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REPORT

Same but different? Zoantharian assemblages (Anthozoa: Hexacorallia) in Bonaire and Curaçao, southern Caribbean

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Abstract Marine community datasets are key to the effective management and conservation of marine ecosystems, including coral reefs, which are increasingly threatened by a myriad of stressors. Although community information exists for many comparatively well-studied taxa, other common groups remain to be examined for even such basic information. In this study, we report on the zoantharian communities (Cnidaria: Anthozoa: Hexacorallia: Zoantharia) on the reefs of Bonaire in the southern Caribbean, and compare current results from 30, 20, 10, and 5 m depths to recent similar surveys from nearby Curaçao. The surveys revealed a total of 17 zoantharian species and epibiotic associations on the reefs of Bonaire.

Additionally, results showed that while zoantharian assemblages around Bonaire at shallow 5 and 10 m depths, dominated by *Palythoa* spp., were similar to those found on Curaçao, diversity and numbers of zoantharians were higher at 20 and 30 m due to more abundant epibiotic Parazoanthidae species associated with sponges. Differences in assemblage structure were seen in deeper 20 and 30 m depths between the two islands, implying that conservation of deeper reef slopes, or along depth gradients, may need to be independently considered and addressed for each location. Analyses with environmental parameters on the Bonaire dataset indicate the potential importance of coral reef rugosity and physical structure in shaping these zoantharian communities, aspects that should be focused on in more detail in future research.

Keywords Cnidaria · Benthos · Coral reefs · Diversity · Symbiosis

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Introduction

Information on marine communities and assemblages is critical in effective management and conservation of marine ecosystems (Edgar et al. 2016), for example in order to increase the accuracy of future predictions (Waldock et al. 2019). Such information is particularly important for Caribbean coral reefs, which face increasing anthropogenic threats and degradation from rising seawater temperatures due to climate change (Sheppard and Rioja-Nieto 2005; McWilliams et al. 2005) and additional negative impacts from diseases (Weil 2004; Walton et al. 2018), over-exploitation (Duran et al. 2018; Shantz et al. 2020; Cramer et al. 2020), coastal development (Burke and Maidens 2004), and pollution (Duran et al. 2018; Cramer

et al. 2020). Coral reefs harbor diverse communities of marine organisms (Roberts et al. 2002), and although much community information exists for some taxa such as hard corals (Goreau 1959; Newman et al. 2006), octocorals (Velásquez and Sánchez 2015; Tsounis et al. 2018), sponges (Zea 1993; Wulff 2001; Alcolado 2004), and fish (Gladfelter et al. 1980; Pinheiro et al. 2016), there are only scarce community and assemblage datasets for many other less prominent coral reef taxa. One such group lacking data is the zoantharians.

Zoantharians (Cnidaria: Anthozoa: Hexacorallia) are common benthic colonial components of tropical Caribbean coral reefs. Members of the order Zoantharia (= Zoanthidea) include two major groups. The first group (suborder Brachycnemina) are taxa symbiotic with photosynthetic Symbiodiniaceae, such as the genera *Palythoa* (Kemp et al. 2006) and *Zoanthus* (LaJeunesse 2002). The other major group (suborder Macrocnemina) are taxa epibiotic on other benthos, including the family Parazoanthidae with species associating with demosponges, such as the genera *Parazoanthus*, *Bergia*, and *Umimayanthus*, as well as the family Hydrozoanthidae and genus *Hydrozoanthus* on hydrozoans (Swain and Wulff 2007; Swain 2009; Montenegro et al. 2020).

Caribbean zoantharians have been well studied since the beginnings of modern marine science compared to zoantharians in other regions of the world, with research spanning from taxonomy to ecology (Ellis 1768; Crocker and Reiswig 1981; Sebens 1982; Varela et al. 2002; Montenegro and Acosta 2010; Swain 2012). The identification of most Caribbean zoantharian species is possible from external appearances and the identity of associated host species (if present), which has been confirmed with molecular analyses (West 1979; Lewis 1982; Swain and Wulff 2006; Swain 2012; Montenegro et al. 2020). From past ecological research, it is known that some Caribbean zoantharian species play a dominant role in the competition for space with scleractinian corals and other benthic reef invertebrates (e.g., *Palythoa caribaeorum*) (Suchanek and Green 1981; Bastidas and Bone 1996; Ladd et al. 2019; Hoeksema et al. 2020; Hill et al. 2021). However, most zoantharian ecological research in the Caribbean has remained limited to shallow waters (depths < 10 m) and primarily focused on the zooxanthellate genera *Palythoa* and *Zoanthus* (e.g., Belford and Phillip 2012, but see Swain 2012).

In 2017, the zoantharian communities on the fringing reefs of the leeward side of Curaçao in the southern Caribbean were surveyed from depths of 5–30 m (Reimer et al. 2018). Their results showed depths of 5 and 10 m harboring small numbers of zoantharians, mainly zooxanthellate *Palythoa* colonies, while deeper depths of 20–30 m harbored higher abundances of zoantharian species,

primarily epibiotic species such as associations with demosponges (Reimer et al. 2018). While these results provide an important baseline dataset for understanding patterns of zoantharian assemblages and diversity in Curaçao, the study was limited to a single island, and thus questions remain as to whether the Curaçao results can inform us on zoantharian communities of the coral reefs surrounding other nearby islands. In an attempt to broaden our understanding of Caribbean zoantharian communities and their patterns of diversity and associations, we report on the observed patterns of zoantharian diversity and communities at sites around Bonaire, approximately 80 km to the east of Curaçao. We then compared results from both islands. We also analyze the obtained Bonaire zoantharian community dataset with respect to various environmental parameters from previous research, and discuss future avenues of continued research. This study will provide a baseline for additional, more elaborate studies, working toward a better understanding of Caribbean zoantharian communities.

Materials and methods

Surveys

The surveys in the current study utilized the methodology outlined by Reimer et al. (2018). Surveys were conducted at coral reefs around the islands of Bonaire and Klein Bonaire by SCUBA between 22 October and 7 November 2019. A total of 22 sites were investigated, mainly on the leeward western coast of Bonaire, but also two sites on the windward east coast, and three sites around Klein Bonaire Island, located off the central west coast of Bonaire (Table S1, Fig. 1). The sites ranged from directly next to the town of Kralendijk (e.g., Something Special at Playa Pabou and Bari's Reef) to remote areas in the north (e.g., Playa Frans and Boka, Playa Funghi, Slagbaai) within Washington-Slagbaai National Park and to the south (e.g., Willem's Tower and Red Slave). The eastern (windward) side of the island was not surveyed in detail as dive sites were hard to access, and weather conditions very rarely permitted entry into the ocean. As in Reimer et al. (2018), at each site, we examined the zoantharian abundance at 30, 20, 10, and 5 m (± 1 m depth) (Table S1). We surveyed 22 sites in total. Of these, at Playa Funghi, we did not perform a survey at 30 m as the site did not reach this depth, and at Dolphin Beach we did not survey 5 m due to limited time (Table S1). Thus, the total number of surveys in this study was 86.

