Original Articles

Coral-associated invertebrates as indicators of reef health in the Caribbean

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ABSTRACT

Coral reef biodiversity is partially comprised of macro-invertebrates that live partially embedded inside the skeletons of live corals, from where they may potentially cause extensive damage to their host's external polyp tissue. In the present study, six dominant groups of Caribbean coral associates were investigated for adverse effects on their host's health. Internal damage of the coral's skeleton was not considered. The associates can be categorized into two groups, i.e., those with small coral wounds (boring mussels of the genus *Leiosolenus*, coral barnacles of the family Pyrgomatidae, and gall crabs of the family Cryptochiridae) and those with larger coral injuries (feather duster worms of the genus *Anamobaea*, worm snails of the genus *Petaloconchus*, and serpulid worms of the genus *Spirobranchus*). A positive relationship was found between the surface area occupied by the associated invertebrate and the size of the surrounding damage. Damage caused by one particular associate could also vary among host corals, probably indicating host-specific resistance to symbiont-related damage. Some coral species showed pigmented tissue adjacent to the symbiont, possibly indicative for regenerative growth, disease, or a chemical defence mechanism. Hence, this study clarifies the nature of the symbiotic relationships between various coral-associated invertebrates and their hosts and demonstrates the variation in harmful impact of widespread coral-associated fauna in the Caribbean. This information helps to clarify the potential use of coral-associated invertebrates as bioindicators of reef health: their presence is a contribution to reef biodiversity, but when they reach high densities (like in eutrophic conditions), some of them are capable of causing serious harm to their host corals.

1. Introduction

Macro-invertebrates form a crucial component of coral reef ecosystems, with an estimated diversity exceeding 168,000 species (Ray and Grassle, 1991; Ruppert et al., 2004). Only a small fraction (0.5 %) of these species is known as associated fauna of live corals (Stella et al., 2011), but their record has increased recently due to the discovery of various cryptic invertebrate species, such as endolithic gall-forming snails (Gittenberger and Gittenberger, 2011 and barnacles (Kolbasov et al., 2025), camouflaged corallivorous sea slugs (Hu et al., 2020; Jia et al., 2023; Mehrotra et al., 2020, 2024), epibiotic hydroids (Maggioni et al., 2022), and commensal shrimps (Rauch et al., 2019). Thus, coral-associates may play an underestimated role in marine biodiversity (Montano, 2020, 2022).

This species richness is vulnerable because of their strong dependence on the coral's health and survival (Goulet and Goulet, 2021; van der Schoot and Hoeksema, 2022, 2024). Not only the presence of host corals (e.g., Cleary et al., 2006; Hoeksema et al., 2019a; 2022d), but also the composition of their associated fauna depends on environmental factors, such as depth, water movement and nutrients (Lymperaki et al., 2022; van der Schoot and Hoeksema, 2022; Becking et al., 2024). As a specific example, the presence of coral-associates can be positively related to local eutrophication, with densities reaching up to five individuals per 10 cm^2 coral tissue (Le Grand and Fabricius, 2011; van der Schoot and Hoeksema, 2022). This raises a critical ecological question: how do these associated species influence their host's health? In some cases, these associations may enhance host resistance against external threats, such as coral predation by deterrence of predators (DeVantier et al., 1986; Montano et al., 2017), sedimentation by cleaning the coral surface of the precipitated material (Stewart et al., 2006) and coral bleaching by a mechanism that is still unknown (Ben-Tzvi et al., 2006), potentially improving conditions for their mutual survival. However, many studies describe a negative impact on the host's health (Hutchings, 2008; Nogueira et al., 2014; Barton et al., 2020; Hoeksema et al., 2022a, 2022b, 2022c), where the presence of these symbionts might exacerbate coral decline, potentially triggering a negative feedback process that

poses a threat to both the host and the associated species.

