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Variable effects of substrate colour and microtexture on sessile marine taxa in Australian estuaries

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ABSTRACT
Concrete infrastructure in coastal waters is increasing. While adding complex habitat and manipulating concrete mixtures to enhance biodiversity have been studied, field investigations of sub-millimetre-scale complexity and substrate colour are lacking. Here, the interacting effects of ‘colour’ (white, grey, black) and ‘microtexture’ (smooth, 0.5 mm texture) on colonisation were assessed at three sites in Australia. In Townsville, no effects of colour or microtexture were observed. In Sydney, spirorbid polychaetes occupied more space on smooth than textured tiles, but there was no effect of microtexture on serpulid polychaetes, bryozoans and algae. In Melbourne, barnacles were more abundant on black than white tiles, while serpulid polychaetes showed opposite patterns and ascidians did not vary with treatments. These results suggest that microtexture and colour can facilitate colonisation of some taxa. The context-dependency of the results shows that inclusion of these factors into marine infrastructure designs needs to be carefully considered.

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Ecological engineering; sessile species; complexity; temperate; tropics

Introduction

Coastal areas around the world are becoming hotspots of urbanisation, with more than 2.4 billion people (approx. 40% of the population) living in the coastal zone (UN2016). As a result of this, a considerable amount of artificial substrate has been added to coastal areas for the purpose of coastal protection (e.g. seawalls), recreation (e.g. marinas) and maritime industries (e.g. ports) (Bulleri and Chapman 2010, Mineur et al. 2012). Globally, more than 70% of the shoreline has already been modified (Dafforn et al. 2015), and further increases are projected for the future (Bugnot et al. 2020, Floerl et al. 2021). However, a majority of studies suggest that artificial structures are not surrogates for the natural habitat they have replaced, causing biodiversity loss, alterations in community structure, and facilitation of invasive species (Airoldi et al. 2015, Bulleri and Chapman 2010, Connell 2001), though some exceptions exist (e.g. Baxter et al. 2023, Hawkins et al. 1983, Holloway and Field 2020).

Differences in the ecological communities of artificial structures and natural habitats reflect differences in their chemical and physical properties (Coombes et al. 2010, Jang et al. 2015), geomorphological processes (weathering, wetting/drying, bioprotection) (Coombes and Naylor 2012, Coombes et al. 2013), complexity (Lawrence et al. 2021), environmental setting (i.e. exposure to waves, orientation, inclination) (Firth et al. 2016), and associated changes in recruitment and biotic interactions (Drakard et al. 2021, Hanlon et al. 2018, Jackson et al. 2008, Klein et al. 2011, Perkol-Finkel and Benayahu 2007). Artificial habitats are often constructed of unnatural materials (Bulleri and Chapman 2010) and are often more homogenous than natural habitats,

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lacking habitat features (i.e. rock pools, crevices) commonly found on natural habitats such as rocky shores (Chapman and Bulleri 2003, for an exception, see Baxter et al. 2023). Similarly, natural materials like rock are often 'older', displaying more heterogeneous surface microtextures (sub-mm scale) and porosity as a result of longer weathering and erosion processes compared to 'newer' artificial materials (Bulleri and Chapman 2010, Coombes et al. 2015). Additionally, artificial materials, or even 'processed' natural materials (e.g. quarried rock) can vary from naturally occurring materials in colour and/or brightness (e.g. grey concrete, quarried and natural sandstone), as a consequence of weathering, oxidation processes, chemical additives, and/or UV exposure (Rivas et al. 2020). These differences in characteristics can influence the 'bioreceptivity', or potential for a substrate to support colonisation of biological life, of material (Guillitte 1995, Sanmartín et al. 2021). While artificial materials inevitably cannot recreate all characteristics of natural materials, efforts are being taken to improve the bioreceptivity of artificial materials to achieve better ecological outcomes. Understanding the independent and interactive effects of characteristics of artificial materials on colonising biota is therefore an important to maximise the potential of artificial structures as habitat for native marine organisms.

