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A centuries-old manmade reef in the Caribbean does not substitute natural reefs in terms of species assemblages and interspecific competition

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ABSTRACT

With increasing maritime activities in the proximity of coral reefs, a growing number of manmade structures are becoming available for coral colonisation. Yet, little is known about the sessile community composition of such artificial reefs in comparison with that of natural coral reefs. Here, we compared the diversity of corals and their competitors for substrate space between a centuries-old manmade structure and the nearest natural reef at St. Eustatius, eastern Caribbean. The artificial reef had a significantly lower species richness and fewer competitive interactions than the natural reef. The artificial reef was dominated by a cover of crustose coralline algae and zoantharians, instead of turf algae and fire corals on the natural reef. Significant differences in species composition were also found between exposed and sheltered sites on both reefs. Our study indicates that even a centuries-old manmade reef cannot serve as a surrogate for natural reefs.

1. Introduction

Despite occupying less than 1% of the global marine benthic environment, coral reefs are considered to be one of the most diverse and productive ecosystems worldwide, supporting ~830,000 multi-cellular species, and underpinning a spectrum of ecosystem goods and services that contribute to the welfare of millions of people (Martínez et al., 2007; Fisher et al., 2015; Woodhead et al., 2019). Regardless of their importance, coral reefs are threatened by a combination of global climate change and local anthropogenic activities including over-fishing, shipping, agriculture (nutrient run-off) and coastal development (Burke et al., 2011). The effect of these stressors manifest themselves in various ways on coral reefs, causing mass bleaching and mortality (Graham et al., 2007; Ainsworth et al., 2016; Hughes et al., 2018), reduced calcification and skeletal density (Foster et al., 2014; Mollica et al., 2018) and declines in the physical structure of reef habitats (Pratchett et al., 2014), to name a few. Due to slow natural recovery and because of high economic and ecological value, restoration efforts are essential to facilitate reef redevelopment and to ensure that coral reefs will not be lost altogether (Soong and Chen, 2003).

One major approach to coral reef restoration is the construction of artificial reefs. Artificial reefs contribute to conservation firstly, by providing extra substrate surface and refuge for juveniles of rare/endangered species, and secondly, by diverting human activity away from the nearby natural reef, thereby alleviating it from tourism and fishing pressures (Abelson, 2006). With increasing urbanisation, the number of manmade structures such as oil and gas platforms, seawalls, breakwaters, piers and jetties in the marine environment is increasing, and gradually natural marine habitats are being replaced by artificial ones (Tan et al., 2012; Heery et al., 2018; Masucci and Reimer, 2019; Todd et al., 2019; Kikuzawa et al., 2020). While such structures are not placed with the intention of recruiting marine life, the colonisation of corals onto these urban structures is apparent (Bulleri and Chapman, 2010; Chou et al., 2010; Dafforn et al., 2015; Gilbert et al., 2015), resulting in the formation of more artificial reefs. In some cases, these urban structures have even been found to host a higher abundance and diversity of fish, corals and other benthic organisms than on nearby natural reefs (Pondella et al., 2002; Burt et al., 2009a, 2009b).

The installation of artificial reefs should be considered carefully however, with thorough analysis of environmental risk prior to installation, and long-term management and monitoring thereafter. This is because artificial substrates facilitate the invasion or range expansion of non-native species, by serving as their 'stepping stones'. For example, three non-native coral species of the genus *Tubastraea* were able to settle

and expand at both sides of the Atlantic by use of man-made substrates, such as docks, pontoons, oil platforms, and shipwrecks (Boschma, 1953; Creed et al., 2017; Kolian et al., 2017; Soares et al., 2018, 2020; López et al., 2019; Derouen et al., 2020). In addition, artificial reefs are unable to provide comparable geo-ecological functions to natural reefs, meaning that reef framework production, sediment generation, growth potential and the maintenance of habitat complexity will differ (Perry and Alvarez-Filip, 2018), potentially resulting in different community compositions to those on natural reefs.

To gain a thorough understanding of community development on artificial reefs, the community composition of artificial reefs should be compared to that of the nearest natural reef (Carr and Hixon, 2011). Studies in past years that have made comparisons of the kind, have focussed predominantly on the development of early benthic communities on young artificial reefs (Aseltine-Neilson et al., 1999; Thanner et al., 2006; Higgins et al., 2019), with limited research of mature benthic communities on older structures (Perkol-Finkel et al., 2006; Harrison and Rousseau, 2020). In order for a mature community to establish on a manmade structure, comparable to that of a natural reef, decades to centuries of immersion could be required (Clark and Edwards, 1999; Perkol-Finkel et al., 2006, Perkol-Finkel and Benayahu, 2009). However, Perkol-Finkel et al. (2006) – who compared an ancient artificial reef with a nearby natural reef – concluded that that even after a century, the artificial reef will only mimic the community of the natural reef if it possesses similar structural features. Structural features therefore, seem to play a larger role than age in determining a similar community composition to that of the natural reef. Further research into the structural features of reefs has shown that artificial reefs tend to be more homogenous than natural reefs, supplying fewer and less extensive biogenic and topographic microhabitats, and thus hosting a lower abundance and range of organisms (Moschella et al., 2005; Firth et al., 2013; Aguilera et al., 2014).

In addition to age and structure, another variable found to influence the population and community ecology of reefs is wave exposure. Burt et al. (2010) investigated the influence of wave exposure on leeward and windward breakwater communities, finding that leeward breakwaters had a lower-cover coral community with smaller colonies and higher mortality compared to the windward breakwaters. Previous research has also found that wave exposure influences the distribution pattern of sponges and zoantharians. For example, Roberts et al. (2006) found sponges dominating sheltered sites, with >40% on sheltered reefs, and only 25% on exposed reefs. Meanwhile the body-plan of zoantharians influenced their distribution between wave-exposed sites, with species *Palythoa caribaeorum* occupying exposed sites and *P. variabilis* occupying sheltered sites (Rabelo et al., 2015).

Another key determinant of community composition on reefs is competition for space among sessile reef organisms. This type of interspecific interaction influences reef biodiversity and community composition to a great extent, and is therefore regarded as an important structuring mechanism of benthic assemblages (Aerts and Van Soest, 1997; Tanner, 1997; Chadwick and Morrow, 2011). Interspecific interactions are highly variable, with benthic organisms displaying a range of strategies to compete with others for space. Scleractinian corals, for example, have developed defence mechanisms against adjacent competing corals. They use either mesenterial filaments or sweeper tentacles to directly harm their competitors' tissues (Den Hartog, 1977; Richardson et al., 1979; Wellington, 1980; Lang and Chornesky, 1990; Lapid and Chadwick, 2006; Roff et al., 2009), or indirectly affect their competitors by overshading or overtopping them (Lang, 1971; Lang and Chornesky, 1990; Álvarez-Noriega et al., 2018). Corals and sponges are renowned competitors for space, with most research documenting the success of sponges outcompeting corals by overgrowing them, excavating their skeletons, or releasing toxic compounds to kill them (Porter and Targett, 1988; López-Victoria et al., 2006; Wulff, 2006, 2012; Loh et al., 2015). There are few examples however, in which corals are known to overgrow sponges (García-Hernández et al., 2017) or – in the

case of free-living corals – cause damage to sponges by dropping on top of them (Hoeksema et al., 2014) or move away from them (Hoeksema and De Voogd, 2012). Zoantharians also engage in interspecific competition. The zoantharian *Palythoa caribaeorum* is a notoriously aggressive competitor, due to its fast and continuous growth rate – which is far superior to that of co-occurring scleractinian corals – (Silva et al., 2015), and its ability to produce an allelochemical known as palytoxin (Gleibs et al., 1995; Deeds et al., 2011).

Minimal research has been carried out on interspecific interactions in benthic communities on artificial substrate. One study however, by Ng et al. (2012), found that hard coral assemblages on seawalls in Singapore averaged a large distance of 1 m apart, which could be caused by differences in key ecological processes, such as competition, predation and facilitation between artificial and natural substrates that determine ecological interactions (Bulleri and Chapman, 2010). Due to a scarcity of information on reef community development on non-natural/ artificial reefs over extended periods of time, we were looking for possibilities to study much older man-made structures that could act as candidate substrate for reef benthos. Our research was carried out on an ancient reef discovered on St. Eustatius, an island situated in the eastern Caribbean. Such an old artificial reef – or similar structures– have to our knowledge not been studied before. It therefore served as an ideal research object given it had the prospect of harbouring a mature and well-established artificial reef community, and could contribute to research on urban structures serving as artificial reefs.

