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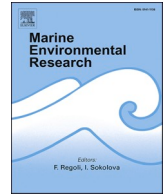
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# Abundance of coral-associated fauna in relation to depth and eutrophication along the leeward side of Curaçao, southern Caribbean

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## ABSTRACT

Coral-associated invertebrates contribute much to the biodiversity of Caribbean coral reefs. Although the nature of their symbiotic relation is usually not fully understood, they can cause damage to their hosts, especially when they occur in high densities. The abundance of seven groups of coral-associated invertebrates was investigated on reefs along the leeward side of Curaçao, southern Caribbean. In particular, coral barnacles (Pyrgomatidae), boring mussels (Mytilidae: *Leiosolenus* spp.), gall crabs (Cryptochiridae), and Christmas tree worms (Serpulidae: *Spirobranchus* spp.) were recorded together with their host corals by means of a photo survey at four depths (5, 10, 15, 20 m) and across seven sites with high and five sites with low eutrophication values (based on  $\delta^{15}\text{N}$  isotope data). Feather duster worms (Sabellidae: *Anamobaea*), coral blennies (Chaenopsidae: *Acanthemblemaria*), and worm snails (Vermetidae: *Petalocochnus*) were insufficiently abundant for thorough quantitative analyses. The results show a decrease in the number of barnacles and Christmas tree worms per host over depth, which could be related to the availability of their host corals. Sites with high  $\delta^{15}\text{N}$  values show a higher abundance of barnacles and Christmas tree worms per host than sites with low values. This indicates that eutrophication could be favourable for these filter feeding organisms but when their densities become too high, they tend to overgrow their hosts and may become a threat to them.

## 1. Introduction

Coral reefs are the most species-rich ecosystems of the world's oceans and seas, while covering only 0.2% of their surface area and containing about 35% of their species (Reaka-Kudla, 1997). Around 30,000 species have been described from Caribbean coral reefs, which make up 8% of the global coral reef surface area (Bryant et al., 1998; Reaka-Kudla, 2005). Their biodiversity is largely explained by the presence of scleractinian corals as bioengineers (Ponti et al., 2021), which create complex three-dimensional structures that provide shelter and habitat for various biotic groups, such as fish, invertebrates, and algae (Gates and Ainsworth, 2011; Brandl et al., 2019; Bowden et al., 2022).

Coral-associated fauna is usually depending on the host coral on which they live as epibionts, either as encrusting epifauna on its surface or by living partly embedded in the coral skeleton. This symbiotic relation can be facultative, in which the symbiont can survive without the host, or obligatory, in which the associate cannot exist without the host (Stella et al., 2011). From ecological and conservational

perspectives, it is important to understand the impact of epifauna on their hosts. In some associations, the epibiont offers protection against predators and diseases (DeVantier et al., 1986; Ben-Tzvi et al., 2006; Montano et al., 2017; Samsuri et al., 2018) or provides cleaning services (Stewart et al., 2006), while in others they wound their hosts, obstruct the host's growth, or smother them entirely (Shima et al., 2010; de Bakker et al., 2018; Turicchia et al., 2018; Barton et al., 2020; Allchurch et al., 2022).

A basic question is whether the nature of their relation is strictly mutualistic, commensalistic, or parasitic. In the last case they may even become pest species when they reach high abundances (Samimi-Namin et al., 2010; Wong et al., 2015; Adhavan et al., 2021). In addition, they may also become harmful when they almost tend to behave more as predators than parasites (Scaps and Denis, 2008; Potkamp et al., 2017; Kaullysing et al., 2019) and also if they represent a catalyst or a vector in the spread of coral diseases as observed in corallivorous snails (Nicolet et al., 2018; Montano et al., 2022). Additional information about these relationships can tell us more about how the symbiont impacts its host's health and therefore its presence or absence (Gates and Ainsworth,

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2011).

In the present study, seven groups of coral-associated fauna were investigated in Curaçao to find out about their abundance, their preferred hosts, and distributions along the leeward side of the island across pollution categories and a depth gradient: (1) coral barnacles (Pyrgomatidae Gray, 1825), (2) Christmas tree worms (Serpulidae: *Spirobranchus* Blainville, 1818), (3) boring mussels (Mytilidae: *Leiosolenus* Carpenter, 1857), (4) coral gall crabs (Cryptochiridae Paulson, 1875), (5) Feather duster worms (Sabellidae: *Anamobaea* Krøyer, 1856), (6) Coral blennies (Chaenopsidae: *Acanthemblemaria* Metzelaar, 1919) and (7) worm snails (Vermetidae: *Petalconchus* H.C. Lea, 1843). So far, little or nothing is known about how these groups are distributed over coral reefs and also not how their distribution is affected by variation in eutrophication caused by sewage output. Previous studies reported mostly on their host ranges but they did not provide quantitative ecological data. The present study will therefore help to increase our understanding of how epibiont distribution and diversity on coral reefs may depend on biotic factors (through host relations), and abiotic factors, either natural (depth) or anthropogenic (eutrophication). The purpose of this study was not to look at specific host-symbiont relationships, which could not be done at this large scale, but to get more insight in how the different groups overall differ in their distributions by use of the same localities at the same time with the same method.

Coral barnacles of the family Pyrgomatidae form a common group of symbionts, which are widespread and can form high densities on the surface of coral colonies. This group is represented by several species in the Atlantic Ocean, which range from host-specific to generalist, without a clear relation with depth (Scott, 1987; Ogawa and Matsuzaki, 1992). Most coral-barnacles are suspension feeders, and therefore do not directly consume coral tissue, like species of the genus *Hoekia* Ross and Newman, 1973 (Ross, 2000), which have been observed to digest organic matter expelled by the host coral (Achituv et al., 1997). The settlement process of the barnacles is disadvantageous for the host as their larvae penetrate the coral tissue with their antennules, which triggers a physical defence response (Liu et al., 2016). It is also thought that occupying host surface by the barnacles might inhibit coral growth (Barton et al., 2020). Besides these negative influences, hydrocorals acting as hosts were thought to recycle organic material excreted by the barnacles, indicating a mutualistic symbiosis (Cook et al., 1991). The effect of eutrophication on the distribution of coral barnacles is currently unknown. Macro-bioeroders however have been observed to occur predominantly in eutrophicated waters (Le Grand and Fabricius, 2011).

Christmas tree worms are tube-building polychaetes and among the most commonly known coral associates, as they are easily noticed by their colourful cone-shaped branchial crowns, which can be retracted under threat (Hoeksema and ten Hove, 2017b). Of this group, three species have been described in the Caribbean, of which *S. giganteus* has the widest host range, including 28 species of stony coral (Hoeksema and ten Hove, 2017a; Hoeksema et al., 2020). *Spirobranchus* worms are known to impose damage to their host's polyps through abrasion caused by contact with the worm's operculum and its epibiont turf algae (Hoeksema et al., 2019a, 2019b). Depth profiles of *Spirobranchus* have been studied very little. In South Africa, corals showed decreasing densities of *Spirobranchus* worms down to a maximum survey depth of 18 m (Floros et al., 2005) and at Curaçao they have not been reported at depths over 39 m (Hoeksema and ten Hove, 2017a).

