Interspecific interactions of scleractinian corals on artificial and natural hard substrates at Curaçao, southern Caribbean

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Abstract

Coral reefs worldwide have come under increasing pressure caused by anthropogenic activities over the last decades. The deployment of artificial reef structures, to provide substrate for settlement of benthic reef organisms, is a commonly applied approach in reef conservation and restoration efforts. Yet, there are few studies that compared competition for space between sessile reef organisms, as one of the key factors determining community structure between reef communities on artificial and natural hard substrates. In this study the intra- and interspecific interactions of Scleractinia, as major reef building organisms on tropical coral reefs, were compared for multiple reef sites on different types of substrata along the leeward side of the island of Curaçao, southern Caribbean, in regard to their distribution, as well as differences in their frequency and dominance hierarchy. The colonies of scleractinian coral on an artificial structure at Boca Samí were found to be evenly distributed, with on average large distances between each other. In contrast to earlier studies that found artificial reefs to generally host a lower abundance and range of organisms and fewer competitive interactions, there was no significant difference in the frequency of scleractinian interactions observed between artificial and natural reefs. An effect of substrate type on the outcomes of competitive interactions between scleractinian corals could not be proven. This indicates similar community structures on artificial and natural reefs of Curaçao, which is likely the result of the complex, heterogenous surface structure of the breakwaters sampled as artificial reef structures in this study, which closely resembles that of natural rocky reefs found around the island and results in more nature-like communities. The present study therefore indicates that increased surface structure of the settlement substrate can increase the effectiveness of artificial structures as tools in reef conservation.

1. Introduction

Coral reefs are important ecosystems that, despite making up less than 1% of the world's benthic marine environment, provide habitat, nurseries, and foraging grounds for roughly 830,000 multi-cellular species and several valuable ecosystem goods and services that benefit

millions of people around the globe (Martínez et al., 2007; Fisher et al., 2015; Woodhead et al., 2019). These valuable ecosystems have come under increasing pressure caused by anthropogenic activities on a global and local scale over the last decades (Burke et al., 2011; Vermeij, 2012). The main threats are over-harvesting, pollution, outbreaks of diseases and pests and climate change (reviewed by Bellwood et al., 2004) and manifest themselves in the occurrence of mass bleaching and mortality events (Ainsworth et al., 2016; Hughes et al., 2018), reduced calcification and skeletal density (Foster et al., 2014; Mollica et al., 2018) and overall declines in reef structures and habitats (Pratchett et al., 2014; De Bakker et al., 2016). Due to their slow natural recovery rates, restoration is of key importance in ensuring the survival of these crucial ecosystems (Soong and Chen, 2003; Ng et al., 2016; Lymperaki et al., 2022). One major approach is the installation of artificial reefs, which restore lost three-dimensional structures of the reef matrix, provide hard substrate for polyp settlement and refugia for individuals of many species and divert human activity away from nearby natural reefs (Abelson, 2006; Hylkema et al., 2021; Hill et al., 2021; Monchanin et al., 2021).

Due to ongoing marine construction of manmade structures, such as seawalls, breakwaters, piers, oil platforms, bridges and marine wind parks, artificial hard substrate in the oceans is steadily increasing and natural ecosystems are gradually replaced by artificial ones (Heery et al., 2018; Masucci and Reimer, 2019; Todd et al., 2019; Kikuzawa et al., 2020). While these structures are usually constructed without the intention of recruiting marine life, it has been proven that corals settle on them (Bulleri and Chapman, 2010; Chou et al., 2010; Dafforn et al., 2015; Hill et al. 2021) and that in some cases they even host a higher abundance and diversity of fish and benthic organisms than nearby natural reefs (Burt et al., 2009a, 2009b; Lymperaki et al., 2022). Despite their apparent use in restoration efforts, deployment of artificial reefs should be thoroughly considered regarding potential environmental risks and long-term management and monitoring needs after installation (Hylkema et al., 2021). Artificial hard substrate can function as "steppingstones" for non-native species, facilitating an expansion of range or even invasions (Soares et al., 2018, 2020; López et al., 2019; Hylkema et al., 2021). Additionally, it has been shown that artificial reefs will differ in reef framework production, sediment generation, growth potential and maintenance of habitat complexity from natural reefs, which potentially results in different community compositions than those of natural reefs (Perry and Alvarez-Filip, 2018; Hill et al., 2021; Monchanin et al., 2021; Lymperaki et al., 2022). Also, studies have shown that even after centuries of submersion, artificial reefs only mimic natural reef communities and tend to be more homogenous than natural reefs, resulting in a lower abundance and range of organisms (Perkol-Finkel et al., 2006;

Moschella et al., 2005; Firth et al., 2013; Aguilera et al., 2014; Hill et al., 2021; Monchanin et al., 2021; Lymperaki et al., 2022). Based on these observations, it is apparent that further knowledge of how and why community structures differ between artificial and naturals reefs is of crucial importance to improve design and long-term management strategies, as well as reduce potential negative environmental effects of artificial reef structures designated to be used in future reef conservation efforts.

One key factor determining community composition on reefs is the competition for available space by sessile reef organisms. This specific form of interspecific interaction has a great influence on reef biodiversity and community structure (Tanner, 1997; Chadwick and Morrow, 2011; Hill et al., 2021). Scleractinian corals are some of the major reef building organisms, particularly on tropical reefs (de Bakker et al., 2016). By using endosymbiotic algae, called zooxanthellae, Scleractinia can derive energy from photosynthesis, while also feeding heterotrophically using their polyps' tentacles (Porter, 1976; Madl and Witzany, 2014). As they grow, they build and maintain a carbon skeleton underneath the living tissue made up of the polyps, which shapes the overall structure of the coral colony and its geometric properties (e.g., surface area, volume, perimeter), which in turn creates the structure of coral reefs from cellular to ecosystem scales (George et al., 2021).

Scleractinian corals compete with other organisms for sunlight and settlement space on the reef (Jackson, 1977; Sheppard, 1979; Dai, 1990; George et al., 2021). Scleractinia can fight out competitive interactions in various ways: they can directly attack their opponents' tissue, such as by mesenterial digestion or developing sweeper tentacles (Lang, 1973; Sheppard, 1979; Richardson et al., 1979; Wellington, 1980; Dai, 1990; Lapid and Chadwick, 2006; Roff et al., 2009; George, et al. 2021), or they outgrow and overshadow them (Sheppard, 1979; Dai, 1990; Álvarez-Noriega et al., 2018).

Reef coral species of the Atlantic and the Indo-Pacific have been grouped by previous studies into aggressive, intermediate, and submissive species, based on how well they performed in competitive encounters with other benthic organisms, such as turf algae, sponges, and other corals (Lang, 1973; Logan, 1984; Sheppard, 1979; Dai, 1990; Barott et al., 2012; Swierts and Vermeij, 2016). These hierarchies have originally been believed to be consistent. However, some studies showed that coral interspecific competition is not always as hierarchical and consistent and the outcomes can be influenced by external factors like environmental conditions, colony size, position of contact, the development of sweeper tentacles or presence of epifauna (Sheppard, 1979; Bak et al., 1982; Dai, 1990). Despite this long history of research

on coral interactions and their competitive abilities, studies on coral interspecific interactions on artificial substrates are rare (Hill et al., 2021).

A study by Ng et al. (2012) found that scleractinian coral colonies on seawalls in Singapore grew on average 1 m apart, which indicates that interactions between corals on artificial substrate are less likely to occur than on natural reefs. Hill et al. (2021) also found a higher number of interactions between sessile reef organisms on a natural reef than on a nearby artificial one. These findings support the suggestions of Bulleri and Chapman (2010), that structures of anthropogenic origin cannot replace natural environments, due to differences in key ecological factors, such as predation, facilitation, and competition. However, the scarcity of studies directed specifically at the differences in the interspecific interactions of Scleractinia (Hill et al., 2021), as some of the major reef building organisms with profound influence on reef structure, biodiversity, and community composition of tropical reefs (Tanner, 1997; Chadwick and Morrow, 2011; de Bakker et al., 2016; George et al., 2021; Hill et al., 2021), requires further research.

The aim of the present study was to investigate how scleractinians are distributed on artificial structures in relation to their nearest neighbor and how the inter- and intraspecific interaction between scleractinian corals differs between natural and artificial substrate, both in frequency and in the competitive hierarchy of the coral species involved. Based on the findings of Ng et al. (2012), who found coral colonies on seawalls in Singapore to grow on average 1 m apart, it was hypothesized that i) scleractinian corals on artificial structures would be distributed evenly, with large distances between neighboring colonies. Secondly, it was hypothesized that ii) inter- and intraspecific interactions between scleractinian corals would be less frequent on artificial than on natural substrate. This was expected, as previous studies (Perkol-Finkel et al., 2006; Moschella et al., 2005; Firth et al., 2013; Aguilera et al., 2014; Hill et al., 2021; Lymperaki et al., 2022) consistently found artificial reef structures to host a lower abundance and diversity of organisms and fewer interactions between sessile reef organisms than natural reefs. Additionally, it was hypothesized that iii) Scleractinia species would be grouped into different hierarchical categories regarding their competitive abilities on different substrata. This assumption is based on the results of earlier research (Sheppard, 1979; Bak et al., 1982; Dai, 1990) that the outcomes of interactions between corals can be influenced by external factors.

2. Materials and Methods

2.1 Study Area

The study was conducted on the island of Curaçao, situated in the southern Caribbean and off the northern coast of Venezuela. The island is part of the Dutch Caribbean, has 444 km^2 of land surface area and is dominated by a semi-arid climate, with seawater temperatures varying around 27 °C. Curaçao is surrounded by fringing reefs and known for steep reef slopes close to the shoreline (Bak, 1975; van Duyl, 1985). Data was collected at seven different reef sites along the southern leeward coastline of the island (Fig. 1): (1) Aqualectra Desalination Plant (henceforth referred to as "Water Factory" (WF)) (12°06′33.3″N 68°57′15.3″ W), (2) Blue Bay Beach (henceforth "Blue Bay" (BB)) (12°08'02"N 68°59'07"W), (3) Tugboat Beach (TB) (12°04'10"N 68°51'44"W), (4) Marie Pampoen Beach (henceforth "Marie Pampoen" (MP)) (12°05'24"N 68°54'18"W), (5) Sportcentrum Marie Pampoen (henceforth "Marie Pampoen Sewage" (MS)) (12°05'34"N 68°54'35"W), (6) Substation Curaçao at the Sea Aquarium (henceforth called "Sea Aquarium" (SA)) (12°05'00"N 68°53'49"W) and (7) Boca Sami Beach (BS) (12°08'48"N 68°59'57"W).
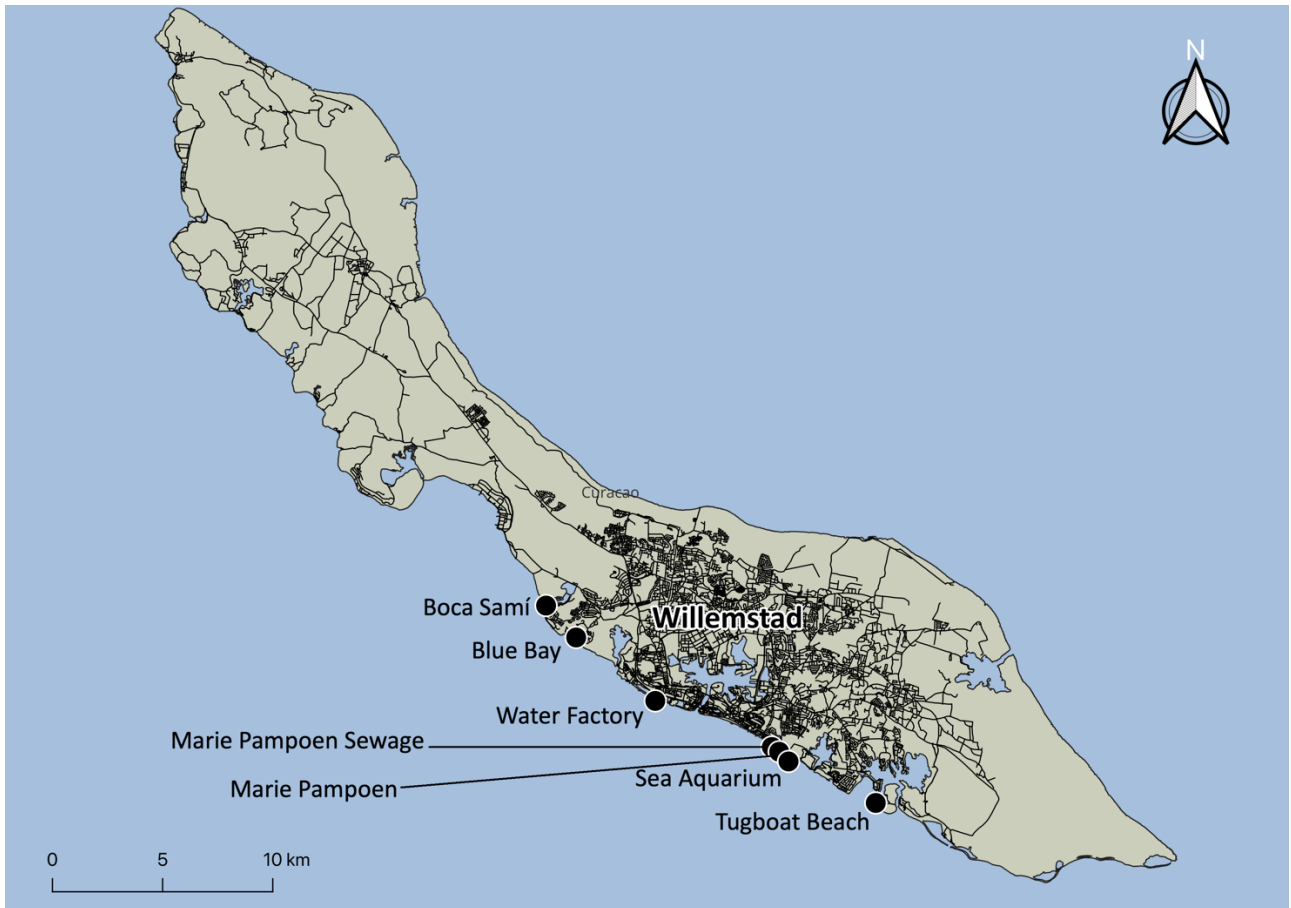
Figure 1. Map of the island of Curaçao, southern Caribbean showing the seven sites sampled in this study.