The aim of our research was to compare the community composition and benthic structure between the historic artificial reef and the nearest natural reef (including corals and their competitors for space), enabling us to understand the role of an artificial reef in the biodiversity of this environment (Carr and Hixon, 2011). We hypothesised that the artificial reef would have lower benthic cover, abundance and species richness than the natural reef. We expected this finding due to the homogenous nature of artificial structures, lacking biogenic and topographic microhabitats that are generally present on a natural reef (Moschella et al., 2005; Firth et al., 2013; Aguilera et al., 2014). Secondly, we hypothesised that there would be fewer interspecific interactions on the artificial reef compared to the natural reef. We expected this because in a previous study looking at a similar urban structure in Singapore, few interspecific interactions were found, with coral colonies averaging a large distance apart (Ng et al., 2012). Thirdly, we hypothesised that there would be different species assemblages on exposed and sheltered sites on both reefs, with lower cover and abundance of corals and sponges on wave-exposed sites –as found by Burt et al. (2010) and Roberts et al. (2006) respectively– and higher cover and abundance of zoantharians on sheltered sites, as found by Rabelo et al. (2015) for certain species.

2. Material and methods

2.1. Study site

St. Eustatius (popularly known as 'Statia') is a small volcanic island (Moolengraaff, 1931), with a land area of 21 km^2, and politically a special municipality of the Caribbean Netherlands in the eastern Caribbean (Collier and Brown, 2008; Hoeksema et al., 2017; Van der Loos et al., 2017). The eastern (Atlantic) side of the island has a wave-exposed coastline, while the western (Caribbean) side has a sheltered coastline (Fig. 1; Debrot et al., 2014; Hoeksema, 2016).

The reefs focussed on in this study were located nearshore of the sheltered Caribbean coastline (Fig. 1). The locality of the ancient artificial reef coincides with that of a jetty in the 18th century (Barka, 1985; Triplett, 1995; Eastman, 1996) and a breakwater in the 19th century that was built in 1829 but largely washed away in 1834 (Stelten, 2019: p. 85). St. Eustatius was once known as one of the world's leading ports and lost this reputation due to the impact of frequently occurring hurricanes and successive wars between European colonial powers (Stelten,
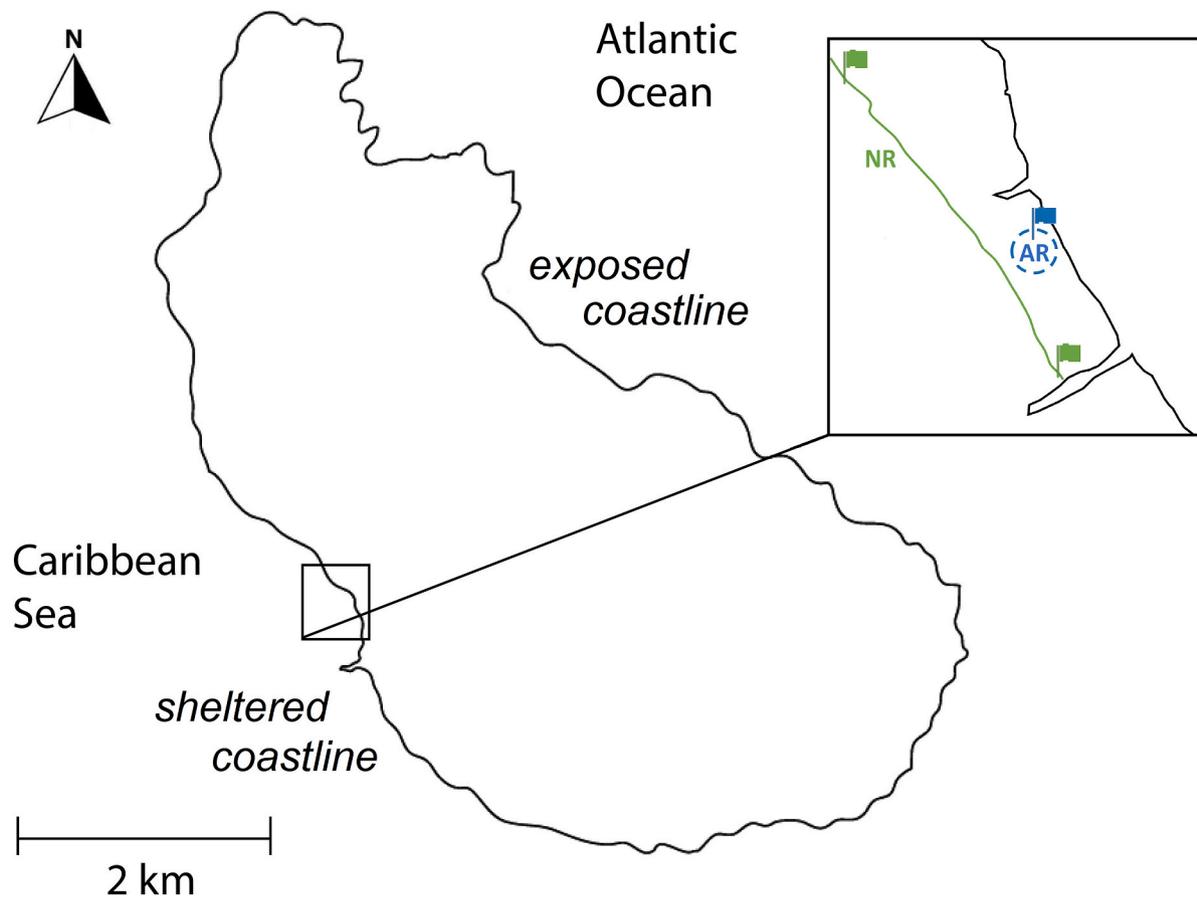
Fig. 1. Map displaying the location of the field sites at St. Eustatius, eastern Caribbean. The area marked 'AR' indicates the site of the artificial reef, with all 12 outcrops located within the blue dashed circle (5–35 m offshore; 17°28′53.14"N, 62°59′15.40"W). The green line marked 'NR' indicates the range of the natural reef (50–75 m offshore; 17°28′56.16"N, 62°59′19.26"W to 17°28′49.97"N, 62°59′15.13"W). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2019). Since these hurricanes were powerful (Cambers, 1997; Lugo, 2000) and capable of demolishing buildings and piers along the shoreline of St. Eustatius, we can confidently assure that these hurricanes were responsible for the condition of the ancient manmade reef as it is today, remaining submerged and recruiting marine benthos ever since its demolition (Fig. 2a-c).
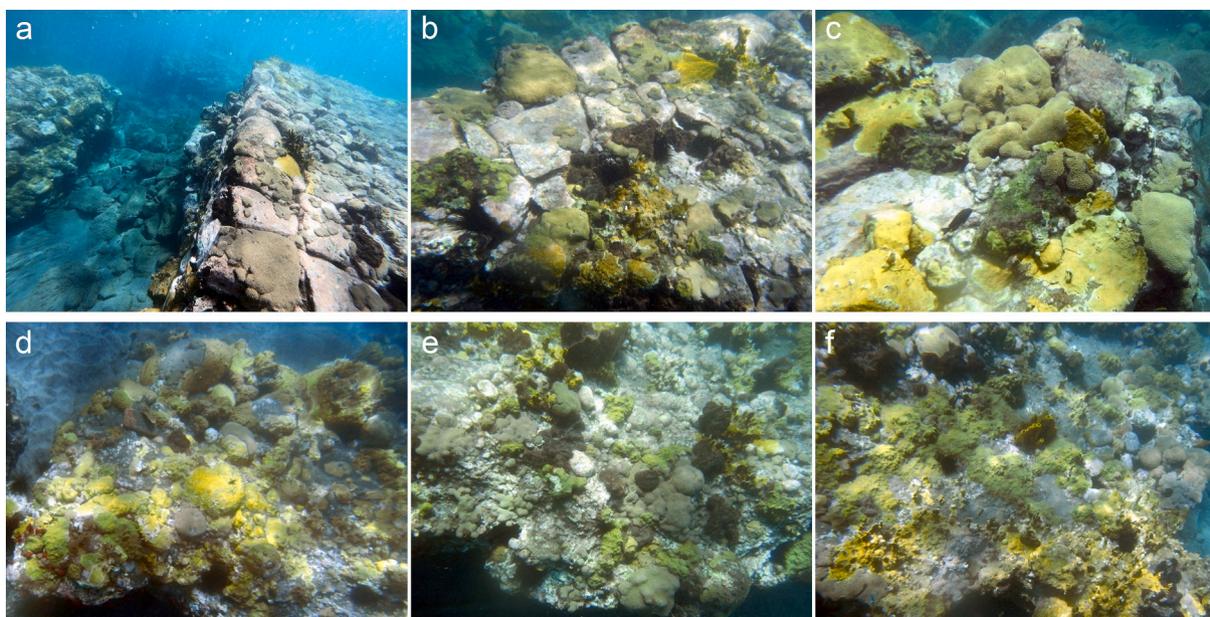

Fig. 2. Impressions of the artificial reef (**a, b, c**) and the natural reef (**d, e, f**).

