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The implications of artificial substrate material type for sessile fouling communities along the South African east coast

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Introduction: The growing blue economy and rapid development and urbanisation of coastal areas drive an increase in marine infrastructures. These structures are built with artificial materials and the submerged parts thereof become substrates for colonisation by fouling biota which are often dominated by invasive alien species. However, knowledge on the ecological implications of artificial substrate material for marine biota remains limited, with a notable research gap with respect to Africa.

Methods: This field study assessed how artificial substrate material type might influence sessile fouling communities along the South African east coast. Fiberglass, High-Density Polyethylene (HDPE) and Polyvinyl Chloride (PVC) panels were used as artificial substrates for biofouling community settlement over a period of three months.

Results: Differences in artificial substrate material type influenced sessile fouling community structure, with fiberglass panels showing a dominant effect than the other two types of materials. Fiberglass panels also supported higher species diversity and percentage cover than the HDPE and PVC panels. Notably, no significant effect of species status (invasive and native) was detected on overall percentage cover.

Discussion: These results highlight the dominant influence of fiberglass materials on sessile assemblages. Overall, this study suggests that the type of material used in artificial marine structures may have ecological implications and therefore, should be included as an important consideration in material selection criteria.

KEYWORDS

biofouling, artificial substrate material, community ecology, marine invertebrates, marine structures, South Africa

1 Introduction

The growing blue economy, urbanisation and increasing human population in coastal areas drive the proliferation of man-made infrastructures in marine environments (Dafforn et al., 2015; Firth et al., 2016a; Dodds et al., 2022). These structures can include seawalls, docks or jetties, buoys, marinas, ports, and/or ripraps or breakwaters made of artificial materials such as concrete, plastics or metals (Sempere-Valverde et al., 2018). With the growing population and related activities, artificial infrastructure is rapidly destroying and fragmenting natural habitats (Bishop et al., 2017), but also providing surfaces for colonisation by distinct marine assemblages (Mayer-Pinto et al., 2017). These changes could alter the connectivity of the seascape at local to regional scales, and ultimately, impair the structure and functioning of marine ecosystems (Bulleri and Chapman, 2010; Mayer-Pinto et al., 2018; Porter et al., 2018).

The literature on the ecological implications of artificial and natural structures show that benthic communities that recruit and develop on artificial substrata are different from those on nearby natural reefs, often displaying relatively lower coverage, species richness and diversity (Moschella et al., 2005; Tyrrell and Byers, 2007; Pister, 2009; Bulleri and Chapman, 2010; Sedano et al., 2019; Dodds et al., 2022). This is because substrates built from artificial materials commonly differ from natural substrata in terms of colour (Lathlean and Minchinton, 2012; Dobretsov et al., 2013; Ells et al., 2016), surface chemistry (Anderson, 1996; Sella and Perkol Finkel, 2015), chemical composition and physical properties such as microtexture and porosity (Bulleri and Chapman, 2010; Terlizzi and Faimali, 2010; Loke and Todd, 2016). For example, artificial substrate materials made from concrete, depending on its composition, could have a higher pH than seawater (Perkol-Finkel and Sella, 2014). Certain concrete formulations can leach heavy metals into the surrounding water column (McManus et al., 2018). Moreover, concrete substrate types are less heterogenous in microtexture than wood and natural rock (Coombes et al., 2015). All these factors could have implications for colonising marine biota by influencing species richness and abundance and ultimately, altering community structure (Hsiung et al., 2020; Dodds et al., 2022; Grasselli et al., 2024). Recently, there has been considerable interest in biocompatible concretes, which aim to reduce environmental impact and enhance sustainability (Gowell et al., 2015; Chlayon et al., 2018; Pioch et al., 2018; Hayek et al., 2022). This area is growing rapidly and represents a significant commercial and research focus (Gowell et al., 2015; Chlayon et al., 2018; Pioch et al., 2018; Hayek et al., 2022). Besides concrete, artificial structures as substrate types are generally less likely to offer refuge from adverse abiotic and biotic conditions compared to natural substrates (Firth et al., 2013; Loke et al., 2015), especially in intertidal environments (Ostalé-Valriberas et al., 2018). Therefore, there is a need to comprehensively investigate and understand the implications of structures made from artificial materials for marine biota to contribute data towards exploring avenues for adopting infrastructures with less ecological impacts.

Studies use different types of man-made materials to investigate the influence of artificial substrata on marine biota. These often include acrylic, High-Density Polyethylene (HDPE), Polyvinyl Chloride (PVC), fiberglass, steel, rubber, metal and concrete (Dodds et al., 2022; Grasselli et al., 2024). While most of these materials are used to construct marine infrastructures, concrete is by far the most ubiquitous (Bhattacharyya and Deb, 2022). Moreover, fiberglass and steel are also commonly used to construct small boats and recreational yachts (Sakinah et al., 2023; Ciocan et al., 2024) while concrete, acrylic, HDPE and PVC are widely used as artificial substrates in biofouling studies (Tyrrell and Byers, 2007; Dobretsov, 2015; Chase et al., 2016; Pinochet et al., 2020; Loureiro et al., 2021a; Dodds et al., 2022; Jewett et al., 2022; Grasselli et al., 2024).

