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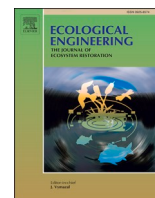
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The effects of wave exposure and host cover on coral-associated fauna of a centuries-old artificial reef in the Caribbean

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ABSTRACT

An increasing number of artificial reefs (ARs) are constructed to compensate for the loss of natural reefs (NRs), but little is known about their benthic community composition. Here, we compared the densities of coral-associated fauna (CAF) between a centuries-old manmade structure and the nearest NR at St. Eustatius, eastern Caribbean. Overall, no significant difference in the density of CAF (coral-dwelling barnacles, crabs, worms) was found between the NR and the AR, nor between the exposed and sheltered sides of each. Significantly different densities of CAF related to host cover were observed among corals on both the AR and the NR. Per host species, the AR did not show such differences in density between exposed and sheltered sides, although these differences were observed on the NR. Thus, turbulence and host cover regulate the density of CAF, while differences also depend on host species composition. Furthermore, from an ecological engineering perspective, the present AR resembles the NR in overall design, but not in relief rugosity and surface structure, which are also considered important contributors to the difference in species assemblages of the host corals and their CAF, even after many decades of community development.

1. Introduction

Coral reefs are the most diverse marine ecosystems worldwide and can thrive in remote oligotrophic tropical environments but also in close proximity to human settlements, where they are exposed to overfishing, eutrophication, sedimentation and various other kinds of land-based pollution (Miloslavich et al., 2010; Hughes et al., 2017, 2018; Heery et al., 2018). Elevated seawater temperatures due to climate change have also accelerated damage to the biological and structural complexity of tropical reefs around the world (Hughes et al., 2003; Carpenter et al., 2008). Consequently, coral reefs are globally recognised as a major ecosystem in need of conservation (Crosby et al., 2002; Klein et al., 2010; Burke et al., 2011). Therefore, various coral-reef restoration and rehabilitation techniques have been developed within recent years (Jaap, 2000).

Artificial reefs are submerged manmade structures consisting of synthetic or natural materials which can be designed specifically for the purpose of restoring or enhancing marine life, often recruiting reef-

associated organisms, such as macroalgae, invertebrates, and fishes (Seaman and Jensen, 2000; Baine, 2001; Schuhmacher, 2002; Svane and Petersen, 2001; Hylkema et al., 2021; Mathews et al., 2021; Reis et al., 2021). Artificial structures are likely to be colonised by marine organisms like algae and invertebrates within two to four weeks of deployment (Bailey-Brock, 1989; Bohnsack et al., 1994; Plass-Johnson et al., 2016). Overtime, communities of artificial reefs (ARs) may resemble those of natural reefs (NRs) and can even compete with them in terms of abundance and diversity of fish and benthic organisms (Rilov and Benayahu, 2000; Pondella et al., 2002; Perkol-Finkel and Benayahu, 2004). However, the patterns and mechanisms driving differences in species composition between ARs and adjacent NRs are yet to be fully understood (Burt et al., 2009a). Typically, differences in coral assemblages usually result from structural dissimilarities between natural and artificial substrates (Perkol-Finkel et al., 2005, 2006; Hill et al., 2021).

The most common factors influencing the composition and abundance of colonisers, and therefore the success of an AR, are reef size, surface area, complexity, water quality and local hydrodynamics

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(Baynes and Szmant, 1989; Connell, 1999; Glasby, 2000; Burt et al., 2009a). Depth is also a factor that influences the development rate on artificial structures, with a higher biomass of fish and epifauna found on shallower ARs, with a subsequent decrease towards greater depths (Shinn and Wicklund, 1989; Svane and Petersen, 2001). Other important factors affecting species assemblages are the design and the type of material used in the construction of ARs (Hylkema et al., 2020; Monchanin et al., 2021; Ramm et al., 2021; Reis et al., 2021). Geochemical signatures released by substrates can be detected by several benthic organisms in their larval phase, which could lead to the development of different communities (Maldonado and Uriz, 1998; Qian, 1999).

Most studies on fauna associated with ARs focus on fish assemblages (Tupper and Hunte, 1998; Burt et al., 2013; Mills et al., 2017; Komyakova et al., 2019) or benthic assemblages covering artificial structures (Burt et al., 2011; Grizzle et al., 2016; Chou et al., 2017; Higgins et al., 2019; Biondi et al., 2020; Kikuzawa et al., 2020; Hill et al., 2021; Mamo et al., 2021), but little attention has been paid to the importance of coral-associated fauna on benthic assemblages on manmade reefs. This is remarkable because corals are known to harbour many different species of invertebrates and fish that have an obligate symbiotic relationship with their host, and this associated fauna can potentially be used as an indicator for the condition of coral reefs (Risk et al., 2001; Scaps and Denis, 2007; Stella et al., 2011; Hoeksema et al., 2012; Biondi et al., 2019; Montano, 2020). Many of these associated species are small and inconspicuous and are therefore called cryptobenthic reef fauna (Ahmadia et al., 2012; Hoeksema, 2017; Brandl et al., 2020). This reef cryptofauna can be harmful to their host corals when they live on the coral upper surface and damage, overgrow or smother polyps (Samimi-Namin et al., 2010; Hoeksema and Farenzena, 2012; Wijgerde et al., 2013; Hoeksema et al., 2019a, 2019b); or as endofauna boring into the coral skeleton (Gittenberger and Gittenberger, 2011; Printrakoon et al., 2016; de Bakker et al., 2018), while others dwell between the coral tentacles, in crevices, or underneath corals without causing visible damage (Brinkmann and Franssen, 2016; Rauch et al., 2019; García-Hernández and Schizas, 2021).

The nature of these symbiotic relationships is not always clear (Hoeksema, 2017), but in many cases the associated species use the host as a food source (Gittenberger and Hoeksema, 2013; Potkamp et al., 2017b; Scott et al., 2017; Kaullysing et al., 2019), while in other cases, the host coral predominantly appears to be used as shelter (van der Meij, 2014; García-Hernández et al., 2020; Hoeksema and García-Hernández, 2020), or substrate (Hoeksema et al., 2013; Ivanenko et al., 2018; Korzhavina et al., 2019; Maggioni et al., 2020). On the other hand, there are also examples of associated fauna possibly aiding the protection of their host against predation (DeVantier and Endean, 1998; Pratchett, 2001; Montano et al., 2017; Samsuri et al., 2018), reducing their host's susceptibility to disease (Pollock et al., 2013; Montano et al., 2017), and minimising the negative effects of sedimentation (Stewart et al., 2006).

Since this cryptobenthic fauna appears to play relevant roles in the biodiversity and condition of coral communities, it seems opportune to study their representation on ARs as well. While corals need their time to settle and grow on ARs, it may take even more time for them to become infested by associated fauna. The older and larger a host can grow, the more time and surface area it will make available for the colonisation of symbionts. Therefore, in an ideal situation, the AR should be as old as possible.

On the Caribbean island of St. Eustatius, a manmade reef is present at the western shoreline, consisting of basalt structures that have been submerged since the 19th century and have been researched in a previous study with focus on the cover, species composition and interspecific competition of corals and other benthic organisms (Hill et al., 2021). Given the fact that similar old structures have not previously been studied regarding coral-associated invertebrates, the presence of this coral community on old manmade structures at St. Eustatius offered the opportunity to compare the roles of its coral-associated fauna with those of a nearby natural reef. We hypothesised that the density of coral-

associated fauna would be lower on the AR at comparable depths. This is because in a previous study that compared the benthic cover between the same AR and NR as in the present study, lower cover was found on the AR (Hill et al., 2021), meaning there are fewer coral hosts available for the associated fauna to colonise. In addition, artificial structures have been reported to have higher homogeneity and less microhabitats, which suppress the increase of biodiversity (Moschella et al., 2005; Aguilera et al., 2014; Kikuzawa et al., 2020). These results will help us to ascertain if centuries-old man-made structures provide a suitable substrate for the development of a well-established reef community.

