Coral Reefs
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RESEARCH

Depth influences coral-dwelling faunal symbiont communities in the Caribbean, independently of colony size

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Abstract The characteristics of stony corals and their environmental conditions play a critical role in shaping the abundance and composition of their associated faunal symbionts. Studies have consistently shown a positive correlation between symbiont community assemblages, number of symbionts and the size of branching coral colonies, as well as habitat depth. However, symbiont assemblages associated with non-branching corals, such as plating or massive species, remain underexplored. To address this gap, we conducted visual surveys of coral-dwelling faunal symbionts on three non-branching coral species—*Agaricia agaricites*, *Porites astreoides*, and *Siderastrea siderea*—at two depths (6 and 15 m) along the leeward coast of Curaçao. Symbiont species and abundance were recorded for 585 coral colonies, yielding a total of 4,969 records representing over 15 species. Observed symbiont species included barnacles, polychaete worms, gall crabs, boring bivalves, and blennies. We examined the relationship between overall symbiont abundance (irrespective of species), colony size, and depth, as well as the relative proportion of colonies hosting varying numbers of symbiont taxa. For all three coral species, the number of individual symbionts was uncorrelated with colony size. Depth significantly influenced symbiont abundance in the massive corals *P. astreoides* and *S. siderea*, but not in *A. agaricites*. Across all species, most coral colonies hosted one or two symbiont taxa, and this reduced symbiont composition became more prevalent at greater depths. These findings underscore the complexity of coral-symbiont assemblages and highlight the important role of environmental factors, such as depth, in structuring these communities.

Keywords Coral-associated fauna · Community ecology · Coral reefs · Curaçao · Scleractinia

Introduction

Tropical coral reefs offer a wide variety of habitats that support a rich diversity of associated taxa, and many of these species live in symbiosis with a sessile host. Coral-dwelling faunal symbionts (e.g., decapods, molluscs, worms) inhabit scleractinian hosts on which they rely for food, shelter and/or reproduction (Stella et al. 2011; Hoeksema et al. 2012). Some symbionts can negatively impact coral health and increase mortality through activities such as feeding or boring (Scott and Risk 1988; Shima et al. 2010). However, many others provide essential protective benefits to their coral hosts (Glynn 1976; Stier and Leray 2014), enhancing the fitness and survival of the corals they inhabit (Stewart et al. 2006; Montano et al. 2017). The assemblages of coral-associated organisms (e.g., symbiont abundance and composition) can also influence the services provided to the

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coral host (McWilliam et al. 2018). For example, Stier et al. (2012) demonstrated that a higher number of associated decapod taxa can improve the removal of sediments from the coral surface, providing a beneficial service to the coral. Additionally, the presence of two or more coral guard-crabs species (*Trapezia* spp.) resulted in a notably superior performance of safeguarding their coral hosts from seastar predators compared to a single species (McKeon et al. 2012).

A coral's growth form plays a critical role in shaping the assemblages of its associated faunas (Abele and Patton 1976; Pisapia et al. 2020; Britayev et al. 2023). Branching corals, e.g., most Acroporidae and Pocilloporidae species, exhibit the highest structural complexity (Graham and Nash 2013; Hermosillo-Nuñez et al. 2015; Britayev et al. 2023), creating niches and opportunities for symbionts to exploit diverse environmental resources (Tews et al. 2004). In these corals, symbiont richness and abundance are positively correlated with colony size (Abele and Patton 1976; Leray et al. 2012). The extensive surface area and intricate topographic structure of large branching colonies provide abundant habitats for symbiotic species, fostering highly diverse communities (Pisapia et al. 2020). Additionally, factors such as depth (Smallhorn-West et al. 2017), location (López-Pérez et al. 2017), host coral density (Britayev et al. 2023), wave energy (Depczynski and Bellwood 2005), and water flow (McWilliam et al. 2018) have all been documented to influence the symbiont assemblage of branching corals. Plating and massive corals, characterised by simpler macromorphologies and reduced structural complexity, provide fewer available niches and habitats for symbionts (Kerry and Bellwood 2012). As a result, compared to branching corals, the assemblages associated with non-branching corals have received relatively little attention in the scientific literature.

The coral-associated fauna of Caribbean scleractinian corals has been documented in several studies (e.g., Scott 1987, 1988; van der Meij 2014; van der Schoot and Hoeksema 2022). These organisms play crucial roles in these reef ecosystems, influencing coral health and growth through various interactions. Key groups include crustaceans (barnacles, gall crabs), fish (blennies), polychaetes (Christmas tree worms) and molluscs (boring mussels) (van der Schoot and Hoeksema 2022). Each of these groups exhibits unique relationships with their coral hosts, ranging from obligate to facultative, and from mutualistic to parasitic. For example, coral barnacles are known to form high-density colonies on coral surfaces, potentially inhibiting coral growth (Vago et al. 1994), while Christmas tree worms can damage coral polyps through abrasion (Hoeksema et al. 2019). The distribution and prevalence of these taxa are likely influenced by various factors, such as depth and environmental conditions, but the processes governing these symbiont assemblages are poorly understood. Generally speaking, there is a significant portion of coral symbionts that are rare, with a few dominant and abundant species (Abele and Patton 1976; Austin et al. 1980). A declining coral cover will likely exacerbate the decrease of all symbionts, with the impacts expected to affect those that are already rare (Idjadi and Edmunds 2006; Bravo et al. 2021). Therefore, understanding the factors that shape symbiont assemblages is crucial for the effective management and conservation of coral reef biodiversity.