At each depth, a diver swam for approximately 10 min parallel to the shore along the same depth and took macro images of every zoantharian colony encountered. The same
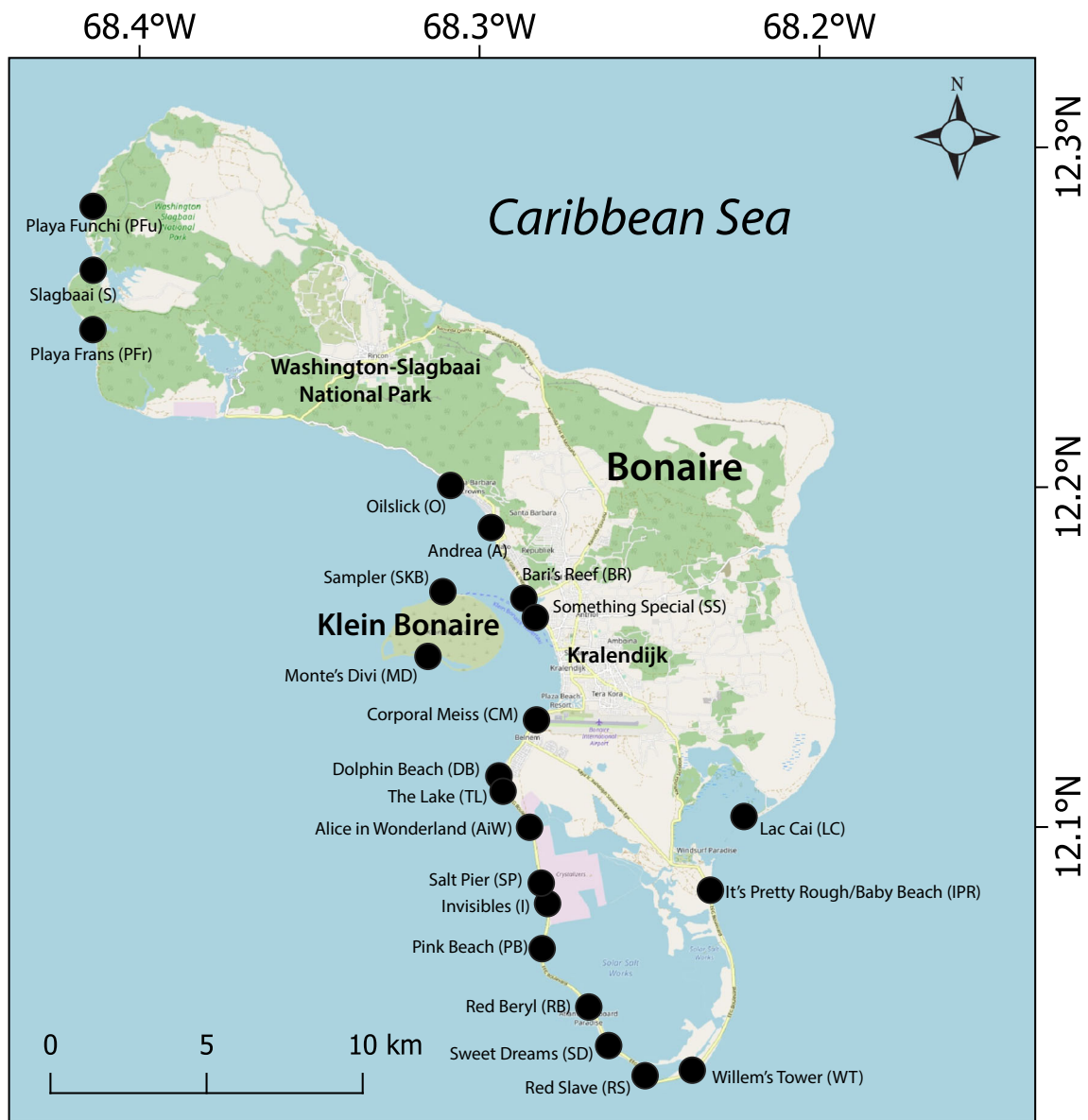
Fig. 1 Map of Bonaire showing sites and their abbreviations where zoantharian community surveys were performed in this study. Map from OpenStreetMap loaded into QGIS

diver (first author) collected and analyzed the photographic data for all dives in this study, as in the 2018 study of Curaçaoan reefs (Reimer et al. 2018). In some dives, survey times slightly deviated from the 10 min in the interest of maintaining a safe dive profile, in such cases, the survey times were noted from digital information on acquired images to allow subsequent standardization of data. Distances swam during the 10 min at each depth were approximately 150–200 m, with a transect width of approximately 2 m. No strong currents were encountered during surveys, and the surveyor swam at a consistent speed in all surveys, but the overall numbers of zoantharians observed may still include some effect of variations in distances surveyed.

Information from the timed-dive method utilized in this study does not generate density or abundance (e.g., m²) data, unlike transect or quadrat surveys. However, this timed survey method (during SCUBA diving, usually limited to one hour of air supply) is ideal when studying small and/or cryptic (hidden) species (Lincoln Smith 1988; Montano et al. 2020), such as many zoantharian species (polyp diameters of < 1 cm), or when the goal of the study is to assess biodiversity via finding as many species as possible (Condor-Lujan et al. 2018; Hill and Wilkinson 2004; Hoeksema and Koh 2009; Holt et al. 2013; Munro 2005; Schmidt et al. 2002).

Digital images from each dive were analyzed, and the numbers of zoantharians and their host organisms (only

Porifera and Hydrozoa observed) were recorded. All zoantharian and host species were identified to species level from photographs based on previous literature (Reimer et al. 2012, 2018; Montenegro et al. 2020; Swain, 2009 for Zoantharia; Zea et al. 2014 for Porifera). We grouped observations into 'associations' (zoantharians of genera *Umimayanthus*, *Bergia*, *Parazoanthus*, *Hydrozoanthus*+host), as the same zoantharian species may be found on different host species, and 'species' (for non-epibiotic zoantharians of the genera *Palythoa* and *Zoanthus*). From these analyses, we obtained total numbers of zoantharian colonies and species/associations for each depth at each site; these data were used for all subsequent analyses.

Data analyses

Two sets of biological data (dependent variables), and the total number of zoantharian colonies and species/association (henceforth known as species/association) compositions were compiled for each station (sites+depth). The compiled data were further transformed to encounter per 10 min of survey. The transformed data were then combined with the raw data from Curaçao (Reimer et al. 2018) for inter-island comparisons. Each site was designated with two independent variables: islands (Bonaire and Curaçao) and depths (5, 10, 20, and 30 m). The prepared data table was imported into R Console (4.0.3) running in RStudio (1.4.1106) for further analyses (R Core Team 2020; RStudio Team 2020). The data associated with this study are available online as Supplementary Material 1.