Additionally, in order to gain a more thorough understanding of the associated-fauna community, we investigated the preferences of the associated fauna between the sheltered and exposed sides of both reefs to wave and current action, because it is possible that wave exposure has a selective effect on this (Hill et al., 2021). We hypothesised that associated species living attached and partly embedded inside the host coral, such as Christmas tree worms and coral barnacles (Nishi and Nishihira, 1996; Liu et al., 2016) would be more resistant to wave action and therefore have a higher density on the exposed sides than associated fauna predominantly living inside dwellings on the host surface, such as crabs and fish (García-Hernández et al., 2020; Böhm and Hoeksema, 2017).

2. Materials and methods

Data was collected in conjunction with the study of Hill et al. (2021) at St. Eustatius, with both studies using a similar methodology to compare communities between an ancient AR and an adjacent NR. The present study differs from this companion study in that it focuses on coral-associated fauna instead of the main benthic organisms, their cover, and interactions.

2.1. Locality

Both reefs are located nearshore of the sheltered Caribbean coastline of St. Eustatius, eastern (Dutch) Caribbean. The artificial reef (17°28'53.14"N, 62°59'15.40"W) is situated at a maximum depth of 2 m, at a distance of 5–35 m from the shoreline (Fig. 1a). It consists of 12 independent rock formations that are remnants of an ancient manmade breakwater (from the 19th century) that were demolished by the regular occurrence of forcible hurricanes (Hill et al., 2021). The AR has a distinctly manmade appearance, with large smooth basalt stones visibly cemented together, showing little relief rugosity (Fig. 1b).

The natural reef (17°28'56.16"N, 62°59'19.26"W to 17°28'49.97"N, 62°59'15.13"W) runs parallel to the coastline at a total length of 260 m, and is situated 50–75 m away from the shore, at a maximum depth of 4 m (Fig. 1a). It is located on top of a lava underground, which has a rough surface and much relief rugosity, shown by numerous crevices and overhangs that offer various sheltered habitats (Fig. 1c).

2.2. Data collection

Data was collected via underwater photography using SCUBA in February and March of 2020. A photo quadrat of 25 × 25 cm² (Hill et al., 2021: Fig. 3a) was used to take images of all host corals and their associated fauna across both reefs. Most species included anthozoans of the subclass Hexacorallia (belonging to various families in the orders Scleractinia and Zoantharia) and hydrozoans of the subclass Hydrozoa (order Anthoathecata: family Milleporidae). As coral-associated fauna we only counted invertebrate fauna living on top of the host corals, some of which were located inside holes with openings at the coral surface. Sessile invertebrates living next to live corals were not included, such as feather duster worms of the family Sabellidae (Tovar-Hernández and Salazar-Vallejo, 2006), which were found on dead corals during the present study.

For every image taken, the exposure to wave-force was recorded as

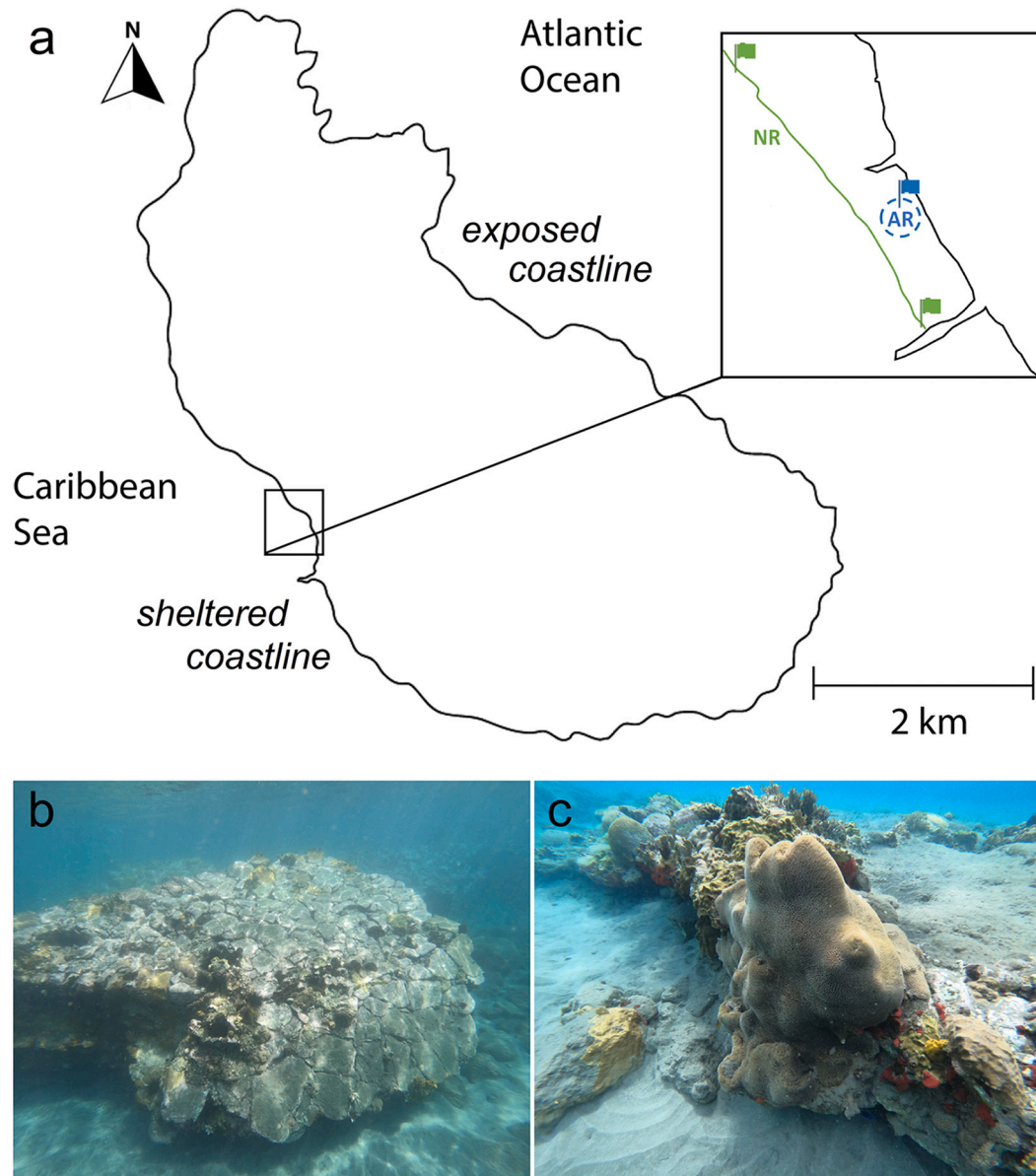


Fig. 1. (a) Map indicating the locality of the field sites on the sheltered coast of St. Eustatius; the natural reef site (marked by the green line labelled 'NR') runs parallel to the shoreline at a length of 260 m, 50–75 m offshore; the artificial reef site (located within the dashed circle labelled 'AR') constitutes 12 rock formations, 5–35 m offshore (after Hill et al., 2021). (b) An outcrop of the artificial reef. (c) A subsection of the natural reef. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

either 'sheltered' if the coral-associated invertebrates were within a crevice or beneath an overhang, or 'exposed' if they inhabited the reef flat or sides. A total of 1865 images were taken across the NR (80%) and the AR (20%). From this, we calculated the total photographed surface area of each reef by multiplying the quadrat area ($25 \times 25 \text{ cm}^2$) with the number of images taken on each reef. Additional images were taken of smaller more cryptic fauna using a higher resolution camera (Fujifilm XP) to aid taxonomic identification.