The artificial reef (17°28′53.14″N, 62°59′15.40″W) consisted of 12 rocky outcrops made from cemented smooth basalt blocks and boulders (Fig. 2a–c). It was situated close to the coastline, at a distance of 5–35 m, and at a greatest depth of 2 m (Fig. 1). The natural reef (17°28′56.16″N, 62°59′19.26″W to 17°28′49.97″N, 62°59′15.13″W) was partly biogenic since it was located on top of a rough lava underground (Fig. 2d–f). It ran parallel to the coastline at a length of 260 m, and was situated 50–75 m from the shoreline and at a greatest depth of 4 m (Figs. 1, 2). Both reefs, although situated in close proximity to the shoreline, were subtidal and could most easily be studied by SCUBA diving (Hoeksema, 2016).

2.2. Data collection

Data for both the artificial and natural reef was collected by underwater photography, using SCUBA in the months of February and March 2020. Underwater photography was carried out using a photo quadrat sized 25 × 25 cm^2. A photo quadrat of this size was chosen in order to ensure that smaller species and/or juvenile forms were not overlooked, as also used by Ateweberhan et al. (2006), Milne and Griffiths (2014) and Edmunds and Bruno (1996). The photo quadrat was constructed by mounting a GoPro Hero 7 camera centrally to a frame positioned 25 cm above the quadrat (Fig. 3a). Use of the photo quadrat ensured that all photographs were consistently taken from the same orientation and distance. No auxiliary light was needed to improve the photograph quality, given the shallow-water field site had sufficient natural light.

Overall, 1639 images of the biodiversity across the natural (78%) and artificial (22%) reef were taken. This number was sufficient to include all of the benthic organisms that made up both reefs. Each one of these images was of a separate quadrat, with no quadrats photographed more than once. Although there were considerably fewer images taken on the artificial reef, the sampling effort on both reefs was equal, and instead, this difference is reflective of the artificial reef being smaller in size, and hosting fewer organisms to photograph than the natural reef. The sampling depth however, differed only marginally by 2 m.

For each image taken, the wave-exposure of the organisms photographed was recorded as either 'sheltered' if they were shielded from wave force (within a crevice or beneath an overhang), or 'exposed' if they were unshielded (exposed on the reef flat or sides).

2.3. Benthic structure

To determine the percentage cover (%) and the abundance of benthic organisms, images were individually analysed. Specimen identification was performed with the help of field guides by Humann and DeLoach (2013) and Zea et al. (2014), and organisms were identified to the lowest possible taxonomic rank (species or genus). Some congeneric species were hard to distinguish when the specimens were not full-grown, like abundant fire corals (*Millepora* spp.) starting with an encrusting phase, or many small encrusting corals of the genus *Siderastrea*. The abundance of each species was determined by manually counting the number within each image. Total abundance counts for each species were converted to a density metric (m^{-2}) in order to account for the size difference between the artificial and natural reef. This way, the abundance of organisms on each reef could be fairly compared. Density was calculated through division of the abundance value by the surface area of the relevant reef. Percentage cover was determined by the software 'CoralNet' (Beijbom et al., 2012). Images were uploaded into CoralNet, and a total of 30 points were randomly distributed over every image (Fig. 3b). Every point was manually labelled to the lowest taxonomic rank, and the software accurately calculated the percentage cover of each organism in every image.

2.4. Benthic interactions

Benthic interactions were also determined from individually analysing each image. Any visible physical contact between live benthos types was considered a competitive interaction, and was counted and recorded to the lowest taxonomic rank. This method of assessing interactions is similar to the one used in counts of 'neighbour events' as defined by Bradbury and Young (1983) and 'peripheral contact' by Aerts and Van Soest (1997).

Benthos that did not interact with another live benthos type was recorded as interacting with 'nothing'. Previous studies on interspecific interactions between reef benthos have recorded which species within an interaction pairing had won, lost, or whether the species simply coexisted (Sheppard, 1979; Logan, 1984; Barott et al., 2012; Swierts and Vermeij, 2016). Our purpose for assessing benthic interactions here however, was purely to provide a more complete image of the reef assembly. Winning/losing scores were not relevant to our aim and therefore not recorded.

2.5. Data analyses

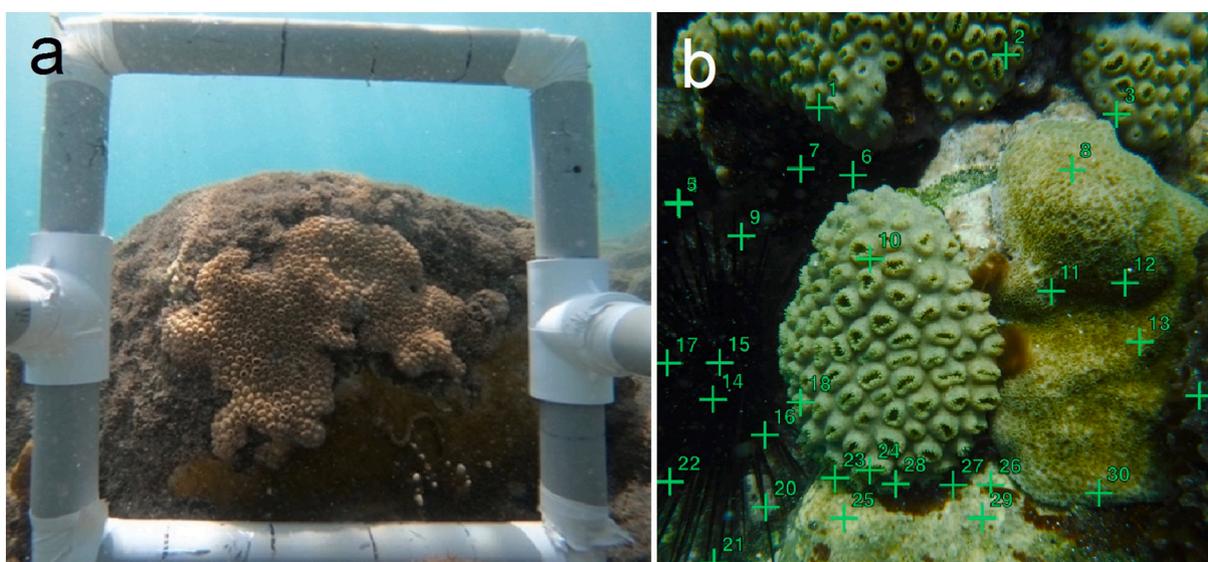Permutational multivariate analysis of variance (PERMANOVA;

Fig. 3. Data collection: (**a**) The photo-quadrat in use; (**b**) Image in CoralNet software to calculate percentage cover.

Anderson, 2017) was used to test for significant community differences between the natural and artificial reef, and between sheltered and exposed sites on both reefs. A total of 999 random permutations were used, in combination with a Bray-Curtis distribution using non-transformed data (Bray and Curtis, 1957). A post-hoc test, namely the similarities percentages procedure (SIMPER) (Clarke, 1993) was used to determine the contributions from individual species to the observed community differences calculated with PERMANOVA. We chose to report SIMPER results of species up to ~70% as each of these species contributed more than 10% to the variance between the reefs.

A paired-samples Wilcoxon test (Wilcoxon, 1945) was used to determine if there were significant differences in the frequency of interspecific interactions between the natural and artificial reef. The same test was also performed on interaction counts that had been corrected to account for the size difference between the natural and artificial reef. Interaction counts were divided by the summed density of both benthic organisms of each interaction pair. These values were subsequently used for the statistical analyses.

All data analyses were carried out in R software (R Core Team, 2019), using packages 'vegan' (Oksanen et al., 2019), 'MVN' (Korkmaz et al., 2014) and 'dplyr' (Wickham et al., 2020) for statistical analyses, and packages 'ggplot2' (Wickham, 2016), 'dplyr' (Wickham et al., 2020), 'tidyr' (Wickham, 2020) and 'ggpubr' (Kassambara, 2020) for the creation of graphs.