Because artificial substrates are constructed from different types of materials as highlighted above, they exhibit differences in physico-chemical properties, which influence marine biota. Varying substratum characteristics include differences in material type, roughness, wettability (water adsorption to surface), thermal capacity or colour (Harlin and Lindbergh, 1977; Jones and Boulding, 1999; Osborn, 2005; Finlay et al., 2008; Coombes, 2011; Firth et al., 2016b; Sempere-Valverde et al., 2018; Grasselli et al., 2024). In terms of artificial material type, composite substrates such as fiberglass and concrete have higher wettability which could allow higher settlement of biota (Dugan et al., 2012; Dyer, 2014; Hsiung et al., 2020; Rubino et al., 2020) when compared to hydrophobic polymeric materials with low wettability including HDPE and PVC (Encinas et al., 2010; Dhandapani et al., 2024). Complex micro-topographies in rough artificial substrates enhance the turbulence of water near the surface, which in turn increases larvae transport to the substratum (Koehl, 2007). This results in higher spore and larval settlement on rough than smooth substrata (Koehl, 2007; Sempere-Valverde et al., 2018). Moreover, elevated surface water retention due to holes and crevices on rough substrates provide cool temperature conditions, lessening the likelihood of desiccation during low tides (Jones and Boulding, 1999; Coombes, 2011; Firth et al., 2016b). Finally, some studies on artificial substratum colour have shown a dominant effect of brightness on ascidian settlement densities (Ells et al., 2016), while others have reported higher densities of biofouling on black than white panels (Swain et al., 2006; Dobretsov et al., 2013; Nall et al., 2022) or no effect of colour on marine invertebrate larval settlement (Schaefer et al., 2024), thereby highlighting context dependency in terms of the effect of colour.

Of marine biota, sessile fouling communities, including algae and basibionts, and often dominated by invasive alien species, are particularly more likely to be influenced by varying artificial substrate types than vagile taxa (Grasselli et al., 2024). This is because the selection of microhabitat by sessile organisms is almost irreversible after metamorphosis, which influences post-settlement community composition (Osborn, 2003). Indeed, studies show that differences in artificial substrate types and overall substratum characteristics can alter fouling community structure by affecting diversity and species abundance (Anderson and Underwood, 1994; Tyrrell and Byers, 2007; Albano and Obenat, 2019; Muthukrishnan et al., 2019) but see Hartanto et al. (2022) who found no effect on macrofaunal species richness, total abundance and community composition. Effects can occur from the initial colonisation of fouling organisms to the development of communities over time (Anderson and Underwood, 1994; Albano and Obenat, 2019). As such, the measure of the density of artificial structures, coupled with their properties, over a gradient of human coastal modification can be used as a predictor for the abundance of species and fouling community diversity (Susick et al., 2020). However, in most regions of the world information about the effects of variable artificial substrates on fouling communities remains limited, particularly in Africa.

In South Africa, the distribution and abundance of fouling taxa along the coast have been assessed, with communities dominated by invasive alien species in harbours and marinas (Peters et al., 2014, 2017, 2019; Loureiro et al., 2021a). These fouling communities are regulated by light and predation (Loureiro et al., 2021b) and are vulnerable to cooling temperatures and ocean acidification (Matikinca and Robinson, 2024a). Moreover, fouling taxa from this coast also show limited tolerance to decreasing pH at different life stages under cooling and restricted food supply conditions (Matikinca and Robinson, 2024b). On the substrate materials side, fiberglass is a dominant material in small boats and recreational yachts, which are important regional vectors for the transfer of alien fouling species in South Africa (Peters et al., 2017, 2019). On the other hand, HDPE is one of the most abundant plastic materials in South Africa's coastal waters and its buoyancy is known to be affected by biofouling (Fazey and Ryan, 2016; Ryan, 2020). Lastly, PVC is a common artificial substrate that has been used by various studies on biofouling dynamics along the South African coast (Peters et al., 2014, 2017, 2019; Loureiro et al., 2021a; Matikinca and Robinson, 2024a). However, notwithstanding the above, no research has considered how these different artificial substrates might simultaneously influence sessile fouling communities along this coast. Previous studies in South Africa have only used PVC panels to collect or monitor biofouling communities. Whether and how assemblages on these panels might compare with those on other artificial substrates, such as fiberglass and HDPE, remains unexplored.

This field study experimentally investigated the implications of artificial substrate material type for sessile fouling community dynamics along the South African east coast. Using fiberglass, HDPE and PVC panels, we tested the hypothesis that differences in artificial substrate material type would influence sessile fouling assemblages by altering community structure and species diversity. Due to the differences in physico-chemical properties of the three