2.3. Data processing

All photographs were individually analysed in order to identify all associated fauna and benthic hosts to the lowest possible taxonomic rank. Specimen identification was aided by the field guides of Humann and Deloach (2013) and Humann et al. (2013). Following identification, the abundance was obtained by manually counting the number of individual organisms within each image. Abundance counts were

converted to density (m^{-2}) values by dividing them by the surface area of the relevant reef, enabling us to compare the AR and NR fairly. The density of coral-associated species per host (dm^{-2}) was also calculated to account for the size difference between the AR and NR.

2.4. Statistical analyses

We used a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) with a total of 999 random permutations and a Bray-Curtis distribution (Bray and Curtis, 1957) to test whether the densities of the associated-fauna communities significantly differed between the NR and AR, and between exposed and sheltered sides of each reef. In addition, we used an analysis of similarity percentages procedure (SIMPER; Clarke, 1993) to determine the contributions of individual coral-associated fauna (%) to the overall differences between the two reefs and between the two sides calculated with PERMANOVA. We reported SIMPER results up to ~70% as each of these taxonomic

groups contributed more than 10% to the variance between the reefs. All of the above data analyses and visualization were carried out in R software (R Core Team, 2019) with use of packages ‘vegan’ (Oksanen et al., 2019), ‘dplyr’ (Wickham et al., 2020), ‘ggplot2’ (Wickham, 2016), and ‘tidyr’ (Wickham, 2020). Results of the density of the coral-associated fauna were interpreted using bar plots.

3. Results

3.1. The host corals and their associated fauna

Among the coral species (milleporids, scleractinians, and zoantharians) on the AR and the NR at St. Eustatius (Hill et al., 2021), several corals were important as hosts for associated fauna. These were the zoantharian *Palythoa caribaeorum* Duchassaing & Michelotti, 1860 (Anthozoa: Hexacorallia: Sphenopidae), the hydrocorals *Millepora alcornis* Linnaeus, 1758 and *M. complanata* Lamarck, 1816 (Hydrozoa: Anthothecata: Milleporidae), and the stony corals *Agaricia humilis* Verrill, 1901, *Dendrogyra cylindrus* (Ehrenberg, 1834), *Madracis decactis* (Lyman, 1859), *Porites astreoides* Lamarck, 1816, *Porites porites* (Pallas, 1766), *Pseudodiploria clivosa* (Ellis & Solander, 1786), *Pseudodiploria strigosa* (Dana, 1846), *Siderastrea radians* (Pallas, 1766), and *Siderastrea siderea* (Ellis & Solander, 1786) (Anthozoa: Hexacorallia: Scleractinia). The two *Millepora* species are referred to as *Millepora* spp. because encrusting parts and juvenile forms could not be identified at species level. Since both *Millepora* spp. tend to start substrate colonisation with an encrusting growth form and, like some congeners, continue to maintain this as dominant shape in turbulent water, this character is usually not reliable in distinguishing species (de Weerd, 1984; Lewis, 2006; de Souza et al., 2017). Similarly, both *Siderastrea* species are referred to as *Siderastrea* spp. because their colonies were usually small and not all of them could be easily distinguished in the photographs.

The associated fauna (Fig. 2) consisted of coral barnacles of the families Balanidae and Pyrgomatidae, the christmas tree worms *Spirobranchus giganteus* (Pallas, 1766) and *S. polycerus* (Schmarda, 1861) of

the family Serpulidae, coral gall crabs of the family Cryptochiridae, and the gaudy clown crab *Platypodiella spectabilis* (Herbst, 1794) of the family Xanthidae. The coral barnacles and the gall crabs were not identified at species level due to photographs being too ambiguous. The two worms are hereafter referred to as *Spirobranchus* spp., because their species identity could not be determined when they were retracted inside their tube. Finally, some holes were found of which the inhabitant could not be identified, and these were classified as “unknown holes”.

3.2. Associated fauna on the natural vs. artificial reef

No significant difference in the density of associated fauna between the NR and AR overall was found (PERMANOVA, pseudo-F = 1.5181, $p > 0.05$). Some patterns were observed, such as higher densities of coral barnacles (40.4 vs. 24.6 m^{-2}), *Spirobranchus* spp. (29.3 vs. 22.6 m^{-2}), and *P. spectabilis* (11.0 vs. 9.7 m^{-2}), and lower densities of unknown holes (1.9 vs. 4.8 m^{-2}) and gall crabs (1.1 vs. 1.4 m^{-2}) on the NR than the AR respectively (Fig. 3). Only coral barnacles contributed ~70% to the overall differences between the natural and artificial reef (Table 1).

3.3. Associated fauna per benthic host on the AR and the NR

Significantly different densities among species of associated fauna related to host cover were observed on both the AR (Table 2; PERMANOVA, pseudo-F = 5.5548, $p = 0.002$) and the NR (Table 2; PERMANOVA, pseudo-F = 3.9404, $p = 0.040$). Densities of *Spirobranchus* spp. found on *Millepora* spp. and *Madracis decactis*, as well as coral gall crabs found on *Pseudodiploria clivosa* and *Pseudodiploria strigosa* contributed ~70% to the overall differences between the host cover on the two reefs (Table 1). Coral barnacles showed little difference in density per host cover of *Millepora* spp. (AR = 0.9, NR = 0.8 m^{-2}) and of *Porites astreoides* (AR = 1.6, NR = 2.0 m^{-2}) on both reefs (Table 2). No difference was observed in the density of *Spirobranchus* spp. per host cover of *P. astreoides* on both reefs (0.9 dm^{-2}) (Table 2). *Platypodiella spectabilis* had a higher density per host cover of *Palythoa caribaeorum* on the NR

