum: Phaeophyta							
Family: Scytosiphonaceae							
Petalonia binghamiae	+				+	+	+
Colpomenia peregrina				+			
Family: Dictyotaceae							
Dictyota dichotoma						+	+
Padina fraseri						+	
Family: Lessoniaceae							
Ecklonia radiata	+	+				+	+
Family: Ectocarpaceae							
Ectocarpus siliculosus	+	+				+	
Family: Ralfsiaceae							
Ralfsia verrucosa	+	+	+	+		+	+
Family: Sargassaceae							
Sargassum sp						+	
Phylum: Rhodophyta							
Family: Hildenbrandiacea							
Hildenbrandia rubra						+	
Family: Corallinaceae							
Corallina officinalis	+					+	+
crustose coralline algae sp.	+					+	+
Family: Geldiaceae							
Gelidium corneum	+					+	+
Gelidium pusillum	+	+				+	+
Family: Gracilariaceae							
Gracilaria arcuata						+	
Gracilaria mammillaris		+				+	+
Hydropuntia preissiana						+	+
Gracilariopsis longissima	+	+				+	+
Family: Bangiaceae							
Pyropia pulchella	+					+	+
Phylum: Arthropoda							
Order: Amphipoda							
Amphipod 1	+	+		+		+	+
Amphipod 2	+						
Amphipod 3	+			+			

	1	2	3	4	5	6	7
Amphipod 4							
Amphipod 5	+			+			
Order: Isopoda							
Isopod 1	+			+		+	
Isopod 2	+					+	
Isopod 3	+						
Isopod 4	+			+			
Isopod 5				+			
Isopod 6	+						
Isopod 7	+						
Isopod 8	+		+				
Isopod 9	+						
Isopod 10	+						+
Isopod 11	+						
Isopod 12	+						
Isopod 13	+						
Family: Ligiidae							
Ligia australiansis	+						
Ligia exotica	+	+	+	+	+	+	+
Family: Austrobalanidae							
Austrominius covertus	+	+	+	+	+	+	+
Hexaminius popeiana	+	+	+	+	+	+	+
Family: Balanidae							
Amphibalanus amphitrite	+		+	+		+	+
Amphibalanus variegatus	+		+	+	+	+	
Megabalanus coccopoma						+	
Family: Catophragmidae							
Catomerus polymerus	+					+	
Family: Tetraclitidae							
Tesseropora rosea	+	+	+	+		+	+
Tetraclitella purpurascens	+		+			+	
Phylum: Cnidaria							
Hydroid 1	+					+	
Hydroid 2						+	
Phylum: Ectoprocta							
Family: Bugulidae							
Bugula neritina	+					+	+
Family: Lepraliellidae							
Celleporaria nodulosa			+				
Family: Cryptosulidae							
Cryptosula pallasiana						+	+
Family: Schizoporellidae							
Schizoporella errata	+					+	+
Family: Candidae							
Tricellaria inopinata	+					+	+
Family: Watersiporidae							
Watersipora arcuata	+		+			+	

Appendix 1/ Table 2 cont.

	1	2	3	4	5	6	7
Watersipora subtorquata	+			+		+	+
Phylum: Mollusca							
Family: Mytilidae							
Mytilus galloprovincialis	+					+	
Trichomya hirsuta						+	
Family: Ostreidae							
Saccostrea glomerata	+	+	+	+	+	+	
Phylum: GASTROPODA							
Family: Patellidae							
Cellana tramoserica	+		+			+	+
Scutellastra chapmani						+	+
Family: Acmaeidae							
Notoacmea petterdi	+	+	+	+		+	
Family: Fissurellidae							
Montfortula rugosa	+						+
Family: Littorinidae							
Afrolittorina acutispira	+	+	+	+	+	+	+
Bembicium auratum		+	+		+	+	
Bembicium nanum		+	+		+	+	
Patelloida mimula		+	+		+	+	
Family: Muricidae							
Bedeva paivae		+	+		+	+	
Tenguella marginalba						+	+
Family: Siphonariidae							
Siphonaria denticulata	+	+	+		+	+	+
Family: Chitonidae							
sypharochiton pelliserpentis					+	+	+
Family: Serpulidae							
Ficopomatus enigmaticus							
Galeolaria caespitosa	+					+	+
Hydroides sp (elegans & ezoensis)	+					+	+
Salmacina australis						+	
Spirorbinae	+		+	+		+	+
Spirobranchus taeniatus						+	
Phylum: Porifera							
Encrusting Sponge 1	+					+	
Family: Pyuridae							
Pyura praeputialis	+					+	+
Family: Sycettidae							
Sycon sponge 1						+	
Sycon sponge 2		+				+	+
Sycon sponge 3		+					
Sycon sponge 4						+	
Sycon sponge 5						+	

Appendix 1/ Table 2 cont.

Phylum: Tunicata			
Family: Botrylloides			
Botrylloides leachii		+	+
Family: Styelidae			
Styela plicata	+	+	+