The Caribbean is home to the highest coral reef diversity in the Atlantic Ocean and approximately 70 hard coral species have been documented from the region (Souter et al. 2021). Average coral cover in Caribbean reefs has experienced a significant decline from ~50 to ~10% since the early 1980's (Gardner et al. 2003; Jackson et al. 2014), with coral diseases and increasing ocean temperatures being the major drivers of this decline (Aronson and Precht 2001; Bruckner and Bruckner 2006; Eakin et al. 2010; Hoegh-Guldberg et al. 2023). Populations of essential framework-building coral genera, such as *Acropora* and *Orbicella*, have been greatly reduced, resulting in a notable shift in the composition of coral communities. *Agaricia agaricites* (Linnaeus, 1758), *Porites astreoides* Lamarck, 1816, and *Siderastrea siderea* (Ellis & Solander, 1786) are now some of the most abundant species throughout the Caribbean (Green et al. 2008; Perry et al. 2015; Bonthond et al. 2018; Eagleson et al. 2023). *Porites astreoides* and *S. siderea* are massive in structure, while *A. agaricites* has highly variable growth forms including flat unifacial plates, upright bifacial plates, and encrusting forms (Helmuth and Sebens 1993), and is hereafter referred to as submassive. Curaçao is located in the Southern Caribbean, where these three coral species are relatively dominant, with a change in abundance over depth (van Tienderen and van der Meij 2016; van der Schoot and Hoeksema 2022). Given the abundant presence of these coral species, they provide a suitable foundation for the focused study of indwelling faunal symbiont assemblages.

In this study, we investigated the effects of colony size and depth on the abundance and composition of coral-dwelling symbiont assemblages in *A. agaricites, P. astreoides* and *S. siderea*. We hypothesised that larger coral colonies would exhibit a positive correlation with higher abundance and diversity of symbiont species, whereas deeper habitats would show a negative correlation. To test these hypotheses, we conducted visual surveys to collect quantitative data on symbiont communities at two depths on reefs in Curaçao. Moreover, we provide a detailed approach on how to estimate coral colony size based on in situ diameter measurements.

Materials and methods

Data collection

Visual surveys were conducted to document the number of indwelling symbionts within colonies of three coral species, including the submassive *A. agaricites* and the massive *P. astreoides* and *S. siderea*. Surveys were conducted via SCUBA diving at 20 dive sites at depths of 6 and 15 m along Curaçao's leeward coast between February 22nd and April 3rd, 2022 (Fig. 1). To ensure accuracy and consistency of symbiont identification, the data collection by each team member was exclusively restricted to selected coral species. All colonies were randomly selected along a predetermined path and depth, irrespective of size (Table S1). The longest axis (in cm) of each coral colony was recorded using a measuring tape, with measurements across the widest part (Fig. S1). In addition, every colony was photographed in situ, allowing for a more accurate estimation of colony area afterwards (see Supplementary Materials part one for a detailed approach to coral size estimations). Most symbiont species (e.g., gall crabs, Christmas tree worms, blennies) were readily identified to species level using a combination of morphological traits and coral host association (Table 1; Fig. S2). The abundance of each symbiont species was recorded in the field. However, for some symbiont taxa (barnacles, boring bivalves) field identification proved challenging, and specimens were collected for molecular and morphological identification at the University of Groningen. DNA barcoding using Cytochrome c oxidase subunit I (Cox1) and 16S ribosomal rRNA (16S) was used to identify unknown symbionts (see Supplementary Materials part two for barcoding protocols). All sequences are deposited in the NCBI GenBank database with the accession numbers shown in Table S2. Not all polychaete worms, except for *Spirobranchus* spp. and *Anamobaea* spp., can be easily identified in the field due to unresolved taxonomy. Therefore, they were identified only to family level, either Serpulidae or Sabellidae. The symbiont communities were described using the concepts assemblage and abundance. Assemblages is used to describe the community composition of symbiont species on a host, whereas abundance refers to the number of symbiont specimens (regardless of species).