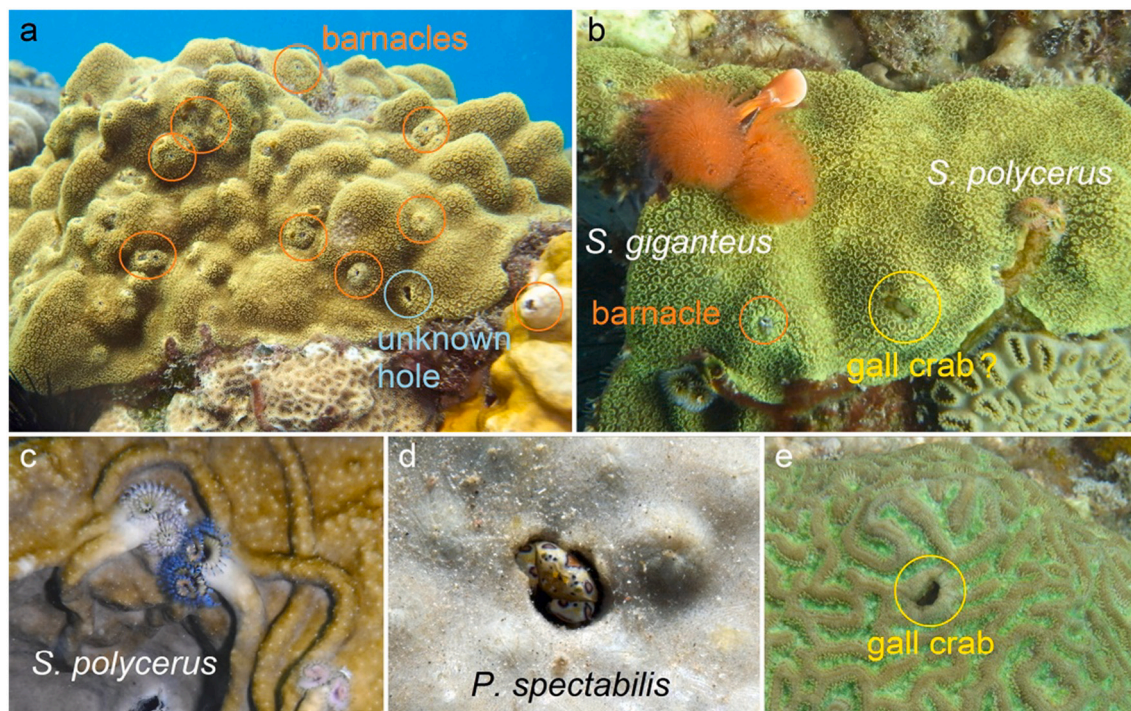


Fig. 2. Examples of coral-associated fauna at the study locality: (a) *Porites astreoides* (center) and *Millepora* sp. (right corner below) with barnacles; the first also showing an “unknown hole”; (b) *P. astreoides* with *Spirobranchus* spp., a coral barnacle, and an apparent gall crab; (c) *Millepora* sp. with *Spirobranchus polycerus*; (d) *Palythoa caribaeorum* with the gaudy clown crab *Platypodiella spectabilis*; (e) *Pseudodiploria strigosa* with a gall crab. Photographs a, b, d, and e were taken in 2015.

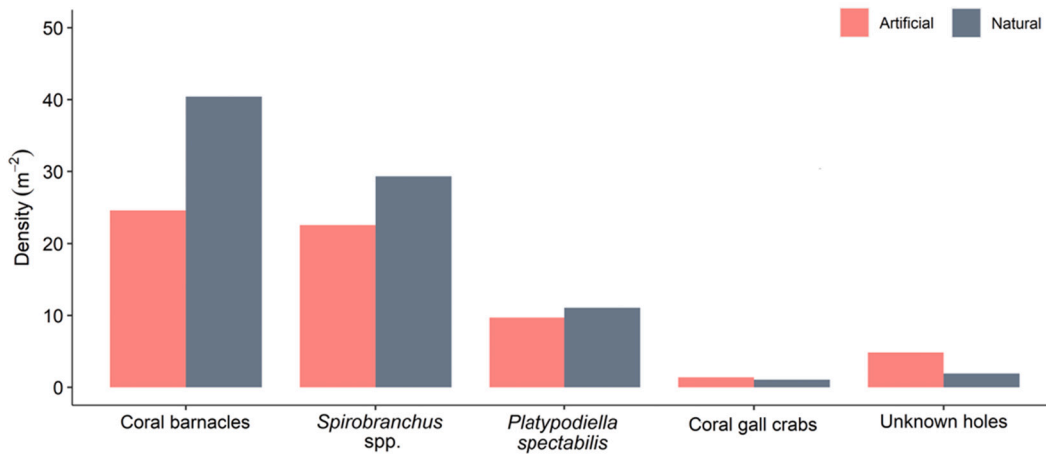


Fig. 3. Densities (m⁻²) of associated fauna on the artificial and natural reef.

Table 1

SIMPER analysis results of the coral-associated fauna that contributed up to ~70% of the observed variance when testing for differences between the artificial and natural reef using PERMANOVA.

Data type	Organisms (associated fauna / benthic hosts)	Cumulative percentage (%)
Abundance	Coral barnacles	58.1
	Coral barnacles - <i>Porites astreoides</i>	34.3
	Coral barnacles - <i>Millepora</i> spp.	58.8
Associated fauna per benthic host	<i>Spirobranchus</i> spp. - <i>Millepora</i> spp.	69.6
	Coral gall crabs - <i>Pseudodiploria clivosa</i>	34.5
	<i>Spirobranchus</i> spp. - <i>Madracis decactis</i>	47.1
	Coral gall crabs - <i>Pseudodiploria strigosa</i>	58.6
	<i>Spirobranchus</i> spp. - <i>Millepora</i> spp.	66.7
Associated fauna per host cover	<i>Platypodiella spectabilis</i>	41.9
	<i>Spirobranchus</i> spp.	34.8
AR exposed vs. sheltered sides	Coral barnacles	66.9
Associated fauna per benthic host on the AR, exposed vs. sheltered sides	<i>P. spectabilis</i> - <i>Palythoa caribaeorum</i>	40.4
	Coral barnacles - <i>P. astreoides</i>	57.3
	<i>P. spectabilis</i> - <i>Palythoa caribaeorum</i>	30.3
	<i>Spirobranchus</i> spp. - <i>P. astreoides</i>	48.3
Associated fauna per benthic host on the NR, exposed vs. sheltered sides	Coral barnacles - <i>P. astreoides</i>	65.8

than the AR (AR = 0.7, NR = 1.3 dm⁻²) (Table 2).

3.4. Associated fauna on exposed vs. sheltered sides

The density of associated fauna did not differ significantly between exposed and sheltered sides on the AR (Fig. 5a; PERMANOVA, pseudo-F = 1.81, $p > 0.05$). Exposed sides had a higher density of *Platypodiella spectabilis* compared to the sheltered sides (15.6 vs. 3.6 m⁻²), which contributed ~70% to the overall differences (Table 1). Coral barnacles (29.0 vs. 20.0 m⁻²) dominated exposed over sheltered sides respectively, while *Spirobranchus* spp. (26.2 vs. 21.6 m⁻²) and coral gall crabs (2.3 vs. 0.5 m⁻²) dominated sheltered over exposed sides respectively. Unknown holes were observed in higher densities on the exposed over the sheltered sides (5.5 vs. 4.2 m⁻²).

On the NR, there was also no significant difference in the density of associated fauna between exposed and sheltered sides (Fig. 5b; PERMANOVA, pseudo-F = 8.796, $p > 0.05$). Coral barnacles (46.2 vs. 31.7 m⁻²) and *Spirobranchus* spp. (23.1 vs. 38.7 m⁻²) contributed ~70% to the overall differences between the exposed and sheltered sides respectively (Table 1). Additionally, exposed sides had a high density of *P. spectabilis* (16.6 vs. 2.7 m⁻²) compared to sheltered sides, while coral gall crabs (1.1 vs. 1.0 m⁻²) had similar densities between the two sides. Lastly, unknown holes were observed in low densities between the exposed and sheltered sides respectively (2.3 vs. 1.3 m⁻²).