*Leiosolenus* is a genus of boring mussels (also known as date mussels) that live in limestone substrate, comprising either live coral or dead rock. They are not always noticed, as their hole orifices are small or covered by black mantle tissue (Hoeksema et al., 2022c). Of the four Caribbean species of coral-dwelling boring mussels (*Leiosolenus* spp.), 22 host-coral species have been reported (Scott, 1986; Kleemann, 1990; Hoeksema et al., 2022c). As macro-boring organisms, date mussels impose structural damage to their hosts and make them more susceptible to diseases and external bioerosion by parrotfish (Scott and Risk,

1988; Wong et al., 2015; Rice et al., 2020). Although the relation between eutrophication and boring mussels has not been described directly, a study on the effect on *Leiosolenus tripartitus* in relation to upwelling showed increased bioeroding activity of boring mussels with higher nutrient concentrations (Wizemann et al., 2018).

Cryptochiridae is a family of brachyuran crabs that live in depressions called cavities or pits or in flattened spherelike deformities in the surface of a host coral (Chan et al., 2020; Carricart-Ganivet et al., 2004). This group is relatively well studied and the species that occur in the Caribbean are known to show relatively high host specificity (van der Meij, 2014). They are therefore dependant on the availability of host species, with maximum records of 26 reef-dwelling scleractinians in the Caribbean and 33 host corals in the whole Atlantic (van der Meij, 2014; Hoeksema et al., 2017; van Moorsel and van der Meij, 2018; García-Hernández et al., 2020). Damage to host corals caused by gall crabs has not been extensively studied although it is known that they cause deformations in the host's surface (Nogueira et al., 2014). Coral tissue around the pit zone may die causing the accumulation of debris and the growth of filamentous algae (Kropp, 1986), which are also known to be harmful to the host (Gowan et al., 2014; Wild et al., 2014). No relation between depth and eutrophication has been described for gall crabs.

Split-crown feather duster worms of the Caribbean genus *Anamobaea* (Sabellidae) have recently been reported as coral associates, consisting of two species with a wide range of host corals, including 25 scleractinians and two milleporids (Hoeksema et al., 2022b). They live in a rigid tube inside the coral skeleton and are easily recognized by their branchial crowns (Tovar-Hernández et al., 2020a). Although some sabellids of the genera *Notaulax* Tauber, 1879 and *Pseudopotamilla* Bush, 1905 have been reported to bore into calcareous substrate (Vinn et al., 2018; Çinar and Dağlı, 2021), it is unclear whether coral-dwelling feather duster worms bore into the coral skeleton or settle on the surface as larvae, after which they eventually get overgrown by the coral tissue. Some sabellid species are known to secrete mucus with antibacterial properties which might have a protective effect on the host (Stabili et al., 2011). However, coral polyps around the worm tubes are often damaged or dead, indicating a negative impact on the host coral (Hoeksema et al., 2022b). The distribution of reef-dwelling *Anamobaea* worms in relation to depth and eutrophication is unknown because most studies on coral-dwelling fan worms are performed on collected specimens or *in situ* photographs, and therefore notes on their substrate are usually absent (Tovar-Hernández and Salazar-Vallejo, 2006; Giangrande et al., 2007; Tovar-Hernández et al., 2020a; 2020b; Capa et al., 2021; Hoeksema et al., 2022b).

Blennies of the genus *Acanthemblemaria* are represented by 11 Atlantic species, three of which predominantly occupy holes in coral at shallow depths, i.e., *A. aspera*, *A. greenfieldi* and *A. spinosa*, the latter being the most common in the Caribbean (Eytan and Hellberg, 2010; Böhm and Hoeksema, 2017). *Acanthemblemaria spinosa* lives in burrows on the vertical part of the host coral, whereas *A. greenfieldi* occupies burrows in the horizontal part (Greenfield and Greenfield, 1982; Clarke, 1989). Coral blennies have not been reported to cause damage to their hosts, although they keep serpulid tubes open after the worms have died, obstructing the coral to grow over the worm hole and heal (Böhm and Hoeksema, 2017). No relation to eutrophication has been described for these fishes.

Gastropods of the genus *Petalconchus* are worm snails that live attached to hard substrate or partly embedded in live corals. There is only one report on coral-associated worm snails in the Caribbean and therefore limited information is available about the impact on their hosts, which comprise 19 scleractinians and two milleporids (Hoeksema et al., 2022a). The vermetid gastropod *Ceraesignum maximum* (Sowerby, 1825) in the Indo-West Pacific is known to reduce coral health by inhabiting skeletal growth and general survival of their hosts by using toxic mucus webs (Adhavan et al., 2021; Shima et al., 2010; Zvuloni et al., 2008). *Petalconchus* species are known to use similar mucus webs (Spotorno-Oliveira et al., 2018).

Curaçao is an island of 444 km<sup>2</sup> in the southern Caribbean. The coral cover on its shallow reefs has been declining in the past decades, resulting in a loss of more than 70% over all depths and up to 79% at 20 m depth (de Bakker et al., 2016). This decrease implies that fewer hosts have become available for coral-associated fauna, possibly leading to a decrease in their diversity. The ecological functioning of coral-associated invertebrates in the light of coral decline is still unclear. In the present study a photo survey was performed on the reefs on the leeward side of Curaçao, with the objective to map the abundance of the described groups of epibionts over a depth gradient and across two longshore pollution zones, and to identify what is the role of the symbiotic relations for the host coral species in a rapidly deteriorating environment (Bak et al., 2005; Vermeij et al., 2011; de Bakker et al., 2016; Webb et al., 2021).

## 2. Materials and methods

### 2.1. Data collection

Surveys were conducted in October and November 2021, at 12 sites located at the leeward side of Curaçao (Fig. 1, Table 1.). Seven sites are located in areas with a high eutrophication ( $\delta^{15}\text{N}$  (‰) ratio between 3.5 and 4.4) and five sites in areas with low eutrophication ( $\delta^{15}\text{N}$  (‰) ratio between 1.3 and 1.7). Eutrophication was measured by the Waitt Institute (2017) to determine the effect of sewage discharge along the coastline of Curaçao. For these measurements, the ratio of the stable isotopes 14N:15N (= of  $\delta^{15}\text{N}$  (‰)) per site was determined as a proxy for sewage output on the reef, as anthropogenic wastewater contains relatively much  $\delta^{15}\text{N}$  compared to  $\delta^{14}\text{N}$ . The ambient  $\delta^{15}\text{N}$  fixed by the thalli of the brown alga *Dictyota* sp. was used as a proxy for anthropogenic wastewater, which is an easy technique (Lin et al., 2007).