Understanding the nature and impact of these interactions is essential for assessing their broader implications for coral reef ecosystems and for exploring the possibilities of coral associated fauna as indicators of coral reef health (Risk et al., 2001; Scaps and Denis, 2008). To date, studies investigating the use of coral-associated fauna as bioindicators have primarily focused on broader aspects, such as overall coral reef health (Risk et al., 2001; Scaps and Denis, 2008), colony-specific health in relation to bioerosion (Fonseca et al., 2006), and environmental parameters like eutrophication (Le Grand and Fabricius, 2011; van der Schoot and Hoeksema, 2022) and sedimentation (Scaps and Denis, 2008; Harty, 2011). However, detailed information on the influence of specific symbiont groups on particular coral species remains scarce, even though such insights could contribute to the development of bioindicators with enhanced sensitivity and specificity.

In this study six groups of coral-associated macro-invertebrates (Fig. 1) are investigated for the damage they inflict to host corals in the Caribbean: (a) boring mussels of the genus *Leiosolenus* (family Modiolidae), (b) coral barnacles (family Pyrgomatidae), (c) coral gall crabs (family Cryptochiridae), (d) split-crown feather duster worms of the genus *Anamobaea* (family Sabellidae), (e) polychaetes of the genus *Spirobranchus* (family Serpulidae), and (f) worm snails of the genus *Petaloconchus* (family Vermetidae).

Boring mussels of the genus *Leiosolenus* (Modiolidae: Botulinae), also called date mussels, are suspension feeders known for the bioerosion of a variety of calcium carbonate structures, among which coral skeletons (Kleemann, 1996; Owada, 2007; Vinagre et al., 2018; Tan and Tan, 2024). These species apply a combined mechanical-chemical approach i. e., pallial glands produce acidic metabolites which weaken the coral skeleton followed by abrasion (Schönberg et al., 2017). These boring bivalves actively excavate the coral skeleton, thereby weakening the host coral and increasing its susceptibility to erosion, which in turn exacerbates the overall degradation process (Jones and Pemberton, 1988; Scott and Risk, 1988; Mizrahi et al., 2023). The presence of date mussels in a coral is recognized from the outside by the figure-eight or dumbbell shape of their boreholes (Kleeman, 1980; Hoeksema et al., 2022b), not showing the real damage of the excavated borehole inside the coral skeleton (Kramer et al., 2024). Moreover, their boreholes form a suitable substrate for micro-endolithic algae, which in turn facilitate colonization of the host by other macroborers (Fordyce et al., 2020).