Concrete is the most commonly used material in artificial structures (Bhattacharyya and Deb 2022) but has a more homogenous surface (Coombes et al. 2015) and higher surface alkalinity than rock (Sella and Perkol-Finkel 2015), and also leaches metals (McManus et al. 2018). Properties of concrete are, however, easily modified through additives to the concrete mix (Dennis et al. 2018, Dhir and Dyer 1996, Dunn et al. 2019), and/or adding fine scale microtexture (µm-mm scale) and larger scale topographic complexity (cm-scale) during the manufacturing process, which can benefit colonisation of target marine biota (Bishop et al. 2022, Coombes et al. 2015, Kosová et al. 2023, MacArthur et al. 2019). For example, the inclusion of pozzolans, recycled or natural materials like oyster shells in the concrete mix can provide positive settlement cues for larvae and reduce the environmental footprint of standard concrete (Anderson 1996, Dennis et al. 2018, Dunn et al. 2019). Efforts to improve the ecological value of marine infrastructure by incorporating ecological principles into their design (e.g. through the manipulation of properties of concrete) is known as ecological engineering (Bergen et al. 2001, Mitsch and Jorgensen 1989), though a diverse range of terminology exists (e.g. ecological enhancement (Naylor et al. 2012); for a range of terminology used see Morris et al. 2018).

The addition of topographic complexity (cm-scale) has been a major focus of past ecological engineering designs (Coombes et al. 2011; Coombes et al. 2015; Firth et al. 2014; Hall et al. 2019; MacArthur et al. 2019; Strain et al. 2018; Strain et al. 2021), because complex surfaces provide a diversity of microhabitats, which can influence the composition of sessile communities by reducing competitive interactions (Klein et al. 2011), providing refuge from predators and/or environmental stressors (Garrity 1984; Scyphers and Powers 2013), and/or by enhancing the diversity of niches available (McGuinness and Underwood 1986). Microtexture (changes to texture on the µm to mm-scale) can, however, be equally important as it is relevant to the scale of larvae or spores of marine organisms during settlement (Carve et al. 2019; Scardino et al. 2008). Microtexture is generally posited to increase the recruitment of sessile invertebrates by increasing the number of attachment points for a settling organism (Callow et al. 2002; Scardino et al. 2008) and by creating hydrodynamic conditions that help retain larvae (Walters et al. 1997). However, effects can vary with the size, shape and wettability of the microtexture, and the species colonising the surface (Carve et al. 2019; Scardino et al. 2008). While many past studies have tested the use of microtexture for its antifouling properties (see Carve et al. 2019 for a comprehensive review and list of microtexture scales tested), more recent studies have shown that specific microtexture designs can be used to increase the bioreceptivity of artificial structures to improve their ecological value, though this was often limited to the intertidal zone (see Supplementary Table). Additionally, field studies assessing the effects of microtexture (sub-mm scale) and topographic complexity (cm-scale) have shown that differences in the environmental context, such as differences in abiotic conditions, tidal rages, functional groups present, and local larval supply can further influence the effectiveness of interventions, highlighting the need for further investigations into what biotic and abiotic factors mediate these relationships (Coombes et al. 2015; MacArthur et al. 2019; Strain et al. 2021). Understanding the influence of microtexture across multiple sites that differ in the local species pool and environmental conditions will inform spatial considerations for designs.

In addition to microtexture, concrete can also be manipulated with oxides to control substrate colour (hue), which affects the intensity and quantity of light reflected (brightness). The settlement of early colonisers such as bacteria and diatoms, as well as dichromatic larvae and algal spores are influenced by

Table 1. Environmental setting at deployment sites.

Site	Direction	Exposure	Tidal range (m)
Townsville	NW	Sheltered	3.8 (Global Environmental Modeling Systems (GEMS)), 2007)
Sydney	SE	Sheltered	2.1 (Johnston et al. 2015)
Melbourne	NNE	Moderate	1 (Bird 2011)

colour, although they predominantly respond to brightness rather than hue (Callow and Callow 2000; Dobretsov et al. 2013; Ells et al. 2016; Fletcher and Callow 1992), as they display phototaxis, i.e. movement towards (positive) or away (negative) from light (Randel and Jékely 2016). Although several species are positively phototactic during the early phases of their larval stages, many become negatively phototactic during settlement, although this can vary across taxa (Thorson 1964). Lighter colours are more reflective and will therefore appear brighter, whilst darker colours absorb most of the light and will appear dull. Some species, such as barnacles, have more developed compound eyes and can also distinguish colours (Matsumura and Qian 2014). Consequently, communities can vary across substrates of different colour (Dobretsov et al. 2013; Satheesh and Wesley 2010; Saucedo et al. 2005; Su et al. 2007; Swain et al. 2006). This knowledge of colour responses, however, predominantly comes from short laboratory experiments (4-40 days) and it is unclear what effect colour has on community development over the longer term.