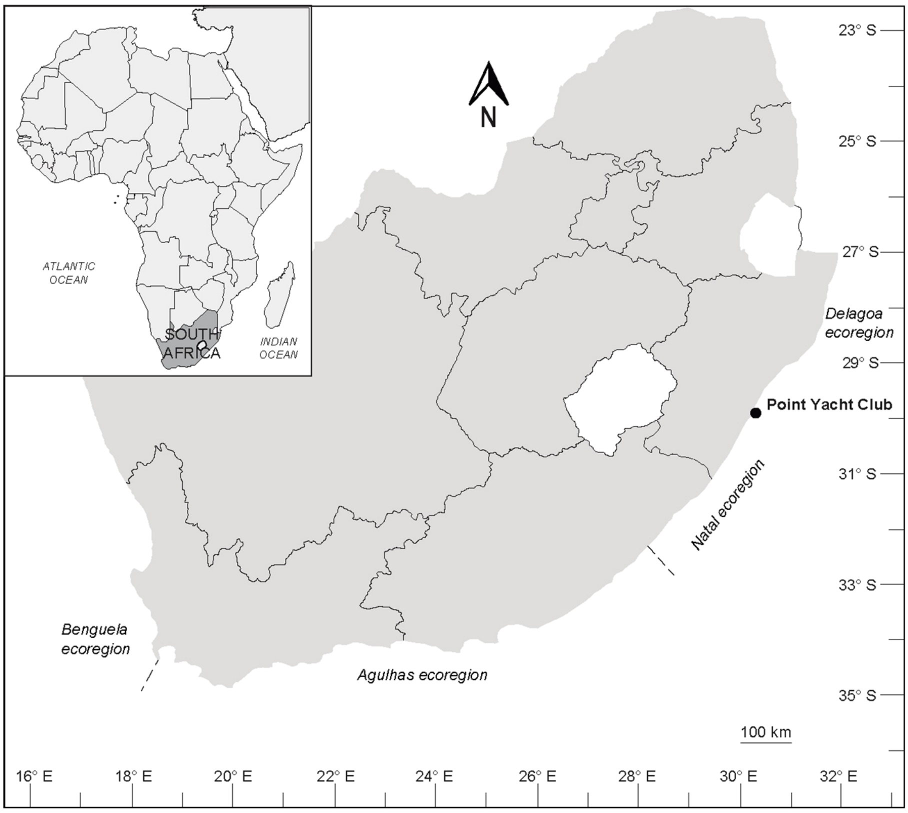

FIGURE 1
Map of the study site along the South African east coast where experimental arrays were deployed to monitor fouling communities. The map was adopted and edited with permission from Loureiro et al. (2021a).

substrate material types, we predicted that fiberglass panels might show a dominant influence on sessile fouling community composition than HDPE and PVC panels.

2 Materials and methods

2.1 Data collection

The study was conducted at Point Yacht Club (29°51’48” S, 31° 01’27” E) on the east coast of South Africa (Figure 1). During the austral Spring of 2023, nine experimental arrays with a total of 27 panels were deployed from floating jetties for three months (September – November) in the marina to collect fouling assemblages. Each array was assembled by fixing three panels (15 x 15 x 0.25 cm) (one fiberglass, one HDPE, and one PVC) perpendicular to a rope and suspended at a depth of 2 m below the water surface (Figure 2). This depth was chosen such that the distance between the panels and water surface was unaffected by tides (Schaefer et al., 2024) and is within the depth range covered by biofouling studies along the South African coast (Peters et al., 2017; Robinson et al., 2017; Loureiro et al., 2021a, b). As the jetties were floating structures, depth remained constant (Loureiro et al., 2021b). Moreover, all arrays were weighted to stabilise the panels and prevent them from posing a safety risk to vessels (Loureiro et al., 2021a). In South Africa, sessile fouling organisms grow facing downward on the underside of the panels (Peters et al., 2017; Robinson et al., 2017; Loureiro et al., 2021a, b). Therefore, the orientation of the panels used in this study followed the same methods as previous studies in this region (Peters et al., 2017; Robinson et al., 2017; Loureiro et al., 2021a, b). This orientation has also been used by studies from other regions such that the experimental surface faces downward parallel to the seafloor to mimic floating jetties (Crooks et al., 2011; Marraffini et al., 2017; Jewett et al., 2022). The panels were randomly attached to a Tremnet/plastic net on each array (Chase et al., 2015) to ensure that they remained in the same position relative to one another. A distance of at least 2 m was maintained between the arrays. Before the experiment, the panels were sanded and soaked in distilled water for 10 days to allow chemicals to leach (Loureiro et al., 2021a).

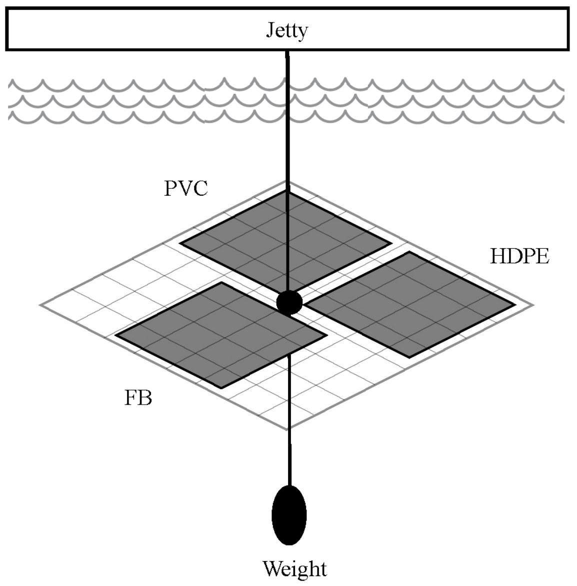

FIGURE 2
Schematic illustration of the experimental setup to monitor fouling biota using fiberglass (FB), High-Density Polyethylene (HDPE) and Polyvinyl Chloride (PVC) panels. not drawn to scale.

2.2 Quantifying sessile community structure

The underside of the panels was photographed using a Canon PowerShot G7 X Mark III camera at the end of the experiment. The identification of specimens was made from the photographs. Specimens whose identification was uncertain were preserved and returned to the laboratory for microscopic analysis. Identifications were carried out to the lowest taxonomic level possible using Darwin (1854); Day (1967); Monniot et al. (2001); Smith and Gordon (2011) and Rocha et al. (2012). Community composition of sessile assemblages was quantified in terms of percentage cover and assessed using 100-point counts generated by overlaying a standardized grid onto the photographs.

2.3 Statistical analyses

A PERMANOVA was conducted to assess the influence of substrate material type on sessile fouling community structure. A square root transformation was applied to the non-standardized data to decrease the influence of the dominant species (Clarke and Warwick, 2001) and all multivariate analyses were underpinned by Bray-Curtis similarities (Bray and Curtis, 1957; Clarke and Warwick, 2001). PERMANOVA routines were based on 9999 permutations and a type III sum of squares. PERMDISP, based on the average distance from the centroid, was used to assess dispersion among the panels within treatments. A SIMPER analysis (with a cut-off of 90%) was performed to identify the species responsible for dissimilarities detected in community structure. All multivariate community analyses were conducted using PRIMER 6.0 (Clarke and Gorley, 2006; Anderson et al., 2008).