Pyrgomatidae Gray, 1825, is a family of obligate coral-dwelling barnacles, which occur mainly on scleractinian corals but also on
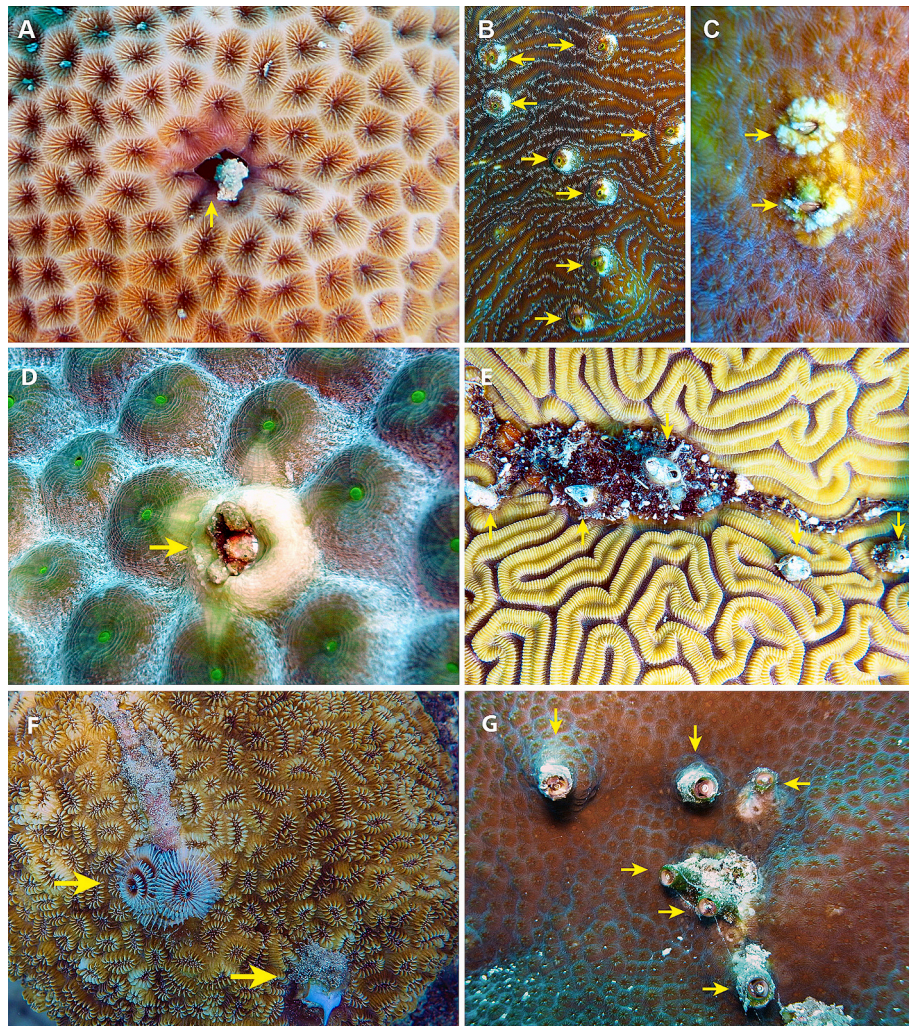
Fig. 1. Coral associates (yellow arrows) and examples of their host corals observed in the present study. (A) A boring mussel (*Leiosolenus* sp.) in *Siderastrea siderea* with pigmentation surrounding the boring bivalve and detritus on top of the borehole opening. Eight coral barnacles (Pyrgomatidae) in (B) *Agaricia lamarcki* and two in (C) *Orbicella faveolata*, surrounded by bleached coral tissue. (D) A gall crab (Cryptochiridae) in *Montastraea cavernosa*, surrounded by bleached tissue. (E) Five feather duster worms (*Anamobaea* sp.) in *Diploria labyrinthiformis*. (F) Two Christmas tree worms (*Spirobranchus* sp.) in *Dichocoenia stokesii*. (G) Six worm snails (*Petaloconchus* sp.) in *O. faveolata*, surrounded by dead coral tissue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

hydrozoans and sponges (Tsang et al., 2014). The group consists of 99 species, 95 of which have been described from over 250 host-coral species (van der Schoot and Hoeksema, 2024). Their host specificity is high, relative to other symbiont groups, such as serpulid tube worms and date mussels (Lithophaginae) (van der Schoot and Hoeksema, 2024). Not much is known about the impact of coral-associated barnacles on their hosts, except that the settlement process of their larvae causes damage to coral's tissue (Liu et al., 2016) and that they produce a tube-shaped base inside the coral skeleton (Yap et al., 2023). Some species feed on their host's tissue and absorb its nutrients (Ross and Newman 1969, 1995, 2000). Since most barnacles are not very large, their densities on a single coral colony can become high, reaching up to 0.5 individual per cm² (van der Schoot and Hoeksema, 2022). Occupancy of the host's tissue has been thought to impede the host's growth (Barton et al., 2020) and possibly limits its range expansion (Sommer et al., 2024).

Coral gall crabs (Cryptochiridae) are obligate symbionts of scleractinian corals, each residing inside a dwelling that has an opening on the coral surface (Castro, 1976; Chan et al., 2020). These crabs are different from the other symbiont groups as they are not attached to the coral but are motile (van der Meij, 2014; García-Hernández et al., 2020). Cryptochirids exploit a strong host-specificity, meaning that each species inhabits a very select group of scleractinian hosts (van der Schoot and Hoeksema, 2024), depending on the host availability within their distribution range (Hoeksema et al., 2018a). Some gall crab species feed on the coral mucus and/or tissue (Bravo et al., 2024) and one species has been observed to impede the growth rate of its host (Nogueira et al., 2014). Other gall crabs were seen to facilitate the growth of filamentous algae on the edges of their dwellings, possibly entrapping sediment and causing damage to their hosts coral tissue (Carricart-Ganivet et al., 2004; Pratte et al., 2018; Bähr et al., 2025).