3. Results

3.1. Percentage cover (%)

The species composition of organisms differed significantly between the artificial and natural reef (PERMANOVA, pseudo-F = 149.62, $p < 0.001$). The artificial reef was dominated by crustose coralline algae
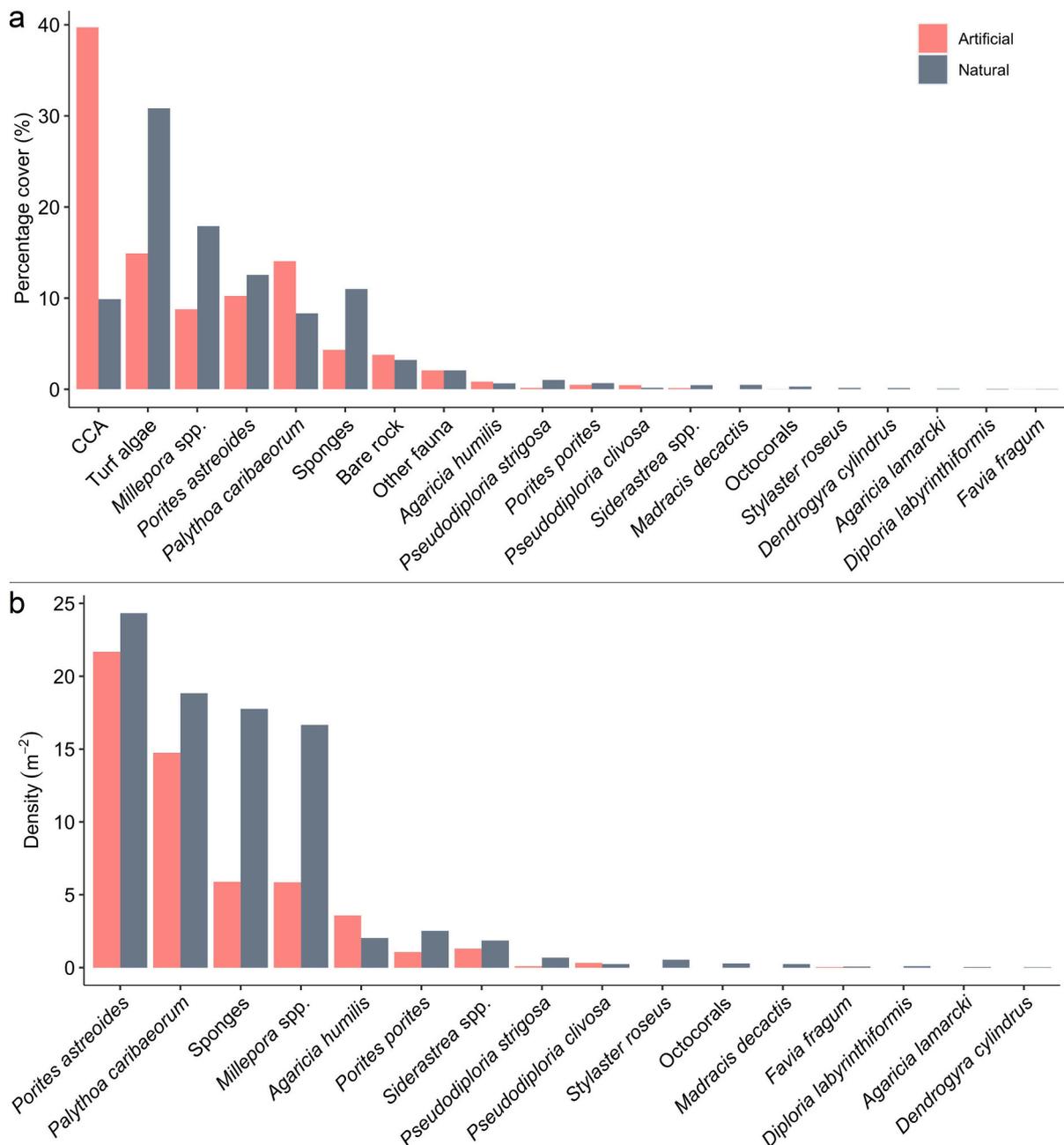

Fig. 4. (**a**) Percentage cover of reef organisms on the artificial and natural reef. (**b**) Densities (m^{-2}) of reef organisms on the artificial and natural reef.

(CCA, 39.7%) and the zoantharian *Palythoa caribaeorum* (14.1%), while the natural reef was dominated by turf algae (30.8%) and *Millepora* spp. (17.9%), all of which contributed ~70% to the community differences between the two reefs (Figs. 4a, 5; Table 1).

3.2. Abundance

The species composition again differed significantly between the artificial and the natural reef (PERMANOVA, pseudo-F = 33.912, $p <$ 0.001). While both reefs were found to have a similar ranking order of the most abundant to the least abundant benthic species or species group, a lower number of benthic organisms was found on the artificial reef ($n = 13$) than on the natural reef ($n = 18$) (Fig. 4). *Porites astreoides* (21.7 vs. 24.3 m^{-2}), *Millepora* spp. (5.9 vs.16.7 m^{-2}), and *Palythoa caribaeorum* (14.7 vs. 18.8 m^{-2}), contributed ~70% to the community differences between the artificial and natural reef respectively (Figs. 4b, 5; Table 1). Furthermore, the five additional taxonomic categories found on the natural reef, ranked in order of decreasing abundance, were: *Madracis decactis, Stylaster roseus, Dendrogyra cylindrus, Agaricia lamarcki,* and *Diploria labyrinthiformis* (Fig. 4b).

3.3. Exposed verses sheltered sites: artificial reef

Here, the species composition differed significantly between exposed (on the reef flat/sides) and sheltered sites (within a crevice or beneath an overhang) (PERMANOVA, pseudo-F = 6.7408, $p < 0.002$). Exposed sites had the highest density of *Porites astreoides* (23.8%) and *Palythoa caribaeorum* (19.4%), which contributed to ~70% to the community differences between the two sites (Figs. 5, 6a; Table 1). Sheltered sites, however, hosted the highest density of sponges (10.2%) compared to the exposed sites (3.3%) (Figs. 5, 6a).

3.4. Exposed verses sheltered sites: natural reef

The species composition differed significantly between exposed (on the reef flat/sides) and sheltered sites (within a crevice or beneath an overhang) (PERMANOVA, pseudo-F = 36.73, $p < 0.001$). Exposed sites had the highest density of *Porites astreoides* (27.1%) and *Palythoa caribaeorum* (22.4%), while sheltered sites again had the highest density of sponges (28.2%) (Figs. 5, 6b). Such differences contributed ~70% to the

Table 1
SIMPER of the species that contributed ~70% of the observed variance when testing for differences between the artificial and natural reef using PERMANOVA.

Data type	Species	Cumulative percentage (%)
Abundance	*Porites astreoides*	
		28.1
	Palythoa caribaeorum	
		50.1
	Millepora spp.	
		68.4
Percentage cover	Crustose coralline algae	
		23.0
	Turf algae	
		42.6
	Millepora spp.	
		57.2
Natural reef, exposed vs. sheltered	*Palythoa caribaeorum*	
		69.5
	Porites astreoides	
		24.7
	Sponges	
		48.0
	Palythoa caribaeorum	
		66.5
tificial reef, exposed vs. sheltered	*Porites astreoides*	
		32.6
	Palythoa caribaeorum	
		57.8

community differences between the two sites (Table 1).