All univariate analyses were conducted using R version 4.4.0 (R Core Team, 2021). Before the analyses, the data were assessed for normality and homogeneity of variances using Shapiro-Wilk and Levene’s tests, respectively (Levene, 1960; Shapiro and Wilk, 1965). A Kruskal-Wallis test was used to assess the influence of substrate material type on the abundance of species responsible for the dissimilarities in community structure (Kruskal and Wallis, 1952). The Shannon-Wiener diversity index (H’) which includes both species richness and evenness (Clarke and Warwick, 1994), was used to assess the effect of substrate material type on diversity through the Kruskal-Wallis test. Likewise, the influence of substrate material type on species richness was also evaluated using the Kruskal-Wallis test. All pairwise comparisons for the Kruskal-Wallis analyses were conducted using Dunn’s test based on the

Bonferroni adjustment method (Dunn, 1961, 1964). Finally, generalized least squares models (GLS) were conducted using the nlme package (Pinheiro and Bates, 2000) to assess the effect of substrate material type and species status (i.e. invasive and native) on the overall percentage cover.

3 Results

A total of seven sessile taxa were identified on the settlement panels (Table 1). The sessile assemblage composition of fouling significantly differed according to the substrate material type (PERMANOVA: $F = 7.40$, $P < 0.001$; Figure 3). Sessile assemblages on High-Density Polyethylene (HDPE) and Polyvinyl Chloride (PVC) panels differed from those on fiberglass panels (HDPE vs fiberglass: $t = 3.27$, $P < 0.001$; PVC vs fiberglass: $t = 3.42$, $P < 0.001$). No significant differences were detected in community structure between HDPE and PVC panels ($t = 1.00$, $P = 0.40$). The differences observed between assemblages on the different materials were not caused by differences in dispersion (PERMDISP: $F = 1.78$, $P = 0.19$).

The SIMPER analysis showed that the differences detected between the types of substrate material were driven by the invasive ascidians *Diplosoma listerianum*, *Styela plicata*, the invasive bryozoans *Watersipora subtorquata*, *Bugula neritina*, the native bryozoan *Menipea triseriata*, the native barnacle *Amphibalanus amphitrite*, and the native polychaete *Spirorbis* sp. (Table 2). These species contributed 42% dissimilarity between PVC and fiberglass communities, 38% between HDPE and fiberglass, and 29% between PVC and HDPE. All these species differed significantly in percentage cover among the different types of substrate material except for *W. subtorquata* (Figure 4; Tables 3, 4). They displayed higher abundance on fiberglass panels than on the other two material types ($P < 0.05$). No significant differences in percentage cover were detected between HDPE and PVC panels for any of the species except for *S. plicata*, which showed a significantly higher abundance on PVC than HDPE panels ($P < 0.05$).

The overall percentage cover was influenced by substrate material type only, with no significant effect of species status (invasive and native) (Figure 5; Table 5). Fiberglass panels supported higher overall percentage cover than HDPE and PVC panels (fiberglass vs HDPE: $P = 0.005$; fiberglass vs PVC: $P = 0.010$). No significant differences in percentage cover were observed between HDPE and PVC panels ($P = 0.828$). Notably, no significant interactions were found between substrate material type and species status.

While no effect of treatment was detected on species richness, species diversity (Shannon-Wiener index) differed significantly between the different types of substrate material (Figure 6; Table 6). Fiberglass panels supported higher species diversity than the other two types of materials (fiberglass vs HDPE: $P = 0.002$; fiberglass vs PVC: $P = 0.022$). No significant differences in diversity were detected between HDPE and PVC panels ($P = 1.00$).

TABLE 1 Species recorded at Point Yacht Club on High-Density Polyethylene (HDPE), Polyvinyl Chloride (PVC), and fiberglass panels.

Taxa	Status	HDPE	PVC	Fiberglass
ANNELIDA				
Polychaeta				
Spirorbis sp. (Daudin, 1800)	Native	X	X	X
CRUSTACEA				
Cirripedia				
Amphibalanus amphitrite (Darwin, 1854)	Native			X
BRYOZOA				
Bugula neritina (Linnaeus, 1758)	Invasive	X	X	X
Menipea triseriata (Busk, 1852)	Native	X	X	X
Watersipora subtorquata (d'Orbigny, 1852)	Invasive	X	X	X
CHORDATA				
Ascidiacea				
Diplosoma listerianum (Milne Edwards, 1841)	Invasive	X	X	X
Styela plicata (Lesueur, 1823)	Invasive	X	X	X

Status of species assigned following Robinson et al. (2016).

4 Discussion

Although fouling communities are well-studied and commonly used as model systems in community ecology (Needles and Wendt, 2013; Robinson et al., 2017), the understanding of how they might be influenced by substrate material remains limited. This study suggests that substrate material type has an influence on the sessile assemblage of fouling communities. Overall, fiberglass appears to have a dominant influence on these assemblages than hydrophobic substrate material types.