The total rate of species/association encounter at each station was grouped based on sites, depths, and islands. Normality (Shapiro–Wilk) and homoscedastic (Fligner-Killeen) tests were conducted on the dataset. For the Bonaire-only dataset, a nonparametric test (Brown-Forsythe test) of total species/association encounters with depths was conducted, with a post-hoc test if significance was detected. For the Bonaire+Curaçao dataset, nonparametric and non-nested tests among factors (Scheire-Ray-Hare test) were conducted to examine the interaction between depths and islands on the total number of species/association encounters. Post-hoc (Dunn test with Holm's correction) were conducted when significant differences were found on interaction(s). The significant values threshold set for this study was $p = 0.05$.

The composition variations of the species/associations at different stations (factors: islands x sites x depths) were examined using ecological statistics based on the techniques as described by Oksanen (2015), with R packages 'vegan', 'Mass', and 'dplyr'. Analyses were conducted for Bonaire only and for comparison between two islands

(Bonaire+Curaçao). The data were transformed into Bray–Curtis dissimilarity matrices.

Without a priori grouping assumed for the sites, a similarity profile analysis (SIMPROF; Clarke et al. 2008) was conducted to explore the compositional structure of the species/associations on reefs around Bonaire. Depths were represented in colors (5 m = red, 10 m = yellow, 20 m = green, 30 m = blue) at the leaf end of the SIMPROF cluster tree. Groupings of the SIMPROF were based on the mean permuted profile with 99% confidence level (default: $p < 0.01$). Two dominant SIMPROF clusters from deeper depths (20 and 30 m) were extracted and plotted on a map of Bonaire to examine the geographical distribution of the composition clusters.

To examine the composition of species/associations among the depths and sites of Bonaire, non-metric Multidimensional Scaling (nMDS) plots were constructed from the Bray–Curtis dissimilarity matrix with stable solution from 100 random restarts. Permutational multivariate analysis of variance (PERMANOVA; permutations = 999) was conducted on the species/association composition of Bonaire with respect to depth factor, followed by post-hoc tests (pairwise.adonis) with Holm's correction (Martinez Arbizu 2020). Similarity percentage (SIMPER) analysis was conducted to determine the species/associations that contributed the most to the dissimilarities among the depth factor groups.

We also combined the Bonaire dataset with that from Curaçao (15 sites, 59 surveys, 958 images, 971 colonies) for a total dataset of 37 sites, 145 surveys, 2492 images, and 2939 colonies. The comparisons of species/associations compositions at sites between Bonaire and Curaçao were conducted with similar steps as per the Bonaire dataset, but no SIMPROF analysis was conducted for this combined dataset. A hierarchical cluster was constructed using the Bray–Curtis dissimilarity matrix of both islands with the leaves represented by depths and islands (Bonaire = circle, Curaçao = square). nMDS plots were constructed representing the distances of species/association composition similarities in two dimensions with regards to depths and islands. PERMANOVA analyses were conducted with the interactions among the island and depth factors, followed by post-hoc test with Holm's corrections for each factor grouping. SIMPER analyses were conducted for each grouping that showed significant difference in order to examine the species/associations that distinguished the dissimilarities.

Analyses with environmental and other parameters

Data for the sites in Bonaire for various environmental parameters and other categories were compiled from previous studies. Specifically, from De Bakker et al. (2019;

Supplemental Table S2) we compiled data from the closest sites to the sites we examined. Curaçao was excluded from these analyses due to incomplete/inconsistent environmental data available. Data were compiled for the following categories: disturbance levels, management practice, type of coast, wave energy (J m^{-3})^2, terrace width (m)^1, hard substratum (m), rugosity, mean vertical height (m), live coral cover (%), coral production (kg m^{-2} yr^{-1}), CCA production (kg m^{-2} yr^{-1}), gross production (kg m^{-2} yr^{-1}), parrotfish bioerosion (kg m^{-2} yr^{-1}), sponge bioerosion (kg m^{-2} yr^{-1}), micro bioerosion (kg m^{-2} yr^{-1}), urchin bioerosion (kg m^{-2} yr^{-1}), gross erosion (kg m^{-2} yr^{-1}), net production (kg m^{-2} yr^{-1}), and estimated accretion rate (mm yr^{-1}) (for definitions of each category see Supplemental Table S2 in De Bakker et al. 2019). We also added wave action/water movement category data for sites based on Fig. 4 in Van Duyl (1985) to the dataset.

Two of the sites we examined in this study, both on the east coast of Bonaire (It is Pretty Rough, Lac Cai), did not have data available, and we removed both sites from these analyses.

The De Bakker et al. (2019) dataset had results from 3 to 7 m (= 'lower coral terrace zone') and 8–12 m (= 'drop-off zone'). Hence, we categorized the 3–7 m data as representing the 5-m surveys in the current study, while the 8–12 m data was represented by our 10, 20, and 30 m datasets (all drop-off zone).

Datasets were prepared based on zoantharian abundances (biological data, = bio), factors (= fac), and environmental data (= env). Factors comprised depth, management practice (marine park, no fishing zone, no diving reserve), disturbance level (low, moderate, high, extreme), and type of coast (low shore, cliff). The remaining data categories from De Bakker et al. (2019) and Van Duyl (1985) comprised the env dataset. The environmental dataset was normalized to even out the weights of the measurements (= env.norm). PERMANOVA was conducted for both bio and env.norm datasets grouped in fac. Except for depth, the factors were not evenly distributed. Hence, no interaction of factors was conducted in the analyses. Factors showed significant differences that were further examined using pairwise PERMANOVA with Holm's correction. The bio dataset was ordinated into nonmetric multidimensional scaling (nMDS) with Bray–Curtis dissimilarity index. The env.norm data was subsequently fitted into the nMDS by means of 'envfit' function to isolate environmental drivers with significant correlation ($p < 0.05$) (Tables S2, S3).

Results

Surveys around Bonaire

We examined a total of 1534 images from these surveys, which contained a total of 1968 colonies, with some images containing more than one colony. During the surveys in this study, we observed 17 species/associations (Fig. 2). In general, similar to as observed in the previous surveys at Curaçao, Brachycnemina colonies (*Palythoa*, *Zoanthus*) were more common at 5- and 10-m depths, while Macrocnemina species and associations were more common at 20- and 30-m depths.