Split-crown feather duster worms of the genus *Anamobaea*, consist of two species, *A. orstedii* and *A. phyllisae,* both of which occur on dead and living corals in the Caribbean Sea. They form a leathery tube, which can extend deep inside the coral skeleton (Tovar-Hernández and Salazar-Vallejo, 2006; Hoeksema et al. 2022c). They can reach high densities and cause large injuries and peak-shaped skeleton deformities in their hosts (Hoeksema et al., 2022c).

Serpulid polychaetes of the genus *Spirobranchus* form a group of tube worms, some of which have been recorded as facultative coral associates while others occur on non-living substrates (van der Schoot and Hoeksema, 2024). They are easily recognizable by their colorful radiolar crown, which can be subtracted into their tube when disturbed, particularly by predators (Hoeksema and ten Hove, 2017b; Pezner et al., 2017). Within this genus, *S. giganteus* is the most common coral-associated species in the Caribbean where it has been recorded from at least 23 different host species (Hoeksema et al., 2019c, 2020). Based on anecdotal observations, they were initially seen as harmless or even contributing to the survival of their hosts by predator deterrence (DeVantier et al., 1986; Pratchett 2001), by enhancing coral feeding through improved water circulation (Strathman et al., 1984), and by stimulating polyp regeneration after bleaching (Ben-Tzvi et al., 2006). Pigmented areas of coral tissue are regularly observed in the area where the operculum touches the host's surface when the worm is extended out of its tube, indicating a possible stress response of the host (Hoeksema et al., 2018b, 2019b, 2019c; Afkar et al., 2024) or a disease, such as dark spot syndrome (Borger, 2005; Nugues and Bak, 2007). Additional damage has been recorded in the area around the worm tube, which is often bleached or dead and covered by filamentous algae (van der Schoot and Hoeksema, 2022; Afkar et al., 2024). The growth of such algae depends on the presence of nutrients (Isdianto et al., 2024). Furthermore, the worms were observed to reach high densities, predominantly in areas with high mineral and chlorophyll-a concentrations (van der Schoot and Hoeksema, 2022). Serpulids also have been reported to reach high densities during red tides, causing severe damage to their hosts by smothering their polyps (Samimi-Namin et al., 2010).

Coral damage caused by worm snails of the genus *Petaloconchus* was recently reported in the Caribbean for the first time (Hoeksema et al., 2022a). This worm snail was probably introduced by hull-fouling and may have arrived in the Caribbean before 1955 (Hoeksema et al., 2023, 2025). The large coral injuries observed around the worm snails may be caused by the toxic mucus nets as observed in other worm snail species (Hadfield et al., 1972; Klöppel et al., 2013). Other possible causes for the detrimental effect of the worm snails are overgrowth of healthy coral polyps and damage caused by turf algae on their shells, similar to those on calcareous worm tubes (Hoeksema et al., 2019b, 2019c, 2022a).

As specific information about the nature of symbiotic relationships between coral-associated fauna and their host species remains scarce, this study aims to quantify and characterize the damage caused by different symbiont groups to their host corals. In particular, it distinguishes between damage occurring directly within the area occupied by the symbiont (primary damage) and damage around it (surrounding damage). Based on earlier studies, both the symbiont group and the identity of the host species are expected to determine the extent and nature of tissue damage (Hoeksema et al., 2019b, 2019c, 2022a, 2022b, 2022c; Barton et al., 2020; van der Schoot and Hoeksema, 2022).

By providing detailed insights into these interactions, this study aims to contribute to a better understanding of the health implications that these associations have for the hosts. The findings help to develop bioindicators based on the host-specific responses to symbiont pressure. Ultimately, this information may support the design of management protocols for coral reef conservation and restoration, offering guidance for mitigating threats to coral reef health posed by harmful symbiotic interactions.