Effects of microtexture and colour may vary spatially and temporally according to variation in environmental conditions and the identity of key colonists. They are predicted to be greatest when there is bare substrate with which colonists can interact (Dayton 1971). Effects of microtexture and colour are also predicted to be greatest for small-bodied, phototactic species that respond to colour and fit within microtextures. Consequently, factors such as water temperature and day length, which determine the timing and rate of colonisation (Lord and Whitlatch 2015; O'Connor et al. 2007; Stachowicz et al. 2002) and the identity of key colonists (Sams and Keough 2012), may influence microtexture and colour effects. Effects of colour may also vary spatially and seasonally according to the intensity and duration of sunlight to illuminate surfaces. Testing manipulation of microtexture and brightness across a wide range of ecological and environmental ranges will help determine the universal applicability of these factors.

Here, the interactive effects of surface microtexture (using a single grooved design at the µm-scale) and substrate achromatic colour (hereafter referred to as 'colour') were manipulated in a fully orthogonal design that assessed their independent and interactive effects on colonising biota at three sites along the east coast of Australia. Because sessile invertebrates dominate the communities on artificial structures in the local area (Bracewell et al. 2017; Mayer-Pinto et al. 2018; Susick et al. 2020) greater recruitment to dark surfaces was expected. Greater overall recruitment was also expected onto textured surfaces, due to the increased number of attachment points. Therefore, the greatest cover of colonising biota was expected on textured dark surfaces, and lowest cover of sessile biota on smooth light surfaces. Overall, effects of brightness and microtexture were expected to be stronger in the tropics than at temperate sites, reflecting the longer day length and increased recruitment during deployment in Austral summer (and therefore shorter time over which substrate is bare) in the latter.

Methods

Experimental design

The experiment was conducted at three sites along the east coast of Australia, one tropical; Ross Creek near the Port of Townsville (Townsville, Queensland) (-19.26 'S, 146.82'E) and two temperate; Port Jackson Bay (Sydney, New South Wales) (-33.87'S, 151.2'E) and Port Phillip Bay (Melbourne, Victoria) (-37.86'S, 144.91'E). At each location, the experiment was conducted at a single site during Austral summer (9 – 15 December 2019 to 28 February– 4 March 2020) (Table 1).

This geographical range was selected to include ecological and environmental gradients known to influence patterns in the abundance and diversity of species. All sites were urban with adjacent hard substrates mainly comprising of seawalls, breakwaters, and pylons. Sites were selected based on availability and so that two stainless steel frames, containing tiles, could be hung vertically from the pontoon at a depth of 2 m, and not shaded by surrounding infrastructure or the pontoon itself. All pontoons were located in estuarine settings, but varied slightly in their direction and thus the orientation of settlement plates towards the sun, their exposure to wave action, and the extent of the tidal range (Table 1).

At each site, substrate colour (with 4 levels, 'white', 'grey' and 'black' tiles, as well as procedural control tiles with no oxides addition) and microtexture (with 2 levels, smooth and textured) were manipulated on concrete settlement tiles (150×150 mm) in a fully orthogonal design, totalling eight treatments, with 5 tiles per treatment. Thus, 40 tiles were deployed per site and 120 tiles across the three sites.

Colour was manipulated using a grey scale of "white", "grey" and "black" tiles to represent, light, medium and dark brightness intensities respectively, by adding oxides to an off-white cement base (Table S1, Figure S1). White tiles did not contain oxide, whilst grey and black coloured tiles were created by adding grey oxide and black oxide respectively. To test for any potential confounding effect of variation in oxide chemistry, additional control tiles were fabricated from a grey 'general purpose' cement base without oxide and compared to grey tiles with oxide (Table S1, Figure S1).