3.5. Associated fauna per benthic host on exposed vs. sheltered sides

On the AR, overall, densities of associated fauna observed per benthic host species did not differ significantly between the exposed (E) and sheltered (S) sides (Fig. 6a; PERMANOVA, pseudo-F = 0.156, $p > 0.05$). Coral barnacles were abundant on *Millepora* spp. (E = 9.9, S = 6.0 m⁻²) and *P. astreoides* (E = 19.2, S = 14.1 m⁻²), which together with *Platypodiella spectabilis* observed on the zoantharian *P. caribaeorum* (E = 15.7, S = 3.6 m⁻²) contributed ~70% to the overall differences between the exposed and sheltered sides (Table 1). Coral gall crabs were observed on *P. clivosa* (E = 0.0, S = 1.9 m⁻²), *A. humilis* (E = 0.1, S = 0.4 m⁻²), and *P. strigosa* (E = 0.4, S = 0.0 m⁻²). *Spirobranchus* spp. was observed on *Millepora* spp. (E = 14.0, S = 16.1 m⁻²) and *P. astreoides* (E = 7.3, S = 10.4 m⁻²). Unidentified holes were only observed on *P. astreoides* (E = 4.2, S = 3.1 m⁻²) and *P. porites* (E = 1.3, S = 1.1 m⁻²).

On the NR, significantly different densities of associated fauna were observed per benthic host species between exposed and sheltered sides (Fig. 6b; PERMANOVA, pseudo-F = 2.674, $p = 0.048$). Coral barnacles observed on *P. astreoides* (E = 29.1, S = 21.0 m⁻²), *P. spectabilis* observed on *P. caribaeorum* (E = 16.6, S = 2.7 m⁻²), and *Spirobranchus* spp. observed on *P. astreoides* (E = 7.5, S = 15.8 m⁻²) contributed ~70% to the overall differences between the exposed and sheltered sides (Table 1). Other coral barnacles were found in lower densities on *Millepora* spp. (E = 17.1, S = 10.7 m⁻²). Members of *Spirobranchus* spp. were also observed on *Millepora* spp. (E = 15.3, S = 21.9 m⁻²), *P. strigosa* (E = 0.1, S = 0.3 m⁻²), *A. humilis* (E = 0.0, S = 0.3 m⁻²), *M. decactis* (E = 0.2, S = 0.3 m⁻²), *Siderastrea* spp. (E = 0.0, S = 0.1 m⁻²), and *P. porites* (E = 0.0, S = 0.1 m⁻²). Gall-crab holes were observed on *P. strigosa* (E = 0.7, S = 0.4 m⁻²), *P. clivosa* (E = 0.1, S = 0.3 m⁻²), *A. humilis* (E = 0.0, S = 0.2 m⁻²), *D. cylindrus* (E = 0.1, S = 0.0 m⁻²), and *Siderastrea* spp. (E = 0.0, S = 0.1 m⁻²). Lastly, some holes were unidentifiable on *P. astreoides* (E = 1.9, S = 1.2 m⁻²), *P. porites* (E = 0.3, S = 0.4 m⁻²), and on *M. decactis* (E = 0.1, S = 0.1 m⁻²).

Table 2

Density of coral-associated species per reef area (m^{-2}) and per host cover (dm^{-2}) on both the artificial (AR) and natural reef (NR). The five most abundant associated taxa are indicated in **bold** script. Host cover data derived from Hill et al. (2021).

Associated fauna	Host species	AR density (m^{-2})	NR density (m^{-2})	AR host cover (%)	NR host cover (%)	AR density per host cover (dm^{-2})	NR density per host cover (dm^{-2})
Coral barnacles	<i>Millepora</i> spp.	8.0	14.6	8.9	18.1	0.9	0.8
	<i>Porites astreoides</i>	16.7	25.9	10.3	12.7	1.6	2.0
<i>Spirobranchus</i> spp.	<i>Agaricia humilis</i>	0.0	0.1	4.1	3.0	0.0	0.0
	<i>Madracis decactis</i>	0.0	0.2	0.0	0.2	0.0	1.1
	<i>Millepora</i> spp.	15.1	17.9	8.9	18.1	1.7	1.0
	<i>P. astreoides</i>	8.8	10.8	10.3	12.7	0.9	0.9
	<i>Porites porites</i>	0.0	0.0	0.2	0.3	0.0	0.1
	<i>Pseudodiploria strigosa</i>	0.0	0.2	0.1	0.5	0.0	0.4
	<i>Siderastrea</i> spp.	0.0	0.0	0.1	0.2	0.0	0.2
	<i>A. humilis</i>	0.3	0.1	4.1	3.0	0.1	0.0
	<i>Dendrogyra cylindrus</i>	0.0	0.1	0.0	0.1	0.0	0.7
	<i>Pseudodiploria clivosa</i>	0.9	0.2	0.2	0.1	4.6	1.6
Coral gall crabs	<i>Pseudodiploria strigosa</i>	0.2	0.6	0.1	0.5	2.2	1.2
	<i>Siderastrea</i> spp.	0.0	0.1	0.1	0.2	0.0	0.3
	<i>Palythoa</i>	9.8	11.0	14.2	8.6	0.7	1.3
	<i>caribaeorum</i>						
	<i>Platypodiella spectabilis</i>						

4. Discussion

4.1. The host corals and their associated fauna

The purpose of this research was to study differences in reef-associated fauna between an ancient artificial reef and the nearest natural reef. The results indicated that there were no clear differences in species composition in the associated fauna between the AR and NR. *Millepora* spp., *Porites astreoides*, and *Palythoa caribaeorum* were the most common hosts. Barnacles were the most dominant associated invertebrates on both reefs followed by serpulid polychaete worms (*Spirobranchus* spp.), and the gaudy clown crab (*Platypodiella spectabilis*), whereas coral gall crabs were recorded in lower densities. Some associated fauna known from other localities were missing. Details are discussed in the following paragraphs.

4.1.1. Coral barnacles

The coral barnacles found in *Millepora* spp. and *P. astreoides* (Fig. 2a) were not identified at species level but based on their host choice they are likely the balanid *Megabalanus stultus* (Darwin, 1854) and the pyrgomatid *Ceratoconcha quarta* (Kolosváry, 1947), respectively. *M. stultus* is a conical-shaped, protruding species (Lewis, 1992), while *C. quarta* is the only barnacle species recorded for its host (Scott, 1987), remaining low and embedded in the coral surface (Fig. 2b).

Coral barnacles were most abundant on the NR and more abundant on the exposed sides than on the sheltered sides of each reef. Besides studies on host choice, distribution ranges, settlement and development (Brickner et al., 2010; Liu et al., 2016; Chan et al., 2018; Chan et al., 2020), very little is known about the ecology of coral barnacles (Lewis, 1992). The higher abundance on NRs can partly be explained by their higher cover of hosts and the same counts for the exposed sides (Hill et al., 2021). This simple effect of habitat availability can be enforced by the tendency of barnacles to form aggregations (Gebauer et al., 2020), but this may be less clear in coral barnacles that tend to keep distance from coral polyps (Liu et al., 2016). With regard to wave exposure, barnacles are well known to resist turbulence and they are generally known to be abundant in shallow-water at wave-exposed shorelines (e.g., Pardal et al., 2021). Higher densities of barnacles and other filter-feeders in response to wave exposure is a commonly known pattern, as the elevated water flow can increase the food availability (Leonard et al., 1998; McQuaid and Lindsay, 2000).