In order to collect data on the species and number of epibionts on coral colonies, photographs of corals and their symbionts were taken at 5, 10, 15 and 20 m depth with an Olympus OM-D E-M5II system camera with a 14–42 mm lens in an Olympus PT-EP13 underwater housing with external flash. A ruler was photographed on the coral surface as scale. Host colonies were only recorded when at least one symbiont was observed at the coral surface. A time frame of 15 min per depth per site was spent on searching and photographing each symbiont encountered in a direction parallel to the shoreline, adapted after the survey method

**Table 1**

Localities at the Leeward side of Curacao where surveys were performed in October 2021. High  $\delta^{15}\text{N}$  values are eutrophic; low  $\delta^{15}\text{N}$  values are non-eutrophic.

Location	Coordinates	$\delta^{15}\text{N}$
Daaibooi	N12°12'40.9", W69°05'13.9"	Low
Kokomo Beach	N12°09'37.4", W69°00'20.8"	Low
Lagun	N12°19'05.1", W69°09'09.6"	Low
Playa Kalki	N12°22'28.8", W69°09'29.8"	Low
Santa Martha	N12°16'00.4", W69°07'42.2"	Low
Piscadera Bay (Carmabi)	N12°07'13.6", W68°58'16.5"	High
St. Michielsbaai	N12°08'48.0", W69°00'03.5"	High
Marie Pampoen	N12°05'23.3", W68°54'21.1"	High
Seaquarium	N12°05'03.7", W68°53'54.6"	High
Tugboat Beach	N12°04'04.8", W68°51'44.2"	High
Waterfactory	N12°06'32.2", W68°57'15.7"	High
Blue Bay	N12°08'04.9", W68°59'17.5"	High

used by Reimer et al. (2018, 2022), which was aimed at recording zoantharian species, including those in association with other benthic animals, such as sponges. This method has as an advantage that it also includes uncommon symbiotic species. Distances swam during the 15-min timeframe were approximately 200–300 m, depending on symbiont density, and symbionts were counted within an area of circa 2 m width.

### 2.2. Data analysis

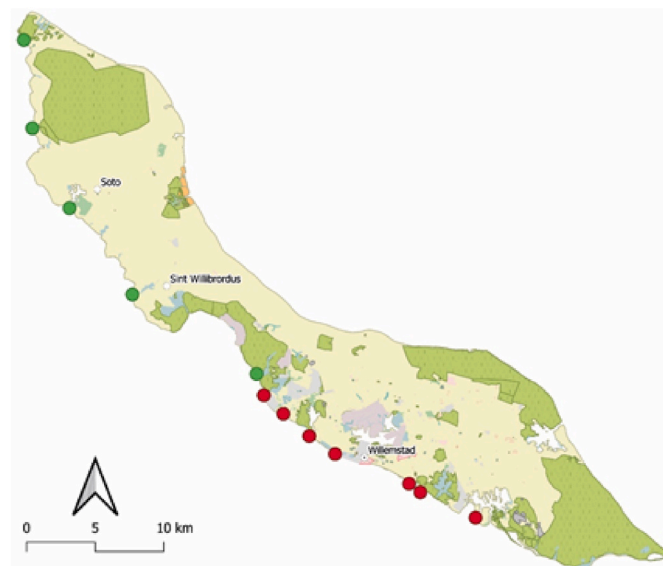
A total of 2413 pictures of 982 host corals were taken. The corals were identified to species level with the help of the field guides by Humann and Deloach (2013) and Hoeksema et al. (2022: ESM 1), with nomenclatural updates presented by the World List of Scleractinia (Hoeksema and Cairns, 2022). The colony size was calculated by use of the software program ImageJ (Schneider et al., 2012). The width and length of the colony were measured with a ruler that was included in each photograph to determine the scale. For most growth forms i.e., encrusting, foliose, massive, submassive, open and complex branching, these dimensions were used to calculate the projected surface area (PA) with the following formula:

$$PA = \pi r^2 \text{ in which } r^2 = \frac{\text{width} * \text{length}}{2}$$

The PA was multiplied with the surface index (SI) corresponding to the growth form of the coral (Holmes, 2008). For small massive colonies that were ball-shaped, the Knud Thomsen approximation for ellipsoids with unequal  $r$  values was used to directly calculate the surface area (Xu et al., 2009). The symbionts were counted per host coral and determined to family or subfamily level (i.e., Cryptochiridae, Pyrgomatidae) or genus level (i.e. *Leiosolenus*, *Spirobranchus*, *Petalocochus*, *Anamobaea*) with the use of available literature (Humann et al., 2013; van der Meij, 2014; Hoeksema et al., 2022a, 2022b, 2022c). Sponges and algae were not recorded. Symbionts that could not be identified are referred to as 'unknown'. The average number of symbionts per host and the symbiont density is calculated per depth or pollution zone. In order to calculate the symbiont density, the number of symbionts is divided by the occupied colony surface area, and of these values the average is calculated.

### 2.3. Statistical analysis

A taxon of coral-associated species was included in the analysis when 15 or more records were present per nominal variable i.e., depth, therefore worm snails were not included. The data was analysed with the software program R (R Core Team, 2021). To test for significant differences between groups the data was fitted into a Generalized Linear model (GLM, package: stats), for count data the Poisson distribution was applied, for continuous data the inverse gaussian or gamma distribution was used. Both fitted models were checked visually for normally



**Fig. 1.** Map of Curaçao with survey sites indicates by red (high  $\delta^{15}\text{N}$  representing high sewage output) and green dots (low  $\delta^{15}\text{N}$  representing low sewage output).



distributed residuals with a Q-Q plot and a density plot, in the case the continuous data showed strong skewed data the inverse gaussian or Gamma distribution was applied. If the GLM returned a significant result ( $p < 0.05$ ) a pairwise comparison test was performed using the “glht” function with the Tukey post hoc test with adjusted p-values by the single step method in the “multcomp” package (Hothorn et al., 2008). The regressions of the number of symbionts to host size were performed with the “ggplot” function to obtain a visual representation in combination with the “stat\_cor” function with the “pearson” method to retrieve the  $R^2$  and the p-value.

### 3. Results

#### 3.1. Host species

A total of 982 host corals was recorded belonging to 29 scleractinian species (Table 3), of which *Porites astreoides* was the most common at all depths (Fig. 2). The abundance of this species decreased with depth as also seen in the common hosts *Pseudodiploria strigosa*, *Siderastrea siderea*, *Orbicella annularis*, and *Montastraea cavernosa*. In contrast, the records of other hosts increased with depth, such as *Agaricia agaricites*, *A. humilis*, *A. lamarcki*, *Orbicella faveolata*, *O. franksi*, and *Stephanocoenia intersepta*. The average size of *P. astreoides* hosts was significantly larger at 20 m depth in comparison to 5, 10, and 15 m (GLM, Inverse Gaussian: 5–20 m,  $p = 0.012$ ; 10–20 m,  $p = 0.002$ ; 5–20 m,  $p < 0.001$ ) (Fig. 3). Other host species did not show a significant change in size over depth. The largest recorded host coral belonged to *Madracis auretenra* with 56 m<sup>2</sup> live coral surface area at 10 m depth (not shown).