3.5. Interactions

Overall, the artificial reef hosted significantly less interspecific interactions than the natural reef (Wilcoxon, $p < 0.001$). In total, 1338 interactions were documented spanning the artificial reef (Table 2; Fig. 7). *Porites astreoides* was most commonly found without interaction ($n = 196$), while the interactions of *Palythoa caribaeorum* ($n = 184$) and *P. astreoides,* each with their conspecifics ($n = 169$) followed thereafter (Table 2). It was found that *Palythoa caribaeorum* most frequently
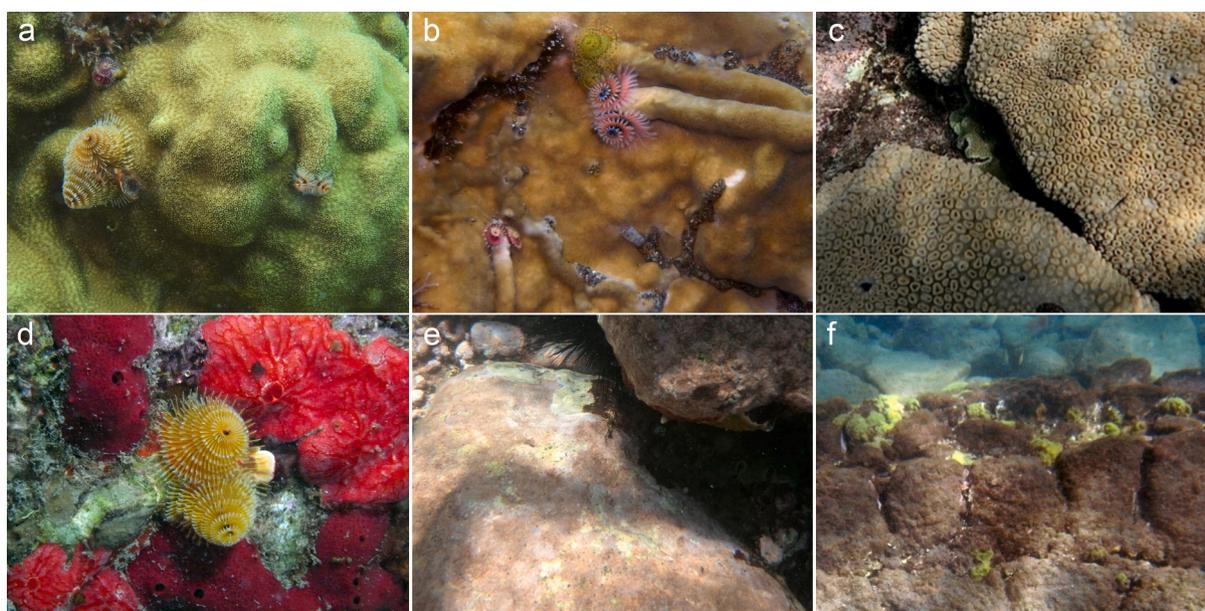

Fig. 5. Key players found on both types of reefs: (**a**) *Porites astreoides*, (**b**) *Millepora* spp., (**c**) *Palythoa caribaeorum*, (**d**) sponges (**e**), crustose coralline algae (CCA), (**f**) turf algae.
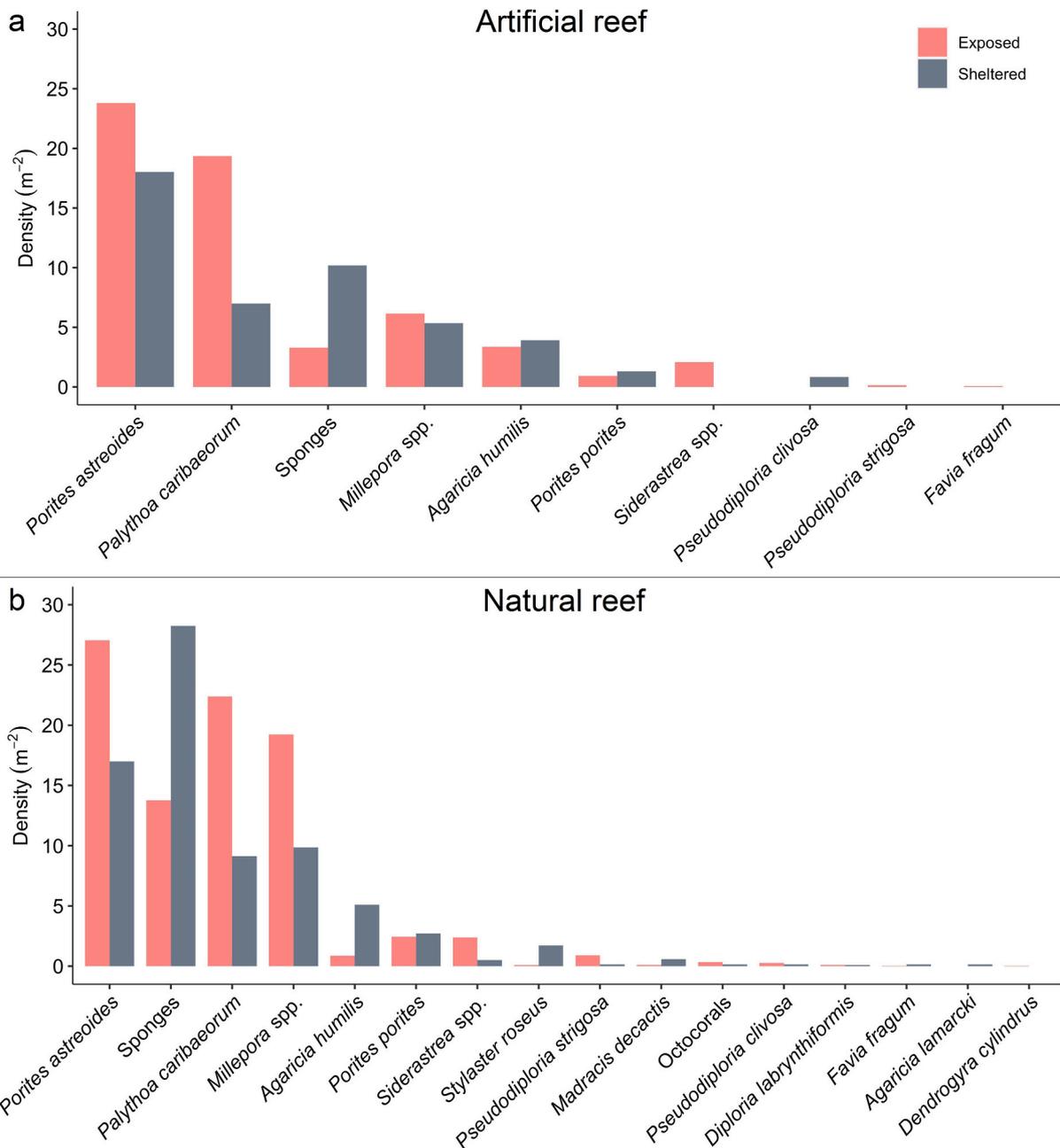
Fig. 6. Densities (m^{-2}) of reef organisms on the exposed and sheltered sides of (**a**) the artificial reef, and (**b**) the natural reef.

interacted with conspecifics (6.2 m^{-2}) and *Millepora* spp. interacted the most with sponges (4.3 m^{-2}) (Table 2). Whereas, *Siderastrea* spp. (28.6 m^{-2}), *Porites porites* (17.7 m^{-2}), *Agaricia humilis* (12.0 m^{-2}) and *Porites astreoides* (9.0 m^{-2}) were most commonly found alone, and interacted very little with other reef species (Table 2). In total, 6927 interactions were recorded across the natural reef (Table 3; Fig. 7). Of these, interactions between *P. astreoides* with conspecifics was the most frequent interaction type (*n* = 749), followed by *Palythoa caribaeorum* with conspecifics (*n* = 692), and *Millepora* spp. with sponges (*n* = 624) (Table 3). A review of relative numbers highlights *Porites astreoides* was most frequently found without interaction (20.5 m^{-2}), followed by interactions with conspecifics (15.4 m^{-2}), with sponges (12.7 m^{-2}), with *Millepora* spp. (7.9 m^{-2}), and with *P. caribaeorum* (6.1 m^{-2}) (Table 3). *Palythoa caribaeorum* was most frequently found interacting with conspecifics (18.4 m^{-2}), followed by interactions with sponges (11.3 m^{-2}), nothing (11.1 m^{-2}) and with *Millepora* spp. (10.2 m^{-2}) (Table 3).

Millepora spp. was found most frequently without interactions (23.2 m^{-2}) and interacting with sponges (18.1 m^{-2}). Lastly, *Porites porites* (33.0 m^{-2}), *Siderastrea* spp. (76.4 m^{-2}) and *Agaricia humilis* (28.0 m^{-2}) were found most frequently by themselves, with very few interactions with other reef species (Table 3).

4. Discussion

4.1. Species richness and substrate cover

The lower species richness on the artificial reef compared to the nearby natural reef (Fig. 4) was expected, and in line with findings of previous research comparing biodiversity between artificial and nearby natural reefs (Moschella et al., 2005; Carr and Hixon, 2011; Firth et al., 2013; Aguilera et al., 2014; Kikuzawa et al., 2020). For example, Aguilera et al. (2014) found that the consistently lower species richness

Table 2
A summary of all interspecific interactions on the artificial reef per unit area (m^{-2}).