2. Materials and methods

2.1. Data collection

Surveys were conducted in March 2023 at 23 sites at the leeward side of Curaçao (Fig. 2, Table S1). Using underwater photography, the following data were recorded: host-coral species, symbiont taxon, surface area occupied by the symbionts (primary damage) and the area around the symbionts affected by injuries (surrounding damage). Photographs were taken by two divers at depths ranging from 5 to 20 m, one of them using an Olympus OM-D E-M5II camera with a 14–42 mm lens, housed in an Olympus PT-EP13 underwater housing, with an INON Z-330 strobe, and the other one using a Sea&Sea DX-2G camera with an
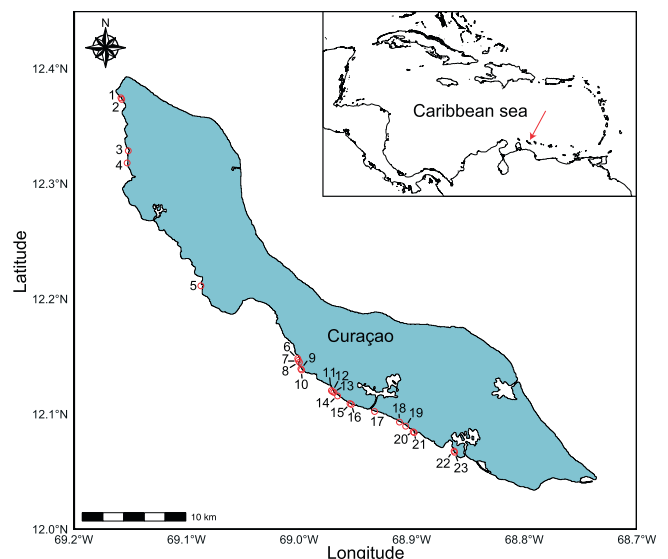

Fig. 2. Map of Curaçao indicating field localities used for data collecting in March 2023. Coordinates of localities are mentioned in Table S1.

external YS-D2 strobe.

To provide scale, two quadrat sizes were used: a 100 × 100 mm for small areas and 140 × 140 mm for larger areas. A time-swim survey method was employed during each 60-minute dive, similar to the approach described by van der Schoot and Hoeksema (2022). The dive began at a depth of 20 m, moving parallel to the shoreline. During weak currents, the direction was reversed after 30 min; during stronger currents, 40 min were spent against the current and 20 min with the current. All live coral colonies, except for *Millepora* spp., with at least one visible symbiont within a belt width of 2 m were recorded. No selection was made regarding the type of symbionts at this stage. Each symbiont was photographed at the center of the quadrat.

2.2. Data analysis

A total of 7,279 photographs were taken during 46 dives across 23 sites. Host corals were identified to species level, while symbionts were classified to family level (e.g., Cryptochiridae, Pyrgomatidae) or genus level (e.g., *Spirobranchus, Leiosolenus, Petaloconchus, Anamobaea*). Identifications of both host and symbiotic species were performed based on the photo records using relevant identification guides and literature (Humann and Deloach, 2013, Human et al., 2013, van der Meij, 2014, Breves et al., 2017; Hoeksema et al., 2022a, 2022b, 2022c).

Surface areas of primary and surrounding damage were calculated using the software ImageJ version 1.54j (Schneider et al., 2012). The number of square pixels in a manually selected area (ImageJ function: "polygon selections") of each photograph (for both the quadrat and damage regions) was measured (Fig. 3).