Overall, there were an average of 51.2 ± 34.8 ($n = 21$ sites) zoantharians observed at 30 m depth during 10 min, 42.0 ± 39.0 (n = 22 sites) at 20 m, 7.6 ± 16.9 (n = 22 sites) at 10 m, and 2.0 ± 3.3 ($n = 21$ sites) at 5 m (Fig. 3a). There were no zoantharians observed in several surveys, primarily at 5-m depths ($n = 12/21$ sites), but also occasionally at 10 m ($n = 5/22$ sites) and 20 m ($n = 1/22$ sites). Zoantharians were always observed at 30 m. The test of group variance showed a significant difference of total zoantharian/associate encounters among depths (Brown-Forsythe test: $F = 15.983$, d$f = 3$, $p < 0.01$). Posthoc tests showed significant differences between most depths, but not for the deeper reef (20 and 30 m; pairwise Wilcoxon: $p > 0.251$). Although there were sometimes more zoantharians at 20 m than 30 m ($n = 8/21$ sites), in general there were increasing numbers and diversity of zoantharians as depth increased (Fig. 3a).

By depth, a total of 15 species/associations were observed in 30-m surveys, 12 in 20-m surveys, nine in 10-m surveys, and only four at 5 m. On average, 5.4 species/associations were observed per site at 30 m depth, 4.3 at 20 m, 1.8 at 10 m, and only 0.3 species/associations at 5 m (Fig. 3b).

A total of at least 12 sponge species were observed in association with zoantharians during the course of the surveys across the depth ranges; *Niphates erecta* Duchassaing & Michelotti, 1864, *N. amorpha* van Soest, 1980, *Callyspongia (Cladochalina) aculeata* (Linnaeus, 1759), *N. caribica* (Pulitzer-Finali, 1986), *Petrosia (Petrosia) weinbergi* van Soest, 1980, *Agelas conifera* (Schmidt, 1870), *Svenzea zeai* (Alvarez, van Soest & Rützler, 1998), *Xestospongia muta* (Schmidt, 1870), *Xestospongia* sp., *Iotrochota birotulata* (Higgin, 1877), *Cliothosa delitrix* (Pang, 1973), *Dragmacidon* sp., as well as on unidentified encrusting sponges. These sponges were in association with a total of five zoantharian species; *Umimayanthus parasiticus* (Duchassaing & Michelotti, 1860), *Bergia catenularis* Duchassaing & Michelotti, 1860, *B. puertoricense* (West, 1979), *Parazoanthus swiftii* (Duchassaing &
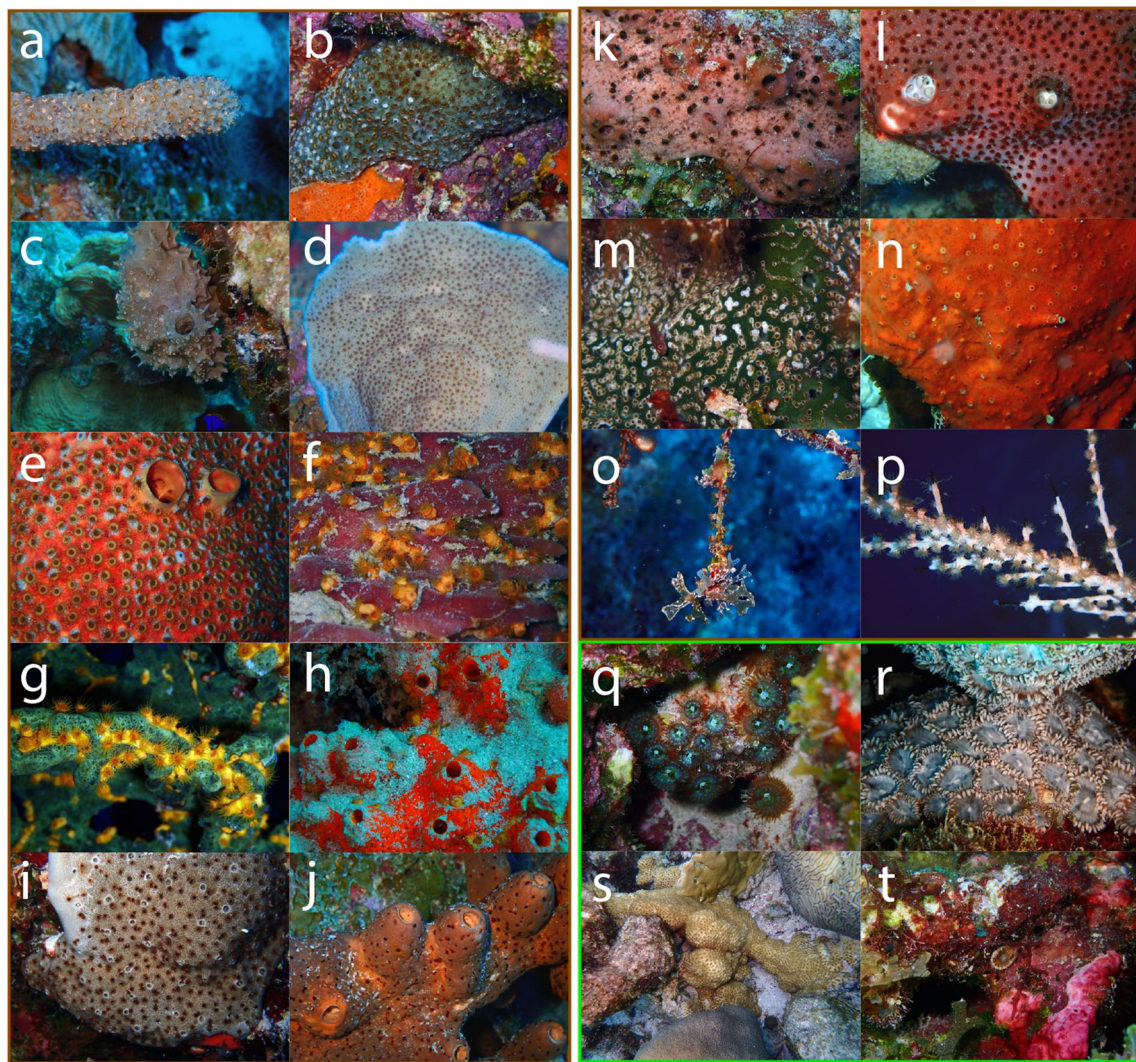
Fig. 2 Species and associations of zoantharians observed in surveys around Bonaire in this study. Macrocnemina species in brown boxes, Brachycnemina in green. (a) *Umimayanthus parasiticus* on *Niphates erecta*; (b) *U. parasiticus* on *N. amorpha*; (c) *U. parasiticus* on *Callyspongia aculeata*; (d) *U. parasiticus* on *N. caribica*; (e) *U. parasiticus* on *Cliothosa delitrix*; (f) *Parazoanthus swiftii* on *Xestospongia muta*; g) *Par. swiftii* on *Iotrochota birotulata*; (h) *Par. swiftii* on *Dragmacidon* sp.; i) *Bergia puertoricense* on *Petrosia weinbergi*; (j) *B. puertoricense* on *Agelas conifera*; (k) *B. puertoricense* on *Xestospongia* sp.; (l) *B. puertoricense* on *Svenzea zeai*; (m) *B. catenularis* on *Pe. weinbergi*; (n) unidentified Parazoanthidae species on an encrusting sponge; (o) *Hydrozoanthus antumbrosus* on *Dentitheca dendritica*; (p) *H. tunicans* on *D. dendritica*; (q) *Zoanthus solanderi*; (r) *Zoanthus pulchellus*; (s) *Palythoa caribaeorum*; (t) *Pal. grandiflora*