#### 3.2. Symbiont distribution and diversity

The analysis of the pictures resulted in eight categories of symbionts i.e., seven taxonomic groups, and when a symbiont or its hole could not be determined, it was placed in the group ‘unknown’ (Fig. 4, Table 2). The most abundant symbionts were the coral barnacles and the Christmas tree worms, of which comparable numbers of coral colonies were found, with on average twice as many barnacles per host in comparison to Christmas tree worms. Worm snails were the least-abundant symbiont group.

#### 3.3. Symbiont abundance over depth

The abundance of symbionts is expressed in two ways: the number of symbionts per host coral and the density over the host’s live surface area, the maximum density (0,50 barnacles/cm<sup>2</sup>) was observed at a colony of *Porites astreoides*, which hosted 52 barnacles at a surface area of 104 cm<sup>2</sup>. The data of the four most observed symbiont groups is shown in Figs. 5 and 6. The abundances of the other three groups were not sufficiently high for thorough quantitative analyses. The records of all symbiont taxa with a complete list of host species is presented in

**Table 2**

Taxonomic symbiont categories with their totals of recorded symbionts and numbers of host corals measured in 12 sites along the leeward coast of Curaçao.

Symbiont categories	Number of symbionts	Number of host corals
Coral barnacles (Pyrgomatidae)	3457	459
Christmas tree worms ( <i>Spirobranchus</i> )	1764	475
Boring mussels ( <i>Leiosolenus</i> )	234	76
Coral-gall crabs (Cryptochiridae)	174	125
Feather duster worms ( <i>Anamobaea</i> )	121	53
Coral blennies ( <i>Acanthemblemaria</i> )	102	77
Worm snails ( <i>Petalocochnus</i> )	24	18
Unknown	246	166
<b>Total</b>	<b>6122</b>	<b>982</b>

Supplementary Material Table S1. Variety in host species was found both between symbiont groups and across depths. The most colonized host species in terms of number of symbionts per host was *O. annularis* at 5 m depth by Christmas tree worms (*Spirobranchus* spp.). For density this was *S. siderea* at 5 m by the coral barnacles (Pyrgomatidae). However at 10, 15 and 20 m depth, *S. siderea* was hardly present as a host. A similar trend was observed for *Spirobranchus* as number of symbionts per host, in which *O. annularis* was not recorded at 20 m depth, whereas it was the most common host at 5, 10 and 15 m. This symbiont group can be discerned in the density, which appeared equal over the depth gradient, and the number of worms per colony, which decreased with depth (Fig. 4). Host corals inhabited by Cryptochiridae were recorded more frequently with increasing depth. The average number per host and the density did however not change over depth (see Figs. 5 and 6).

The number of *Spirobranchus* worms showed significant differences across all depths with the exception of 15 vs. 20 m (GLM, Poisson;  $p < 0.001$ ). The Pyrgomatidae showed significantly different numbers per host colony between all depths, except for 10 vs. 20 m (GLM, Poisson;  $p < 0.001$ ). The number of *Leiosolenus* was significantly different between 10 vs. 15 m depth (GLM, Poisson;  $p < 0.001$ ), between 5 vs. 10 (GLM, Poisson;  $p < 0.001$ ), and 5 vs. 20 m (GLM, Poisson;  $p = 0.003$ ). The records of *Anamobaea*, *Acanthemblemaria*, and Cryptochiridae did not show significant differences over depth. *Petalocochnus* sp. was not included as not enough records were present.

Considering density (Fig. 6), Pyrgomatidae showed significantly more individuals per cm<sup>2</sup> coral-surface area at 5 m depth in comparison to 15 and 20 m (GLM, Gamma;  $p < 0.001$ ). *Spirobranchus* did not show any significant difference. Of the other symbiont groups, only *Leiosolenus* showed a significant difference between 5 and 20 m (GLM, Gamma;  $p = 0.047$ ).

#### 3.4. Symbiont abundance between eutrophication categories

Regarding the numbers of symbionts per host coral in sites with high  $\delta^{15}\text{N}$  ratio (eutrophic zone) and sites with low  $\delta^{15}\text{N}$  ratio (non-eutrophic zone) (Fig. 7), the coral barnacles are significantly more abundant in the eutrophic zone at 5, 10 and 20 m depth (GLM, Poisson;  $p < 0.001$ ).

*Spirobranchus* was significantly different at 5 m (GLM, Poisson;  $p < 0.001$ ), 10 m (GLM, Poisson;  $p < 0.001$ ), and 15 m (GLM, Poisson;  $p = 0.033$ ), the number of worms per host at 5 m, however, was higher in the non-eutrophic zone than in the eutrophic zone, at 10 and 15 m depth the number of worms per host was higher in the eutrophic zone. The observation at 5 m depth can be explained by one colony of *P. astreoides* hosting 334 worms. After removal of this value no significant difference was found.

*Leiosolenus* occupied most hosts in the eutrophic zone at 10 m depth (GLM, Poisson;  $p = 0.0498$ ) however at 20 m it was more abundant in the non-eutrophic zone (GLM, Poisson;  $p < 0.001$ ). This can be explained by a single colony of *M. pharensis* that was infested by 14 individuals and a colony of *S. intersepta* that was infested by 10 individuals. These corals were relatively small, respectively 227 and 105 cm<sup>2</sup>.

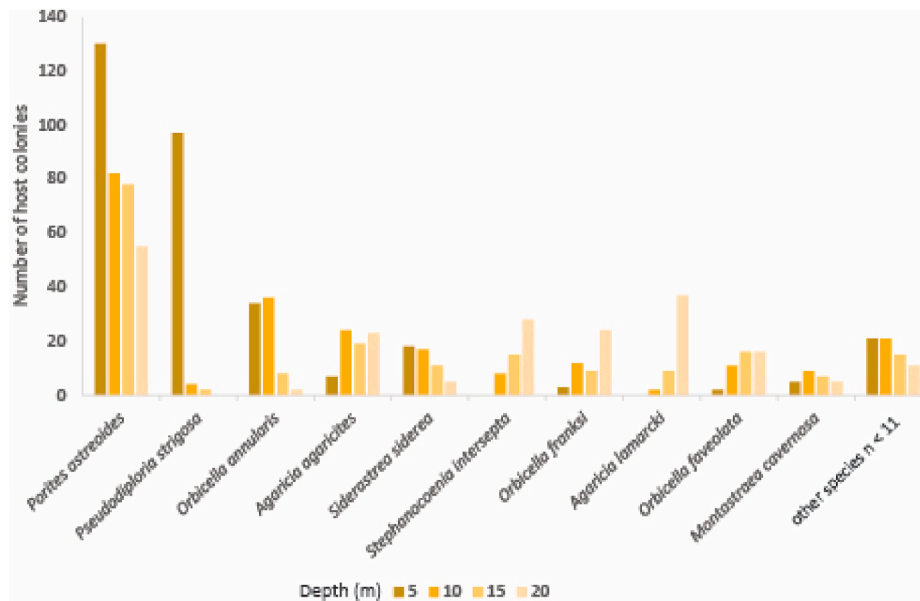
#### 3.5. Numbers of symbionts in relation to host size