2.1.1 Data Collection

For the analysis of differences in the frequencies of intra- and interspecific scleractinian coral interactions and the dominance of scleractinian species in interactions between natural and artificial reef structures, data was collected by underwater photography along 25-m long transect lines, using SCUBA between April 4th and May 22nd, 2022, at Water Factory, Sea Aquarium, Blue Bay, Tugboat Beach, Marie Pampoen and Marie Pampoen Sewage. Pictures were taken using a Sea&Sea DX-1G, a Sea&Sea DX-6G and a GoPro Hero 10. Transects were set up by placing a 25-m long measurement tape along the sea floor at different depths, parallel to the coast. One exception was the transect at Marie Pampoen Sewage, which followed a sewage pipeline down the reef slope. At Marie Pampoen, Marie Pampoen Sewage and Water Factory transects were taken both on the breakwaters (WF, MP) and the sewage pipeline (MS) as artificial reef structures (3- and 4-m depth transects, pipeline transect (3–7 m depth)) and on natural reefs, between the breakwaters and the reef slopes (5-m depth transects). At Sea Aquarium, the sea wall extended down deeper, so transects were also set up at 10 and 15 m

depth. Furthermore, at all four of the sites, transects were deployed at 4 and 5 m depth on stretches of reef flat bottom mostly covered by sand, next to the natural reefs. At Tugboat Beach and Blue Bay, transects were deployed at 4 and 5m depth along sea floor strewn by rocks and boulders broken off from the cliffs above. Therefore, all transects at these sites were on natural hard substrate only (Fig. 2).
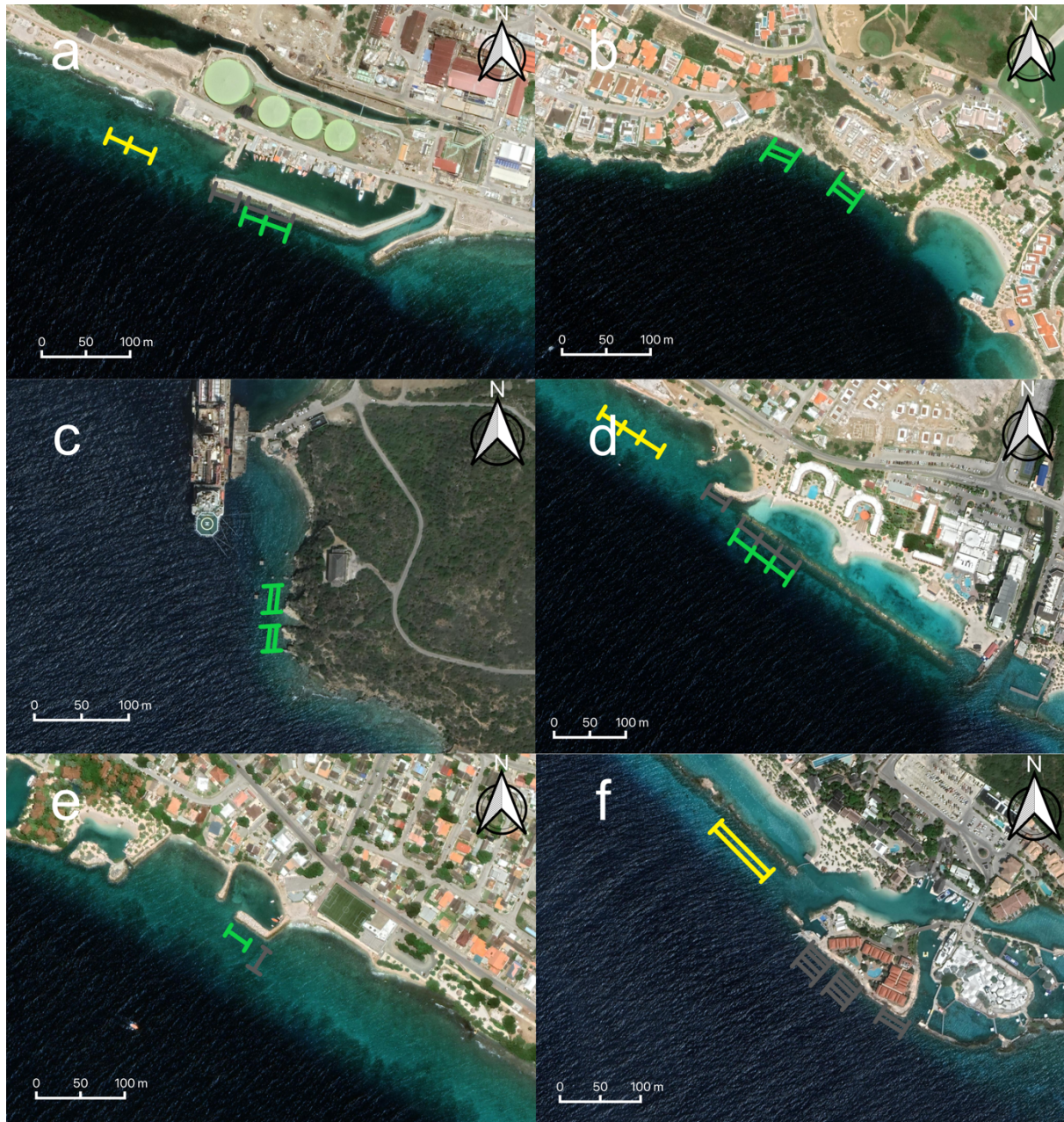
Figure 2. Aerial pictures of the transect sampling sites: a) Water Factory, b) Blue Bay, c) Tugboat Beach, d) Marie Pampoen, e) Marie Pampoen Sewage and f) Sea Aquarium. Green lines = transects on natural hard substrate, grey lines = transects on artificial hard substrate and yellow lines = transects on reef flat bottom.

Following the methodology of Hill et al. (2021), photos were then taken by diving along the transects using a 25x25 cm^2 photo quadrat (Fig. 3), which ensured that smaller coral colonies were not overlooked. Each photo subsequently equals one quadrat, without the same

quadrat being photographed twice. In total 18 transects were taken on artificial reef structures (112.5 m^2), 14 on natural reefs structures (87.5 m^2) and 11 on reef-flat bottom surface (68.75 m^2).

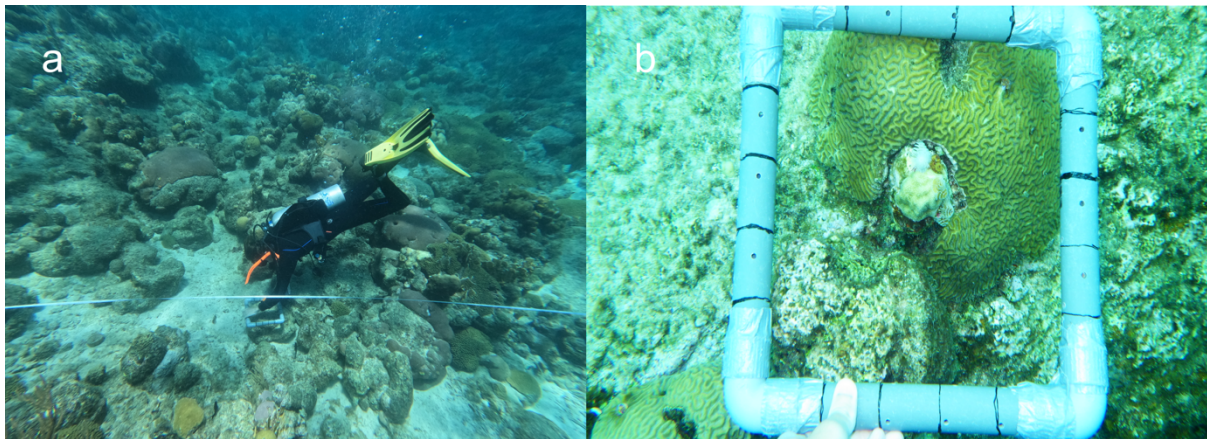*Figure 3. Picture showing the transect sampling method (a) and an example picture as used in the identification (b). Scale on the photo quadrat: 5 cm.*

The photographs were then used to identify all scleractinian coral species using the photographic guide to coral species in Hoeksema et al. (2022: ESM1) in each quadrat down to the lowest possible taxonomic level. As this study specifically targeted hard corals, sponges and soft corals were not counted and fire corals were only identified as *Millepora* sp. If the quality of the pictures did not allow for the identification of a colony, they were listed as 'unclear'.

The number of colonies of each of the identified corals that were found in each picture, as well as their percentage cover of the surface area in the picture were recorded. Furthermore, all occurring interactions between scleractinian corals were recorded. Every direct physical contact between two coral colonies, as well as colonies that abutted or were growing in close proximity (< 5 cm in distance) were counted as interactions. For every interaction recognized, it was noted which coral species interacted, and as each colony found was listed, interactions between colonies were always counted twice - once for each interaction partner. These interactions were identified following the definitions used by Dai (1990) as overgrowth, direct interaction, or stand-off. If two colonies of the same species made physical contact and fused together to form a bigger colony, this was recognized as an interaction labelled fusion. Additionally, for interactions that could not be clearly identified in the pictures, another category was added: unclear (Fig. 4). Coral colonies without interactions were listed as having 0 interactions (n interactions = 0). Interactions with *Millepora* sp. were not regarded (n interactions = NA), as this study was focused on scleractinian species.

For the comparison of coral dominance in interactions, it was also identified which involved coral showing overgrowth or direct interaction was winning and which one was losing, or if they were in a tie. For overgrowth, the coral that was physically growing over the other was recorded as winning, the overgrown coral as losing. For direct interaction the coral showing more tissue damage around the area of contact, was recorded as losing, the other one as winning. If there was equal or no visible tissue damage on both interacting corals at the area of contact, the direct interaction was counted as a tie (Fig. 3).
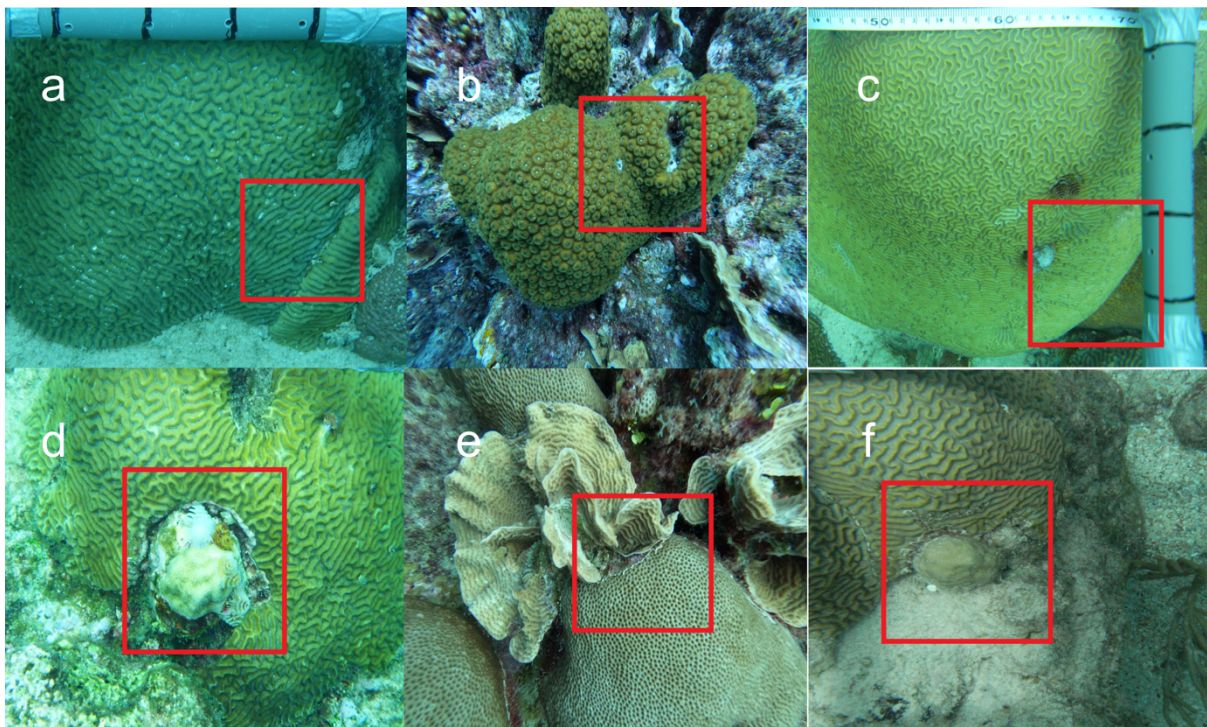

Figure 4. Examples of interaction types. a) Direct interaction (tie): No tissue damage seen on either colony along border of contact. b) Fusion: Two distinct colonies of the same species growing into one colony. c) Unclear: Due to the angle of the picture it cannot be established if the two colonies interact directly or are merely in a stand-off. d) Stand-off: Two colonies within less than 5 cm distance, but no direct tissue contact. No sign of tissue damage on either colony. e) Overgrowth: One colony visibly growing over the other. f) Direct interaction (win/loss): Two colonies with tissue contact. One colony shows tissue damage around the area of contact, signifying a loss against the colony without visible tissue damage.