Statistical analyses

Colony size was calculated based on the recorded longest axis (see Supplementary Materials part three). Colony sizes,

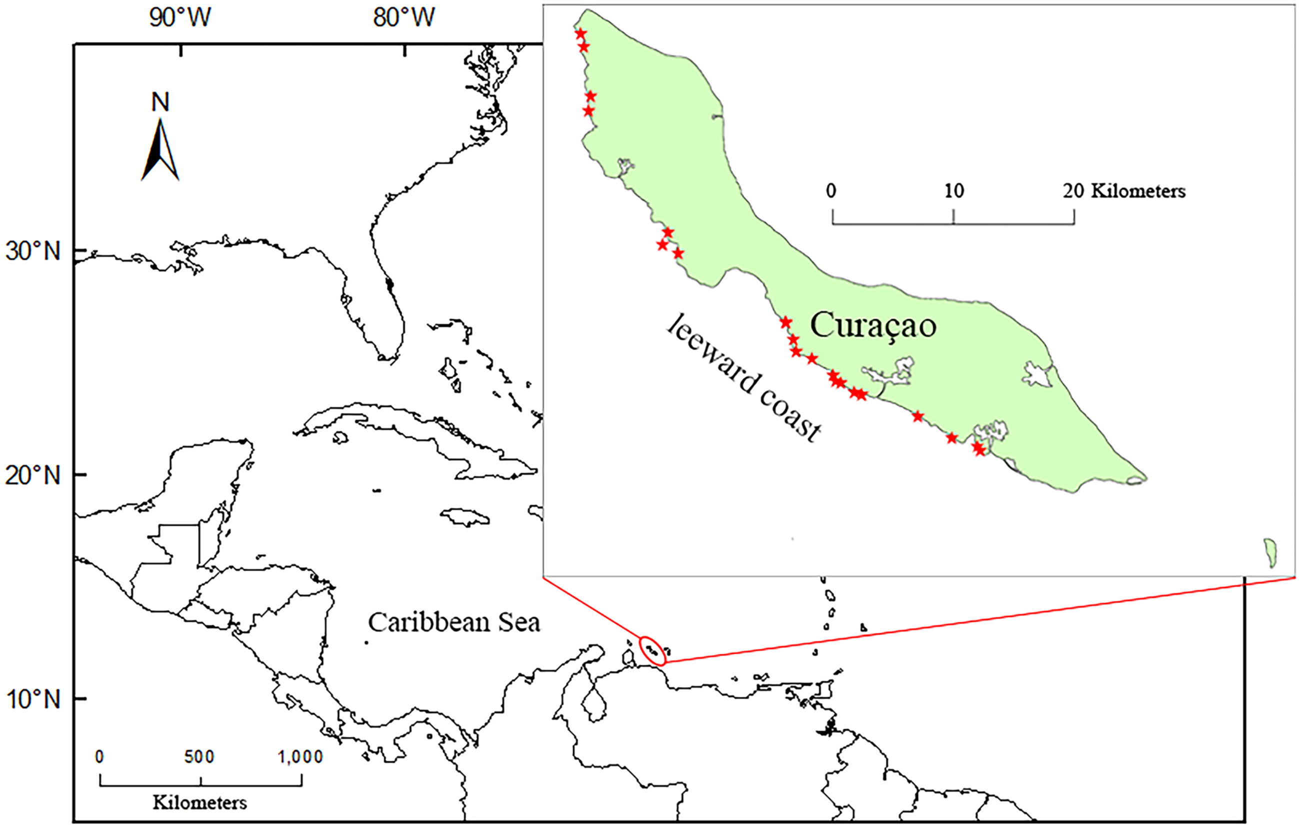


Fig. 1 Location of the 20 sampling sites (indicated with a red star) along the leeward side of Curaçao

Table 1 Symbiont species, and their respective abundances, found in three coral species across the two depths (6 m and 15 m)

Group	Species/OTU	Aaga 6 m	Aaga 15 m	Past 6 m	Past 15 m	Ssid 6 m	Ssid 15 m
Gall crabs (Cryptochiridae)	*Opecarcinus hypostegus* (Shaw & Hopkins, 1977)	17 (n=14)	22 (n=11)	0	0	0	0
	Kroppcarcinus siderastreicola Badaro, Neves, Castro & Johnsson, 2012	0	0	0	0	148 (n=42)	16 (n=11)
Blennies (Chaenopsidae)	*Acanthemblemaria spinosa* Metzelaar, 1919	1 (n=1)	0	7 (n=6)	4 (n=4)	16 (n=13)	0
	Emblemariopsis pricei Greenfield, 1975	0	0	1 (n=1)	0	1 (n=1)	0
Polychaete worms	*Spirobranchus giganteus* (Pallas, 1766)	11 (n=9)	10 (n=9)	128 (n=51)	49 (n=25)	30 (n=16)	6 (n=4)
	Spirobranchus polycerus (Schmarda, 1861)	2 (n=2)	5 (n=3)	12 (n=8)	1 (n=1)	2 (n=2)	0
	Anamobaea sp.	2 (n=2)	3 (n=3)	0	37 (n=3)	2 (n=2)	0
	Sabellidae sp.	0	0	0	0	1 (n=1)	0
	Serpulidae sp.	9 (n=7)	6 (n=5)	9 (n=7)	22 (n=12)	20 (n=13)	8 (n=7)
Barnacles (Pyrgomatidae)	*Ceratoconcha* sp. OTU Aaga	581 (n=44)	886 (n=95)	0	0	0	0
	Ceratoconcha sp. OTU Past	0	0	1039 (n=82)	543 (n=76)	0	0
	Ceratoconcha sp. OTU Ssid	0	0	0	0	1011 (n=58)	33 (n=8)
Gastropods	*Petaloconchus* sp.	2 (n=2)	5 (n=4)	6 (n=4)	1 (n=1)	19 (n=7)	2 (n=2)
Bivalves	*Leiosolenus* sp.	1 (n=1)	1 (n=1)	12 (n=11)	20 (n=15)	32 (n=23)	15 (n=15)
	Gastrochaenidae sp.	0	0	2 (n=1)	0	3 (n=2)	1 (n=1)
	Totals	627 (n=51)	938 (n=102)	1216 (n=100)	677 (n=113)	1286 (n=109)	225 (n=110)