Michelotti, 1860), and an unidentified Parazoanthidae-species. We also observed three zooxanthellate species; *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860), *P. grandis* (Verrill, 1900), and *Zoanthus solanderi* Le Sueur, 1817 (Fig. 2). During the course of the current study, we observed two zoantharian-sponge associations not previously reported in the recent literature (Swain and Wulff 2007, Swain 2009, Reimer et al. 2018), namely *B. puertoricense* on *N. caribica*, and *P. swiftii* on *X. muta*. We also observed four additional species/associations outside of the transect surveys; *Zoanthus pulchellus* (Duchassaing & Michelotti, 1860) at 18 m depth and *Parazoanthus atlanticus* Montenegro et al., 2020 on

various encrusting sponges at 16 m depth, both at Small Wall, and *Hydrozoanthus tunicans* (Duerden, 1900) *H. antumbrosus* (Swain, 2009) on *Dentitheca dendritica* (Nutting, 1900) on the windward eastern coast (It is Pretty Rough) at 25 m depth (Fig. 2).

Overall, ten different species/associations were observed to be the most dominant zoantharians in individual surveys; *U. parasiticus* on *N. erecta* in eight surveys (four surveys at 30 m, three surveys at 20 m, and one survey at 10 m), *U. parasiticus* on *N. amorpha* in 36 surveys (11 surveys at 30 m, 12 at 20 m, 11 at 10 m, and one at 5 m), *U. parasiticus* on *C. aculeata* in one survey at 5 m, *U. parasiticus* on *C. delitrix* in one survey at 30 m, *B. catenularis* on
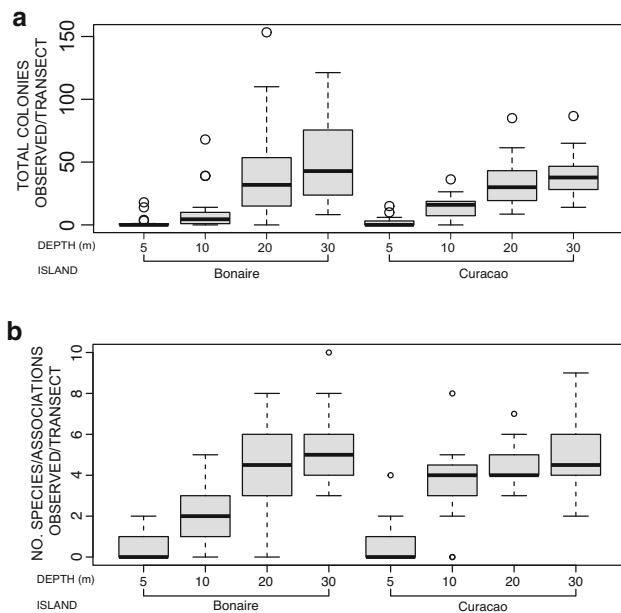
Fig. 3 Comparisons of a. number of zoantharians per survey depth for Bonaire and Curaçao, and b. number of species/associations per survey depth for Bonaire and Curaçao. Data for Curaçao reported in Reimer et al. (2018)

P. (*Petrosia*) *weinbergi* in two surveys at 20 m, *B. puertoricense* on *A. conifera* in 16 surveys (five surveys at 30 m, seven surveys at 20 m, and four surveys at 10 m), *B. puertoricense* on *S. zeai* in one survey at 20 m, *P. swiftii* on *I. birotulata* in one surveys at 10 m, *Palythoa caribaeorum* in six surveys (three surveys at 10 m, three surveys at 5 m), and *P. grandis* in one survey at 5 m. Note that at some sites two or more species/associations were co-dominant.

In the SIMPROF (Fig. 4) and nMDS (stress = 0.093; Fig. S1) plots of the Bonaire dataset, the large majority of the 5- and 10-m surveys were clustered together, while those of the 20- and 30-m surveys were more spread out. We observed six main clusters of zoantharian communities based on the SIMPROF. Half (*n* = 3) of the clusters were dominated by *U. parasiticus* on *N. amorpha* (Fig. 4: Red, Green, Blue clusters), but each with a different co-dominant zoantharian species/association. Among the clusters there was one major shallow cluster (Green, 5–10 m; *n* = 43), and two major deep clusters (Red and Blue, 20–30 m; *n* = 21, 17, respectively; Fig. 4). These clusters could be characterized as follows: (1) Green (*n* = 43) characterized by a lack of or only very few zoantharians (encounter rate = 3.31 ± 4.81), with *P. caribaeorum* (31.28%) as the second-most dominant encounter; (2) Red cluster (*n* = 21) consisting of 10-, 20-, and 30-m sites with secondary dominance of *B. puertoricense* on *A. conifera* (22.19%); (3) deeper Blue cluster (*n* = 17) with *U. parasiticus* on *N. erecta* (31.83%) as the second-most dominant

encounter; (4) Indigo cluster (*n* = 3) with the highest encounter rate of zoantharian/associations (86.52 ± 12.62), dominated by *U. parasiticus* on *N. erecta* (38.31%); and two single sites that recorded only one zoantharian species/association of (5) *P. caribaeorum* (Yellow), and 6) *P. grandiflora* or *P. grandis* (Orange), respectively.

Of the two most common deep clusters (Red and Blue clusters), the Red cluster sites were mostly found along the central and northwest coast of Bonaire, while the Blue sites were predominantly found along the southwest coast, although these geographic patterns were not absolute (Fig. S2). In addition, there were seven sites where the Red and Blue clusters were both present at different depths (e.g., Red at 20 m and Blue at 30 m or vice versa); these sites are purple in Fig. S2.

Depth played an important role in driving the composition of species/association (PERMANOVA: D*f* = 3; R^2 = 0.303; *p* < 0.001). This was also reflected in further statistical analyses of the Bonaire data, in which all depth comparisons were statistically different except for the 20-m and 30-m comparison (pairwise adonis: R^2 = 0.027; *p* = 1.00). The dominant driver of composition dissimilarity between the depths was the *U. parasiticus* on *N. amorpha* association (SIMPER > 30%). Other major associations that drove the compositional differences were *U. parasiticus* on *N. erecta*, *B. puertoricense* on *A. conifera*, and the non-associated encrusting and zooxanthellate *P. caribaeorum*.