In order to exclude the possible effect of high relief in the artificial boulder substrates of breakwaters, the surface of a large relatively flat concrete structure at Boca Sami used to anchor a mooring buoy (Fig. 5) was photographed by using a mosaic of photo quadrats over a large homogenous area instead of along a transect line over heterogenous boulders. The photographs were then mounted together using Microsoft Paint® to form a complete picture of a part of the structures surface and to enable measurements of the distance between

neighboring coral colonies. Distances were always measured in cm between the central points of each colony using ImageJ (Version 1.53u, MacOSX-Java8) (Schneider et al., 2012). The 5-cm markings of the photo quadrats were used as a reference.
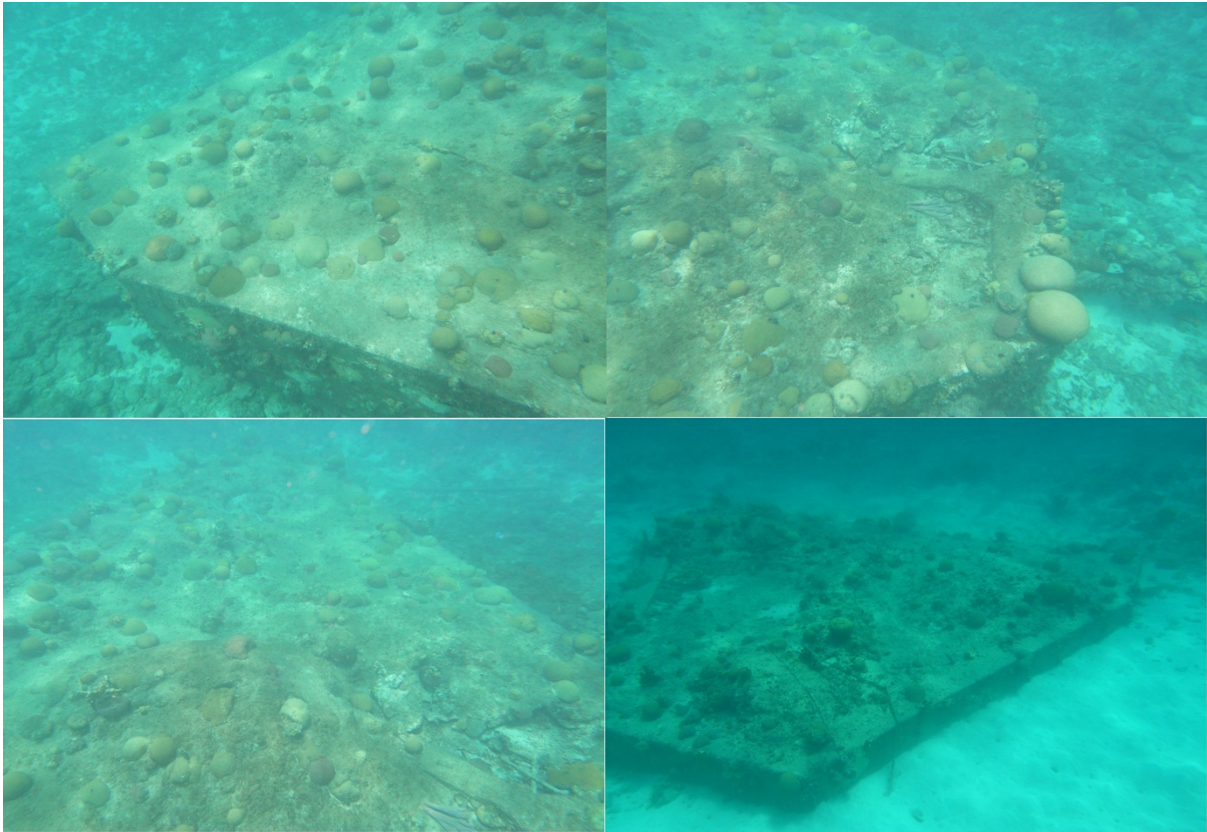
Figure 5. Pictures showing the concrete structure at Boca Sami that was used for the Nearest Neighbor Analysis.

2.2 Data Analysis

The distances between neighboring coral colonies measured for the flat concrete structure at Boca Samí were used to perform the Clark-Evans Nearest Neighbor Analysis to determine whether scleractinian corals on this artificial structure were dispersed in an even, random, or clustered pattern. For this an R value is calculated as the measure of the degree to which the observed distribution departs from that expected in a hypothetical random distribution with respect to the distance to nearest neighbor. For this the formula **R = rA / rE**, where rA is the mean of the nearest neighbor distances measured and rE is the mean distance to nearest neighbor expected in an infinitely large random distribution of a density rho (Clark and Evans, 1954).

To compare the frequency of interactions between scleractinian coral species on the different substrate types, multiple tests were performed using RStudio (Version R 4.0.2) (R Core Team, 2020), which was also used to create boxplot graphs for better visualization. To test for statistically significant differences in the frequency of interactions occurring on the different substrate types, the number of interactions recorded was tested against the substrate types using non-parametric analysis of variance (Kruskal-Wallis-Test) using data of all transects and of the sites with multiple reef substrate types (WF, MP, MS, SA) separately, as environmental factors like available sunlight, water quality and wave exposure have a profound influence on the fitness and distribution of scleractinian species (e.g., Vermeij, 2012; de Bakker et al., 2016; Hill et al., 2021) and can vary substantially between sampling sites. Sea Aquarium was the only site where transects were carried out at 15 m depth, and the environmental conditions here vary considerably from the shallower depth at 3 to 10 m, thus the tests for all transects and for the Sea Aquarium transects were also carried out excluding the 15-m transect data.

To enable a more detailed comparison, the frequency of inter- and intraspecific interactions was tested for each species. For this, all occurring interactions of a coral species were counted separately for each observed interaction pairing. Colonies that were found without interaction were counted as interacting with nothing for this analysis. To account for the difference in transect area covering the different reef substrate types, an interaction per density value was calculated for each interaction pairing by dividing the interaction counts by the summed density of both interacting coral species, following Hill et al. (2021). Both the interaction counts and the interaction per density value were then used for a Kruskal-Wallis-Test to check for significant differences between the different substrate types. If an interaction pairing was not found on all substrate types, the number of interactions and the interaction per density value for this pairing was set as equal to 0 for the substrate types it was not found on, to enable a statistical comparison.

To compare the competitive abilities of scleractinian coral species on different substrate types, a coral interaction dominance index (CI) was calculated based on the recorded interaction outcomes, where **CI = (n (wins) − n (losses)) / n (total)** (see Dai, 1990). The calculated results for each species can range from +1 to -1, where +1 indicates a species winning all interactions and -1 indicates a species that loses all interactions. The species were then grouped into five different categories based on their calculated CI. These categories (Dai, 1990) are: aggressive (CI = 0.6 to 1.0), moderately aggressive (CI = 0.2 to 0.59), intermediate

(CI = -0.2 to 0.19), moderately subordinate (CI = -0.6 to -0.21), and subordinate (CI= -0.61 to -1).

3. Results

3.1 Nearest neighbor analysis

For the analysis of the distribution pattern of scleractinian corals in relation to their nearest neighbor on the concrete structure at Boca Samí (Fig. 4), an area of 45,625 cm^2 (~73 photo quadrats) was used to measure distances between coral colonies. Seventy-one scleractinian coral colonies were found within this area, equaling a density of 15.56 individuals*m^{-2}. The mean distance to nearest neighbor calculated for a hypothetical random population distribution using this density (rE) was 12.7 cm, the one calculated using the measured distances between colonies (rA) was 17.2 cm. An R value of R = 1.35 was calculated using the formula for an analysis of nearest neighbor by Clark and Evans (1954). This value is >1, indicating that the distribution pattern of scleractinian colonies on the concrete structure was even. A standard error δrE of 0.8 has been calculated for the mean distance to nearest neighbor in a randomly distributed assemblage of this density. This means that the probable range of distance to nearest neighbor in an assemblage of random distribution would have been between 11.9 and 13.5 cm.

The measured mean distance to nearest neighbor of 17.2 cm lies outside this range, and it can thus be assumed with certainty that the distribution pattern of scleractinian colonies on this artificial structure is even, not random. For a summary of the measurements and calculated values see the Appendix (Table S1).

3.2 Frequency of interactions by species

3.2.1 All-transect comparison

In total 3,639 interactions of 23 different species of Scleractinia have been found on all artificial hard substrate transects, over an area of 112.5 m^2 (Table 1). *Porites astreoides* was most commonly found interacting with nothing (n = 844), followed by *Agaricia humilis*, *Siderastrea siderea*, *Pseudodiploria strigosa* and *Favia fragum* – also without interaction (n = 661, 399, 312, and 203 respectively) (Table 1). All species were found to occur most often

interacting with nothing. Seven of the 23 observed species were only found without any interaction.

Of the interactions between two colonies the most common pairings were *Pseudodiploria strigosa* and *Siderastrea siderea* with their conspecifics (16.3 m^{-2} and 9.92 m^{-2}), *Pseudodiploria strigosa* and *Siderastrea siderea* with each other (4.63 m^{-2}), *Agaricia agaricites* with *Madracis decactis* (4.29 m^{-2}) and *Porites astreoides* with its conspecifics (3.65 m^{-2}) (Table 1).

When the 15-m depth transects at Sea Aquarium are excluded, the sampling area on artificial hard substrate equals 100 m^2. *Porites. astreoides*, *Agaricia humilis*, *Siderastrea siderea*, *Pseudodiploria strigosa* and *Favia fragum* – each without interaction – were still the most commonly found (n = 830, 661, 369, 312 and 202 respectively).

Also, all recorded species were still most often found without interaction. *Agaricia lamarcki* was only found in the 15-m-depth transects, reducing the number of species observed on artificial substrate to 22. The most commonly encountered interaction remained the same, even though the interaction per density value changed, as the sampling area changed as well (Appendix Table S2).

Table 1. Summary of all species interactions recorded in all transects on artificial hard substrate per unit area (m^{-2}).

Interaction name	n interactions	Density (m^{-2})	Interaction/density
Acropora cervicornis - Nothing	15	0.13	112.5
Acropora palmata - Nothing	5	0.06	80.36
Acropora palmata - *Pseudodiploria strigosa*	2	4.76	0.42
Agaricia agaricites - Nothing	14	0.13	110.53
Agaricia agaricites - *Madracis auretenra*	2	1.42	1.41
Agaricia agaricites - *Madracis decactis*	1	0.23	4.29
Agaricia agaricites - *Meandrina meandrites*	1	0.3	3.29
Agaricia agaricites - *Orbicella annularis*	1	1.1	0.93
Agaricia fragilis - Nothing	1	0.01	112.5
Agaricia humilis - Nothing	661	6.39	103.42
Agaricia humilis - *Agaricia humilis*	12	12.78	0.94
Agaricia humilis - *Madracis auretenra*	1	7.68	0.13
Agaricia humilis - *Madracis decactis*	1	6.5	0.15
Agaricia humilis - *Orbicella annularis*	3	7.34	0.41
Agaricia humilis - *Porites astreoides*	16	15.42	1.04
Agaricia humilis - *Porites porites*	1	6.46	0.16
Agaricia humilis - *Pseudodiploria strigosa*	18	11.08	1.62
Agaricia humilis - *Siderastrea siderea*	11	11.64	0.95
Agaricia lamarcki - Nothing	2	0.02	112.5
Colpophyllia natans - Nothing	2	0.06	32.14
Colpophyllia natans - *Favia fragum*	3	2.01	1.49
Colpophyllia natans - *Madracis auretenra*	1	1.35	0.74
Colpophyllia natans - *Pseudodiploria strigosa*	2	4.76	0.42
Diploria labyrinthiformis - Nothing	18	0.29	61.36
Diploria labyrinthiformis - *Porites astreoides*	8	9.32	0.86