Values represent the total number of specimens of the respective symbiont species. "n" is the number of coral colonies inhabited by their respective symbiont species (e.g. *O. hypostegus* had 17 occurrences in 14 *A. agaricites* corals at 6 m, meaning that some colonies had more than one individual). The bottom row corresponds to the total number of symbiont specimens found in the respective coral species. Aaga: *Agaricia agaricites*; Past: *Porites astreoides*; Ssid: *Siderastrea siderea*

as independent variables, were tested for normality and variance heterogeneity before conducting regression analyses. Simple regression analyses were performed to examine the correlation between symbiont abundance and colony size across two depths and three host species. The same tests for normality and variance heterogeneity were applied to depth-grouped data. The '*wilcox.test*' function in R was used to compare differences between the depths (v2.18; R Core Team 2020). To visualise the data a box plot was created using '*ggplot2*' (v3.4.0; Wickham 2016). Additionally, a stacked bar plot with percentage labels was generated to display the proportion of coral colonies hosting different numbers of symbiotic species (ranging from 0 to 7 species).

Occurrence rates were calculated by dividing the number of colonies (NC) harbouring a specific symbiont by the total number of all sampled colonies (TNC) from two depths. A bipartite network of symbiotic relationships based on the occurrence rates (NC/TNC; Table S3) of each symbiont on each colony across the three coral species was constructed using the '*bipartite*' package in R (v2.18; Dormann et al. 2008). Lastly, we used the package '*cooccur*' to examine symbiont co-occurrences on a coral host across two depths (v1.3; Griffith et al. 2016).

Results

A total of 4,969 individual symbionts, representing at least 15 symbiotic species, were recorded across 585 host colonies (Table 1). Based on Cox1 barcoding data we identified several Operational taxonomic units (OTUs) in *Ceratoconcha*, which are here used as *Ceratoconcha* sp. OTU Aaga, *C.* sp. OTU Past, and *C.* sp. OTU Ssid. Boring mussels were identified as *Leiosolenus* sp. for now, but *Leiosolenus aristatus* (Dillwyn, 1817) or *L. bisulcatus* (d'Orbigny, 1853) are the most likely candidates for this species. Polychaete tube worms were identified to family level, but more diversity at species level is expected.

Agaricia agaricites, *P. astreoides*, and *S. siderea* hosted 9, 10 and 12 different symbiont species respectively, with each coral exhibiting distinct composition of these species (Fig. 2; Table 1). The gall crab *Opecarcinus hypostegus* occurred exclusively in *A. agaricites*, inhabiting 16.34% of the colonies. Meanwhile, *Kroppcarcinus siderastreicola* was found only in *S. siderea*, inhabiting 24.2% of the colonies. The blenny *Acanthemblemaria spinosa* was most abundant in shallow colonies of *S. siderea* and of *P. astreoides*. The Christmas tree worm *Spirobranchus giganteus*