4.1.2. Coral gall crabs

Because most Caribbean host coral species are inhabited by a single symbiotic gall crab species (van der Meij, 2014; Hoeksema et al., 2017; García-Hernández et al., 2020), it is possible to link host corals to their most probable associated crab species. The cryptochirid *Opecarcinus hypostegus* (Shaw & Hopkins, 1977) is the single candidate species living on *Agaricia humilis*, whereas *Troglocarcinus corallicola* Verrill, 1908, is known as the only associated crab living in the scleractinians *Dendrogyra cylindrus* (tentatively), *Pseudodiploria clivosa*, and *P. strigosa*. Host corals of *Siderastrea* form an exception with three possible crab symbionts (van der Meij, 2014). Although no gall crab has ever been reported from *P. astreoides* or any other *Porites* species (Chan et al., 2020), the photograph in Fig. 2b suggests that a gall crab may occur in this host, although its identity is unclear. More research is needed to verify this possible association.

Host diversity is slightly lower on the AR ($n = 3$) compared to the NR ($n = 5$), but due to multiple hosts sharing the same crab species, the difference in crab diversity is even less with $n = 2$ and $n = 3$, respectively. The variations in gall crab density between the AR and the NR and between exposed and sheltered sides are too small for drawing conclusions.

4.1.3. Christmas tree worms

Spirobranchus spp. are tube-dwelling polychaetes that usually have their tube overgrown and incorporated in the host coral (Nishi and Nishihira, 1996), which can be either scleractinians or milleporids (Floros et al., 2005; Montebon and Yap, 2009). They commonly settle on the surface of the host coral where they build their calcareous tubes, without excavating the coral (Hunte et al., 1990). In this study, both, the large *Spirobranchus giganteus* and the smaller *S. polycerus* were recorded with overlapping host choice (Fig. 2). The first one has a wide depth range and can be found in many host species (Hunte et al., 1990; Hoeksema and ten Hove, 2017a), while the second one is most common in shallow-water hosts (Hoeksema and ten Hove, 2017b; Hoeksema et al., 2020). Due to the shallow position of both reefs, both *Spirobranchus* species were encountered (Fig. 6).

4.1.4. The gaudy clown crab

Platypodiella spectabilis is exclusively associated with zoantharians, including those in symbiosis with sponges (García-Hernández et al., 2016), and in particular *Palythoa caribaeorum*, which is very common in shallow Caribbean waters (Reimer et al., 2018; Montenegro et al., 2020). In the present research, this crab was also found exclusively in

P. caribaeorum, which has been reported to occur in relatively high densities at the study site (Hill et al., 2021).

4.1.5. Unknown holes

Holes of unknown origin were observed in the corals *M. decactis*, *P. astreoides*, and *P. porites* (Figs. 4, 6). These coral species have so far not been recorded as hosts of gall crabs (Kropp and Manning, 1987; van der

Meij, 2014), although this needs to be verified (Fig. 2b). A possible candidate species using the unknown holes could be the Atlantic coral shrimp *Pomatogebia operculata* (Schmitt, 1924), family Upogebiidae, which has been reported most frequently from *P. astreoides* and less from some other scleractinians (Kleemann, 1984; Scott et al., 1988; Coelho et al., 2000), but not yet from *M. decactis* and *P. porites*.

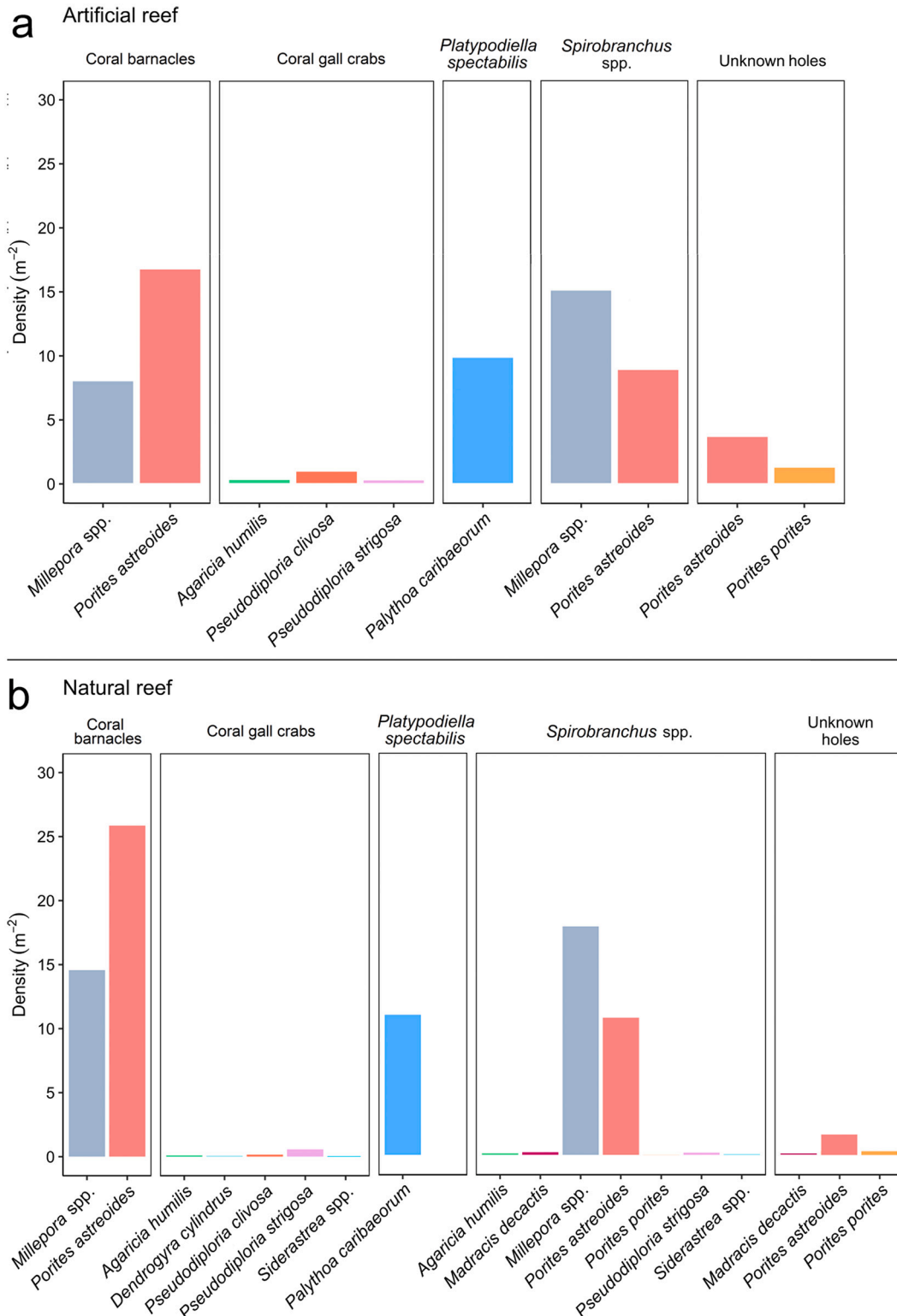


Fig. 4. Densities (m⁻²) of associated fauna per benthic host species (x-axis) on the artificial reef (a) and the natural reef (b).