The microtexture on 'textured' tiles consisted of a series of rectangular ridges and depressions, running the length of the tile, with depressions 500 µm in width and depth (Figure S2, S3). This was the finest scale microtexture that could be fabricated using 3D printing but had a larger feature size than most sessile larvae/spores (Carve et al. 2019). The microtexturing was done during fabrication of the tiles by using a textured rubber mould created with a 3D resin laser printer. The smooth tiles were created using a mould without texture. Moulds were fabricated by Reef Design lab, and tiles manufactured by SVC Products.

At each site, five replicate tiles of each treatment were attached to two galvanised wire frames 2.4 m x 0.5 m in dimension using cable ties. Tiles were attached in two rows, 0.1 m apart on each frame, with microtextured surfaces oriented outwards and the ridges on the textured tile running vertically across textured tiles. Tiles for each treatment were evenly distributed between the two frames and two rows and the position in each row determined randomly. The frames were submersed at ~2 m depth from floating pontoons, such that the distance between the frames and water surface was unaffected by tides and tiles were submersed throughout the entire experiment. After three months of deployment, tiles were collected, removed from the frames and transported back to the laboratory in seawater. Care was taken to avoid damage or dislodgement of attached organisms.

Biological census

Each tile was placed under a dissection microscope to assess the abundance and diversity of sessile taxa on each tile (mobile species were not included). To assess the percent cover of sessile taxa, a 9×9 cm grid with 81 evenly spaced intersection points was placed over the centre of each tile (leaving a 3 cm border that was excluded from analysis to avoid any edge effects). The taxa under each of the 81 points was classified using a combination of functional group and morphology into 11 categories: algae; colonial and solitary ascidians; barnacles; bivalves; sabellid, spirorbid and serpulid polychaetes; unidentified worm tubes; solitary and encrusting sponges. Both dead and live organisms were censused. This 'high level' approach was chosen as previous studies assessing biofouling on artificial structures have found differences in community composition that were related to species morphology and physiology rather than identity (Holloway and Connell 2002; Irving and Connell 2002; Perkol-Finkel et al. 2008). If both primary (directly attached to the substrate) and secondary (growing on top of epibiota) cover were present, only primary cover was assessed, as this reflects responses to the factors manipulated and not the primary coloniser.

Brightness measurements

To evaluate if brightness is a possible mechanism by which colour and microtexture affect early settlement of colonising communities, the starting brightness of 5 tiles per treatment was measured using tiles that were fabricated in addition to the 120 tiles that were fabricated for deployment in the field. The initial brightness of these tiles was measured after a brief (24h) submersion in filtered seawater to clean them of any potential manufacturing residues and because brightness is influenced by water absorption. Light spectra of each tile were then measured with an Ocean Optics JAZ-EL200 with a PX Lamp. The spectrometer was set to have the light source running continuously in strobe mode, an integration time of 30 s, a boxcar value of 10 and an averaging value of 5 (Montgomerie et al. 2006). Black and white reference spectra were collected for calibration purposes. Spectra of five random points per tile were measured and brightness values (B2) for each tile were calculated by averaging the five resulting spectra and smoothing data to remove electrical noise arising from the spectrometer following Maia et al. (2013).

Statistical analysis

Brightness

Substrate brightness measurements were analysed using the 'pavo' package (Maia et al. 2013). To assess effects of colour and texture on brightness, a linear model was used. The model included the fixed factors colour (3 levels: 'black', 'grey' and 'white'), microtexture (2 levels: 'textured' and 'smooth') as well as an interaction term. A separate analysis, comparing grey tiles with oxides to grey controls, assessed effects of oxides on brightness, with the factors colour (2 levels: 'grey', 'control'), microtexture (2 levels: 'textured' and 'smooth') as well as an interaction term. Model residuals were visually inspected for normality and heteroscedasticity by plotting Pearson residuals against fitted values. Transformations of brightness data did not improve residual plots and therefore untransformed data were used and significance determined using a more conservative p-value of $\alpha < 0.01$. P-values were obtained using the Anova function (type III) in the R package 'car' (Fox et al. 2012). Tukey's post hoc pairwise comparisons in the R package 'emmeans' (Lenth et al. 2018) identified sources of significant (at $\alpha = 0.05$) treatment effects.