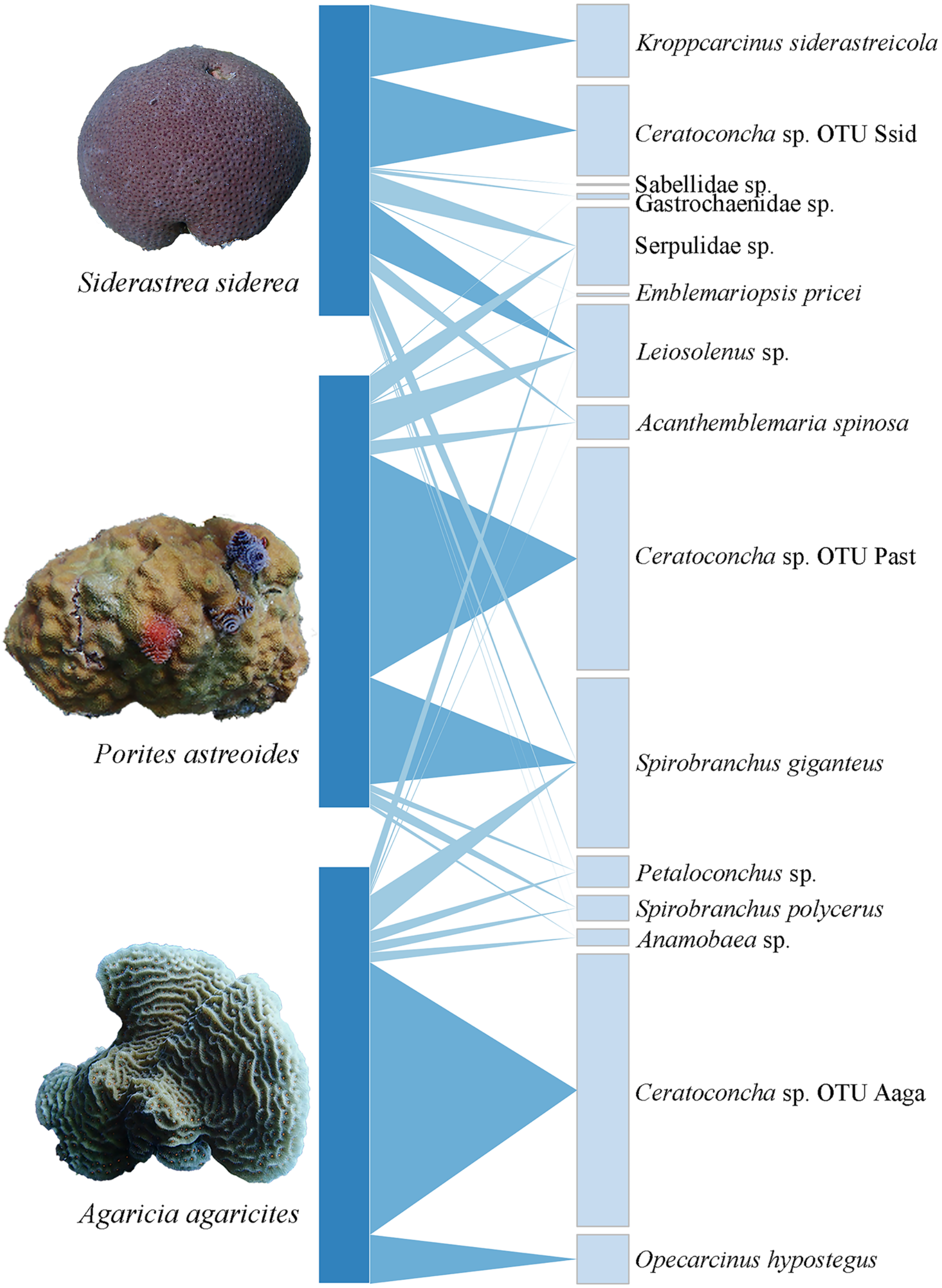


Fig. 2 A bipartite network illustrating the occurrence rates of various symbiont species on three coral host species, regardless of depth. The vertical bars on the left represent each coral species, connected to their respective symbiont species on the right. The width and colour of the connecting bands indicate occurrence rates of the respective symbiont species (dark blue >15% and light blue <15%), with dark blue bands wider than light blue bands. The length of the right vertical bars represent occurrence rates, with larger bars indicating higher occurrence rates for the respective symbiont species/OTUs

was most commonly observed in *P. astreoides*, occurring in 35.68% of the surveyed colonies, but also associated with the other two coral species in this study (11.76% in *A. agaricites* and 9.13% in *S. siderea*). Only one Sabellidae worm was observed living in association with *S. siderea*. Serpulidae worms were present in all coral species and decreased with depth in both *A. agaricites* and *S. siderea*, but showed the opposite trend in *P. astreoides*. Barnacles *Ceratoconcha* sp. OTU Aaga, *C.* sp. OTU Past, and *C.* sp. OTU Ssid dominated the symbiotic assemblage across all three species accounting for 90.85%, 74.18%, and 30.14% of the communities in *A. agaricites*, *P. astreoides*, and *S. siderea*, respectively. Lastly, boring mussels of the genus *Leiosolenus* were commonly found in *P. astreoides* and *S. siderea*, but not in *A. agaricites*.

Correlation between colony size and symbiont abundance

The scatter plot revealed no correlation between colony size and symbiont abundance across the three coral species at both 6 and 15 m depths (Fig. S3; Table S4). Colonies of varying sizes hosted a wide range of symbiont numbers. Results from a simple linear regression confirmed that symbiont abundance was not correlated with colony size at either depth for the three coral species studied (Table S3).

Symbiont abundance and community composition across depth

There was a significant impact of depth on symbiont abundance in *P. astreoides* and *S. siderea*, but not in *A. agaricites* (Fig. 3). At a depth of 6 m, *P. astreoides* typically hosted an average of 9.00 ± 7.92 symbiont individuals, whereas at 15 m, this number decreased to 3.90 ± 3.93 symbionts. *Siderastrea siderea* hosted an average of 4.09 ± 5.19 symbionts at 6 m depth, significantly more than the 0.35 ± 0.59 symbionts found at greater depths. In contrast, the average number of symbionts in *A. agaricites* showed no notable difference between shallow (7.24 ± 5.14) and deeper (7.53 ± 6.91) depths.