Surface area (cm^2) of injuries was measured by relating the number of pixels in the damaged region to the number of pixels in the quadrat that was used. Absent surrounding damage was recorded as 0. Primary damage was defined as the area occupied by the symbiont itself, for *Spirobranchus*, and *Anamobaea* the diameter of the tube opening was measured, for cryptochirid epibionts the opening of the pit or dwelling was measured, for *Leiosolenus* the opening of the borehole was measured, for pyrgomatid symbionts the orifice size (barnacle opening) was measured, and for *Petaloconchus* the part of the tube above the coral surface, including the tube opening, was measured. Opercular plates of

barnacles overgrown by coral tissue were recorded as zero damage, unless this coral tissue was damaged, in which case it was recorded as surrounding damage. Four damage types for surrounding damage were distinguished: (a) bleached tissue, (b) dead tissue, (c) pigmented tissue, (d) and skeleton covered by algae (Fig. 3). Pigmentation was defined as a visible deviation from the predominant coral tissue color (Fig. 1A, 3C). At most three individuals per symbiont taxon on the same host coral were used to allow for sufficient sample variation within the available survey time and to minimize pseudo-replication. Each host-symbiont combination was limited to a maximum of 50 records; host-symbiont combinations recorded less than 40 times were not included in the data analysis.

2.3. Statistical analysis

In the first analysis (Fig. 4), all host coral species were grouped together, and the primary, surrounding, and total damage were compared across symbiont groups. Analyses were conducted using the R software (R Core Team, 2024). A generalized linear model (GLM) with a Gamma distribution was fitted to the data for primary, surrounding, and total damage (package: "stats, function: glm()"). To address zero inflation in the surrounding damage data, a Box-Cox transformation was applied (Box and Cox, 1964; package: "MASS, function: boxcox()"), with a small constant (1.1) added to both avoid the production of negative numbers and taking the natural log (ln) of zero.