Biota

Total cover (dead and live organisms) and percent covers of taxonomic groups were compared between the different colour and microtexture treatments using generalised linear models in the package 'glmmTMB' (Magnusson et al. 2017). Only groupings with >5% cover in at least one treatment combination were analysed. Given dead tests (e.g. of barnacles) and empty tubes (e.g. polychaete or amphipod tubes) were of similar size of their live counterparts, they were counted in the cover as their mortality was likely caused by other factors, rather than anything related after their immediate settlement. Models included the fixed factors colour (3 levels: 'black', 'grey' and 'white'), microtexture (2 levels: 'textured' and 'smooth') and an interaction term. A unique row identifier (unique per data row) was added as a random factor to improve residual plots. Data were analysed separately for each site because of large spatial differences in the dominant space occupiers which otherwise dominated analyses. Artefacts of oxides on total cover of all organisms were assessed separately using analogous analyses to those for brightness measurements. Analyses of cover assumed a binomial family distribution. The total number of occurrences was 81, representing the total number of points assessed on the tile. P-values were obtained using the ANOVA function (type III) in the R package 'car' (Fox et al. 2012). If interactions were non-significant, an additive model was tested using the same ANOVA function (type II). To account for an inflated Type I error associated with doing multiple tests, p-values were adjusted using the p.adjust function and the method 'holm' using the R package '*stats*'. Tukey's post hoc test in the R package 'emmeans' (Lenth et al. 2018) was used to assess differences among groups of significant factors. Due to high amounts of sediments on some tiles in Sydney, 13 tiles (a mix of smooth and textured tiles) were excluded. Therefore, replicates in Sydney ranged between 3-4 tiles per treatment combination (Table S2). Non-significant trends were reported to allow for comparisons across sites.

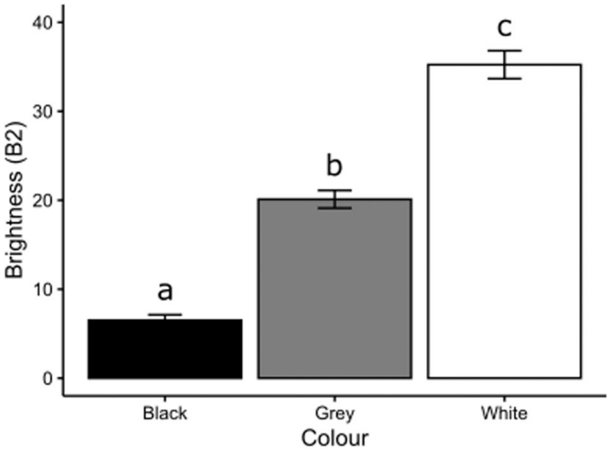

Figure 1. Mean (±SE) of brightness values (B2) of tiles of different (A) colours averaged across microtexture, and (B) microtexture averaged across colours. Different letters represent significant differences among colour treatments. Means were averaged across (A) microtexture and (B) colour treatments, resulting in $n = 10$ tiles per colour and n = −15 tiles per microtexture treatment.

All statistical analyses were undertaken using R (v 4.2.2).

Results

Brightness measurements

Overall, brightness (B2) was influenced by colour, but not microtexture (Figure 1, Table S3). White tiles were significantly brighter than grey tiles, which were in turn brighter than black tiles (Figure 1, Table S3). No difference in brightness was found between the grey (with grey oxide) and grey control (no oxide) tiles (Table S3).

Biological census

General

Despite being deployed for the same amount of time, tiles from the different sites had different amounts of colonisation. Bare space was greatest on Sydney tiles (mean ± SE = 53 ± 3.8%) followed by tiles from Townsville (mean ± SE = 13 ± 2.7%), whereas tiles in Melbourne had almost no bare space (mean ± SE =

0.4 ± 0.1%). There were also differences in the dominant taxa among sites. In Townsville, colonial ascidians (mean ± SE = 61.8 ± 3.6%) and sponges (mean ± SE = 10.9 ± 2%) were the most abundant taxa, whereas the major space occupiers in Sydney were serpulid polychaetes (mean ± SE = 21.6 ± 3%) and encrusting bryozoans (mean ± SE = 12.2 ± 2.1%). In Melbourne, barnacles occupied most space on tiles (mean ± SE = 78.6 ± 2.4%). Total cover did not vary between grey (with grey oxide) and grey control (no oxide) tiles (see Table S4). Thus, it is likely that any differences between the colour treatments were due to colour, and not artefacts of oxide chemistry.