The composition of symbiont assemblages in the surveyed coral colonies varied between the two depths. The proportion of colonies without any symbionts increased markedly with depth for both *P. astreoides* (4.0% at 6 m and 23.01% at 15 m) and *S. siderea* (25.69% at 6 m and 66.36% at 15 m), but remained relatively consistent for *A. agaricites* (3.92% at 6 m and 4.90% at 15 m). At 6 m, most colonies were observed with one or two symbiont species, with total percentages of 86.26, 79.0, and 51.38% for *A. agaricites*, *P. astreoides*, and *S. siderea*, respectively. The pattern was even pronounced at 15 m for *A. agaricites*, with corresponding percentages reaching 92.16%, whereas it was less evident in *P. astreoides* and *S. siderea*, at 69.02% and 32.73%, respectively. Colonies associated with more symbiont species represented a small proportion at both depths (Fig. 4).

Species' co-occurrence, an analysis of the observed and expected frequencies of co-occurrence between each pair of symbionts on a coral host, revealed mostly random associations. No negative associations were found, while some positive associations were observed, particularly in *S. siderastrea* at 6 m depth (Fig. S4, S5).

Discussion

Coral diseases have been a major driver of significantly decreasing coral cover in previously dominant framework-building genera like *Acropora* and *Orbicella* in the Caribbean (Bruckner and Bruckner 2006; Eakin et al. 2010). In contrast, *A. agaricites*, *P. astreoides*, and *S. siderea* have seen increases in coral cover, contributing to the formation

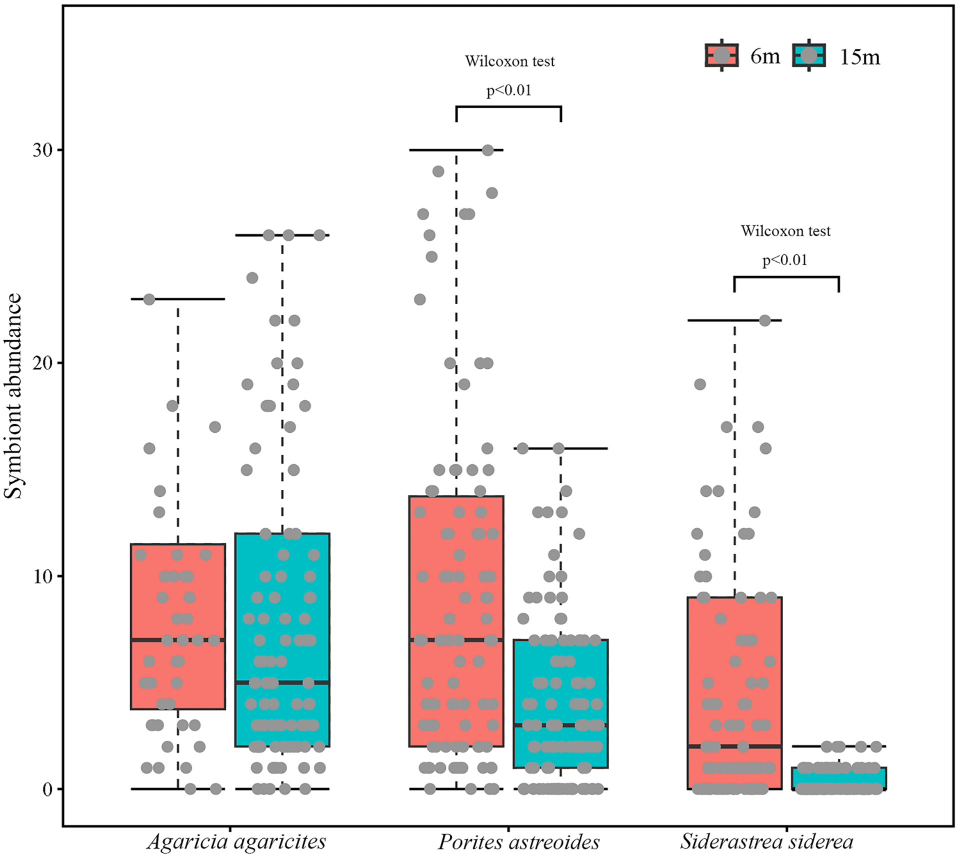
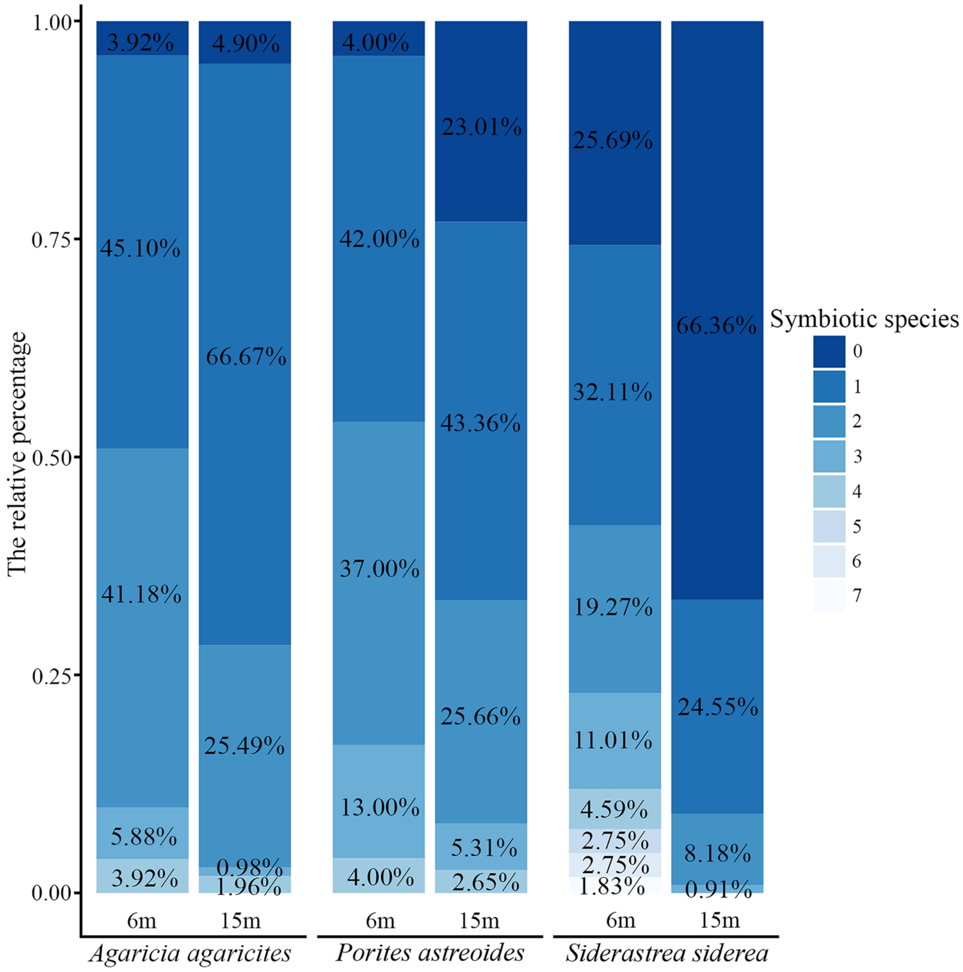