As hypothesised, artificial substrate material type influenced community structure and altered diversity in sessile fouling assemblages. At the community level, these changes can be attributed to the differential responses of species within the community to different substrate material types with varying physico-chemical properties. For example, in the present study *Watersipora subtorquata*, *Bugula neritina*, *Spirorbis* and *Diplosoma listerianum* showed high abundance across the experimental panels while the low occurrence of *Styela plicata* and *Amphibalanus amphitrite* was noted. These results align with previous research which shows that benthic invertebrate communities are influenced by the type of substrate material they settle on (Tyrrell and Byers, 2007; Dobretsov, 2015; Giangrande et al., 2021; Dodds et al., 2022; Grasselli et al., 2024). For example, recent meta-analyses reported differences in biofouling between artificial and natural substrate materials (Dodds et al., 2022; Grasselli et al., 2024). In Muscat, Sultanate of Oman, biofouling communities structurally differed on different artificial substrates in

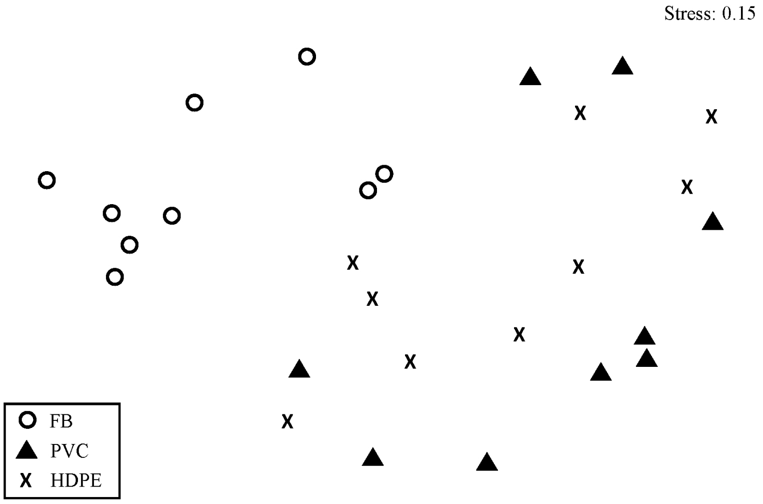

FIGURE 3
Two-dimensional multidimensional scaling plot based on standardised square root-transformed percentage cover of fouling communities at Point Yacht Club on the east coast of South Africa. The different symbols represent artificial substrate material types including High-Density Polyethylene (HDPE), Polyvinyl Chloride (PVC) and fiberglass (FB) panels.

two marinas (Dobretsov, 2015; Muthukrishnan et al., 2019). In Port Pendennis Marina, Falmouth, surface heterogeneity, orientation and chemical composition of subtidal artificial substrates were found to influence benthic biological community recruitment patterns across temporal scales (Hanlon et al., 2018). Overall, the above studies, together with the findings of the present study, suggest that the type of material used in constructing artificial marine structures and their ecological implications should be included as important aspects of material selection criteria.

Following biofouling studies from South Africa (Peters et al., 2017; Robinson et al., 2017; Loureiro et al., 2021a, 2021b) and other regions (Crooks et al., 2011; Marraffini et al., 2017; Jewett et al., 2022), the present study mimicked floating jetties by deploying the substrate panels in a horizontal orientation with the experimental surface facing downward parallel to the seafloor. With this orientation, organic matter collects on the top side of the panels. Therefore, since we analysed the underside of the panels where fouling organisms grow in South Africa (Peters et al., 2017; Robinson et al., 2017; Loureiro et al., 2021a, b), the influence of organic matter on the colonisation of biota was likely negligible. However, much more work is needed to develop a holistic understanding of the implications of different substrate orientations (i.e. horizontal vs vertical) and deposition of organic matter for the colonisation of biofouling communities along the South African coast.

Fiberglass panels, more than High-Density Polyethylene (HDPE) and Polyvinyl Chloride (PVC) panels, supported higher species diversity and percentage cover. This may be due to differences in structural properties such as the physico-chemical composition of these artificial substrates (Wieczorek and Todd, 1998). Fiberglass is a composite substrate material with higher wettability than HDPE and PVC which are hydrophobic polymeric materials (Encinas et al., 2010). Hydrophilic substrates, more than their hydrophobic counterparts, favour the settlement and attachment of fouling organisms (Roberts et al., 1991; Becker, 1993; Sudhakar et al., 2008; Kumar et al., 2014; Muthukrishnan et al., 2019), which explains the higher values of species diversity and percentage cover on fiberglass panels observed in the present study. On the other hand, hydrophobic substrates have a less potential to be colonised because they exhibit low surface energy, which reduces adhesion strength of fouling organisms, making them easily removable from the surface (Callow and Fletcher, 1994; Liu et al., 2022; Romeu and Mergulhão, 2023). Our findings align with previous work which has also found that hydrophobic polymeric substrates generally support lower abundances of fouling organisms than hydrophilic surfaces (Muthukrishnan et al., 2019; Dodds et al., 2022). For example, surface hydrophobicity has been found to exhibit an antifouling effect, which delays the development of biota in the initial stages of biofouling (Cho et al., 2013). Studies have reported an increase in the settlement and attachment of fouling biota such as barnacles and polychaetes on wood and steel, which are hydrophilic, than on polyethylene terephthalate (PET) and polyethylene (PE) surfaces, which are hydrophobic substrates (Roberts et al., 1991; Becker, 1993; Sudhakar et al., 2008; Kumar et al., 2014). A similar pattern was observed for micro-and macrofouling organisms on the same set of substrates (steel, wood, PET and PE) in two locations in Muscat, Oman (Muthukrishnan et al., 2019). It is, however, important to also highlight that some biota are still able to settle on substrate materials with low wettability and may benefit from reduced competition for space (Rittschof and Costlow, 1989; Dodds et al., 2022). For example, a laboratory study on the influence of substrate material on ascidian larval settlement showed that *Ciona intestinalis* (Linnaeus, 1767) and *Botrylloides violaceus* (Oka, 1927) exhibit species-specific settlement preferences, with more individuals settling on HDPE than PVC panels in the absence of competition (Chase et al., 2016). Similarly, another study reported preference of *Bugulina flabellata* (Thompson in Gray, 1848) and *B. neritina* larvae for plastic substrate materials with low wettability rather than settling on wood or concrete

TABLE 2 Results of SIMPER analyses based on Bray–Curtis dissimilarity of square root transformed species percentage cover (%C) among artificial substrate material types including High-Density Polyethylene (HDPE), Polyvinyl Chloride (PVC) and fiberglass panels.