A regression analysis of all cumulative symbionts and the size of their corresponding hosts only revealed a significant relation at 5 m depth, which did not hold when the strongly deviating value of 334 *Spirobranchus* worms (>80 times the median) on *O. annularis* was removed. The Pyrgomatidae were tested at each depth with all corresponding host species pooled, which showed no significant relation to host size. *Spirobranchus* worms showed a significant relationship to host size at 5 m, both with ( $R^2 = 0.072$ ;  $p < 0.001$ ) and without the above-mentioned deviating value ( $R^2 = 0.8$ ;  $p < 0.001$ ).

When symbiont taxa and hosts were assessed per depth and host species (with  $n > 20$ ), several relations between host size and number of

**Table 3**  
Scleractinian host species and their associated fauna found in the present study.

Coral genus/species	Cryptochiridae	Pyrgomatidae	Spirobranchus sp.	Leiosolenus sp.	Acanthemblemaria sp.	Petalocoenochus sp.	Anamobaea sp.
<i>Acropora palmata</i>	–	–	–	x	–	x	–
<i>Agaricia agaricites</i>	x	x	x	x	x	–	–
<i>A. fragilis</i>	x	x	–	–	x	–	–
<i>A. humilis</i>	x	x	x	–	–	–	–
<i>A. lamarcki</i>	x	x	–	–	x	–	–
<i>Colpophyllia natans</i>	x	–	x	x	x	–	–
<i>Dendrogyra cylindrus</i>	–	–	x	–	–	–	–
<i>Dichocoenia stokesii</i>	–	–	x	–	–	x	–
<i>Diploria labyrinthiformis</i>	–	x	x	–	–	–	–
<i>Eusmilia fastigiata</i>	–	–	x	–	–	–	–
<i>Favia fragum</i>	–	–	–	–	x	–	–
<i>Madracis auretenra</i>	–	–	x	–	–	–	–
<i>M. decactis</i>	–	–	–	–	x	–	–
<i>M. pharensis</i>	–	x	x	x	x	–	–
<i>M. senaria</i>	–	x	x	x	x	–	x
<i>Meandrina meandrites</i>	–	–	–	x	–	x	–
<i>Montastraea cavernosa</i>	x	–	x	x	x	x	x
<i>Mycetophyllia aliciae</i>	x	–	–	–	x	–	–
<i>Orbicella annularis</i>	x	x	x	x	x	x	x
<i>O. faveolata</i>	x	x	x	x	x	x	–
<i>O. franki</i>	x	x	x	x	x	x	x
<i>Porites astreoides</i>	–	x	x	x	x	x	x
<i>P. porites</i>	–	–	x	–	–	–	–
<i>Pseudodiploria strigosa</i>	x	x	x	x	x	x	x
<i>Scolymia lacera</i>	x	–	–	–	–	–	–
<i>Siderastrea radians</i>	–	x	–	–	x	–	–
<i>S. siderea</i>	x	x	x	x	x	x	x
<i>Stephanocoenia intersepta</i>	x	x	x	x	x	x	–
<i>Tubastraea coccinea</i>	–	–	x	–	–	–	–
Number of host species	14	15	20	14	18	11	7



**Fig. 2.** Records of scleractinian host species for all symbiont taxa at 5, 10, 15 and 20 m depth measured in 12 sites along the leeward coast of Curaçao.

symbionts were found (Table 4). The relations at 5 and 10 m depth of *O. annularis* and *Spirobranchus* were both dominated by extreme values i. e., the largest value at 5 m is > 100 the median and at 10 m it is 10 times the median, when these values were excluded, no relationship was found.

**4. Discussion**

The assemblage of coral-associated invertebrates showed both

variety over depth and between sites with high and low  $\delta^{15}N$  values along the leeward coast of Curaçao. The number of symbionts per host coral decreased with depth for Pyrgomatidae and *Spirobranchus*, which is in contrast with an earlier study in the Caribbean, in which no relationship to depth was found (Scott, 1987). For all taxa there were strong indications for host specificity as the most frequently colonized host species varied per symbiont group at all depths. Furthermore, both *Spirobranchus* and Pyrgomatidae, and occasionally also *Leiosolenus*, were found to show high densities on their hosts with harmful effects, as coral

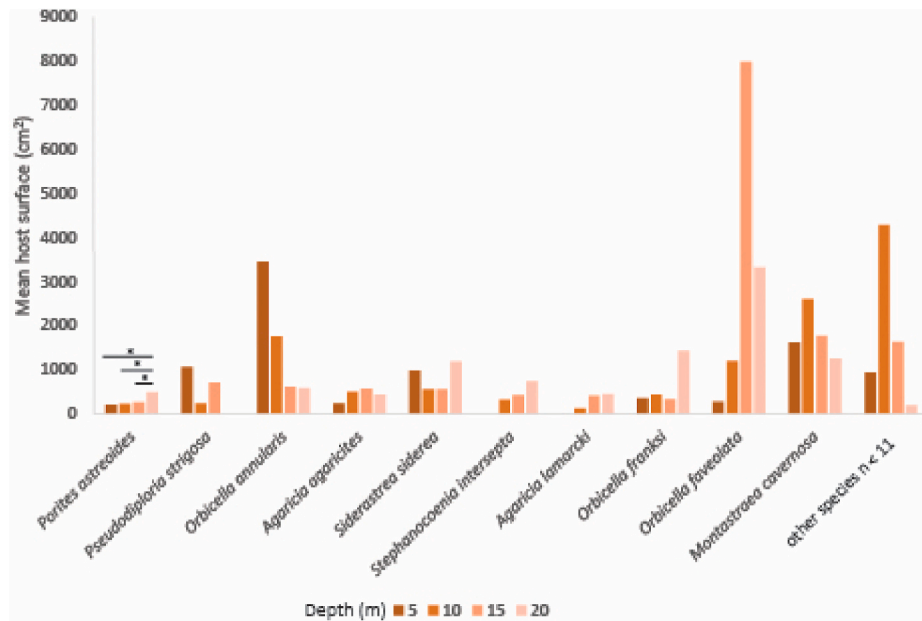


Fig. 3. Mean surface area of host corals for all symbiont taxa ( $\text{cm}^2$ ) at 5, 10, 15 and 20 m depth. Significant differences: \* =  $p < 0.05$ .