Diploria labyrinthiformis - Pseudodiploria strigosa	7	4.99	1.4
Diploria labyrinthiformis - Siderastrea siderea	5	5.54	0.9
Favia fragum - Nothing	203	1.95	104.28
Favia fragum - Colpophyllia natans	3	2.01	1.49
Favia fragum - Favia fragum	10	3.89	2.57
Favia fragum - Porites astreoides	4	10.98	0.36
Favia fragum - Pseudodiploria strigosa	2	6.64	0.3
Madracis auretenra - Nothing	133	1.29	103.19
Madracis auretenra - Agaricia agaricites	2	1.42	1.41
Madracis auretenra - Agaricia humilis	1	7.68	0.13
Madracis auretenra - Colpophyllia natans	1	1.35	0.74
Madracis auretenra - Orbicella annularis	4	2.24	1.79
Madracis auretenra - Pseudodiploria strigosa	1	5.98	0.17
Madracis auretenra - Siderastrea siderea	6	6.53	0.92
Madracis decactis - Nothing	10	0.11	93.75
Madracis decactis - Agaricia agaricites	1	0.23	4.29
Madracis decactis - Agaricia humilis	1	6.5	0.15
Meandrina meandrites - Nothing	16	0.18	90
Meandrina meandrites - Agaricia agaricites	1	0.3	3.28
Meandrina meandrites - Porites astreoides	2	9.21	0.22
Meandrina meandrites - Siderastrea siderea	1	5.42	0.18
Montastraea cavernosa - Nothing	11	0.12	95.19
Montastraea cavernosa - Pseudodiploria strigosa	2	4.81	0.42
Orbicella annularis - Nothing	80	0.95	84.11
Orbicella annularis - Agaricia agaricites	1	1.08	0.93
Orbicella annularis - Agaricia humilis	3	7.34	0.41
Orbicella annularis - Madracis auretenra	4	2.24	1.79
Orbicella annularis - Orbicella annularis	6	1.9	3.15
Orbicella annularis - Porites astreoides	4	9.98	0.4
Orbicella annularis - Porites porites	1	1.02	0.98
Orbicella annularis - Pseudodiploria strigosa	5	5.64	0.89
Orbicella annularis - Siderastrea siderea	5	6.2	0.81
Orbicella faveolata - Nothing	18	0.16	112.5
Porites astreoides - Nothing	844	9.03	93.46
Porites astreoides - Agaricia humilis	16	15.42	1.04
Porites astreoides - Diploria labyrinthiformis	8	9.32	0.86
Porites astreoides - Favia fragum	4	10.98	0.36
Porites astreoides - Meandrina meandrites	2	9.21	0.22
Porites astreoides - Orbicella annularis	4	9.98	0.4
Porites astreoides - Porites astreoides	66	18.06	3.65
Porites astreoides - Pseudodiploria strigosa	39	13.72	2.84
Porites astreoides - Siderastrea siderea	47	14.28	3.29
Porites furcata - Nothing	2	0.02	112.5
Porites porites - Nothing	5	0.07	70.31
Porites porites - Agaricia humilis	1	6.46	0.16
Porites porites - Orbicella annularis	1	1.02	0.98
Porites porites - Siderastrea siderea	1	5.32	0.19
Pseudodiploria clivosa - Nothing	3	0.03	112.5
Pseudodiploria strigosa - Nothing	312	4.69	66.48
Pseudodiploria strigosa - Acropora palmata	2	4.76	0.42
Pseudodiploria strigosa - Agaricia humilis	18	11.08	1.62
Pseudodiploria strigosa - Colpophyllia natans	2	4.76	0.42
Pseudodiploria strigosa - Diploria labyrinthiformis	7	4.99	1.4
Pseudodiploria strigosa - Favia fragum	2	6.64	0.3
Pseudodiploria strigosa - Madracis auretenra	1	5.98	0.17
Pseudodiploria strigosa - Montastraea cavernosa	2	4.81	0.42
Pseudodiploria strigosa - Orbicella annularis	5	5.64	0.89

Pseudodiploria strigosa - Porites astreoides	39	13.72	2.848
Pseudodiploria strigosa - Pseudodiploria strigosa	153	9.39	16.3
Pseudodiploria strigosa - Siderastrea siderea	46	9.94	4.63
Pseudodiploria strigosa - unclear	1	4.78	0.21
Siderastrea radians - Nothing	8	0.07	112.5
Siderastrea siderea - Nothing	399	5.24	76.087
Siderastrea siderea - Agaricia humilis	11	11.64	0.95
Siderastrea siderea - Diploria labyrinthiformis	5	5.54	0.9
Siderastrea siderea - Madracis auretenra	6	6.53	0.92
Siderastrea siderea - Meandrina meandrites	1	5.42	0.18
Siderastrea siderea - Orbicella annularis	5	6.2	0.81
Siderastrea siderea - Porites astreoides	47	14.28	3.29
Siderastrea siderea - Porites porites	1	5.32	0.19
Siderastrea siderea - Pseudodiploria strigosa	46	9.94	4.63
Siderastrea siderea - Siderastrea siderea	104	10.49	9.92
Stephanocoenia intersepta - Nothing	7	0.06	112.5
unclear - Nothing	9	0.09	101.25
unclear - *Pseudodiploria strigosa*	1	4.78	0.21

On a sampling area of 87.5 m^2 of natural hard substrate, a total of 2,468 interactions of 25 species of scleractinian corals was found (Table 2). *Porites astreoides* was found most frequently among coral colonies without interaction (n = 459). *Madracis auretenra*, *Pseudodiploria strigosa* and *Siderastrea siderea* interacting with nothing followed thereafter (n = 394, 217 and 214 respectively). Like on artificial substrate, all species were most often found interacting with nothing and ten species were only found without interactions. The most common interactions between two colonies on natural hard substrate were *Siderastrea siderea* with its conspecifics (7.7 m^{-2}), *Diploria labyrinthiformis* with its conspecifics (6.56 m^{-2}), *Madracis auretenra* with *Orbicella annularis* (4.85 m^{-2}), *Pseudodiploria strigosa* with its conspecifics (3.99 m^{-2}), and *Pseudodiploria strigosa* with *Siderastrea siderea* (3.1 m^{-2}) (Table 2).

Table 2. Summary of all species interactions recorded in all transects on natural hard substrate per unit area (m^{-2}).

Interaction name	n interactions	Density (m^{-2})	Interaction/density
Acropora cervicornis - Nothing	1	0.01	87.5
Agaricia agaricites - Nothing	65	0.93	70.22
Agaricia agaricites - Agaricia agaricites	4	1.85	2.16
Agaricia agaricites - Agaricia humilis	1	3.87	0.26
Agaricia agaricites - Eusmilia fastigiata	3	0.98	3.05
Agaricia agaricites - Madracis auretenra	1	6.14	0.16
Agaricia agaricites - Orbicella faveolata	2	1.25	1.61
Agaricia agaricites - Porites astreoides	1	6.81	0.15
Agaricia agaricites - Siderastrea siderea	6	4.43	1.35
Agaricia humilis - Nothing	244	2.95	82.75
Agaricia humilis - Agaricia agaricites	1	3.87	0.26

Agaricia humilis - Montastraea cavernosa	1	4	0.25
Agaricia humilis - Orbicella annularis	2	5.15	0.39
Agaricia humilis - Porites astreoides	4	8.83	0.45
Agaricia humilis - Pseudodiploria strigosa	1	6.21	0.16
Agaricia humilis - Siderastrea siderea	6	6.46	0.93
Agaricia lamarcki - Nothing	1	0.01	87.5
Cladopsammia manuelensis - Nothing	1	0.01	87.5
Colpophyllia natans - Nothing	4	0.05	87.5
Dendrogyra cylindrus - Nothing	5	0.06	87.5
Dichocoenia stokesii - Nothing	8	0.09	87.5
Diploria labyrinthiformis - Nothing	24	0.46	52.5
Diploria labyrinthiformis - Diploria labyrinthiformis	6	0.91	6.56
Diploria labyrinthiformis - Madracis auretenra	3	5.67	0.53
Diploria labyrinthiformis - Madracis decactis	1	0.64	1.56
Diploria labyrinthiformis - Orbicella annularis	2	2.66	0.75
Diploria labyrinthiformis - Porites astreoides	4	6.34	0.63
Diploria labyrinthiformis - Pseudodiploria strigosa	1	3.71	0.27
Diploria labyrinthiformis - Siderastrea siderea	3	3.97	0.76
Eusmilia fastigiata - Nothing	2	0.06	35
Eusmilia fastigiata - Agaricia agaricites	3	0.98	3.05
Eusmilia fastigiata - Orbicella annularis	1	2.26	0.44
Eusmilia fastigiata - Siderastrea siderea	4	3.57	1.12
Favia fragum - Nothing	15	0.18	82.03
Favia fragum - Orbicella annularis	1	2.39	0.42
Madracis auretenra - Nothing	394	5.21	75.6
Madracis auretenra - Agaricia agaricites	1	6.14	0.16
Madracis auretenra - Diploria labyrinthiformis	3	5.67	0.53
Madracis auretenra - Madracis auretenra	2	10.42	0.19
Madracis auretenra - Montastraea cavernosa	1	6.26	0.16
Madracis auretenra - Orbicella annularis	36	7.42	4.85
Madracis auretenra - Orbicella faveolata	2	5.53	0.36
Madracis auretenra - Porites astreoides	3	11.1	0.27
Madracis auretenra - Porites furcata	2	5.5	0.36
Madracis auretenra - Pseudodiploria strigosa	9	8.47	1.06
Madracis auretenra - Siderastrea siderea	8	8.72	0.92
Madracis decactis - Nothing	14	0.18	76.56
Madracis decactis - Diploria labyrinthiformis	1	0.64	1.56
Madracis decactis - Orbicella annularis	1	2.39	0.42
Madracis senaria - Nothing	1	0.01	87.5
Meandrina meandrites - Nothing	15	0.19	77.21
Meandrina meandrites - Orbicella faveolata	1	0.51	1.94
Meandrina meandrites - Pseudodiploria strigosa	2	3.45	0.58
Montastraea cavernosa - Nothing	81	1.05	77.04
Montastraea cavernosa - Agaricia humilis	1	4	0.25
Montastraea cavernosa - Madracis auretenra	1	6.26	0.16
Montastraea cavernosa - Montastraea cavernosa	4	2.1	1.9
Montastraea cavernosa - Orbicella annularis	1	3.26	0.31
Montastraea cavernosa - Pseudodiploria strigosa	3	4.31	0.7
Montastraea cavernosa - Siderastrea siderea	5	4.56	1.1
Orbicella annularis - Nothing	139	2.21	63.02
Orbicella annularis - Agaricia humilis	2	5.15	0.39
Orbicella annularis - Diploria labyrinthiformis	2	2.66	0.75

Orbicella annularis - Eusmilia fastigiata	1	2.26	0.44
Orbicella annularis - Favia fragum	1	2.39	0.42
Orbicella annularis - Madracis auretenra	36	7.42	4.85
Orbicella annularis - Madracis decactis	1	2.39	0.42
Orbicella annularis - Montastraea cavernosa	1	3.26	0.31
Orbicella annularis - Porites furcata	2	2.49	0.8
Orbicella annularis - Pseudodiploria strigosa	4	5.46	0.73
Orbicella annularis - Siderastrea siderea	7	5.71	1.23
Orbicella faveolata - Nothing	19	0.32	59.38
Orbicella faveolata - Agaricia agaricites	2	1.25	1.61
Orbicella faveolata - Madracis auretenra	2	5.53	0.36
Orbicella faveolata - Meandrina meandrites	1	0.51	1.94
Orbicella faveolata - Porites astreoides	1	6.21	0.16
Orbicella faveolata - Pseudodiploria strigosa	4	3.58	1.12
Porites astreoides - Nothing	459	5.89	77.99
Porites astreoides - Agaricia agaricites	1	6.81	0.15
Porites astreoides - Agaricia humilis	4	8.83	0.45
Porites astreoides - Diploria labyrinthiformis	4	6.34	0.63
Porites astreoides - Madracis auretenra	3	11.1	0.27
Porites astreoides - Orbicella faveolata	1	6.21	0.16
Porites astreoides - Porites astreoides	22	11.77	1.87
Porites astreoides - Porites furcata	1	6.17	0.16
Porites astreoides - Pseudodiploria strigosa	12	9.14	1.31
Porites astreoides - Siderastrea siderea	13	9.39	1.38
Porites furcata - Nothing	18	0.29	63
Porites furcata - Madracis auretenra	2	5.5	0.36
Porites furcata - Orbicella annularis	2	2.49	0.8
Porites furcata - Porites astreoides	1	6.17	0.16
Porites furcata - Siderastrea siderea	3	3.79	0.79
Porites porites - Nothing	10	0.11	87.5
Pseudodiploria strigosa - Nothing	217	3.26	66.62
Pseudodiploria strigosa - Agaricia humilis	1	6.21	0.16
Pseudodiploria strigosa - Diploria labyrinthiformis	1	3.71	0.27
Pseudodiploria strigosa - Madracis auretenra	9	8.47	1.06
Pseudodiploria strigosa - Meandrina meandrites	2	3.45	0.58
Pseudodiploria strigosa - Montastraea cavernosa	3	4.31	0.7
Pseudodiploria strigosa - Orbicella annularis	4	5.46	0.73
Pseudodiploria strigosa - Orbicella faveolata	4	3.58	1.12
Pseudodiploria strigosa - Porites astreoides	12	9.14	1.31
Pseudodiploria strigosa - Pseudodiploria strigosa	26	6.51	3.99
Pseudodiploria strigosa - Siderastrea siderea	21	6.77	3.1
Siderastrea radians - Nothing	12	0.14	87.5
Siderastrea siderea - Nothing	214	3.51	60.99
Siderastrea siderea - Agaricia agaricites	6	4.43	1.35
Siderastrea siderea - Agaricia humilis	6	6.46	0.93
Siderastrea siderea - Diploria labyrinthiformis	3	3.97	0.76
Siderastrea siderea - Eusmilia fastigiata	4	3.57	1.12
Siderastrea siderea - Madracis auretenra	8	8.72	0.92
Siderastrea siderea - Montastraea cavernosa	5	4.56	1.1
Siderastrea siderea - Orbicella annularis	7	5.71	1.23
Siderastrea siderea - Porites astreoides	13	9.39	1.38
Siderastrea siderea - Porites furcata	3	3.79	0.79