Fig. 3 Box plot depicting overall symbiont abundance on coral colonies at 6 and 15 m depth for the three studied coral species. Outliers are not shown for better visualisation. Significance values are included, where the difference in symbiont abundance across depths was significant for a particular coral species

Fig. 4 The relative percentage of colonies hosting between 0 and 7 symbiotic taxa at 6 and 15 m depth in *Agaricia agaricites*, *Porites astreoides*, and *Siderastrea siderea*



of novel coral assemblages (Green et al. 2008; Perry et al. 2015). The proliferation of these coral species enhances the availability of suitable habitats for both specialist and generalist symbionts. In this study we recorded at least 15 symbiont species, associated with *A. agaricites*, *P. astreoides* and *S. siderea,* on Curaçaoan reefs. Only a few species were abundant, each exceeding 15% in relative abundance. These included barnacles (*Ceratoconcha* spp.), polychaete worms (*S. giganteus*), bivalves (*Leiosolenus* sp.), and gall crabs (*K. siderastreicola* and *O. hypostegus*).

The impact of colony size on symbiont abundance and community

In this study, we investigated how coral colony size influences the abundance of coral-associated symbiont species. The results of our simple linear regression analyses yielded low R-squared values, suggesting a limited correlation between the abundance of associated infauna and colony size across the three non-branching coral species at both studied depths. In Indo-Pacific branching corals, such as *Pocillopora verrucosa* (Ellis and Solander, 1786) and *P. meandrina* Dana, 1846, a positive correlation between colony size and symbiont abundance has been observed (Counsell et al. 2018; Britayev et al. 2023). However, the observed patterns in our study on non-branching corals cannot directly be compared to those observed in branching corals. Most studies on faunal symbionts focus on mobile epifaunal assemblages, likely related to different niche availability in branching and non-branching corals. Branching corals possess a complex structure that offers a more diverse habitat compared to non-branching coral morphologies and are particularly favoured by decapod crustaceans (Austin et al. 1980; Stella et al. 2011). Nevertheless, some non-branching corals also host a plethora of symbiont species. Massive corals with a high diversity of symbionts may exhibit specific ecomorphological traits favoured by associated coral-dwelling fauna. For example, traits such as coral dimensions (diameter and thickness) and tentacle size in mushroom corals (Fungiidae) have been shown to influence symbiont community composition (Hoeksema et al. 2012). Besides ecomorphological features, environmental factors (such as wave height, chlorophyll-a, and current flow speed) also play a significant role in shaping the composition of coral-associated assemblages (Counsell et al. 2018; Pisapia et al. 2020), highlighting the importance of considering other factors in addition to coral colony size.

Our results indicate that symbiont species occurrence (1 or 2 species) appears to be unrelated to colony size (Fig. S6; Table S5). The data show that large colonies can host either a high number of symbiotic species or none at all, a pattern consistent across all three coral species and at both depths. The surface area of the sampled coral colonies varied widely, suggesting differences in colony age (Green et al. 2008). This variability suggests that symbiont occurrence may not be linked to colony age and that other factors, such as environmental conditions or microhabitat characteristics, influence symbiont settlement instead.