Comparisons of Curaçao and Bonaire datasets

In the combined quantitative dataset, across all depths by median, there were fewer zoantharians at sites around Bonaire (median number of zoantharian colonies per site = 10.5) than Curaçao (median = 17.5), but the difference was not statistically significant (Scheirer-Ray-Hare: D*f* = 1; *H* = 0.540; *p* = 0.462). On the other hand, comparisons of numbers of zoantharians among depths (without considering islands) showed significant differences (Scheirer-Ray-Hare: D*f* = 3; *H* = 85.813; *p* < 0.001), with post-hoc tests showing significant differences between most depth comparisons except for 20 and 30 m (Dunn test: *Z* = 1.154; *p* = 0.248). Furthermore, when compared by depths with islands, there were more zoantharians (in terms of median) at 10-m depths at Curaçao (10 m = 16.0) sites compared to sites around Bonaire (10 m = 4.5), while there were slightly more at Bonaire sites at 20 and 30 m (20 m = 31.9; 30 m = 42.9) than at Curaçao (20 m = 30.0; 30 m = 37.7) (Fig. 3a). However, the differences were not significant (Scheirer-Ray-Hare: D*f* = 3; *H* = 0.617; *p* = 0.892) (Fig. 3a). Hence, based on the interaction between islands and depths, both islands presented a
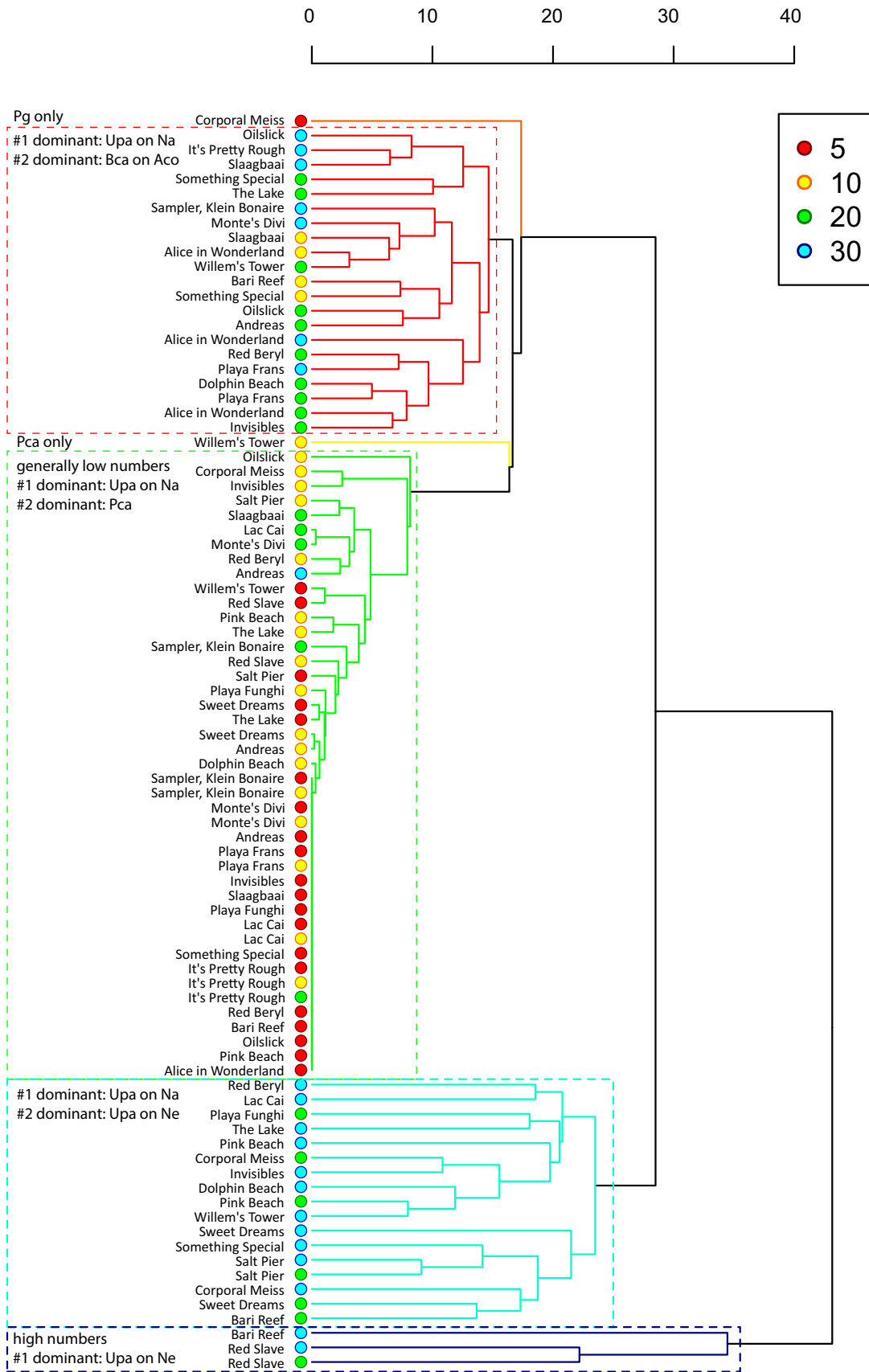
◄Fig. 4 SIMPROF analyses of Bonaire zoantharian communities in this study. Colored circles below phylogram indicate depth of surveys, colors in phylogram indicate the six major groupings observed. Color of the branch represent the groups based on 99% ($p < 0.01$) confidence level in order: Orange, Red, Yellow, Green, Blue and Indigo

consistent increase in zoantharian encounters with an increase in depth.

With regards to average numbers of species/associations encountered at each depth for each island, both Bonaire and Curaçao showed very similar patterns, with very few at 5 m (averages < 1.0 species/associations for both islands). Curaçao showed slightly more species/associations at 10 m than Bonaire, but Bonaire had higher numbers at both 20 and 30 m (Fig. 3b). The number of species/associations encountered in islands (Scheirer-Ray-Hare: Df = 1; $H = 1.038$; $p = 0.308$), depths (Scheirer-Ray-Hare: $Df = 3$; $H = 84.734$; $p < 0.001$) and their interactions (Scheirer-Ray-Hare: $Df = 3$; $H = 3.937$; $p = 0.268$) showed the same patterns as numbers of zoantharians.

With regards to zoantharian communities, island (PERMANOVA: $Df = 1$; $R^2 = 0.032$; $p = 0.002$), depth (PERMANOVA: $Df = 3$; $R^2 = 0.292$; $p < 0.001$), and their interactions (PERMANOVA: $Df = 3$; $R^2 = 0.027$; $p = 0.021$) showed significant differences on the overall dataset. Similar to the Bonaire-only results, all depths were significantly different from each other, except for 20–30 m (pairwise adonis: $R^2 = 0.015$; $p = 0.338$). *U. parasiticus* on *N. amorpha* and *U. parasiticus* on *N. erecta* were the dominant associations which influenced the dissimilarities with depth (SIMPER > 52.2%). Other major associations that drove the composition differences were *B. puertoricense* on *A. conifera,* and non-associated *P. caribaeorum.* Furthermore, the island+depth interaction comparisons were also significantly different, except for 20- and 30-m (pairwise adonis: $R^2 > 0.055$; $p > 0.537$) at each island, and both 5 m and 10 m between both islands (pairwise adonis: $R^2 > 0.013$; $p > 0.112$).