Siderastrea siderea - Pseudodiploria strigosa	21	6.77	3.1
Siderastrea siderea - Siderastrea siderea	54	7.02	7.7
Stephanocoenia intersepta - Nothing	1	0.01	87.5
unclear - Nothing	6	0.07	87.5

A total area of 68.75 m^2 was sampled on reef flat bottom. On this area, 18 species of Scleractinia and a total of 693 interactions were recorded (Table 3). *Pseudodiploria strigosa* was most commonly found interacting with nothing (n = 131), followed by *Siderastrea siderea* (n = 127), *Porites astreoides* (n = 118), and *Siderastrea radians* (n = 78), respectively. All species recorded on reef-flat bottom surface transects were most frequently observed without interaction and eight species were only found interacting with nothing. Of the interactions between two colonies the most commonly found one was *Pseudodiploria strigosa* interacting with its conspecifics (5.03 m^{-2}). *Siderastrea siderea* interacting with its conspecifics (2.29 m^{-2}) and with *Pseudodiploria strigosa* (2.19 m^{-2}), *Porites astreoides* interacting with conspecifics (2.1 m^{-2}), and *Agaricia agaricites* interacting with *Orbicella annularis* (1.64 m^{-2}) followed thereafter (Table 3).

Table 3. Summary of all species interactions recorded in all transects on reef flat bottom per unit area (m^{-2}).

Interaction name	n interactions	Density (m^{-2})	Interaction/density
Acropora cervicornis - Nothing	36	0.52	68.75
Agaricia agaricites - Nothing	1	0.03	34.38
Agaricia agaricites - Orbicella annularis	1	0.61	1.64
Agaricia humilis - Nothing	20	0.31	65.48
Agaricia humilis - Pseudodiploria strigosa	1	2.69	0.37
Colpophyllia natans - Nothing	5	0.07	68.75
Dichocoenia stokesii - Nothing	1	0.02	68.75
Diploria labyrinthiformis - Nothing	3	0.04	68.75
Favia fragum - Nothing	15	0.23	64.45
Favia fragum - Porites astreoides	1	2.14	0.47
Madracis auretenra - Nothing	1	0.02	68.75
Madracis decactis - Nothing	5	0.09	57.29
Madracis decactis - Siderastrea siderea	1	2.27	0.44
Meandrina meandrites - Nothing	3	0.04	68.75
Montastraea cavernosa - Nothing	5	0.15	34.38
Montastraea cavernosa - Montastraea cavernosa	2	0.29	6.88
Montastraea cavernosa - Pseudodiploria strigosa	2	2.53	0.79
Montastraea cavernosa - Siderastrea siderea	2	2.33	0.86
Orbicella annularis - Nothing	37	0.58	63.59
Orbicella annularis - Agaricia agaricites	1	0.61	1.64
Orbicella annularis - Siderastrea siderea	2	2.76	0.72
Orbicella faveolata - Nothing	6	0.1	58.93
Orbicella faveolata - Pseudodiploria strigosa	1	2.49	0.4
Porites astreoides - Nothing	118	1.91	61.93

Porites astreoides - Favia fragum	1	2.14	0.47
Porites astreoides - Porites astreoides	8	3.81	2.1
Porites astreoides - Pseudodiploria strigosa	3	4.29	0.7
Porites astreoides - Siderastrea siderea	1	4.09	0.25
Porites porites - Nothing	4	0.06	68.75
Pseudodiploria strigosa - Nothing	131	2.39	54.92
Pseudodiploria strigosa - Agaricia humilis	1	2.69	0.37
Pseudodiploria strigosa - Montastraea cavernosa	2	2.53	0.79
Pseudodiploria strigosa - Orbicella faveolata	1	2.49	0.4
Pseudodiploria strigosa - Porites astreoides	3	4.29	0.7
Pseudodiploria strigosa - Pseudodiploria strigosa	24	4.77	5.03
Pseudodiploria strigosa - Siderastrea siderea	10	4.57	2.19
Siderastrea radians - Nothing	78	1.13	68.75
Siderastrea siderea - Nothing	127	2.18	58.21
Siderastrea siderea - Madracis decactis	1	2.27	0.44
Siderastrea siderea - Montastraea cavernosa	2	2.33	0.86
Siderastrea siderea - Orbicella annularis	2	2.76	0.72
Siderastrea siderea - Porites astreoides	1	4.09	0.25
Siderastrea siderea - Pseudodiploria strigosa	10	4.57	2.19
Siderastrea siderea - Siderastrea siderea	10	4.36	2.29
unclear - Nothing	3	0.04	68.75

The Kruskal-Wallis-non-parametric analysis of variance showed a significant difference for both the number of interactions by species (df = 2, p = $2.29*10^{-14}$) and the interaction per density values (df = 2, p = $2.14*10^{-12}$) between the different substrate types. The Dunn's post-hoc test showed that artificial and natural hard substrate each hosted significantly higher numbers of interactions and interaction per density values than the reef flat bottom but did not differ from each other significantly (Figures 6a, 7a; Tables 4, 5).
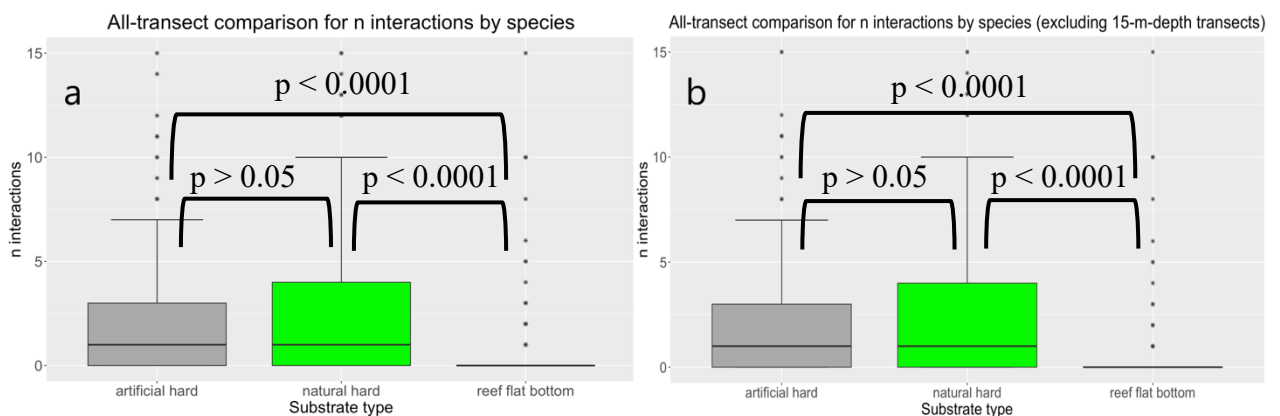

Figure 6. Boxplot showing the number of interactions for the comparison of the frequency of interactions by species against substrate type for all transects a) with and b) without the 15-m-depth transects.
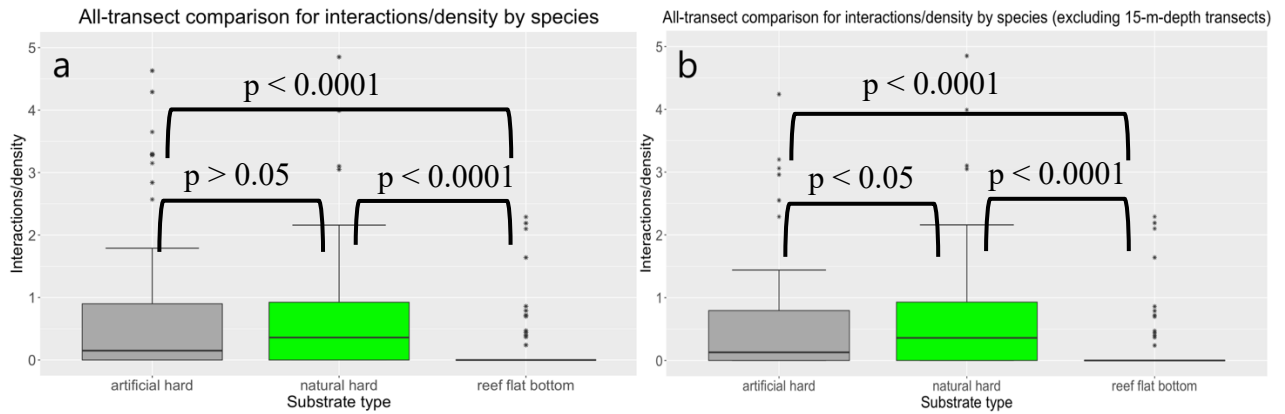
Figure 7. Boxplot showing the interactions/density values for the comparison of the frequency of interactions by species against substrate type for all transects a) with and b) without the 15-m-depth transects.

The tests excluding the 15-m depth transects at Sea Aquarium also showed significantly higher values for each of the hard substrata than for the reef flat bottom (Figures 6b, 7b; Tables 4, 5). A significant difference was also found between artificial and natural hard substrate, but only for the test run with the values corrected for differing sizes in sampling area. This test showed that the interaction per density values were higher on natural than on artificial hard substrate (Figure 7b; Table 5).

3.2.2 Comparison for sampling sites with multiple substrate types

3.2.2.1 Comparison for Water Factory

At Water Factory, an area of 18.75 m^2 was sampled on artificial hard substrate. In total, 15 scleractinian species and 894 interactions were recorded on these transects. The most common finding was *Porites astreoides* interacting with nothing (n = 206), followed by *Agaricia humilis* and *Pseudodiploria strigosa* without interaction (n = 151 and 124 respectively) and *Pseudodiploria strigosa* interacting with conspecifics (n = 108). With the exception of *Porites porites*, which was only found interacting with other species, all species were most frequently found occurring without interaction. Four of the 15 species were only recorded without interactions. Of the interaction between two colonies *Pseudodiploria strigosa* interacting with conspecifics was the most frequent (4.07 m^{-2}). *Pseudodiploria strigosa* interacting with *Siderastrea siderea* (0.93 m^{-2}), *Porites astreoides* interacting with its conspecifics (0.9 m^{-2}), *Pseudodiploria strigosa* interacting with *Porites astreoides* (0.87 m^{-2}) and *Siderastrea siderea* with its conspecifics (0.75 m^{-2}) followed thereafter (Appendix Table S7).

An area of 12.5 m^2 was sampled in natural hard substrate transects, in which 14 species and 402 interactions were found. Among corals without interaction, *Madracis auretenra* was most common (n = 91), followed by *Pseudodiploria strigosa* (n = 38), and *Agaricia humilis* (n

= 35). Four species were only observed without interactions. *Porites furcata* was only observed with interaction, while all other species occurred most often without interaction. Of the recorded interactions between colonies the most common was *Siderastrea siderea* interacting with conspecifics (2.65 m^{-2}), followed by *Madracis auretenra* with *Orbicella annularis* and *Pseudodiploria strigosa* with its conspecifics (1.73 m^{-2} respectively) and *Diploria labyrinthiformis* with conspecifics (1.56 m^{-2}) (Appendix Table S8).

In an area of 12.5 m^2 of reef flat bottom transects, nine species and 217 interactions were recorded. The most common records were *Pseudodiploria strigosa* interacting with nothing (n = 60) and *Porites astreoides* and *Siderastrea siderea* without interactions (n = 46 and 33 respectively). Three of the nine observed species were only found interacting with nothing. *Montastraea* cavernosa and *Orbicella faveolata* were only recorded with interactions. The other species were most often found without interaction. With a value of 1.6 interactions per m^2, *Pseudodiploria strigosa* interacting with conspecifics was the most frequent interaction between colonies. *Pseudodiploria strigosa* interacting with *Siderastrea siderea* (0.68 m^{-2}) and *Siderastrea siderea* with its conspecifics (0.6 m^{-2}) followed thereafter (Appendix Table S9).

The Kruskal-Wallis-Test showed significant differences in both the number of interactions (df = 2, p = 5.87*10^{-5}) and the interactions per density values (df = 2, p = 6.73*10^{-5}). The Dunn's post-hoc test revealed that there was a significant difference between reef flat bottom and both artificial and natural hard substrate respectively, but not between the two hard substrate types (Tables 4, 5). Both hard substrate types showed significantly higher values than the reef flat bottom (Figures 8a, 9a).