Interaction name	Interaction number	Density (m^{-2})	Interaction/ density
P. astreoides - Nothing	196	21.7	9.0
P. caribaeroum - P. caribaeorum	184	29.5	6.2
P. astreoides - P. astreoides	169	43.4	3.9
P. astreoides - Sponge	149	27.6	5.4
P. astreoides - P. caribaeorum	62	36.4	1.7
Sponge - Sponge	60	11.8	5.1
P. caribaeorum - Nothing	58	14.8	3.9
Millepora spp. - Sponge	51	11.8	4.3
P. caribaeorum - Sponge	49	20.7	2.4
Sponge - Nothing	45	5.9	7.6
P. astreoides - Millepora spp.	43	27.5	1.6
A. humilis - Nothing	43	3.6	12.0
Siderastrea spp. - Nothing	37	1.3	28.6
A. humilis - Sponge	31	9.5	3.3
P. astreoides - A. humilis	25	25.3	1.0
Millepora spp. - Nothing	25	5.9	4.3
Millepora spp. - Millepora spp.	22	11.7	1.9
P. porites - Nothing	19	1.1	17.7
P. caribaeorum - Millepora spp.	16	20.6	0.8
P. porites - Sponge	9	7.0	1.3
P. astreoides - P. porites	13	22.8	0.6
P. astreoides - P. strigosa	7	21.8	0.3
A. humilis - A. humilis	5	7.2	0.7
A. humilis - P. caribaeorum	5	18.3	0.3
P. clivosa - Nothing	4	0.3	12.8
P. clivosa - Sponge	3	6.2	0.5
A. humilis - Millepora spp.	2	9.4	0.2
P. strigosa - Sponge	2	6.0	0.3
P. porites - Millepora spp.	1	6.9	0.1
P. porites - P. caribaeorum	1	15.8	0.1
P. strigosa - Nothing	1	0.1	11.2
F. fragum - Nothing	1	0.1	22.4

and abundance of organisms found on the artificial reef was due to fewer and less extensive biogenic and topographic microhabitats, compared to those available on natural platforms. The provision of such microhabitats usually centres around the characteristics of the substrate. For example, an experiment carried out by Mijan et al. (2011), found that use of cockle shells in the construction of artificial reefs encouraged greater settlement of benthic organisms. The shells created a substrate with greater micro-topography, with a rougher, uneven surface that supplied more microhabitats in the form of crevices and holes that would favour the early life-history processes of sclerobionts (Bohnsack and Sutherland, 1985; Mallela, 2018).

The artificial reef in our study was made of cemented basalt blocks, which had a considerably smoother and less porous surface (Fig. 2a–c) than the rougher and more porous surface of the biogenic reef, mainly consisting of coral located on top of a rough lava underground (Fig. 2d–f). Consequently, the lack of habitat heterogeneity meant that fewer species could be supported on the artificial reef than on the natural reef. However, in an experiment using concrete tiles with three degrees of relief (made of ridges and crevices) it was found that complexity mostly enhances biodiversity and live cover but not always (Strain et al., 2021). Typically, the lower diversity found on artificial reefs in comparison to natural reefs can be explained by the younger age of the artificial reef, because younger reefs have not had the opportunity to establish a mature and comparable community to that of the natural reef (Clark and Edwards, 1999; Perkol-Finkel et al., 2006; Perkol-Finkel and Benayahu, 2009). When artificial reefs are assessed after a longer period, more promising results in support of their role are found, as evidenced by coral cover diversity on a 34-year-old shipwreck being

double that of a 14-year-old shipwreck (Perkol-Finkel and Benayahu, 2004). In our study, age was uniquely removed as a potential explanation for the lower biodiversity found on the artificial reef, as it had been submerged for centuries, thus lending further support to the role of structural features in promoting biodiversity. Our results are consistent with the finding of a 7-year-long experiment by Martins et al. (2016), who found that the surface of artificial substrates should be made less smooth in order to enhance their performance.

4.2. Key players

Having discovered which specific benthic reef organisms contributed the most towards the dissimilarity between the artificial and natural reef communities, it was worth exploring these 'key players' further to understand why they dominated one reef over another.

4.2.1. Turf algae and crustose coralline algae

Turf algae are short (<1 cm), dense, multispecies assemblages of small filamentous macroscopic algae, that cover hard substrate on reefs (Steneck and Dethier, 1994; Fong and Paul, 2011; Connell et al., 2014; Tebbett and Bellwood, 2019). Worldwide, turf algae are becoming a dominant component of reef communities, particularly following disturbances such as repetitive bleaching events and during regenerative phases (Tebbett and Bellwood, 2019). This is because turf algae are stress-tolerant (Hay, 1981; Steneck and Dethier, 1994), and rapidly inhabit dead coral skeletons following primary colonisation by cyanobacteria (Diaz-Pulido and McCook, 2002; Arthur et al., 2005).

The dominance of turf algae on the natural reef in this study therefore alludes to the occurrence of some form of disturbance (Fig. 4a). Given turf algae has become the most abundant benthic group on many Caribbean reefs (Mueller et al., 2016; Wells et al., 2021), the possible disturbance experienced by the natural reef is likely widespread. Additionally, this finding of turf algae dominating the natural reef, could be due to a substrate/surface preference. A study carried out by Kardel et al. (2018), investigated the effect of surface topography on turf algal biomass, revealing that turf algae displayed a preference for substrates with more complex topographies than smoother surfaces. This effect even applies to small, ornamented opercula of serpulid worms that function as settlement areas (Hoeksema et al., 2019a, 2019b). The natural biogenic reef in our study had a more complex topography than the artificial reef which had a smoother more regular surface. Turf algal dominance on the natural reef therefore, could be justified by preference for a more complex substrate surface.

Crustose coralline algae (CCA) belong to the order Corallinales and are an important calcifying component in marine benthos (Littler et al., 1985; Steneck, 1986; McCoy and Kamenos, 2015). CCA chemically attract and facilitate the settlement of coral larvae, as well as those of some grazing invertebrates, thereby promoting solidification of the reef framework (Harrington et al., 2004; Vermeij et al., 2011). Cover of CCA in this study was found to dominate the artificial reef. Research on the distribution of CCA reveals that they tend to dominate areas where corals are inhibited by strong wave action (Littler and Littler, 2013). The artificial reef in this study, was located in shallow subtidal water (<2 m depth) and close to the shore (<35 m distance), where wave action was strong. Therefore, the higher cover of CCA on the artificial reef could be explained by the difference in wave action between the two reefs, with CCA having a preference for a more turbulent environment.