At all sites, there was no interactive effect of colour and microtexture on the cover of any of the taxonomic groups analysed (see Table S5 for a list of groups analysed at each site). Therefore, only main effects of colour and microtexture from additive models are reported.

Townsville

In Townsville, there were no significant effects of substrate colour or microtexture on the four taxonomic groups examined (Table S6), but several trends were observed. The cover of serpulid polychaetes (*Hydroides* spp. and *Spirobranchus* spp.) tended to decrease from black to grey to white coloured tiles, whereas the opposite was true for encrusting sponges (*Mycale* spp.) (Figure S3, Tables S6). Serpulid polychaetes and encrusting sponges also appeared to be more abundant on textured than smooth tiles (Figure S3, Tables S6).

Sydney

In Sydney, the cover of spirorbid polychaetes varied with microtexture, with spirorbids having significantly greater cover on smooth than textured tiles, but there was no detectable effect of colour (Figure 2, Table S7). The total cover of algae, encrusting and aborescent bryozoans, as well as serpulid polychaetes did not significantly vary between colours or microtextures, but there was a trend of increasing cover of encrusting bryozoans with decreasing brightness of tiles (Figure S4, Tables S7). Algae were only found on smooth tiles, whereas arborescent bryozoans displayed a non-significant trend for being more abundant on textured than smooth tiles (Figure S4, Table S7).

Melbourne

In Melbourne, the cover of barnacles (*Amphibalanus variegatus*) and serpulid polychaetes (*Hydroides* spp.) varied with colour, but not microtexture (Figure 3, Tables S8). Pairwise comparisons revealed that barnacles occupied significantly less space on white than black tiles, whereas serpulid polychaetes occupied significantly more space on white than black and grey tiles (Figure 3, Tables S8). Colonial ascidians (*Diplosoma listerianum*) did not vary with colour or microtexture (Figure S5, Table S8).

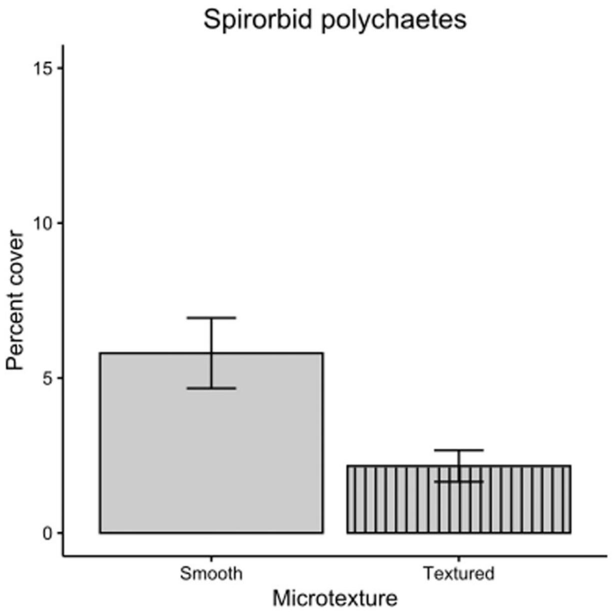

Figure 2. Mean (±SE) percent cover of spirorbid polychaetes on tiles of different microtexture in Sydney. Means were averaged across colour treatments, resulting in $n = 13$ (smooth) and $n = 12$ (textured) tiles per microtexture.

Discussion

This study demonstrated that colour and microtexture of artificial hard substrate independently influenced the settlement of certain taxonomic groups on shallow subtidal substrates, although the effect varied among sites and taxonomic groups. Recruitment patterns of serpulid and spirorbid polychaetes, barnacles and sponges changed with microtexture, and barnacles and serpulid polychaetes differed among colours, although the effects were not consistent among the three sites.