The impact of depth on symbiont assemblage

The abundance of coral symbionts significantly decreased with depth in *P. astreoides* and *S. siderea*, but no difference between the two depths was observed in *A. agaricites* (Fig. 3). Van der Schoot and Hoeksema (2022) reported a decrease in the number of barnacles and Christmas tree worms per host over depth and attributed this decline in symbiont abundance with depth to the availability of host corals. The density of the massive corals *P. astreoides* and *S. siderea* decreases with depth between 6 and 15 m, but the submassive species *A. agaricites* has been observed in higher densities at a depth of 15 m compared to 6 m (van Moorsel 1985; Bongaerts et al. 2013; van Tienderen and van der Meij 2016; van der Schoot and Hoeksema 2022). Our results showed that depth had no significant effect on the overall symbiont abundance of *A. agaricites*, contradicting the hypothesis that host coral availability drives abundance patterns (van der Schoot and Hoeksema 2022). Agariciidae corals prefer deeper depths, and the abundance of *A. agaricites* peaks around 15 m in the shallow zone (Bongaerts et al. 2013). However, there is limited knowledge regarding the prevalence rates of associated fauna in mesophotic zones and beyond (van der Meij et al. 2015; Vimercati et al. 2023). Future studies should include a broader range of depths to better understand the relationship between symbiont abundance and depth.

A large proportion of coral colonies in this study were observed with few symbiont species. This pattern with few symbiont species has also been observed in the branching coral *Pocillopora damicornis* (Linnaeus, 1758) (Austin et al. 1980). Why these coral colonies are deemed unsuitable as hosts by the coral-associated taxa is unclear, but potential reasons could include: distance to other coral hosts (congeners or confamilials; Britayev et al. 2023), limitations imposed by the coral's microbiome (Gates and Ainsworth 2011), or perhaps competition/facilitation (i.e., co-occurrence) with other symbionts (Ladd et al. 2019). A co-occurrence analysis revealed no negative species interactions at each depth in the coral-associated fauna used in this study (Fig. S4, S5), suggesting that co-occurrence is a less likely factor responsible for shaping the simple symbiont assemblages of the three coral species examined. Coral-associated fauna generally seem to prefer shallower depths over deeper depths (Patton 1994; Maher et al. 2018; van der Schoot and Hoeksema 2022). The observed depth patterns of the symbiont species in this study are in agreement with these earlier studies.

Our results show that the relative proportion of reduced symbiont assemblages increases with depth across the three studied coral species. Depth has a strong effect on the orientation choice of larvae (Kramer et al. 2019), the deeper living habitats of colonies may restrict the success rates of the larvae or megalopae to settle down. The exact drivers of this depth preference are unknown, but a multitude of factors, such as the life history of symbiont taxa, larval settlement, and nutrient availability, may play a role in shaping coral-associated symbiont assemblages (Montano et al. 2017; Counsell et al. 2018; Britayev et al. 2023). This latter factor, nutrient availability, may affect symbiont species differently depending on their feeding modes. The gall crabs *K. siderastreicola* and *O. hypostegus* have a higher prevalence rate at 6 m than 15 m (Table 1). Bravo et al. (2024) showed that Atlantic gall crabs mainly dine on coral tissue/mucus, the availability of which is not dependent on depth.

Environmental factors have also been reported to play a key role in shaping the symbiont assemblages in coral ecosystems. High water flow can potentially increase the diversity of the symbiont assemblage by providing nutrient supplies for coral-dwelling organisms (McWilliam et al. 2018; Pisapia et al. 2020), whereas chlorophyll a and wave energy are known to be contributing factors to the community structure of coral-associated fauna (Depczynski and Bellwood 2005; Counsell et al. 2018). While the effects of these potential drivers on community structure may differ for filter-feeding organisms (e.g., *Spirobranchus*; Nishi and Nishihira 1999) or those primarily feeding on their host corals (e.g., Cryptochiridae crabs; Bravo et al. 2024), future research should focus on how these factors interact with each other to better understand their impact on symbiont abundance and composition. The symbiont fauna of non-branching corals is still largely understudied, and further research is needed to unravel the complexities of the factors influencing the composition and structure of symbiont communities in massive, plating and encrusting reef-building corals.

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Author's contribution TX collected the data, analysed the data, prepared figures and/or tables, authored and reviewed drafts of the article, and approved the final draft. HB collected the data, reviewed drafts of the article, and approved the final draft. YJHS collected the data, reviewed drafts of the article, and approved the final draft. NMB collected the data, reviewed drafts of the article, and approved the final draft. SETM conceived and designed the data collection, reviewed drafts of the article, and approved the final draft.

Data availability Data used in this study can be accessed in the online Supplementary file 2. This file includes information on the sampling date, location, depth, diameter (longest axis), species and abundance of symbionts, on each individual coral colony.

Declarations

Conflict of interest The authors declare no competing interests.

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