The smoother more homogenous surface of the artificial reef may have been a preferred substrate for CCA, than the rougher more heterogenous surface of the natural reef that was preferred by turf algae. Currently there appears to be no research on the topic of substrate preference for CCA however, so this is only a theory and further research would be required to support this assertion. It is relevant to note that in a comparison of natural reefs with sea walls in Singapore, turf algae also showed a higher cover on natural reefs, while this difference was less pronounced for CCA (Lai et al., 2018).
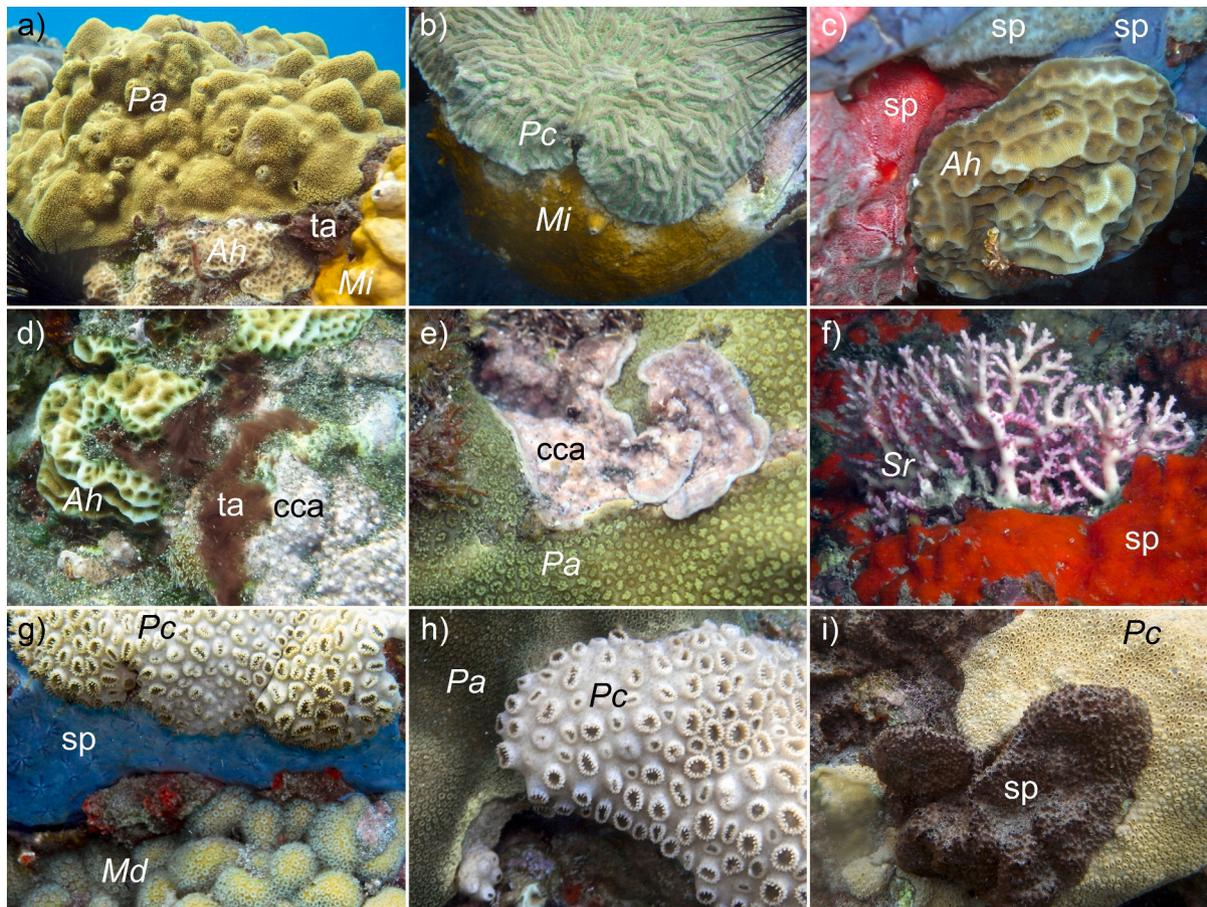
Fig. 7. Examples of interspecific interactions: (**a**) *Pa* = *Porites astreoides, Ah* = *Agaricia humilis, Mi* = *Millepora* spp., ta = turf algae; (**b**) *Pc* = *Pseudodiploria clivosa, Mi* = *Millepora* spp.; (**c**) *Ah* = *A. humilis*, sp. = various sponges; (**d**) cca = crustose coralline algae, ta = turf algae, *Ah* = *A. humilis*; (**e**) cca = crustose coralline algae, *Pa* = *P. astreoides*; (**f**) *Sr* = *Stylaster roseus,* sp . = sponge (*Halisarca caerulea*); (**g**) *Pc* = *P. caribaeorum*, sp. = sponge, *Md* = *Madracis decactis*; (**h**) *Pa* = *P. astreoides*, Pc = *P. caribaeorum*; (**i**) *Pc* = *P. caribaeorum*, sp. = sponge (*Ircinia* sp.).

4.2.2. Palythoa caribaeorum

The zoantharian species *Palythoa caribaeorum* had lower abundance yet higher cover on the artificial reef compared to the natural reef (Fig. 4). The low abundance and high cover indicate the presence of large patches of *P. caribaeorum* on the artificial reef. Our finding corroborates the work of Reimer et al. (2018) and Montenegro et al. (2020) that also found *P. caribaeorum* to occupy the shallow intertidal zone in the Caribbean, showing a preference for turbulent water. *Palythoa caribaeorum's* fast growth rate, encrusting nature, coenenchyme (tissue that surround and link polyps) and high density of symbionts, enable it to persist on shallow water reefs that experience physical disturbance from waves and currents (Santos et al., 2016). Such high cover of zoantharians have even been found to occur on reefs with dead coral and rubble, further evidencing their ability to persist through disturbance that structurally decimates the reef (Karlson, 1983; Cruz et al., 2016). This zoantharian has also been reported on various artificial substrates, such as a shipwreck and concrete blocks (Santos and Reimer, 2018). In this instance, the artificial reef experienced greater physical disturbance than the natural reef, as it was both shallower and closer to the shore. The higher cover of *P. caribaeorum* on the artificial reef, can therefore be justified by the presence of favourable turbulent conditions.

Additionally, the higher cover of *P. caribaeorum* on the artificial reef may be a result of less competition for space among organisms, than on the natural reef. When looking at the summary of all interspecific interactions on both reefs, it is apparent that *P. caribaeorum* had a lower density of interactions on the artificial reef, than on the natural reef (Tables 2, 3), therefore supporting the notion that the higher cover of

P. caribaeorum is facilitated by less interspecific competition. However, research shows that *P. caribaeorum* hinders the growth of competitors with great success (Suchanek and Green, 1981; Acosta, 2001). In addition, other research suggests that *P. caribaeorum* is capable of overgrowing almost every sessile reef invertebrate (Suchanek and Green, 1981; Pérez et al., 2005), with the exception of serpulid worms of the genus *Spirobranchus* (Hoeksema et al., 2020). Based on this, one would expect for *P. caribaeorum* to prevail against competitors, and therefore achieve high cover regardless of the presence or absence of benthic competitors, thus undermining the idea that minimal interspecific competition could be a cause of the large patches of *P. caribaeorum*.

4.2.3. Millepora spp.

Both the cover and density of *Millepora* spp. was high on the natural reef and low on the artificial reef (Fig. 4). *Millepora* spp. are colonial polypoidal hydrozoans, that are conspicuous on shallow tropical reefs and crucial reef- framework builders (Lewis, 2006; De Souza et al., 2017). The morphology of *Millepora* spp. shows much intraspecific variation, which enables them to inhabit reefs with a range of environmental conditions, such as differing current, water movement, depth and turbidity (De Weerdt, 1984). An encrusting calcareous skeleton is the first stage of growth, with numerous perpendicularly oriented protuberances developing later, in the form of branches or plates (De Souza et al., 2017; Arrigoni et al., 2018). The general view is that delicate branched forms persist in calmer conditions, while robust plate forms persist in more turbulent conditions (Stearn and Riding, 1973; Davies and Montaggioni, 1985). In addition, *Millepora* spp. enhance their

Table 3

A summary of all interspecific interactions on the natural reef per unit area (m^{-2}).

Interaction name	Interaction number	Density (m^{-2})	Interaction/ density
P. astreoides - P. astreoides	749	48.7	15.4
P. caribaeroum - P. caribaeorum	692	37.7	18.4
Millepora spp. - Sponge	624	34.4	18.1
Sponge - Sponge	582	35.5	16.4
P. astreoides - Sponge	535	42.1	12.7
P. astreoides - Nothing	498	24.3	20.5
P. caribaeorum - Sponge	413	36.6	11.3
Millepora spp. - Nothing	386	16.7	23.2
P. caribaeorum - Millepora spp.	362	35.5	10.2
P. astreoides - Millepora spp.	323	41.0	7.9
P. astreoides - P. caribaeorum	262	43.2	6.1
Millepora spp. - Millepora spp.	245	33.3	7.4
P. caribaeorum - Nothing	208	18.8	11.1
Sponge - Nothing	194	17.8	10.9
Siderastrea spp. - Nothing	142	1.9	76.4
A. humilis - Sponge	90	19.8	4.6
P. porites - Nothing	83	2.5	33.0
P. porites - Sponge	58	20.3	2.9
A. humilis - Nothing	57	2.0	28.0
P. astreoides - A. humilis	54	26.4	2.1
P. astreoides - P. porites	53	26.9	2.0
P. astreoides - P. strigosa	33	25.0	1.3
P. porites - Millepora spp.	29	19.2	1.5
P. strigosa - Millepora spp.	28	17.4	1.6
M. decactis - Sponge	26	18.0	1.4
P. porites - P. caribaeorum	18	21.4	0.8
Stylaster roseus - Sponge	15	18.3	0.8
A. humilis - A. humilis	14	4.1	3.4
P. strigosa - Nothing	14	0.7	20.4
P. strigosa - Sponge	12	18.4	0.7
Siderastrea spp. - Sponge	9	19.6	0.5
A. humilis - Millepora spp.	9	18.7	0.5
P. astreoides - P. clivosa	8	24.6	0.3
D. labrynthiformis - Nothing	7	0.1	70.2
Siderastrea spp. - Siderastrea spp.	6	3.7	1.6
Siderastrea spp. - P. asteroides	5	26.2	0.2
A. humilis - P. porites	5	4.6	1.1
P. strigosa - P. caribaeorum	5	19.5	0.3
P. clivosa - Nothing	5	0.2	21.1
P. clivosa - Sponge	5	18.0	0.3
M. decactis - P. astreoides	5	24.6	0.2
A. lamarcki - Sponge	5	17.8	0.3
Millepora spp. - Gorgonian	4	17.0	0.2
A. humilis - P. caribaeorum	4	20.9	0.2
P. clivosa - P. astreoides	4	24.6	0.2
M. decactis - Millepora spp.	4	16.9	0.2
Siderastrea spp. - Millepora spp.	3	18.5	0.2
Siderastrea spp. - P. porites	3	4.4	0.7
P. porites - P. porites	3	5.0	0.6
M. decactis - P. caribaeorum	3	19.1	0.2
P. porites - P. strigosa	2	3.2	0.6
M. decactis - Nothing	2	0.2	8.4
M. decactis - A. humilis	2	2.3	0.9
F. fragum - Sponge	2	17.8	0.1
Stylaster roseus - Millepora spp.	2	17.2	0.1
Stylaster roseus- Nothing	2	0.5	3.7
P. astreoides - D. labrynithiformis	1	24.4	0.1
P. astreoides - Gorgonian	1	24.6	0.1
A. humilis - Stylaster roseus	1	2.6	0.4
D. labrynthiformis - P. caribaeorum	1	18.9	0.1
P. clivosa - P. caribaeorum	1	19.1	0.1
M. decactis - P. porites	1	2.8	0.4
F. fragum - Nothing	1	0.1	16.0