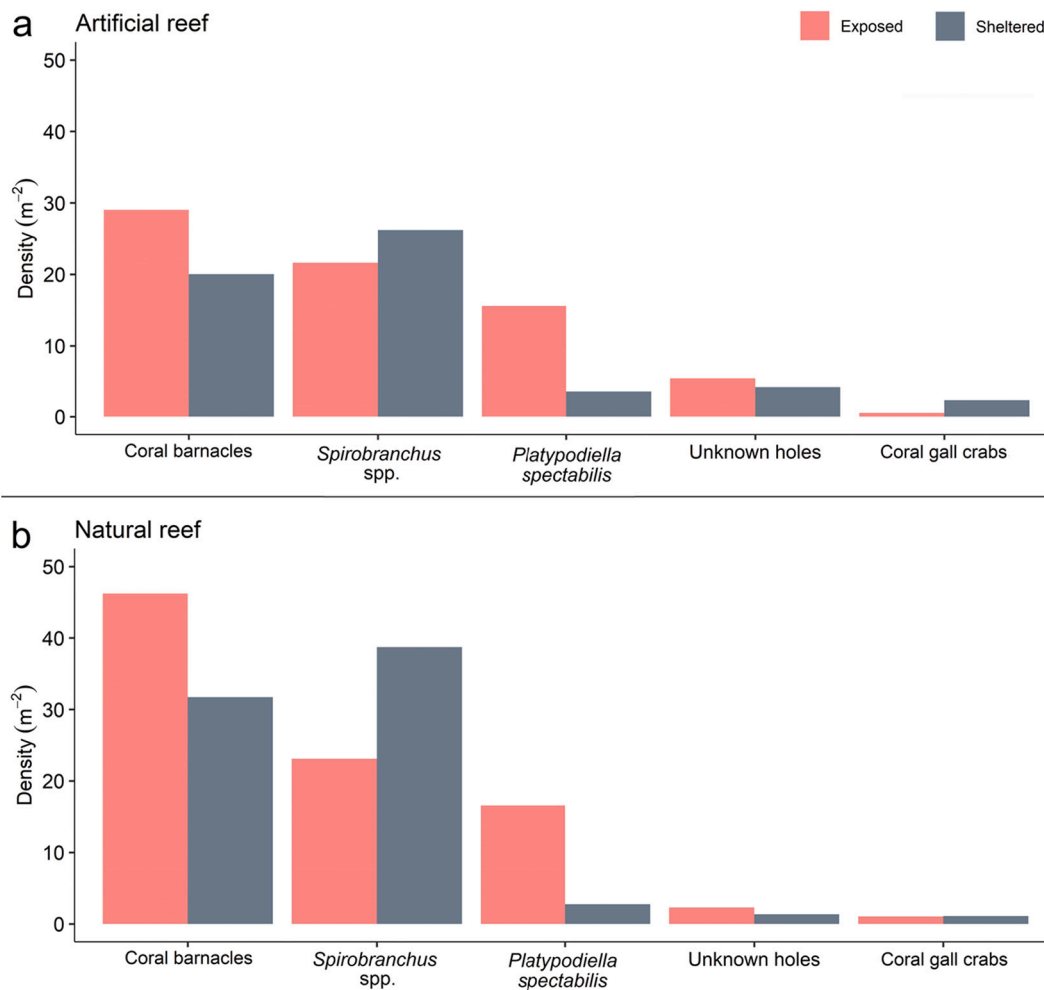


Fig. 5. Densities (m^{-2}) of associated fauna on the exposed and sheltered sides of (a) the artificial reef, and (b) the natural reef.

4.1.6. Missing fauna

The crab *Domecia acanthophora* (Desbonne, 1867) of the family Domeciidae, is known to dwell in holes in shallow-water scleractinians, such as on the surface of the hydrocoral *Millepora complanata* (Scott, 1987; Hoeksema and García-Hernández, 2020), but was not observed in the present research. No coral-dwelling gastropods that usually hide inside crevices in corals, such as the corallivorous *Coralliophila galea* (Dillwyn, 1823), were found. Whereas, in other Caribbean localities these snails can be found in *Pseudodiploria* corals at shallow depths (Potkamp et al., 2017a). Although not invertebrates, coral-dwelling blennies, *Acanthemblemaria spinosa* (Metzelaar, 1919), were also not observed in the quadrats, while their preferred habitat was available, mostly consisting of empty *Spirobranchus* tubes (Böhm and Hoeksema, 2017). This lacking epifauna suggests that the shallow reefs of St. Eustatius were perhaps too exposed to wave action, restricting the settlement of certain coral associates.

4.2. Associated fauna on the natural vs. artificial reef

Our findings revealed that overall, the associated fauna had a lower species diversity and lower densities on the AR compared to the NR, which is consistent with lower densities and cover of host species on the AR. The difference in density was not significant, although there was a general pattern of lower densities on the AR shown by coral barnacles, *Spirobranchus* spp., and *P. spectabilis*, while coral gall crab densities were too low for expressing a clear contrast (Figs. 4, 6). The lower host cover on the AR was attributed to a smoother substrate surface, a less complex

structure, and a lower benthic micro-habitat diversity (Hill et al., 2021). Tomascik et al. (1996) investigated coral colonisation of lava flow in the Banda Sea (Indonesia) and showed that only five years after the eruption of a local volcano, a large area of volcanic substrate was covered by a diverse coral assemblage of 124 species.

Habitat heterogeneity can differ between ARs. Some studies have found ARs to increase diversity on a local scale (Moura et al., 2006; Burt et al., 2009a), while other studies suggest that ARs lack microhabitats, which may be a key factor determining diversity on a local scale (Moschella et al., 2005; Burt et al., 2009b; Carr and Hixon, 2011; Aguilera et al., 2014). Typically, the lower diversity found on ARs vs. NRs can be explained by the older age of NRs, allowing more time to establish a mature community (Clark and Edwards, 1999; Perkol-Finkel et al., 2006; Perkol-Finkel and Benayahu, 2009). This factor can be ignored in the present comparison however, as the manmade reef in question has been submerged for centuries (Hill et al., 2021).

4.3. Associated fauna per benthic host on the AR and the NR

Significant interspecific differences in densities of species inhabiting different corals were observed between both reefs. More specifically, *P. astreoides* and *Millepora* spp. were found to be occupied by high numbers of barnacles on the NR. *Spirobranchus* spp. were present in high densities on *Millepora* and on *P. astreoides*, with only few individuals inhabiting other coral species (*Pseudodiploria strigosa*, *A. humilis*, *Siderastrea* spp. and *P. porites*). As for gall crabs, *Pseudodiploria clivosa*, *P. strigosa* and *A. humilis* had higher densities, compared to other known