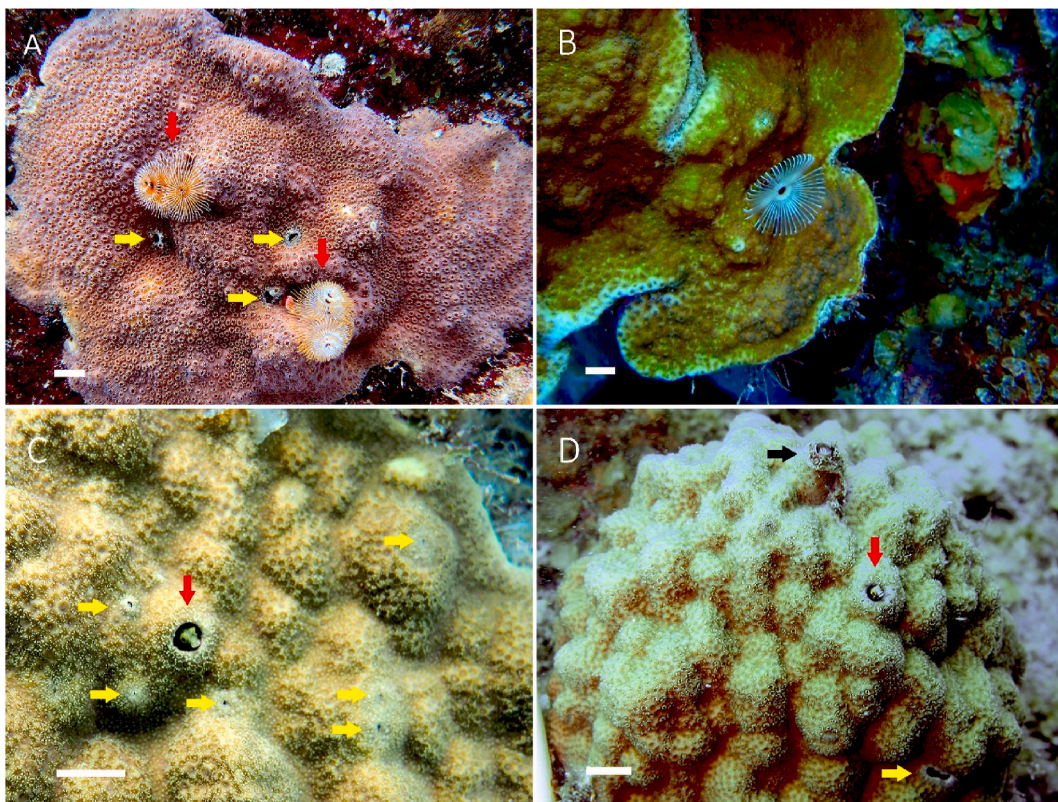


Fig. 4. Seven coral-associated species groups: A *Spirobranchus* spp. (red arrows) and Cryptochirid borings in *Orbicella franki* (yellow arrows). B Feather duster worm (*Anamobaea* sp.) in *O. franki*. C Coral barnacles (Pyrgomatidae, yellow arrows) and a coral blenny (*Acanthemblemaria* sp., red arrow) in *Porites astreoides*. D Wormsnail (*Petalconchus* sp., black arrow), coral blenny (red arrow) and a crevice of *Leiosolenus* sp. (yellow arrow) in *P. astreoides*. Scale bars: 1 cm.

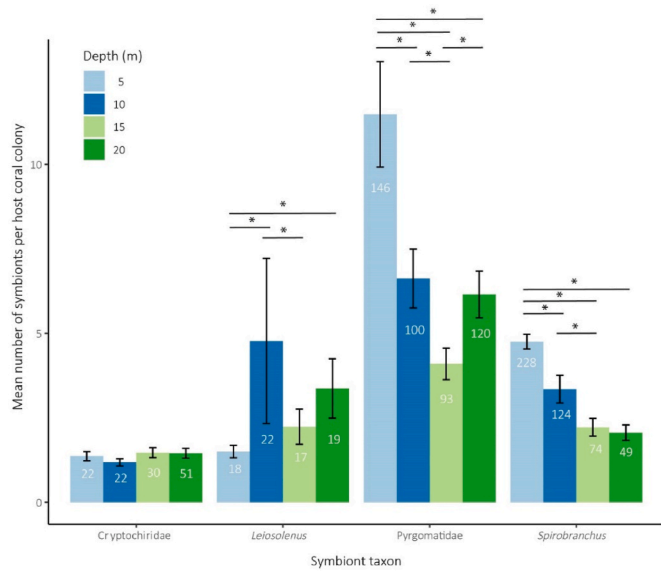
injuries were commonly observed in close proximity to the symbionts (Hoeksema et al., 2019a, 2019b, 2022a, 2022b). Damage caused by boring mussels (*Leiosolenus* spp.) is mostly hidden inside the host's skeleton (Kleemann, 1996) and is hardly visible at the host's surface (Hoeksema et al., 2022c).

#### 4.1. Abundance over depth

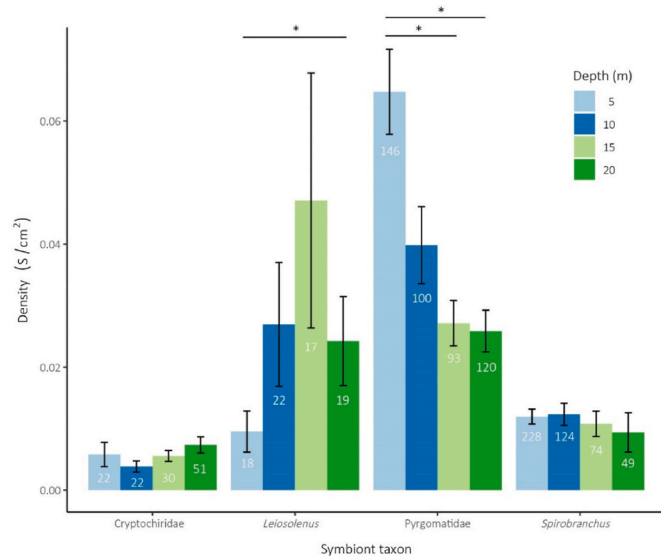
##### 4.1.1. Coral barnacles (Pyrgomatidae)

Coral barnacles were overall the most abundant symbiont taxon, both in terms of individuals per host as in densities. The results show a depth preference for Pyrgomatidae for shallow water as they were more





**Fig. 5.** The mean number of symbionts per host per symbiont taxon across four depths in 12 sites along the leeward coast of Curaçao; error bars = s.e. The number of host corals are indicated in each bar. Significant differences: \* =  $p < 0.05$ .