3.2.2.2 Comparison for Marie Pampoen

At Marie Pampoen, an area of 25 m^2 was sampled on artificial hard substrate. There were 18 species of Scleractinia, and a total of 1187 interactions. *Porites astreoides* was most commonly found without interaction (n = 268). *Siderastrea siderea*, *Agaricia humilis* and *Pseudodiploria strigosa* followed thereafter, each also without an interaction (n = 184, n = 137 and n = 85 respectively) (Appendix Table S12). All coral species – except *Meandrina meandrites* – were found most often without interaction and seven species were only found without any interaction. *Meandrina meandrites* was only found interacting with *Siderastrea siderea*. Of the recorded interactions between two coral colonies the most common interaction was *Siderastrea siderea* with its conspecifics (3.23 m^{-2}), followed by *Pseudodiploria strigosa* interacting with its conspecifics (2.53 m^{-2}), *Siderastrea siderea* with *Pseudodiploria strigosa* (1.44 m^{-2}),

Siderastrea siderea with *Porites astreoides* (1.12 m^{-2}) and *Diploria labyrinthiformis* interacting with *Pseudodiploria strigosa* (0.96 m^{-2}) (Appendix Table S12).

Seventeen species of Scleractinia and 418 interactions were sampled on an area of 18.75 m^2 on natural hard substrate. Most commonly recorded were *Porites astreoides* (n = 86), *Madracis auretenra* (n = 45), *Siderastrea siderea* (n = 44) and *Pseudodiploria strigosa* (n = 39) – each without interaction. All species were found most often interacting with nothing and six of the 17 species were only recorded without interactions. The most common interaction concerned *Diploria labyrinthiformis* with its conspecifics (2.34 m^{-2}). *Siderastrea siderea* with its conspecifics (1.85 m^{-2}), *Madracis auretenra* with *Orbicella annularis* (0.94 m^{-2}), *Siderastrea siderea* with *Porites astreoides* (0.76 m^{-2}) and *Diploria labyrinthiformis* with *Siderastrea siderea* (0.65 m^{-2}) following thereafter (Appendix Table S13).

There were 18.75 m^2 sampled on reef flat bottom at Marie Pampoen. Seven species and 135 interactions were counted. Most commonly found were *Siderastrea siderea* interacting with nothing (n = 36), *Siderastrea radians* interacting with nothing (n = 32) and *Pseudodiploria strigosa* without interaction (n = 27). Again, all species were found mostly without interaction and only *Porites astreoides*, *Pseudodiploria strigosa* and *Siderastrea siderea* were found with interactions. Of the interactions between two colonies, the most common were *Porites astreoides* with *Pseudodiploria strigosa* (0.35 m^{-2}), *Porites astreoides* with *Siderastrea siderea* (0.3 m^{-2}) and *Siderastrea siderea* with *Pseudodiploria strigosa* (0.28 m^{-2}) (Appendix Table S14).

The Kruskal-Wallis-Test showed a significant difference in the number of interactions (df = 2, p = 1.58*10^{-13}) and the interaction per density values (df = 2, p = 2.07*10^{-11}) between the different substrate types. The Dunn's post-hoc test showed that reef flat bottom hosted significantly lower numbers of interactions and interaction per density values than the two hard substrata, but no significant difference between natural and artificial hard substrate (Figures 8b, 9b; Tables 4, 5).
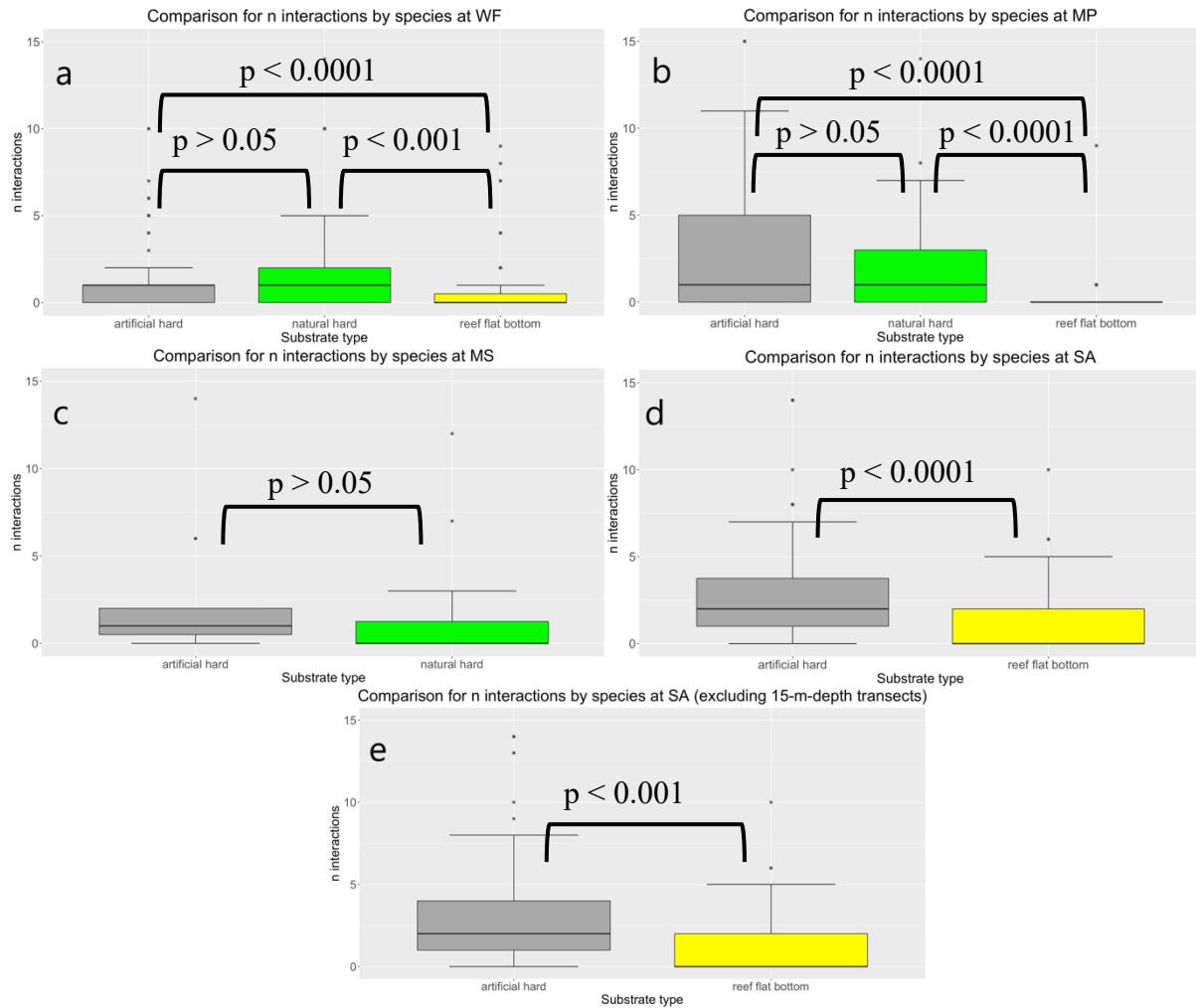
Figure 8. Boxplot showing the number of interactions for the comparison of the frequency of interactions by species against substrate type for a) Water Factory, b) Marie Pampoen, c) Marie Pampoen Sewage and Sea Aquarium d) with and e) without the 15-m-depth transects.

3.2.2.3 Comparison for Marie Pampoen Sewage

At Marie Pampoen Sewage, an area of 6.25 m² of artificial hard substrate was sampled on which six species of scleractinian coral and 109 interactions were found. *Agaricia humilis* was most often encountered interacting with nothing (n = 64), followed by *Pseudodiploria strigosa* without interaction (n = 14), *Madracis decactis*, *Porites astreoides,* and *Siderastrea siderea* also without interaction (n = 6 respectively). All recorded species were most frequently found occurring without interaction and two species were only found without any interaction. The most common interaction concerned *Pseudodiploria strigosa* with *Siderastrea siderea* (0.26 m⁻²), followed by *Agaricia humilis* with *Pseudodiploria strigosa* (0.15 m⁻²) (Appendix Table S17).

An area of equal size was sampled on natural hard substrate. A total of six species and 29 interactions were found. *Pseudodiploria strigosa* was found most often without interaction

(n = 12), followed by *Siderastrea siderea* interacting with nothing (n = 7). Of the six recorded species, only *Orbicella annularis* and *Siderastrea siderea* were found interacting with each other (1.04 m^{-2}), the rest was only encountered without interactions (Appendix Table S18).

The Kruskal-Wallis-Test showed no significant difference for the number of interactions (df = 1, p = 0.059) and the interaction per density values (df = 1, p = 0.3) between the substrate types (Figures 8c, 9c; Tables 4, 5).

3.2.2.4 Comparison for Sea Aquarium

At Sea Aquarium 62,5 m^2 were sampled on artificial hard substrate and a total of 20 species of Scleractinia and 1448 interactions were recorded. *Porites astreoides* (n = 364) was most frequently found, followed by *Agaricia humilis* (n = 309), *Siderastrea siderea* (n = 156), and *Favia fragum* (n = 154), all without interaction. The other encountered species were also found most often without interaction. Nine of the 20 recorded species were only found interacting with nothing.

With 4.17 interactions per m^2, *Orbicella annularis* interacting with conspecifics was the most frequently observed interaction between colonies at Sea Aquarium. *Pseudodiploria strigosa* interacting with its conspecifics (3.98 m^{-2}), *Agaricia agaricites* interacting with *Madracis decactis* (3.68 m^{-2}), *Siderastrea siderea* with its conspecifics (2.63 m^{-2}) and *Agaricia agaricites* interacting with *Meandrina meandrites* (2.16 m^{-2}) followed thereafter (Appendix Table S21).

On reef flat bottom transect an area of 37.5 m^2 was sampled, in which 16 species and 342 interactions were found. The most common findings were *S. siderea* without interaction (n = 58), *Porites astreoides* interacting with nothing (n = 50), *Pseudodiploria strigosa* without interaction (n = 45) and *Orbicella annularis* and *Siderastrea radians* interacting with nothing (n = 37 each). All species were found to occur most often without interaction and seven species were only recorded without interaction.

The most frequently observed interaction between two colonies was *Montastraea cavernosa* interacting with conspecifics (4.69 m^{-2}). *Porites astreoides* interacting with its conspecifics (1.94 m^{-2}), *Siderastrea siderea* with its conspecifics (1.61 m^{-2}), *Montastraea cavernosa* interacting with *Siderastrea siderea* (0.96 m^{-2}) and *Agaricia agaricites* with *Orbicella annularis* (0.89 m^{-2}) followed thereafter (Appendix Table S22).

The Kruskal-Wallis-Test showed a that the number of interactions (df = 1, p = 1.72*10^{-5}) and the interactions per density values (df = 1, p = 2.43*10^{-4}) were significantly higher on artificial hard substrate than on reef flat bottom transects at Sea Aquarium (Figures 8d, 9d; Tables 4, 5).
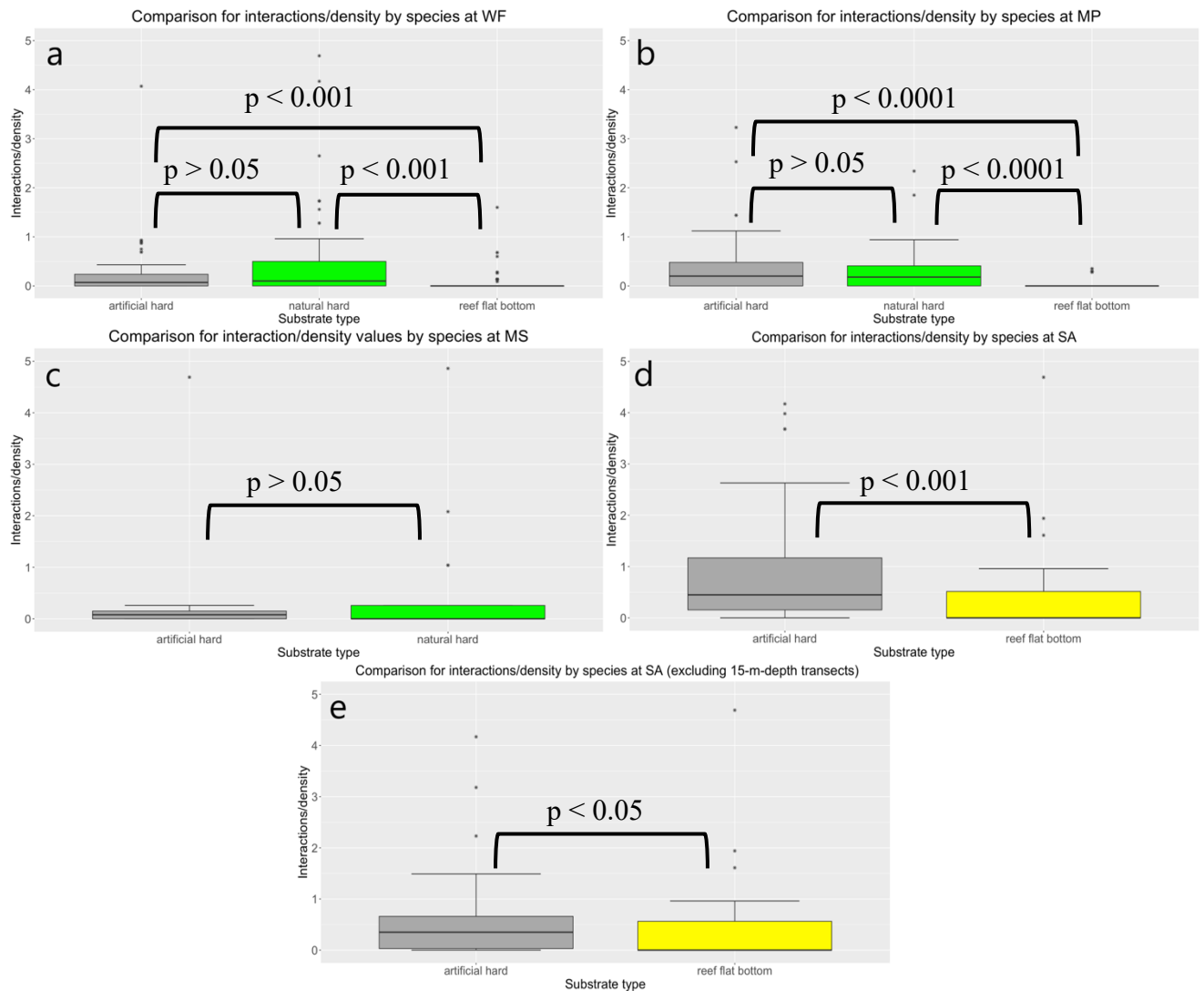
Figure 9. Boxplot showing the interactions/density values for the comparison of the frequency of interactions by species against substrate type for a) Water Factory, b) Marie Pampoen, c) Marie Pampoen Sewage and Sea Aquarium d) with and e) without the 15-m-depth transects.