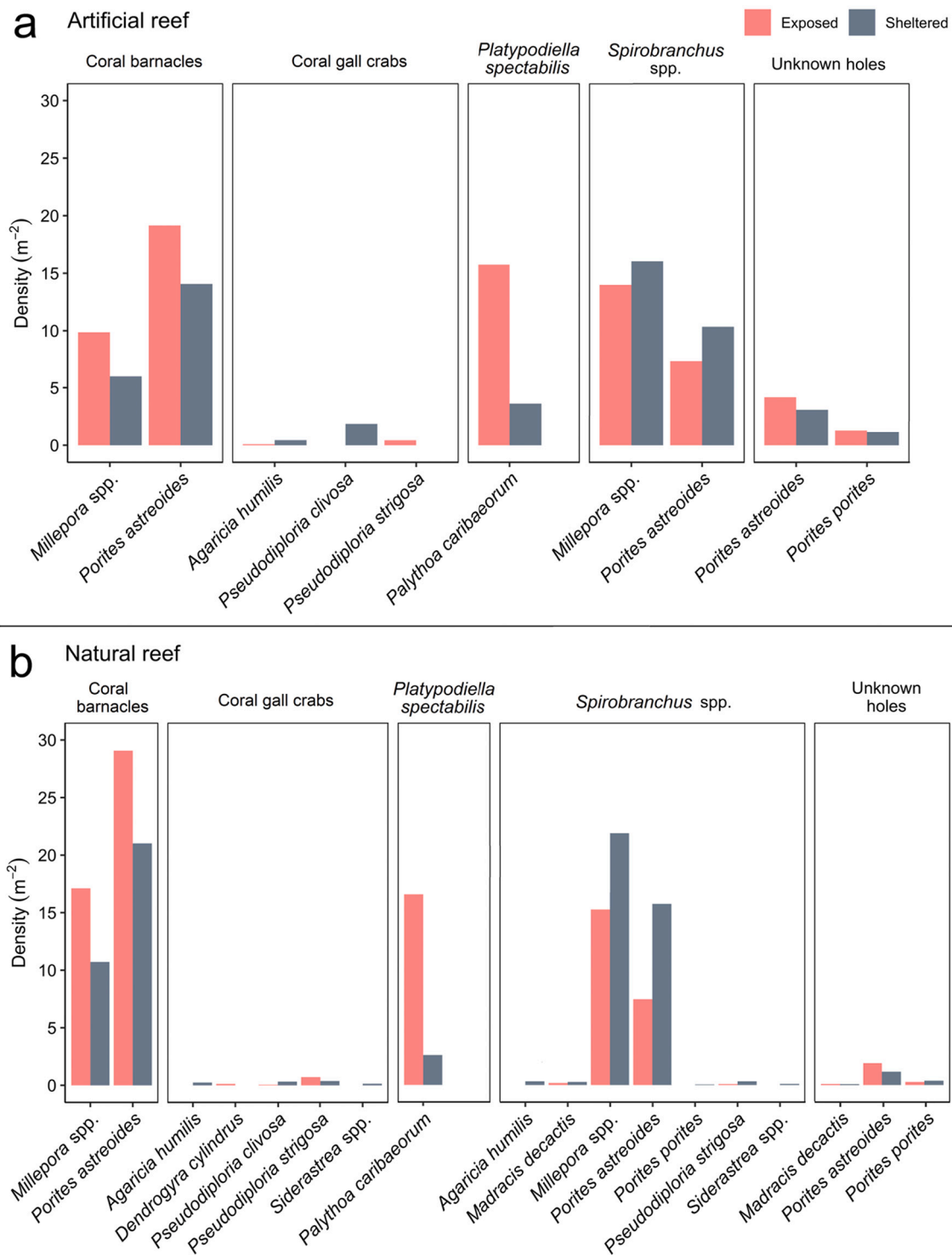


Fig. 6. Densities (m^{-2}) of associated fauna per benthic host organism on the exposed and sheltered sides of (a) the artificial reef, and (b) the natural reef.

host corals. When the numbers are compensated for host cover (Table 2), the differences become less obvious, implying that host density (depending on the reef) is the most important determinant here.

4.4. Associated fauna on exposed vs. sheltered sides

A comparison between coral-associated invertebrates on the sheltered and exposed sides of both reefs revealed significant differences. The density of barnacles on the exposed sides of the NR was much higher, while *Spirobranchus* spp. were observed in higher densities

mostly on the sheltered sides of both reefs. These results suggest that barnacles seem to be more tolerant to high wave action and strong currents, whereas the presence of serpulid worms is affected by such environmental factors, as they prefer more wave-sheltered sides. Thus, the overall densities of coral-associated fauna appeared similar on both sides but their species composition differed.

4.5. Optimal design of artificial reefs for the enhancement of benthic biodiversity

Considering the different designs of ARs (e.g., Hylkema et al., 2020; Komyakova et al., 2021; Mathews et al., 2021), it appears that they are generally not intended to mimic NRs in terms of size and shape. Another important difference is that their surface structure and relief rugosity are usually not designed to resemble that of NRs, which explains why benthic species assemblages of ARs and NRs remain different, even after many decades of community development (Perkol-Finkel et al., 2006; Hill et al., 2021). Breakwaters, like in the present study are usually designed to serve as coastal protection and not as substrate for benthic communities (Cardenas-Rojas et al., 2021; Mamo et al., 2021). Only few artificial substrates in studies offer extra surface roughness and relief rugosity to mimic the surface structure of natural substrates (Martins et al., 2016; Akhwady et al., 2021; Jiang et al., 2021). With dissimilar benthic cover between ARs and NRs (Hill et al., 2021), the associated fauna will also be different as shown in the present study, and in this regard ARs can hardly be considered replacements for NRs (Burt et al., 2009b; Hill et al., 2021; Monchanin et al., 2021). However, ARs may be useful as a possible addition to NRs by creating additional habitats or as a substitute when NRs are lost.

An earlier study on the design of three different types of ARs at St. Eustatius showed that variation in AR shape did not cause significant differences in the species richness of fishes, which used the ARs predominantly for shelter (Hylkema et al., 2020). AR design may be more relevant for the diversity of sessile benthic species, because these cannot move away, unlike fishes. Since the benthic cover of the AR and NR at St. Eustatius mostly consists of zooxanthellate species, such as scleractinians, fire corals (*Millepora*) and zoantharians (*Palythoa*), exposure to light is important and much surface area should be illuminated in daytime, favoured by a horizontal orientation. Because benthic faunas at exposed and sheltered reef sides differ, the design of ARs should also take this variation into account, with one side directed towards the sea and another one towards land, favoured by opposing slopes parallel to the shore line (see Cardenas-Rojas et al., 2021). A combination of sun-exposed surfaces with such slopes could result in structures resembling dikes (Cardenas-Rojas et al., 2021) or pyramids with a flat top (Perkol-Finkel and Benayahu, 2005; Puspasari et al., 2020), or AR types such as 'layered cakes' (Hylkema et al., 2020) and trapezoids (Mathews et al., 2021).

Part of the difference between the AR and NR of the present study can be explained by the variation in depth and the distance from the shoreline. Ideally, to create maximum habitat diversity not a single AR should be constructed, but instead a series of parallel dikes or a field of pyramids/ trapezoids with flat tops (Mathews et al., 2021), varying in depth and distance from the shoreline (Browne and Chapman, 2011).

4.6. Exploration of shallow-water reef communities

The observations of unknown holes in various host corals and the first possible gall crab in *P. astreoides* (Fig. 2) indicate that shallow-water reef communities are not yet fully understood despite their easy access from the shoreline. These findings are from depths <5 m and are consistent with earlier results showing that surveys of reef fauna at shallow reefs may still lead to new and unexpected results (Kuo et al., 2019; Hoeksema et al., 2020; Reimer et al., 2021). Reef communities at mesophotic depths (>30 m) are more challenging to explore from a logistical perspective and it is therefore less surprising that new observations on coral-associated fauna can be made here (Veglia et al., 2019).

5. Conclusions

The companion study of the present work compared the coral assemblages of an old AR and an adjacent NR, showing that the AR appeared to be less rich in species and lower in coral cover than the NR

(Hill et al., 2021). The present study shows that the lower cover of corals on the AR supports lower densities of coral-associated fauna and that exposure to wave action influences the species composition of this fauna. Significant species-dependent differences in densities between exposed and sheltered sides were only found on the AR, with coral barnacles more abundant on the exposed sides and Christmas tree worms more densely distributed on the sheltered sides. The shallow-water zone still requires much more research to be fully understood, yet this study contributes towards a better understanding of communities of coral-associated fauna in the shallow coastal waters of the Caribbean. Part of the difference in benthic community assemblages between our AR and NR can be related to a dissimilar depth and distance from shore, but from an ecological engineering perspective, variation in relief rugosity and surface structure (roughness) are also considered major contributors to this difference, even after many decades of community development.

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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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