**Fig. 6.** The mean density of symbionts ( $\text{cm}^{-2}$ ) on the coral surface per symbiont taxon over across four depths in 12 sites along the leeward coast of Curaçao; error bars = s.e. Significant differences: \* =  $p < 0.05$ . The number of host corals are indicated in each bar. Significant differences: \* =  $p < 0.05$ .

abundant per host at 5 m depth in comparison to 10, 15 and 20 m. Pyrgomatid barnacles appeared to show a preference for wave-exposed hosts in shallow water (Lymperaki et al., 2022), which may explain why they were less abundant at greater depths. In the latter case, a distinction should be made between the Pyrgomatid species that are involved, as some are highly host specific and others are known to be generalists (Ogawa and Matsuzaki, 1992; Chan et al., 2018). The common Caribbean coral barnacle *Megatrema madreporarum* (Bosc, 1812) shows a host range of ten host species over five scleractinian families (Hoeksema et al., 2017c), which indicates a moderate host specificity. For coral species that prefer shallow water, such as *P. astreoides*, *S. radians* and *S. siderea*, only *Ceratoconcha quarta* (Kolosváry, 1947) and *C. floridana* (Pilsbry, 1931) have been described as pyrgomatid symbionts (Scott,

1987; Ogawa and Matsuzaki, 1992), whereas on the deeper coral *A. lamarcki*, *Ceratoconcha domingensis* (Des Moulins, 1866) and *Megatrema madreporarum* (Bosc, 1812) are the only known pyrgomatid symbionts (Veglia et al., 2018; Hoeksema et al., 2017). This might explain the variation in host coral species composition over depth, since at each depth a different dominant coral-barnacle species with a different preferred host could be present.

#### 4.1.2. Christmas tree worms (*Spirobranchus* spp.)

*Spirobranchus* has the highest host record of all studied symbiont taxa, but it is the second most abundant in the coral-associated fauna assemblage per host coral. Its abundance per host was highest at 5 m depth and decreased with greater depths. The high average number of Christmas tree worms per *O. annularis* colony at 5 m (i.e., 14.7 worms per host coral) was mainly caused by a single large colony with 334 worms. When this value is excluded, the average number is 4.0 worms per host, this is similar to the other highly colonized host species at 5 m depth. The mean number at this depth decreases as well without this extreme value, leaving no difference between 5 and 10 m depth, but a strong difference between the two shallowest depths (5 and 10 m) and the two deepest depths (10 and 20 m). Larvae of *Spirobranchus giganteus* have been observed to migrate vertically towards the surface as they respond positively to daylight (Marsden, 1986). This could, together with host specificity, explain the high abundance in the shallow reef area. The four most colonized host species in the present study (*A. agaricites*, *O. annularis*, *P. astreoides*, and *P. strigosa*) were also recognized as such in an earlier study at Curaçao (Hoeksema et al., 2019).

The present study shows a clear difference in host species related to depth, as *O. annularis* was the most preferred host species at 5 m depth and *O. faveolata* at 20 m. An earlier study showed that *O. annularis* and *O. faveolata* both have equal total colony surface area at 5 m depth, *O. annularis* however has smaller, and therefore more colonies present (van Tienderen and van der Meij, 2016). This observation in combination with the weak relationship between the number of worms and the size of the hosts suggests that small colonies are more densely infested by *S. giganteus* larvae than larger colonies. This is possibly related to a preference for a certain microhabitat, for example on top of the colony rather than a lateral position, as is observed with coral blennies (Greenfield and Greenfield, 1982; Clarke, 1989), which usually house in empty *Spirobranchus* tubes (Böhm and Hoeksema, 2017).

#### 4.1.3. Coral gall crabs (*Cryptochiridae*)

Cryptochiridae showed no variation over depth, neither in individuals per host as in density. The number of recorded hosts increased with depth, which was mainly due to a higher abundance of *Agaricia lamarcki* hosts at 20 m. This is in line with an earlier study on Cryptochiridae at Curaçao, in which the gall crab species *Opecarcinus hypostegus* was shown to be predominantly associated with *A. agaricites* colonies, occurring with increasing abundance over depth, corresponding with increasing host availability (van Tienderen and van der Meij, 2016). No high occurrence of Cryptochiridae was found at shallow depths, which is in contrast with the same study that found *Kropocarcinus siderastreicola* to be strongly associated with *S. siderea*, i.e., 59 out of 67 recorded colonies were inhabited by this gall crab species in a belt transect at 6 m depth (van Tienderen and van der Meij, 2016). In the present study 18 colonies of *S. siderea* were recorded at 5 m depth, in which only one gall crab individual was found. As the number of hosts was low, this might be due to chance, since some of the spots determined as 'unknown holes' could possibly have been cryptochirid crevices.

#### 4.1.4. Boring mussels (*Leiosolenus* spp.)

*Leiosolenus* hosts were recorded in equal numbers over depth, *Pseudodiploria strigosa* was the most recorded host at 5 m depth, *Siderastrea siderea* at 10 m, *Porites astreoides* at 15 m, and *Stephanocoenia intersepta*, at 20 m. These coral species are previously only described as hosts for



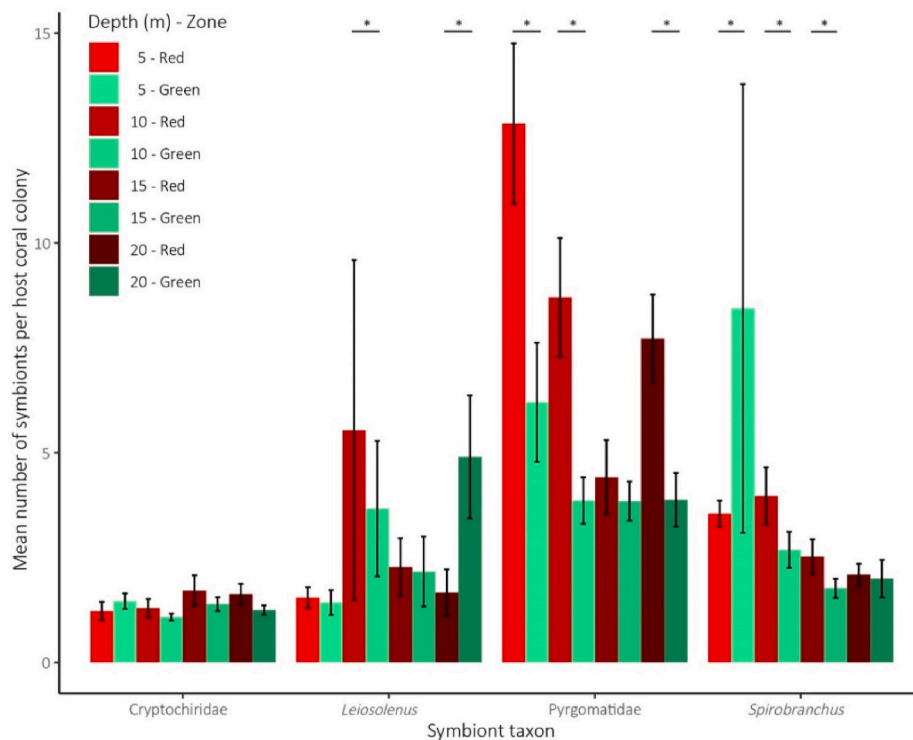


Fig. 7. The symbionts per host were grouped per seven sites with high  $\delta^{15}\text{N}$  ratio (red) and five sites with low  $\delta^{15}\text{N}$  ratio zone (green). Significant differences: \* =  $p < 0.05$ .