Without the 15-m-depth transects, the sampling area on artificial hard substrate is reduced to 50 m^2. *Porites astreoides* (n = 350), *Agaricia humilis* (n = 309), *Favia fragum* (n = 153) and *Siderastrea siderea* (n = 126) – all without interaction – were most commonly found. All species found still occurred most often without interaction, except for *Colpophyllia natans*, which was only found interacting with other species, but not without interaction. *Agaricia lamarcki* was only found on the 15-m-depth transects. Also, when the 15-m-depth transects are excluded, *Agaricia agaricites* was only found occurring without interactions.

Of the interactions recorded between two colonies the most frequently observed was *Orbicella annularis* interacting with its conspecifics (4.17 m^{-2}), followed by *Pseudodiploria strigosa* interacting with its conspecifics (3.18 m^{-2}), *Siderastrea siderea* interacting with

conspecifics (2.23 m^{-2}), *Favia fragum* with its conspecifics (1.49 m^{-2}) and *Porites astreoides* interacting with *Siderastrea siderea* (1.19 m^{-2}) (Appendix Table S23). The non-parametric analysis of variance showed a significantly lower number of interactions (df = 1, p = 8.6*10^{-4}) and interaction per density values (df = 1, p = 1.35*10^{-2}) on reef flat bottom than on artificial hard substrate (Figures 8e, 9e; Tables 4, 5).

Table 4. A summary of the p-values calculated for the comparison of the number of interactions by species by Dunn's post-hoc test for all comparisons.

Comparison	p-Value (Dunn's Test)
All transects: artificial hard – natural hard	p > 0.05
All transects: artificial hard – reef flat bottom	p < 0.0001
All transects: natural hard – reef flat bottom	p < 0.0001
All transects w/o 15 m: artificial hard – natural hard	p > 0.05
All transects w/o 15 m: artificial hard – reef flat bottom	p < 0.0001
All transects w/o 15 m: natural hard – reef flat bottom	p < 0.0001
WF: artificial hard – natural hard	p > 0.05
WF: artificial hard – reef flat bottom	p < 0.001
WF: natural hard – reef flat bottom	p < 0.001
MP: artificial hard – natural hard	p > 0.05
MP: artificial hard – reef flat bottom	p < 0.0001
MP: natural hard – reef flat bottom	p < 0.0001
MS: artificial hard – natural hard	p > 0.05
SA: artificial hard – reef flat bottom	p < 0.0001
SA w/o 15 m: artificial hard – reef flat bottom	p < 0.001

Table 5. A summary of the p-values calculated for the comparison of the interactions per density values by species by Dunn's post-hoc test for all comparisons.

Comparison	p-Value (Dunn's Test)
All transects: artificial hard – natural hard	p > 0.05
All transects: artificial hard – reef flat bottom	p < 0.0001
All transects: natural hard – reef flat bottom	p < 0.0001
All transects w/o 15 m: artificial hard – natural hard	p < 0.05
All transects w/o 15 m: artificial hard – reef flat bottom	p < 0.0001
All transects w/o 15 m: natural hard – reef flat bottom	p < 0.0001

WF: artificial hard – natural hard	p > 0.05
WF: artificial hard – reef flat bottom	p < 0.001
WF: natural hard – reef flat bottom	p < 0.001
MP: artificial hard – natural hard	p > 0.05
MP: artificial hard – reef flat bottom	p < 0.0001
MP: natural hard – reef flat bottom	p < 0.0001
MS: artificial hard – natural hard	p > 0.05
SA: artificial hard – reef flat bottom	p < 0.001
SA w/o 15 m: artificial hard – reef flat bottom	p < 0.05

3.3 Competitive dominance of scleractinian coral species

3.3.1 All-transect comparison

Of the 28 recorded scleractinian coral species that were found in this study, only 18 were observed interacting with either their conspecifics or other species. In total 1,453 interactions between two colonies were observed over the entirety of the sampled area.

For artificial hard substrate only two species were not categorized as intermediate (CI of 0.19 to -0.2) in their competitive abilities: *Acropora palmata* (CI = 1; aggressive) and *Agaricia agaricites* (CI = 0.2; moderately aggressive). *Acropora palmata* was only observed interacting with other species on artificial substrate and won both of its recorded interactions. For *Agaricia agaricites* 5 interactions were observed on artificial hard substrate, of which 4 were neutral interactions and 1 was won by *Agaricia agaricites*. For all recorded species except for *Acropora palmata*, most or all interactions observed on artificial substrate were neutral. *Eusmilia fastigiata*, *Orbicella faveolata* and *Porites furcata* were either not found with interactions, or not occurring at all on the artificial hard substrate transects.

All the species that were found on the natural hard substrate transects had CI values of 0, or close to 0 and were listed as intermediate. *Acropora palmata*, *Colpophyllia natans* and *Porites porites* were not found with interactions on natural substrate.

On the reef flat bottom transects three species were not listed as intermediate: *Agaricia humilis* (CI = -1; subordinate), *Montastraea cavernosa* (CI = 0.33; moderately aggressive) and *Madracis decactis* (CI = 1; aggressive). All other species were either not found occurring with interactions or transects had CI values of 0, or close to 0 and were categorized as intermediate.

Only four species (*Agaricia agaricites*, *Agaricia humilis*, *Madracis decactis* and *Montastraea cavernosa*) were found on all substrate types and categorized differently

regarding their dominance in interactions on different substrata. Each of these species was listed as intermediate for two substrate types, but different on the third (Table 6).

Table 6. A summary of the coral interaction dominance Index (CI) values calculated and the dominance categories of each species of scleractinian corals found interacting with other species or their conspecifics for the all-transect comparison. AHS = artificial hard substrate, NHS = natural hard substrate, RFB = reef flat bottom.

Coral species	Substrate type	n total interactions	n wins	n losses	n neutral	n unclear	Coral interaction dominance Index (CI)	Category
Acropora palmata	AHS	2	2	0	0	0	1	aggressive
Acropora palmata	NHS	NA	NA	NA	NA	NA	NA	NA
Acropora palmata	RFB	NA	NA	NA	NA	NA	NA	NA
Agaricia agaricites	AHS	5	1	0	4	0	0.2	moderately aggressive
Agaricia agaricites	NHS	18	3	1	14	0	0.11	intermediate
Agaricia agaricites	RFB	1	0	0	1	0	0	intermediate
Agaricia humilis	AHS	63	3	0	60	0	0.048	intermediate
Agaricia humilis	NHS	15	0	1	14	0	-0.07	intermediate
Agaricia humilis	RFB	1	0	1	0	0	-1	subordinate
Colpophyllia natans	AHS	6	0	0	6	0	0	intermediate
Colpophyllia natans	NHS	NA	NA	NA	NA	NA	NA	NA
Colpophyllia natans	RFB	NA	NA	NA	NA	NA	NA	NA
Diploria labyrinthiformis	AHS	20	2	0	17	1	0.1	intermediate
Diploria labyrinthiformis	NHS	20	1	1	15	3	0	intermediate
Diploria labyrinthiformis	RFB	NA	NA	NA	NA	NA	NA	NA
Eusmilia fastigiata	AHS	NA	NA	NA	NA	NA	NA	NA
Eusmilia fastigiata	NHS	8	0	0	8	0	0	intermediate
Eusmilia fastigiata	RFB	NA	NA	NA	NA	NA	NA	NA
Favia fragum	AHS	19	0	1	18	0	-0.05	intermediate
Favia fragum	NHS	1	0	0	0	1	0	intermediate
Favia fragum	RFB	1	0	0	1	0	0	intermediate
Madracis auretenra	AHS	15	0	0	14	1	0	intermediate
Madracis auretenra	NHS	67	6	0	60	1	0.09	intermediate
Madracis auretenra	RFB	NA	NA	NA	NA	NA	NA	NA
Madracis decactis	AHS	2	0	0	2	0	0	intermediate
Madracis decactis	NHS	2	0	0	2	0	0	intermediate
Madracis decactis	RFB	1	1	0	0	0	1	aggressive
Meandrina meandrites	AHS	4	0	0	4	0	0	intermediate
Meandrina meandrites	NHS	3	0	0	3	0	0	intermediate
Meandrina meandrites	RFB	NA	NA	NA	NA	NA	NA	NA
Montastraea cavernosa	AHS	2	0	0	2	0	0	intermediate

Montastraea cavernosa	NHS	15	0	1	13	1	-0.07	intermediate
Montastraea cavernosa	RFB	6	2	0	4	0	0.33	moderately aggressive
Orbicella annularis	AHS	29	2	1	26	0	0.03	intermediate
Orbicella annularis	NHS	57	3	1	52	1	0.04	intermediate
Orbicella annularis	RFB	3	0	0	3	0	0	intermediate
Orbicella faveolata	AHS	NA	NA	NA	NA	NA	NA	NA
Orbicella faveolata	NHS	10	0	0	10	0	0	intermediate
Orbicella faveolata	RFB	1	0	0	1	0	0	intermediate
Porites astreoides	AHS	186	9	4	171	2	0.03	intermediate
Porites astreoides	NHS	61	3	2	54	2	0.02	intermediate
Porites astreoides	RFB	13	2	1	10	0	0.08	intermediate
Porites furcata	AHS	NA	NA	NA	NA	NA	NA	intermediate
Porites furcata	NHS	8	0	0	8	0	0	intermediate
Porites furcata	RFB	NA	NA	NA	NA	NA	NA	NA
Porites porites	AHS	3	0	0	3	0	0	intermediate
Porites porites	NHS	NA	NA	NA	NA	NA	NA	NA
Porites porites	RFB	NA	NA	NA	NA	NA	NA	NA
Pseudodiploria strigosa	AHS	278	9	12	245	12	-0.01	intermediate
Pseudodiploria strigosa	NHS	83	1	6	75	1	-0.06	intermediate
Pseudodiploria strigosa	RFB	41	3	3	35	0	0	intermediate
Siderastrea siderea	AHS	225	6	15	200	4	-0.04	intermediate
Siderastrea siderea	NHS	130	2	6	122	0	-0.03	intermediate
Siderastrea siderea	RFB	26	0	3	23	0	-0.12	intermediate
unclear	AHS	1	0	0	1	0	0	intermediate
unclear	NHS	NA	NA	NA	NA	NA	NA	NA
unclear	RFB	NA	NA	NA	NA	NA	NA	NA

3.3.2 Comparison for sampling sites with multiple substrate types

3.3.2.1 Comparison for Water Factory

At Water Factory, 13 species of Scleractinia were found with interactions on the three different substrate types. On artificial hard substrate, all recorded species were categorized as intermediate. Of the 13 total species, three were not found with interactions on artificial hard substrate.

The species found on the transects on natural hard substrate were also all listed as intermediate. Only two of the thirteen total species were not found with interactions on natural hard substrate.

With a CI value of -1 (subordinate), *Agaricia humilis* was the only species of the six with interactions on reef flat bottom not categorized as intermediate. It was also the only species recorded at Water Factory that was grouped into different dominance categories on different substrata. While it was listed as subordinate on reef flat bottom, it was categorized as intermediate on natural and artificial hard substrate (Appendix Table S28).

3.3.2.2 Comparison for Marie Pampoen

A total of 14 species were recorded interacting with either conspecifics or other species at Marie Pampoen. Of these, 11 species were found with interactions on artificial hard substrate. *Acropora palmata* (CI = 1; aggressive) and *Agaricia agaricites* (CI = 1; aggressive) were the only species not categorized as intermediate on artificial substrate.

On the natural hard substrate transects three of the 14 total observed species were not found with interactions. *Agaricia humilis* was categorized as subordinate (CI = -1) and *Montastraea cavernosa* as moderately subordinate (CI = -0.5). The other species were listed as intermediate.