Taxon-specific effects of microtexture on cover may reflect differences in the match between their body size and shape and the type of micotexture provided (Carve et al. 2019). As in previous studies, serpulid polychaetes, dominated by *Hydroides elegans*, showed increased settlement to creviced compared to smooth surfaces (Walters et al. 1997). The long tubes of serpulid polychaetes are able to fit within the crevices and the greater recruitment of these and morphologically plastic sponges to textured surfaces may reflect hydrodynamic effects of the textured surface on colonisation (Carve et al. 2019). By contrast,

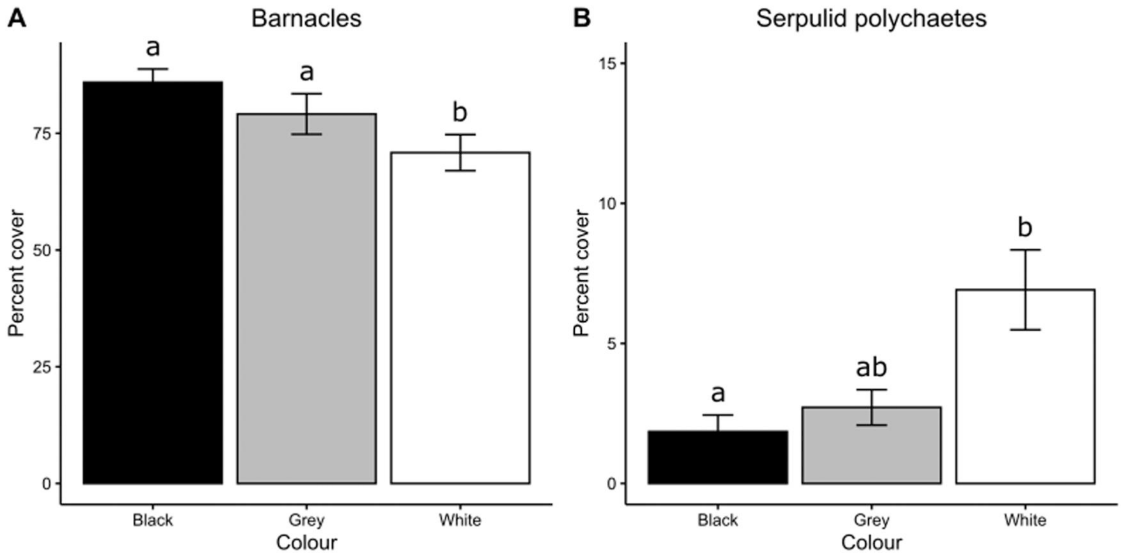

Figure 3. Mean (±SE) percent cover of (A) barnacles and (B) serpulid polychaetes on tiles of different colour in Melbourne. Means were averaged across microtexture treatments, resulting in $n = 10$ tiles per colour treatment. Different letters indicate significant differences among colours. Note the different y-axis scales.

spirorbid polychaetes and barnacles were negatively affected by texture. Within crevices, lateral growth of broad-based spirorbid polychaetes and barnacles may be inhibited, and outside of these adhesion may be limited by the microfeatures (Andersson et al. 1999; Berntsson et al. 2000a; Berntsson et al. 2004; Berntsson et al. 2000b). Lower barnacle recruitment on textured surfaces is in alignment with some, but not all previous studies, which may be related to the profile types and height of the structure chosen here, and the size of the colonising cyprid. For example, Coombes et al. (2015) showed that barnacle recruitment was greater on tiles with a mm-scale textured surface, whereas Berntsson et al. 2000b) found a decrease in barnacle recruitment on textured surfaces at µm-scale compared to smooth surfaces. The size of the microtexture used in this study was slightly smaller than cyprids of *Amphibalanus variegatus* (Wong et al. 2014), the most abundant barnacle in this study, which may have prevented it from recruiting within the features. Multiple scales of microtexture are likely to suit a greater range of target species and may further enhance colonisation (Kosová et al. 2023).