Species	Average %C	Average %C	Contribution (%)	Cumulative contribution (%)
	Fiberglass	PVC		
Average dissimilarity between treatments: 42%				
D. listerianum	3.86	1.69	24.12	24.12
A. amphitrite	1.87	0.00	15.75	39.87
Spirorbis sp.	3.83	2.16	14.31	54.18
M. triseriata	2.07	0.58	14.27	68.45
B. neritina	3.21	1.63	12.72	81.17
W. subtorquata	3.31	2.74	12.37	93.54
	Fiberglass	HDPE		
Average dissimilarity between treatments: 38%				
D. listerianum	3.86	2.06	22.65	22.65
A. amphitrite	1.87	0.00	17.45	40.1
Spirorbis sp.	3.83	2.13	15.83	55.93
M. triseriata	2.07	0.76	15.17	71.1
B. neritina	3.21	1.76	14.04	85.14
W. subtorquata	3.31	2.67	13.21	98.35
	PVC	HDPE		
Average dissimilarity between treatments: 29%				
D. listerianum	1.69	2.06	36.69	36.69
W. subtorquata	2.74	2.67	16.03	52.72
M. triseriata	0.58	0.76	13.97	66.69
S. plicata	0.71	0.00	12.66	79.35
Spirorbis sp.	2.16	2.13	11.09	90.43

substrates (Pinochet et al., 2020). These contrasting findings may be due to differential species-specific responses to substrate material type, different life stages (e.g. larvae, juveniles and adults), different community stages (e.g. micro-and macrofouling communities) and different study designs (e.g. laboratory vs field experiments). This highlights context dependency of biofouling colonisation on substrate material types, which precludes the use of a generic model in understanding fouling dynamics on artificial marine structures. Therefore, there is a need to expand foundational studies on the influence of substrate material on the colonisation of fouling biota as the present knowledge does not enable generalizations to be drawn.

Species richness did not significantly differ between substrate material types. This could be due to the low number of identified species on the panels. Probably, these species can colonise substrates regardless of the material, and/or adapt to the different features of each material. Moreover, these species could be displaying a great colonisation potential, allowing them to displace other competitors during the colonisation process over the three months-period covered in this study. Indeed, previous work has shown that fouling communities that have developed over a relatively short period, such as those in the present study, are generally dominated by few opportunistic species that may be outcompeted over longer time periods and sometimes replaced with more species-rich communities (Hanlon et al., 2018; Dodds et al., 2022). Our findings align with previous studies that show that substrate material type does not influence the number of species in sessile fouling communities (Tyrrell and Byers, 2007; Dodds et al., 2022; Hartanto et al., 2022; Kosová et al., 2023). For example, a study in Australia found that fiberglass and aluminium panels had a similar number of species after 4 months of submersion (Anderson and Underwood, 1994). Similarly, multiple studies comparing the effect of rock and concrete have reported no significant differences in species richness among the two types of substrates (Cacabelos et al., 2016; Hartanto et al., 2022; Kosová et al., 2023). In Wells, Maine USA, natural substrate types (i.e. shell, marble, slate, and wood) and artificial substrates (i.e. aluminium sheet metal, Styrofoam, PVC,

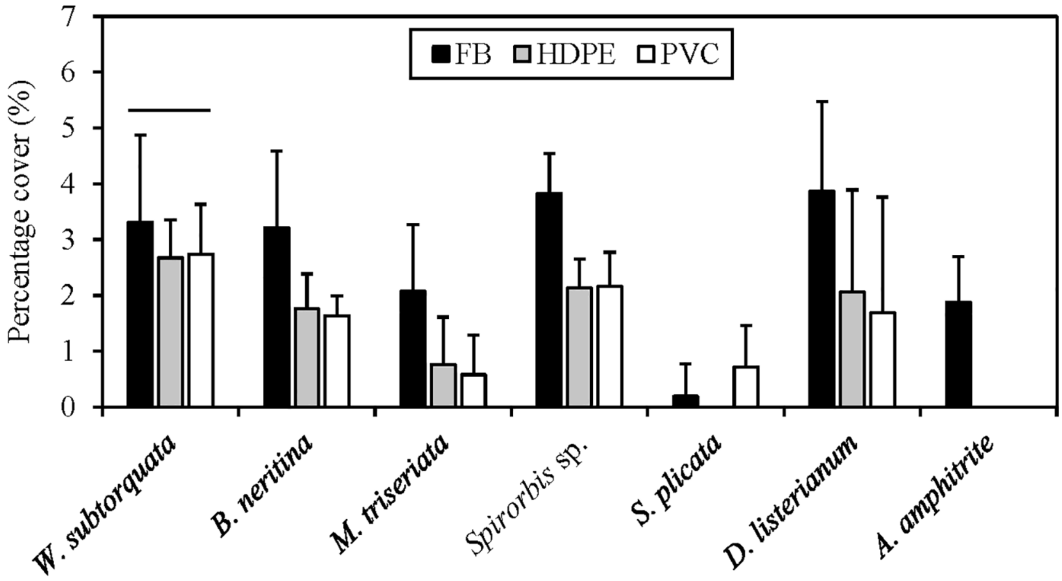

FIGURE 4
Mean (+ SD) square root transformed percentage cover of species most responsible for the dissimilarity in community composition among artificial substrate types. All species but *Watersipora subtorquata* showed higher abundance on fiberglass (FB) than High-Density Polyethylene (HDPE) and Polyvinyl Chloride (PVC) panels. Line above *W. subtorquata* indicates no significant effect of treatment.