On the transect sampled on reef flat bottom at Marie Pampoen only *Porites astreoides*, *Pseudodiploria strigosa* and *Siderastrea siderea* were found interacting with conspecifics or other species and were all categorized as intermediate (Appendix Table S29).

3.3.2.3 Comparison for Marie Pampoen Sewage

At Marie Pampoen Sewage, five species with interactions were found in total, of which only *Siderastrea siderea* was found occurring on both available types of substrata. All species were categorized as intermediate on both hard and artificial hard substrate (Appendix Table S30).

3.3.2.4 Comparison for Sea Aquarium

Twelve species of Scleractinia were found interacting with conspecifics or other species at Sea Aquarium. On artificial hard substrate all species but *Montastraea cavernosa* were found with interactions and all of them were categorized as intermediate.

Agaricia humilis, *Colpophyllia natans* and *Meandrina meandrites* either only occurred without interactions on reef flat bottom or not at all. *Montastraea cavernosa* (CI = 0.5) was categorized as moderately aggressive, *Madracis decactis* (CI = 1) as aggressive and *Siderastrea siderea* (CI = -0.23) as moderately subordinate. All other species were listed as intermediate. *Madracis decactis* and *Siderastrea siderea* were the only species found on multiple types of

substrate and grouped into different dominance categories on the different substrate types (Appendix Table S31).

When excluding the 15-m transects there is no change in the categories the species are grouped into, as the CI values only differ slightly. Additionally, *Agaricia agaricites* and *Madracis decactis* are no longer observed with interactions on artificial hard substrate (Appendix Table S32).

4. Discussion

4.1 Nearest Neighbor Analysis

The results of the nearest neighbor analysis found that the assemblage of Scleractinia growing on a concrete structure at Boca Samí was distributed evenly with individual colonies averaging further apart than would be expected in a randomly distributed population. Even though only a fraction of the total pictures taken of the structure could be pieced together and used for the analysis with confidence, the calculated average distance to the nearest neighbor was well outside the range calculated for a hypothetical randomly distributed population so that a random distribution could be confidentially dismissed. Thus, the hypothesis that scleractinian coral colonies on artificial structures would be distributed evenly can be confirmed. Furthermore, these results are consistent with the findings of Ng et al. (2012), who found coral colonies on seawalls in Singapore were distanced on average 1 m apart and with the findings of Hill et al. (2021) who found significantly less interactions between benthic organisms on an artificial reef compared to a nearby natural reef, even after centuries of submersion. It is a logical assumption that an evenly distributed assemblage of corals with large distances between individual colonies would result in a lower number of interactions, as the likelihood of different colonies coming into direct contact with each other decreases the further they are away from each other. These findings also lend further support to Bulleri and Chapman (2010), suggesting that due to differences in key ecological processes such as predation, competition and facilitation, structures of anthropogenic origin cannot function as surrogates for natural environments (see also Hill et al. 2021).

While the calculated rA value was larger than the value of mean distance to nearest neighbor within a hypothetical assemblage of random distribution of the same density (rE) plus the calculated standard error (δrE), and thus an even distribution could be assumed with

certainty, the sampling method used in this study proved to be susceptible to errors, as only a fraction of the pictures could be pieced together with enough certainty to be used in the analysis. A larger sampling area with more counted coral colonies would improve the resilience of results in future studies. One method to achieve this could be mounting the camera centrally onto a frame a fixed distance above the photo quadrat (Hill et al., 2021), which would ensure consistent orientation and distance from the ground in all pictures, that pictures can be pieced together more easily, and scale and distances within each picture are constant. The option with the most reliable results, however, would be measuring distances between colonies in the field.

4.2 Frequency of Interactions

For the all-transect comparison, as well as for the comparisons at Water Factory, Marie Pampoen and Sea Aquarium (with and without the 15-m transects) both the number of interactions and the interaction by density values were significantly higher for each of the hard substrate types than they were on reef flat bottom. However, there was no significant difference found between the two hard substrata. At Marie Pampoen Sewage, no significant difference was found at all. The only comparison showing a significant difference between artificial and natural hard substrate was the all-transect comparison excluding the 15-m depth transects. This was, however, only true for the test using the interactions per density values, which were higher on natural than on artificial hard substrate (Tables 5, 6). Based on the fact that all other comparisons showed no significant difference in the number of interactions or the interactions per density values between artificial and natural hard substrate, the hypothesis that interspecific interactions between scleractinian corals would be less frequent on artificial than on natural substrate has to be rejected. In addition to the lacking significant difference in the frequency of interactions between artificial and natural hard substrate, there were similarities in the most frequently observed species and interactions: *Porites astreoides*, *Pseudodiploria strigosa* and *Siderastrea siderea* were among the five most commonly found species on each substrate type for all comparisons. *Agaricia humilis* and *Madracis auretenra* were also often among the most frequently found species. *Porites astreoides*, *Pseudodiploria strigosa* and *Siderastrea siderea* interacting with their conspecifics or each other were commonly among the most frequent interactions for each comparison.

These results in combination with the findings that the number of scleractinian species observed on natural hard substrate was lower at Water Factory and Marie Pampoen, and at Marie Pampoen Sewage the number of encountered species was equal on both types of hard

substrate, seems somewhat contradicting to earlier research that found artificial reef communities, even after centuries, tend to be more homogenous than natural reefs, resulting in a lower abundance and range of organisms, as well as fewer interactions between benthic organisms (Perkol-Finkel et al., 2006; Moschella et al., 2005; Firth et al., 2013; Aguilera et al., 2014; Hill et al., 2021; Monchanin et al., 2021; Lymperaki et al., 2022). A possible explanation might be found in the different morphologies of the artificial structures examined. The artificial reef near St. Eustatius examined by Hill et al. (2021) and Lymperaki et al. (2022), for example, had a smoother and less porous surface, while the breakwaters sampled in the present study were made up of rocks and boulders and provided a more complex and variable surface with pores, cracks, and crevices.
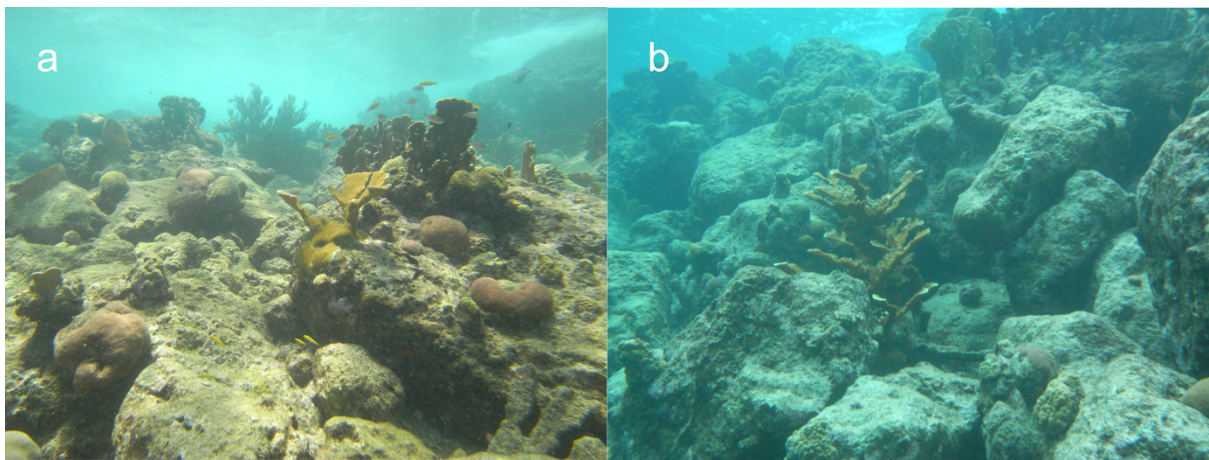

Figure 10. Picture of a) a rocky natural reef at Blue Bay and of b) the artificial breakwater at Marie Pampoen sampling sites.

This complex substrate structure resembles that of rocky natural reefs found around Curaçao (e.g., BB and TB) (Fig. 10) more closely and thus likely results in a more nature like and diverse reef community, which could explain the lack of significant differences in the frequency of interactions between artificial and natural hard substrate observed. This would also align with the results of a seven-year-long experiment by Martins, et al. (2016), who found rougher surfaces of artificial structures enhanced long-term performance and the diversity of the communities they support.

While comparing the frequency of interactions can provide crucial information on differences in reef structure and habitat complexity, other factors such as coral cover or species diversity have to be considered for a more complete comparison of reef communities. Therefore, further research focusing on these factors is needed to confirm the findings of the present study that the communities of Curaçaoan coral reefs on artificial breakwaters do not differ significantly from those on natural hard substrate. Additionally, Caribbean reefs are

generally more homogenous and less diverse than those in the Indo-Pacific region (Veron and Stafford-Smith 2000; Spalding, et al. 2001; Roberts, et al. 2002; Miloslavich, et al. 2010). Thus, further testing is required to see how effective increasing surface complexity of artificial structures is in creating more nature-like communities in more species rich regions.

Also, all breakwaters sampled in this study were comprised of the same materials, yet it is known that many different materials can serve as artificial hard substrate for coral settlement (Fitzhardinge and Bailey-Brock 1989; Lam 2003; Arnold, Steneck and Bell 2011; Hylkema, et al. 2021). Therefore, further investigating the effect of different material types on community structure of reef systems, how structures made of these materials could be manipulated to yield more nature-like communities, and if artificial structures comprised of multiple materials attract more diverse and complex communities than structures made of a single material, could enhance the design and performance of artificial reefs as conservation tools.

4.3 Competitive dominance of scleractinian coral species

Contrary to expectations, the analysis of competitive abilities of scleractinian coral species found most species were grouped into the same category – intermediate – on all substrate types for all comparisons. Only a few species were found on and grouped into different dominance categories on different substrate types. However, they were listed different than intermediate on only one substrate type respectively, on which they were encountered only a few times with interactions. Also, most of these species were grouped differently on reef flat bottom but were in the same category on artificial and natural hard substrate. Only a single species was categorized differently on artificial than on natural hard substrate for the all-transect comparison and two for the comparison at Marie Pampoen. Thus, there is not enough evidence to verify the hypothesis that the dominance of scleractinian corals would differ between artificial and natural hard substrate.

The observed lack of influence of substrate type on the competitive abilities of scleractinian corals in the present study might also be attributed to the complex surface structure of the artificial hard substrate, which closely resembles that of the rocky natural reefs found around Curaçao (Fig. 19) and likely results in more nature-like reef communities with the same competitive hierarchy. This might indicate that among other factors such as wave exposure, position and angle of contact, presence of epifauna, and species-specific competitive strategies (Sheppard, 1979; Bak et al., 1982; Dai, 1990), structural complexity rather than the

type of settlement substrate is one factor deciding the hierarchy in interspecific interactions of sessile reef organisms. However, without further investigation, this assumption is purely speculative. Thus, further research is needed to test for changes in the competitive hierarchy among corals on artificial structures of varying structural complexity compared to nearby natural reefs.

5. Conclusion

The present study provided insights into the distribution of scleractinian corals on artificial structures, as well as the differences in interactions between scleractinian corals on artificial and natural hard substrate in regard to their frequency and competitive hierarchy. In light of the steady increase in artificial hard substrate in the oceans and the decrease in coral health and cover, investigating differences in competitive interactions between scleractinian corals, as major reef building organisms of tropical reefs, might help to improve our understanding of the drivers of differences in reef communities on artificial and natural hard substrate and improve the performance of artificial structures as tools of reef conservation.

An analysis of distance to nearest neighbor between colonies of scleractinian corals on a relatively flat concrete structure at Boca Samí following the methodology of Clark and Evans (1954) showed an even distribution with relatively large distances between individuals. This indicates a lower chance of competitive interactions occurring between scleractinian corals on artificial hard substrate, as large distances between colonies reduces the likelihood of them coming into contact with each other. This aligns with results of earlier studies and supports the suggestion that artificial reefs cannot serve as surrogates for natural reefs, due to differences in key ecological processes.

On the other hand, only a single one of the comparisons of frequency of interactions showed a significant difference between artificial and natural hard substrate. Besides the lack of significant differences in interactions between artificial and natural hard substrate, there were similarities in the number of encountered species, as well as the most commonly encountered species and interaction pairings. These results contradict the consistent findings of earlier research that artificial reefs host a lower range and abundance of organisms, and less competitive interactions than natural reefs. Additionally, there was no change found in the position of scleractinian corals in the competitive interaction hierarchy between artificial and natural hard substrate.

These similarities in the reef communities found on artificial and natural substrate in the present study can be explained by the complex surface structure of the breakwaters sampled as artificial reefs, that closely resembles that of rocky natural reefs found around Curaçao and likely results in more nature-like reef communities. This aligns with the observations of a seven-year-long study by Martins, et al. (2016) that more complex surfaces increase the diversity of communities supported by, as well as the long-term performance of artificial reef structures which could improve the planning and success of artificial structures as conservation tools in the future. Yet further research focused on other factors determining reef community composition, such as species diversity and coral cover, is needed to confirm the findings of the present study. Additionally, further testing is required to see how effective increasing surface structure complexity is in creating more nature-like communities in more species rich and heterogenous regions, like the Indo-Pacific.

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The Appendix is available in separate files. Please contact the author to get access!