Colour had significant effects on settlement patterns of serpulid polychaetes and barnacles at some sites, and trends were also found for encrusting bryozoans and colonial ascidians. Barnacles and enrcusting bryzoans were generally most abundant on black tiles, consistent with a negative phototactic response (Dobretsov et al. 2013, Ells et al. 2016, Satheesh and Wesley 2010, Thorson 1964). Serpulid polychaetes and colonial ascidians were, by contrast more abundant on white tiles. The inverse pattern of serpulids and coloial ascideans to barnacles and bryzoans may reflect positive phototaxis. Other serpulid species, *Hydroides norvegicus* and *Pomatoceros triqueter*, are photopositive or neutral during the settlement phase (as reviewed in Thorson 1964). Alternatively, the greater abundances of serpulids and colonial ascideans on the white panels may reflect the outcome of competition for space with barnacles, which recruited strongly to black panels. The contrasting pattern in other studies of greater ascidean recruitment to darker surfaces (Ells et al. 2016, Thorson 1964) suggests that competition likely contributed to patterns here.

There was considerable variation in the response of individual taxa among the three sites, though not in the way expected. Contrary to expectations that effects would weaken with latitude, stronger effects were seen at Sydney and Melbourne than Townsville and did not directly relate to spatial variation in the availability of bare space. Instead, spatial variation in key colonists and specific competitive interactions may be influencing effects (Lord 2017). Sessile marine invertebrates are typically characterised by high temporal and spatial variability in recruitment in response to local conditions (e.g. food availability, temperature (Coma et al. 2000) and hydrodynamics (Connolly et al. 2001). Varability in these factors can lead to variation in the abundance and type of organisms recruiting at any one time (Sams and Keough 2012). Here, serpulid polychaetes tended to be more abundant on darker tiles in Sydney and Townsville, where bare space was most abundant and competition for space low. In Melbourne, where *Amphibalanus variegatus* barnacles covered >74% of black tiles, serpulids displayed the reverse colour response, with greater cover on white tiles. This suggests that competition rather than settlement cues of microtexture and colour could explain the patterns observed in Melbourne. Consideration of microtexture and brightness effects at additional sites, representing a range of environmental and biotic conditions, may help to illucidate key sources of variation.

The 3-months deployment period allowed for large cover or primary space occupiers, with only little secondary growth. Deployment length is an important factor that can influence the outcome of experimental studies. Competition increases with increasing deployment time as space on recruitment tiles becomes limited, and factors associated with the substrate become less important (Dodds et al. 2022). Additionally, communities undergo succession, by which slower growing species replace fast growing opportunistic species over time (Chalmer 1982). Additionally, some species provide habitat themselves and are overgrown by other species (Russ 1982), reducing the effects of microtexture and colour of primary substrate. Therefore, a longer deployment time could have led to different results.

This study considered effects of colour and sub-mm-microtexture over a 3-month period on macrofouling organisms only. Previous studies have shown that colour and microtexture can also affect the formation of biofilms (Dobretsov et al. 2013, Nanduru et al. 2021), which can modulate subsequent settlement of some but not all macrofouling organisms (Dobretsov and Rittschof 2020, Hadfield 2011, Wieczorek and Todd 1998). Similarly, mobile species can alter recruitment and succession of colonising biota through grazing and/or predation (Anderson and Underwood 1997). These factors should be considered in future studies to determine their influence.

The results of this study suggest that colour and microtexture influence the recruitment of sessile marine invertebrates, but that these effects can vary spatially and among taxonomic groups, which is in line with growing body of evidence that design interventions for the purpose of ecological engineering should be matched to the local environmental context and species pool and not blindly applied across spatial scales (O'Shaughnessy et al. 2021, Strain et al. 2021). Therefore, to determine the suitability of microtexture and colour for new marine infrastructure, baseline surveys should be conducted at the proposed construction site to select the appropriate design for the species or functional groups to be targeted. However, any effects are likely to be limited to early stages of recruitment, as other factors, such as competitive interactions, become more important with time as primary space becomes limited. Testing whether primary colonisers responding to microtexture and brightness affect subsequent secondary colonisers are needed to test the long-term trajectory of communities on artificial habitats with varying colour and microtexture and can help inform the design of ecologically beneficial port infrastructure. Finally, it is important to note that the current study has only tested the effects of micortexture and colour in the subtidal. Colour in particular influences heat absorption of the surface (Kordas et al. 2015), which can cause further thermal stress to intertidal species, some of which are already living close to their thermal limits (Somero 2010). Further field experiments are required to test the suitability of the independent and interactive effects of microtexture and colour on intertidal surfaces of marine infrasrtucture across spatial scales.

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Data availability statement

Data are available upon request.

Supplemental material

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