and rubber) also showed no significant differences in the number of species throughout the study from May to October (Tyrrell and Byers, 2007). Finally, a recent meta-analysis reported a similar pattern of no significant differences in species richness among natural substrates (i.e. wood, biogenic, and rock) and artificial substrates (i.e. concrete, clay, polymers, and metals) (Dodds et al., 2022). Overall, considering the results of the present study and those from the previous work, it can be concluded that species richness does not vary as a function of substrate material type, which suggests that other factors might be more significant or affect different ecological metrices such as abundance rather than richness (Dennis et al., 2018; Kosová et al., 2023). It is important to note, however, that the present study and the previous ones highlighted above were conducted over a relatively short period of time. Going forward, future studies on the effect of substrate material types on biofouling assemblages should consider covering longer time frames to see if species richness remains similar among substrates and to potentially capture species that recruit in different seasons.

TABLE 3 Results of the Kruskal-Wallis test considering the effect of artificial substrate material type on the percentage cover of species responsible for the dissimilarities between treatments.

	df	χ^2	*P*
B. neritina			
Material type	2	12.59	**0.001**
M. triseriata			
Material type	2	7.42	**0.024**
***Spirorbis* sp.**			
Material type	2	16.28	**<0.001**
A. amphitrite			
Material type	2	21.06	**<0.001**
S. plicata			
Material type	2	7.99	**0.018**
D. listerianum			
Material type	2	6.99	**0.030**
W. subtorquata			
Material type	2	1.13	0.567

Values in bold represent significant *P* values.

TABLE 4 Results of the Dunn's test considering the pairwise comparisons for the percentage cover of species between the different types of substrate materials including High-Density Polyethylene (HDPE), Polyvinyl Chloride (PVC) and fiberglass panels.

	Fiberglass – HDPE	Fiberglass – PVC	HDPE – PVC
W. subtorquata	ns	ns	ns
B. neritina	**0.009**	**0.004**	ns
M. triseriata	ns	**0.040**	ns
Spirorbis sp.	**0.001**	**0.001**	ns
S. plicata	ns	ns	**0.021**
D. listerianum	ns	**0.036**	ns
A. amphitrite	**0.0002**	**0.0002**	ns

P-values were adjusted with the Bonferroni method. Values in bold represent significant P-values and ns indicates that the P-values were not significant.

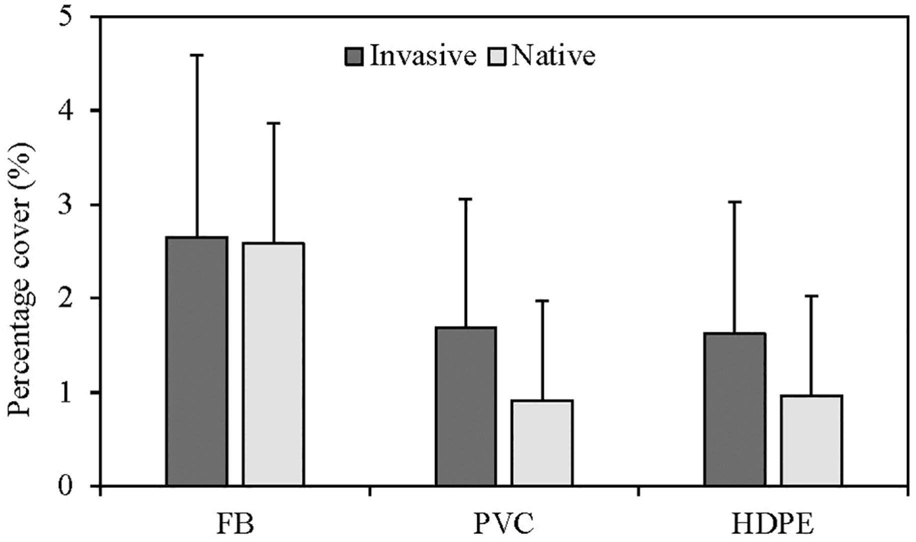

FIGURE 5
Mean (+ SD) overall square root transformed percentage cover considering the effect of substrate material type including High-Density Polyethylene (HDPE), Polyvinyl Chloride (PVC) and fiberglass (FB) panels and species status (invasive and native).

While the present study has contributed important insights into how artificial substrate material type might influence fouling assemblages, it is not without limitations. This study was a field-based experiment, with assemblages exposed to the full spectrum of biotic interactions and abiotic variability that they experience in the field. By the nature of the study design, recruitment was accounted for. However, we could not control for predatory interactions at this level. To understand the implications of predator-prey interactions for fouling community dynamics, knowledge of the predators that feed on these communities need to be held first (Loureiro et al., 2021b; Matikinca and Robinson, 2024a). Such knowledge is currently lacking in the South African context (Loureiro et al., 2021b). Additionally, following previous studies, we relied on photographic and microscopic taxonomic identification of specimens on the panels (Peters et al., 2014, 2017, 2019; Loureiro et al., 2021a; Matikinca and Robinson, 2024a). We acknowledge the probability of misidentifying specimens without DNA analysis. Financial constraints associated with DNA analysis for species identifications are acknowledged below. Finally, the present study was conducted over a relatively short term in one season and may have not captured species that are likely to recruit in other seasons. As such, additional studies that track the development of biofouling assemblages at multiple stages over longer periods of time are needed to investigate the long-term influence of substrate material type. Insightful for such studies, particularly in the South African context, will be considering the potential influence of varying substratum characteristics such as colour, roughness, orientation (i.e. horizontal vs vertical) and thermal capacity over longer time frames. While such studies would generate insightful data, the logistical constraints associated with long-term monitoring biofouling research are acknowledged (Egoh et al., 2020; Loureiro et al., 2021a). These include costs associated with taxonomy workshops with expert taxonomists, buying microscopes, DNA analysis for species identifications, travel time, labour, materials for constructing experimental arrays, preservation of specimens, photography equipment and image analysis (Loureiro et al., 2021a). When scrape samples need to be taken, in addition to using experimental arrays, costs include a dive boat, dive team with their equipment, collection equipment and specimen preservation (Loureiro et al., 2021a).