Shallow sites (5 and 10 m depth) were comparatively homogeneous between the two islands (Fig. 5, Fig. S3). However, at greater depths (20 and 30 m), the assemblage structure deviated slightly but significantly for each island. Furthermore, the zoantharian assemblages of Bonaire were observed to be more diversified than those of Curaçao based on the dispersion in the hierarchical clusters (Fig. 5).

Analyses with environmental and other parameters

For zoantharian communities around Bonaire, depth (PERMANOVA: $R^2 = 0.319$, $p < 0.001$) and disturbance level (PERMANOVA: $R^2 = 0.070$, $p < 0.001$) showed

significant differences within each factor. However, pairwise comparisons only showed significant differences between groups within depth, not for disturbance level. The pairwise comparisons of depth agreed with previous analyses, with only the 20-m to 30-m comparison being not significant (pairwise PERMANOVA with Holm's correction: $R^2 = 0.024$, $p = 0.434$).

Environmental data showed significant differences for all factors: depth (PERMANOVA: $R^2 = 0.150$, $p < 0.001$), management practice (PERMANOVA: $R^2 = 0.086$, $p < 0.001$), disturbance level (PERMANOVA: $R^2 = 0.203$, $p < 0.001$), and type of coast (PERMANOVA: $R^2 = 0.034$, $p = 0.005$). Due to identical data shared for depths of 10 m, 20 m, and 30 m, there was no significance of environmental data ($p > > 0.05$). However, significant differences (pairwise PERMANOVA with Holm's correction: $R^2 > > 0.20$, $p = 0.006$) were detected between the deep (10, 20, 30 m) and shallow (5 m) sites. Regarding management practice, significance differences were detected between marine park and no diving reserve sites (pairwise PERMANOVA with Holm's correction: $R^2 = 075$, $p = 0.006$). For disturbance level, there were significant differences between all levels (pairwise PERMANOVA with Holm's correction: $R^2 > > 0.086$, $p < 0.006$).

The environmental data fitted into the nMDS of zoantharian abundances showed only rugosity ($r^2 = 0.093$, $p = 0.03$), live coral cover ($r^2 = 0.136$, $p = 0.005$), and mean vertical height ($r^2 = 0.118$, $p = 0.005$) correlated significantly with the zoantharian community dataset (Fig. 6).

Discussion

While shallow-water zooxanthellate zoantharians such as *Palythoa* and *Zoanthus* spp. have received some research attention in the Caribbean, it is clear that epibiotic species and associations of suborder Macrocnemina are more common and diverse, at least in the waters around Curaçao and Bonaire. Even though the general patterns of zoantharian diversity are the same between Curaçao and Bonaire, it is important to emphasize that the more diverse and abundant deeper communities at 20- and 30-m depths were statistically different between these two islands. It should be noted that the observed inter-island differences were driven by *U. parasiticus* on *Niphates amorpha* and *U. parasiticus* on *N. erecta*. Additional analyses in which we combined these two associations into one (= *Niphates* sp.) resulted in no statistically significant differences between 20 and 30 m depth zoantharian communities between Curaçao and Bonaire (Fig. S4). Thus, although both of these *Niphates* species are currently taxonomically valid

Fig. 5 Cluster hierarchical analysis of bonaire (circles) and Curaçao (squares) zoantharian communities in this study. Colored circles below phylogram indicate depth of surveys
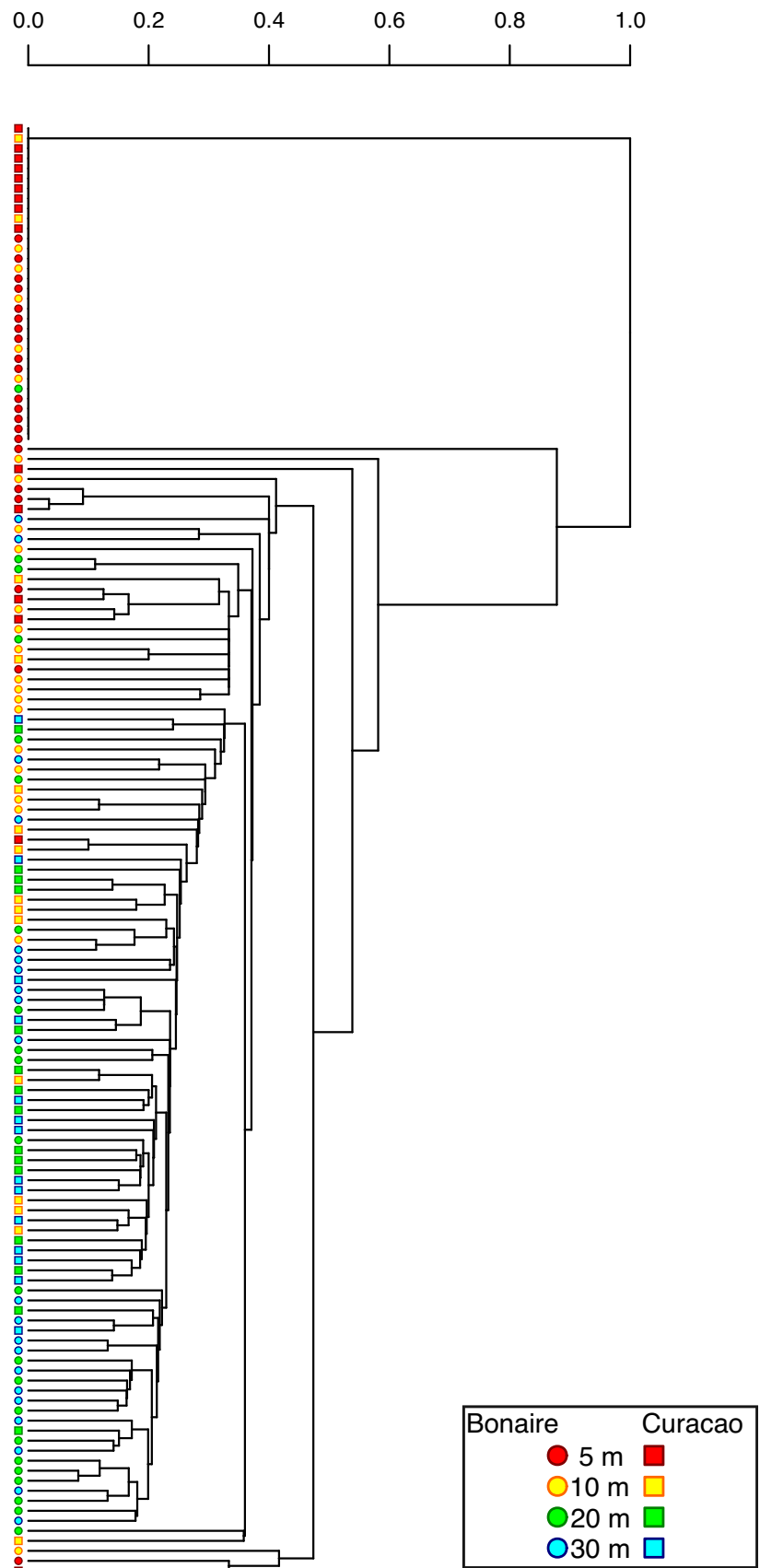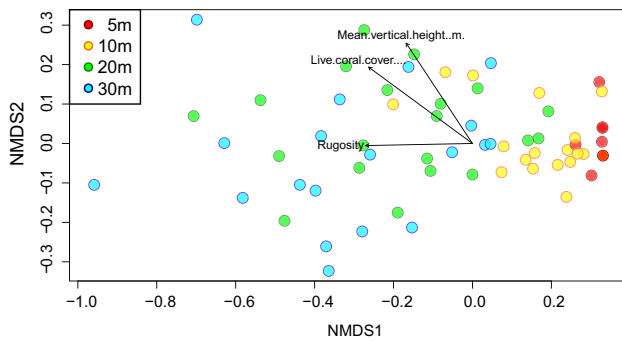
Fig. 6 nMDS analyses (stress = 0.099) of Bonaire zoantharian communities and environmental data in this study. Colored circles indicate different depths of surveys