**Table 4**  
Significant relationships between the size of a host coral species and the number of symbionts.

Host species	Symbiont taxon	n	Depth (m)	R <sup>2</sup>	p
<i>P. astreoides</i>	Pyrgomatidae	111	5	0.29	<0.001
<i>P. astreoides</i>	Pyrgomatidae	49	10	0.11	0.023
<i>P. astreoides</i>	<i>Spirobranchus</i>	79	5	0.11	0.002
<i>P. astreoides</i>	<i>Spirobranchus</i>	43	10	0.17	0.007
<i>O. annularis</i>	<i>Spirobranchus</i>	30	5	0.90	<0.001
<i>O. annularis</i>	<i>Spirobranchus</i>	28	10	0.48	<0.001
<i>P. strigosa</i>	<i>Spirobranchus</i>	80	5	0.05	0.048

*Leiosolenus bisulcatus*, making it plausible that all *Leiosolenus* records in the present study belong to that species (Scott, 1985, 1987; Valentich-Scott and Dinesen, 2004). The variation in most recorded host species over depth appears to depend on their availability, suggesting a generalistic host selection. However both the numbers of *Leiosolenus* per host as their density were significantly higher at 20 m depth, indicating a stronger association with *S. intersepta* at 20 m than with *P. strigosa* at 5 m. This may be related to the immunity of *Leiosolenus bisulcata* to the nematocyst discharge of *S. intersepta*, because this bivalve species is susceptible to nematocysts of other coral species (Scott, 1988). There is another coral-dwelling mussel species known from the Caribbean, i.e. *L. dixonii*, but that one is only known to occur in corals of the genus *Madracis* and not in those of *S. intersepta* (Scott, 1985).

4.1.5. Other symbiont taxa

The other taxa i.e., *Anamobaea* feather duster worms and *Acanthemblemaria* blennies did not show differences across depths. *Petalonchus* worm snails were not included in the depth analysis because not enough records were present. Host corals with associated blennies however, were recorded four times more frequently at 5 m depth than at 10 m, while at 20 m almost no records (n = 2) were found, which suggests a preference for shallow water. This is in line with a decreasing trend over depth found for coral blennies in an earlier study at Curaçao

and their preference for *Spirobranchus* tubes as dwellings (Böhm and Hoeksema, 2017), which are less common at greater depths according to the present study.

4.2. Abundance per eutrophication category

Eutrophication had the most distinct effect on the abundance of Pyrgomatidae per host, which was about twice as much in coastal zones with a high sewage output as zones with less sewage. The number of barnacles per host was high at 20 m depth, whereas there was a decrease from 5 to 15 m, but only in the eutrophic zone. This increase was observed in all host species and therefore might indicate a response to an environmental factor in the surrounding seawater.

For *Spirobranchus* the same effect was observed at 10 and 15 m depth, though at 5 m the effect was reversed, which is due to a large colony of *P. astreoides* hosting 334 worm individuals. *Leiosolenus* mussels are mostly present at 10 m in the eutrophic zone, whereas at 20 m depth they were more abundant in the non-eutrophic zone. This is the first time that the influence of eutrophication is shown for these groups of symbionts. The higher number of epibionts in eutrophic areas is consistent with a study on the relationship between macro-bioeroders and eutrophication (Le Grand and Fabricius, 2011). This shows their potential role as bioindicators for harmful coral reef conditions, which has been proposed earlier based on the impact of water quality on stress in corals through macro-bioeroders (Risk and MacGeachy, 1978; Cooper et al., 2008). It is hypothesized that eutrophicated water is beneficial for filter-feeding organisms such as barnacles and Christmas tree worms because it stimulates the production of phytoplankton, which leads to more dissolved organic matter (DOM) and therefore more food for filter-feeding organisms (D'Angelo and Wiedenmann, 2014). It is also possible that corals become more susceptible to epibionts in water with a high nutrient content because this may decrease their ability to offer resistance to the settlement and overgrowth of harmful epibionts (Holmes et al., 2000; Samimi-Namin et al., 2010).

In the case of barnacles, the settlement of larvae causes stress as it

triggers a chemical defence mechanism. Moreover it has been shown that adult barnacles attract conspecific larvae to settle on the same host (Liu et al., 2016). The impact of *Spirobranchus* larvae on their hosts is less clear as they settle on exposed coral skeleton and let themselves become overgrown by the coral tissue in which they eventually will become embedded (Smith, 1984). *Leiosolenus* species are boring bivalves, whose larvae settle on the living host coral after which they cause extensive erosion of the coral skeleton (Scott, 1988). Future studies with a focus on filter-feeding coral associates (e.g. *Anamobaea* spp.) may perhaps show similar results.

## 5. Conclusions

The present study shows a clear variation in the abundance of coral-associated fauna over depth in relation to host species and eutrophication. The expectation is that most depth-related variation can be explained by host specificity of the coral-associated fauna and by host availability. For Caribbean Cryptochiridae, host specificity has been described in detail (van der Meij, 2014; García-Hernández et al., 2020), whereas many studies on Pyrgomatidae are predominantly focussed on barnacle anatomy and taxonomy (Ross and Newman, 2002; Ogawa and Matsuzaki, 1992) or describe the hosts but not the barnacles down to species level (Scott, 1987). On the other hand, *Spirobranchus giganteus* appears to be a host generalist (Hoeksema and ten Hove, 2017a; Hoeksema et al., 2020), with a preference for shallow water (< 40 m depth). Future studies will have to point out how specific other Caribbean symbiont taxa are in their host choice and to what extent they rely on the availability of particular hosts.

High densities of some symbiont taxa can be harmful to the host coral if the skeleton's integrity becomes affected or if too many polyps become damaged beyond the host's healing capacity, which is observed in cases involving bioeroders (Hutchings 1986; de Bakker et al., 2018; Maher et al., 2018; Hoeksema et al., 2022c) and invertebrates that destroy coral polyps (Potkamp et al., 2017; Hoeksema et al., 2019a, 2019b, 2022a, 2022b). Because this role of coral-associated fauna can be relevant for reef conservation strategies, future studies should focus on the types and degree of the damage caused by the coral-associated fauna and how this may be influenced by the changing environment, in a similar way as we experience an increase in the variety and extent of coral diseases (Gardener et al., 2003; Burge et al., 2014; Randall et al., 2014; Montano et al., 2020; Heres et al., 2021; Meiling et al., 2021).

## CRedit authorship contribution statement

**Roel J. van der Schoot:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Bert W. Hoeksema:** Supervision, Writing – original draft, Writing – review & editing.

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## Declaration of competing interest

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

## Data availability

The data has been added as Electronic Suppl. Material

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2022.105738>.

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