TABLE 5 Results of Generalized Least Squares Models considering the effect of substrate material type and species status on overall percentage cover.

	df	F	*P*
Material type	2	4.57	**0.011**
Species status	1	0.02	0.901
Material type × Species status	2	0.99	0.373

Values in bold represent significant *P* values.

Notwithstanding the above limitations, this study, the first of its kind in South Africa, provides valuable insights into the influence of substrate material type on biofouling communities in an understudied region. Our findings contribute to a broader understanding of how substrate material preferences of sessile fouling biota manifest in the context of marine biological invasions. By examining biofouling communities in this specific region, we offer data that can contribute to predictive modelling and inform management strategies beyond local scales. As such, the significance of the present study extends beyond the South African or African context, as biofouling processes and invasive species dynamics are globally relevant concerns. The increasing movement of marine vessels and the expansion of coastal infrastructure all contribute to the spread of fouling biota, dominated by non-native species (Peters et al., 2014; Mayer-Pinto et al., 2017; Dodds et al., 2022). Understanding the role of substrate type in shaping biofouling communities provides a foundation for predicting

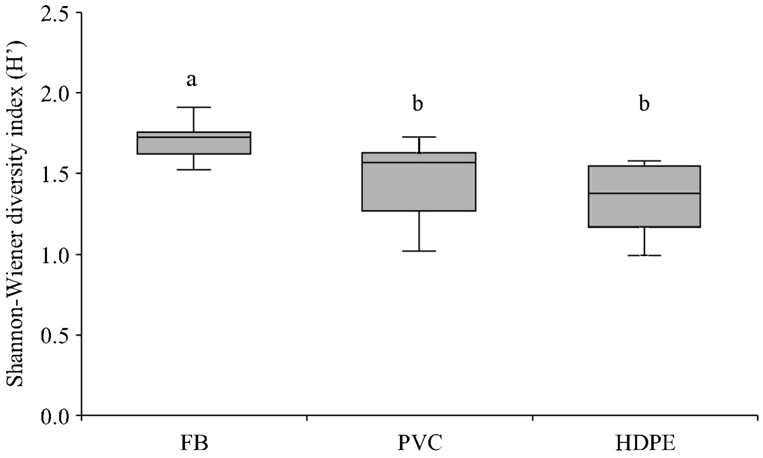

FIGURE 6
Shannon-Wiener diversity index (H′) of fouling communities on fiberglass (FB), High-Density Polyethylene (HDPE) and Polyvinyl Chloride (PVC) panels after three months. Treatments identified by different letters differed significantly ($P < 0.05$).

invasion risks in harbours, marinas, and artificial structures worldwide. Our findings can be compared with similar studies in other regions (i.e. Tyrrell and Byers (2007); Dobretsov (2015); Giangrande et al. (2021); Dodds et al. (2022); Grasselli et al. (2024)) to refine patterns of biofouling community responses to different substrate types. Data from the present study, together with those from the previous work, can inform biosecurity and monitoring programs in other regions, particularly in temperate and subtropical coastal environments where invasion pressures are intensifying due to biofouling. Moreover, this research underscores the importance of investigating biofouling in regions where baseline data are scarce, ultimately contributing to a more comprehensive global perspective on marine biological invasions.

5 Conclusion

This study expands the knowledge of biofouling community composition in the context of varying substrate material type along the South African east coast, an understudied region when it comes to the dynamics of alien fouling biota. The study demonstrated that artificial substrate material type affects sessile fouling community structure along this region. Specifically, this study found that fiberglass panels supported higher species diversity and percentage cover than HDPE and PVC panels, highlighting differences in the ecological implications of hydrophobic and hydrophilic substrates for sessile fouling assemblages. These community-level changes likely stem from a range of responses across different species within community assemblages. Importantly, the differences in material preferences and differential responses among species will preclude the use of a generic model for anticipating how fouling biota may respond to the rapid development of marine infrastructure. Overall, our findings suggest that there is a need to consider the ecological implications of the material used in artificial marine structures during material selection criteria. To understand such implications, ecological studies investigating biofouling dynamics on marine infrastructure should account for the influence of different physico-chemical properties of various substrates on biota. Such properties include differences in orientation, surface microtexture, colour, material type, surface chemistry and wettability. Importantly, studies, particularly in understudied regions with data scarcity, will need to consider these effects over longer time periods across different spatial scales to capture biota that recruit in different seasons. Studies will also need to include comparisons with mature fouling communities on adjacent substrates that have been exposed for a longer duration, paying particular attention to species status (native and invasive alien species). This comparison could help us discern whether the differences observed over a relatively short period of time can be attributed to material type only or whether they simply reflect the natural progression of fouling community development over time.

TABLE 6 Results of the Kruskal-Wallis test comparing the Shannon-Weiner diversity index (H′) and species richness among the different types of artificial substrate materials.

	df	χ^2	*P*
Shannon-Wiener diversity index (H′)			
Material type	2	12.74	**0.001**
Species richness			
Material type	2	5.09	0.078

Values in bold represent significant *P* values.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by School of Life Sciences, University of KwaZulu-Natal and written permission was obtained to conduct the research at the Point Yacht Club in Durban. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

PM: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. VZ: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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