(WoRMS; de Voogd et al. 2021), the question of whether *N. erecta* and *N. amorpha* are truly different species or conspecific morphotypes remains open (West 1979; van Soest 1980; Lewis 1982). This situation strongly demonstrates the need for basic taxonomic reassessment of the sponges of the Caribbean (Wörheide and Erpenbeck 2007; Pomponi et al. 2019).

The patterns of zoantharian diversity and abundance observed around Bonaire in this study reflected those recently observed in Curaçao (Reimer et al. 2018). Both Bonaire and Curaçao had comparatively low zoantharian numbers and diversity at 5- and 10 m-depths, with a preponderance of zooxanthellate species, and then increasing macrocnemic diversity and numbers at 20 and 30 m. As well, all shallow 5 and 10 m zoantharian communities from each island were not statistically different from each other. These results suggest that shallow zooxanthellate communities may not differ much among neighboring islands. Indeed, other studies from the Greater Caribbean on shallow zoantharian communities (e.g., Duerden (1898) in Jamaica; Belford and Phillip (2012) in Tobago) generally report similar *Palythoa* and *Zoanthus* communities, although statistical comparisons with these previous studies were not possible here due to differences in the methodologies employed.

However, the observed differences between zoantharian communities around Curaçao and Bonaire could hold importance for Caribbean coral reef conservation in general. Coral reefs of the Caribbean are known to generally have lower levels of diversity compared to their Indo-Pacific counterparts (Roberts et al. 2002). For Zoantharia, 12 species were observed in the current study, while on Indo-Pacific coral reefs, > 20 species have been reported from the reefs of Okinawa, Japan (Reimer and Fujii 2017; J. D. Reimer, unpubl. data), and 24 morpho-species from the Coral Triangle (Reimer et al. 2014). Although fewer zoantharian species may be present on many Caribbean coral reefs, the communities made by these species may be

different, even around neighboring islands. In particular, in this study, we observed differences in zoantharian communities at 20- and 30-m depths, demonstrating the importance of conservation of deeper reef zones around each island. This also reconfirms that deeper and mesophotic depths (e.g., ≥ 20 m) can act as reserves of coral reef biodiversity (Pomponi et al. 2019). Conservation along depth gradients could be one way to ensure the protection of potentially unique communities.

In the future, it will be important to confirm if the observed patterns in this study hold for other under-examined coral reef taxa. It should be kept in mind that the reefs of both Bonaire and Curaçao are changing due to anthropogenic impacts (Bak and Nieuwland 1995; Bak et al. 2005; De Bakker et al. 2016, 2017), which likely already have and will continue to affect the zoantharian assemblages of these islands. Hence, the present results can also be considered as a baseline for future comparisons. That the shallow reef zones (5 and 10 m) along the leeward coastlines of Bonaire and Curaçao are less different between both islands than the deeper zones may be related to the fact that the shallower reef communities of both islands are more impacted by exposure to wave action (Van Duyl 1985). This could have a similar restricting influence on the variation of their shallow reef faunas, as well as by the presence of fewer zoantharian species, as shown by the current and past (Reimer et al. 2018) studies.

The results of the current study also point toward additional possible avenues of future research topics. Expanding the current research across the greater Caribbean with an added temporal component could provide insights into how zoantharian communities shift and change across different regions. Such a study could be easily performed, as the methodology employed in this and Reimer et al. (2018) is not complex and can be conducted even without training as long as images acquired during dives can be analyzed by trained experts. As well, the combined Curaçao and Bonaire results show increasing zoantharian diversity with increasing depth, and thus surveys deeper into mesophotic depths will undoubtedly expand our knowledge on these important components of Caribbean coral reefs. Although some differences in the zoantharian communities between Curaçao and Bonaire exist, it should also be stressed that the similarities were many, pointing toward the possibility of a general pattern of zoantharians on reefs in the Caribbean that remains to be confirmed.

As well, many additional aspects of zoantharian communities on coral reefs remain to be explored. Most importantly, continued research into the drivers that shape zoantharian communities on these coral reefs is the next logical step to be investigated in detail. For example, it has been shown that the density and numbers of sponges

increases with depth in the Caribbean (Lesser and Slattery 2018), which fits well with the observed zoantharian community data. It remains to be seen if the composition of the host sponge community is critical to the formation of the Parazoanthidae assemblage. As well, it can be speculated that other, environmental factors play a role in the formation and maintenance of zoantharian assemblages. Among these factors, the roles of water quality (Yang et al. 2013; Amato et al. 2016; Cruz et al. 2018) and the physical structure of each reef (e.g., steepness of slope, size of cracks, amount of hard substrate, etc.; Santos et al. 2020) should be investigated. Our initial analyses in this study indicate a good fit with the zoantharian assemblage results to rugosity, live coral cover, and mean vertical height (height of tallest scleractinian coral colonies; De Bakker et al. 2019). These environmental parameters are all related to the physical structure and complexity of reef habitat, and future zoantharian surveys should aim to better quantify each examined site. Such data, combined with information on sponge density and abundance, should result in a more comprehensive understanding of the drivers of zoantharian communities and diversity on Caribbean coral reefs.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states there is no conflict of interest.

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