Table 3 (*continued*)

Interaction name	Interaction number	Density (m^{-2})	Interaction/ density
F. fragum - Millepora spp.	1	16.7	0.1
A. lamarcki - Nothing	1	0.1	26.7
A. lamarcki - P. astreoides	1	24.4	0.1
Gorgonian - Nothing	1	0.3	3.5
D. cylindrus - Sponge	1	17.8	0.1
D. cylindrus - P. astreoides	1	24.4	0.1

survival in turbulent conditions by densely packing numerous colonies together, to trap any broken fragments between upright blades (Lewis, 1991). Based on the existence of such a wave-resistant form and behavioural characteristics that would enable survival in a turbulent environment, it is surprising that the abundance and cover of *Millepora* spp. was significantly lower on the more turbulent artificial reef.

Although unevidenced, it remains a possibility that *Millepora* spp. have a preference for settlement on a more textured and porous surface as provided by the natural reef, as it hosts a significantly higher cover and abundance of *Millepora* spp. This theory, however, requires further research to justify –as similarly to CCA and turf algae– there appears to be no literature covering substrate preference for *Millepora* spp.

4.2.4. Porites astreoides

Similarly, the cover and density of *P. astreoides* was high on the natural reef and low on the artificial reef (Fig. 4). *Porites astreoides* is one of the most abundant species in the Caribbean and is known for its broad ecological range and 'weedy' life history strategy, making it highly abundant, even in adverse conditions (Bak, 1975; Chornesky and Peters, 1987; McGuire, 1998; Knowlton, 2001; Rivera and Goodbody-Gringley, 2014). Therefore, the low abundance and cover on the artificial reef compared to the natural reef was surprising. However, research on the distribution of *P. astreoides* has revealed that it exhibits a preference for calm conditions, in habitats sheltered from wave force (Bayraktarov et al., 2014). This could explain its higher presence on the natural reef than on the slightly more turbulent artificial reef.

Another potential explanation for this difference is interspecific competition. On the artificial reef, there was a higher cover of *P. caribaeorum*, a profound competitor for space, as mentioned above. The defensive mechanisms employed by sessile encrusting organisms to actively fight off their opponents, such as the production of secondary metabolites, are costly. The allocation of energy to defence, instead of growth, could explain the lower cover of *P. astreoides* on the artificial reef, in the presence of the aggressive competitor *P. caribaeorum* (Lang and Chornesky, 1990; Karlson, 1983; Endara and Coley, 2011).

4.3. Species assemblages on wave-exposed vs. wave-sheltered sites

As expected, our study found a significant difference in species assemblages between exposed and sheltered sites on both reefs (Fig. 6). Exposed sites were dominated by *Porites astreoides* and *Palythoa caribaeorum*, while sheltered sites were dominated by sponges (Fig. 6).

Findings by Rabelo et al. (2015), match those of our study, with *P. caribaeorum* also found as large crusts in areas exposed to strong wave action, like around Ascension Island in the middle of the Atlantic Ocean (Reimer et al., 2017). As mentioned above, the morphology of *P. caribaeorum* provides an adaptive advantage in exposed environments, with the presence of coenenchyme tissue that minimises the mechanical effect of constant water flow, thereby enabling them to resist waves, and persist in exposed environments (Koehl, 1977).

Previous findings on the distribution of *P. astreoides* are consistent with those of our study. Research carried out by Bak and Steward-Van Es (1980) found that *P. astreoides* has a high regenerative ability when damaged. This ability of *P. astreoides* to regenerate living coral tissue could enable it to survive in a wave-exposed environment, and therefore justify our findings.

The dominance of sponges on sheltered sites included the blue encrusting sponge *Halisarca caerulea*, a dark brown encrusting sponge, *Ircinia* sp., the red encrusting sponge *Spirastrella coccinea*, and the cylindrical shaped sponge *Aplysina* sp. Generally speaking, erect sponges dominate sheltered sites, while encrusting sponges dominate exposed sites (Readman, 2018; Bell and Barnes, 2000), yet here, we found a mix of encrusting and erect forms on sheltered sites. We did not however, specifically investigate sponge distribution across exposed and sheltered sites according to their body-plan. It is important to note, that while erect sponges tend to predominate sheltered sites (Roberts et al., 2006), they do not occupy sheltered sites exclusively, thereby supporting our findings.

4.4. Interspecific interactions

From observing the interspecific interactions between organisms, a more complete image of the species assemblages and community structure on each reef type was formed (Tables 2, 3; Fig. 7).

The natural reef had a higher number of interactions than the artificial reef (Tables 2, 3). This was anticipated given the natural reef was also found to have a higher density of organisms than the artificial reef, therefore making interactions far more likely, as found in previous studies (e.g., Logan, 1984).

The fewer interactions found on the artificial reef than on the natural reef in our study align with the findings of Ng et al. (2012), where colonies on an artificial structure in Singapore averaged a large distance of 1 m apart. The consistent finding that artificial structures display significantly reduced interactions, lends support to the suggestion of Bulleri and Chapman (2010) that man-made structures cannot serve as surrogates for natural environments due to their differences in key ecological processes such as competition, predation and facilitation.

It does appear, however, that there are similarities when looking at the top most common interaction pairings on both reefs. For example, among the top three most common interaction pairings on both reefs are *Porites astreoides* and *Palythoa caribaeorum* interacting with their relative conspecifics (Tables 2, 3). It is plausible that *P. caribaeorum* had fewer interactions with other benthic organisms, and more with its conspecifics due to its notoriously aggressive nature and excellent defence strategy of releasing a palytoxin to kill competitors (Gleibs et al., 1995). *Porites astreoides* on the other hand, displays minimal aggression towards competitors and therefore likely interacts with its conspecifics frequently to aggregate colonies and promote survival this way (Rivera and Goodbody-Gringley, 2014). In addition, the interaction of sponges with *P. astreoides* was among the top five most common pairings on both reefs (Tables 2, 3). Given corals and sponges are renowned competitors for space (Wulff, 2006, 2012) it is unsurprising to find many interactions between them. Overall, these similarities suggest that the community structure on the natural and artificial reef is partly more alike than initially thought.

4.5. Conclusions

Our study provides a much-needed comparison between old artificial coral substrates and natural reefs, removing the variable of age, to effectively compare mature species assemblages. In addition, our focus on urban coastal structures is crucial in a world where coastal development is increasing at an exponential rate, yet with minimal literature comparing their biodiversity with natural reefs.

The significant differences of cover, density and interaction frequency found between the artificial and natural reef, suggest that artificial reefs cannot serve as surrogates for natural reefs. A more valid comparison, however, is needed to back up this assertion as environmental factors –such as turbulence– interfered with the fair comparison of community composition between the two reefs in this study. Further research comparing artificial and natural reefs should therefore focus on reefs that are situated at slightly more similar depths and distances from the shoreline, with more equal environmental conditions.

While the artificial reef had a significantly different community composition to the natural reef, it still serves as a healthy and diverse reef in its own right. It is important, therefore, to not neglect the role of artificial reefs in conservation work just because they do not harbour identical communities to natural reefs. With that said, careful consideration is essential both prior to and post-installation of an artificial reef, due to its ability to facilitate the invasion of non-native species, potentially inducing unwanted negative effects on the surrounding ecosystems.

CRediT authorship contribution statement

Claudia E.L. Hill: Investigation, Writing – original draft, Writing – review & editing, Visualization. **Myrsini M. Lymperaki:** Investigation, Writing – review & editing, Visualization. **Bert W. Hoeksema:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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