The model's goodness-of-fit was evaluated using diagnostic plots. A Q-Q plot was used to assess the normality of deviance residuals, and a density plot was examined to check for symmetry around zero (package: "stats, functions: resid(), fitted(), qqnorm(), qqline(), density(); package: graphics, function: plot()"). Pairwise comparisons among symbiont categories were performed using Tukey's HSD (Honestly Significant Difference) post-hoc test, controlling for family-wise error rate with corresponding adjusted p-values (Hothorn et al., 2008; package: "multcomp, function: glht()"). The above-described method was also applied to assess the differences in surrounding damage between host species within macro-invertebrate groups. To assess (a) differences in primary damage between host species within a macro-invertebrate group, (b) differences in damage types between host species of a
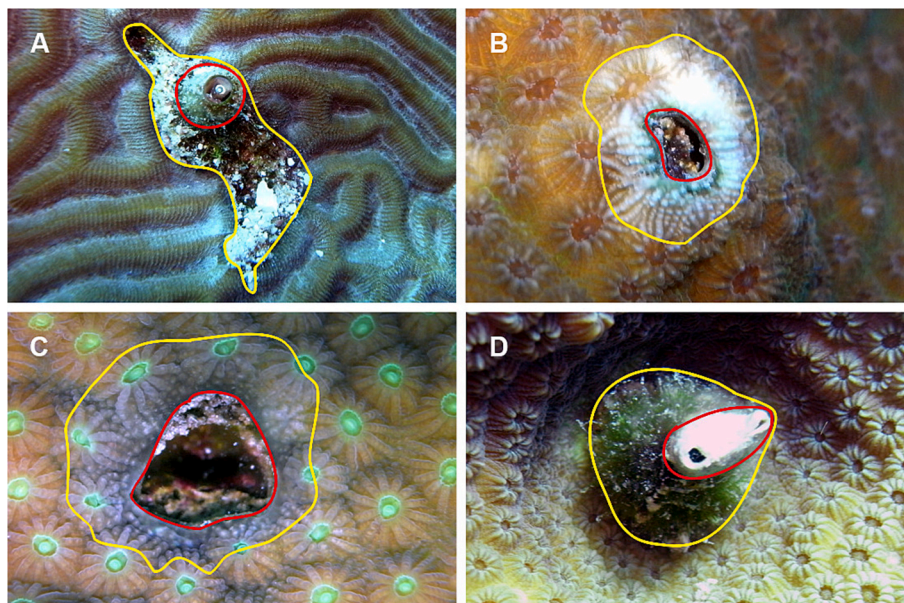
Fig. 3. Different kinds of damage caused by Caribbean coral-associates: primary damage (inside red outlines) and total damage consisting of primary damage plus surrounding damage (enclosed by yellow outlines). (A) *Petaloconchus* sp. in *Pseudodiploria strigosa* host, surrounded by dead tissue, (B) Pyrgomatid in *Orbicella faveolata* host, surrounded by bleached tissue, (C) Pyrgomatid in *O. faveolata* host, surrounded by pigmented tissue and (D) feather duster worm (*Anamobaea* sp.) in *O. faveolata* surrounded by algae. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
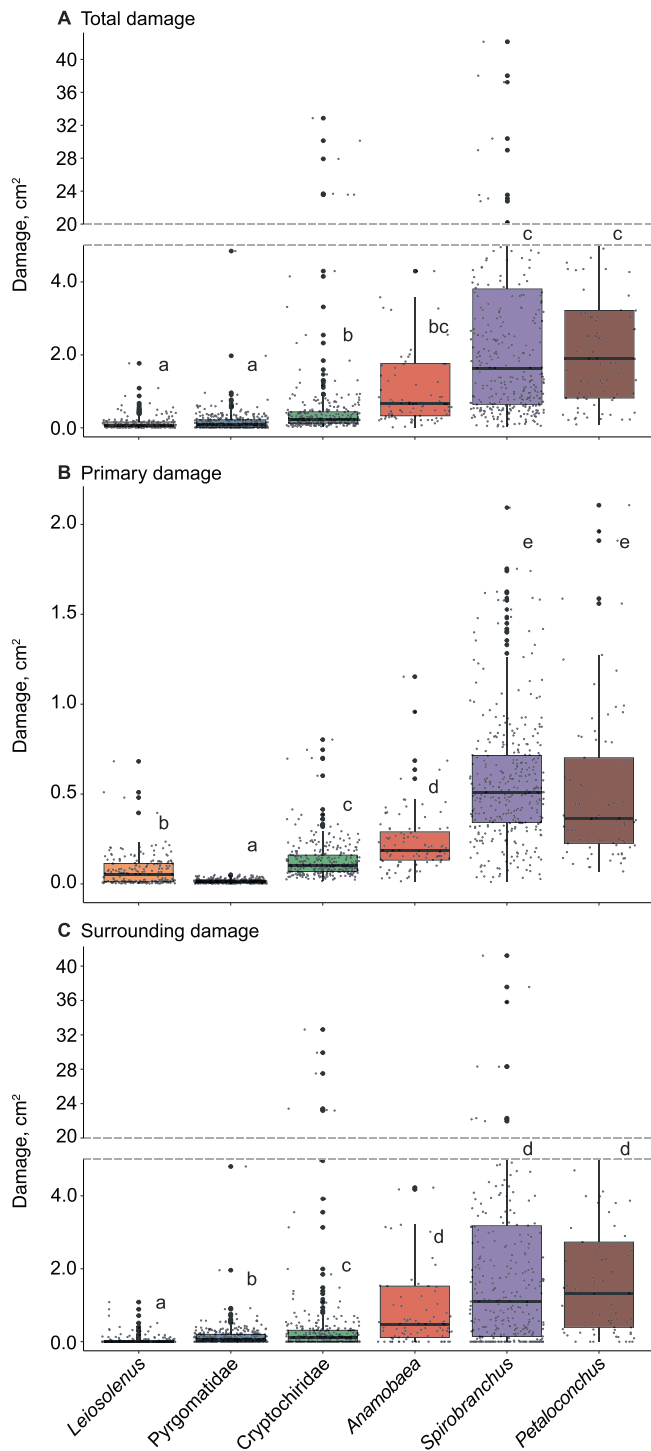
Fig. 4. Damage of host corals caused by the presence of associated fauna belonging to six symbiont groups: A distinction is made between (A) Total damage, divided in (B) Primary damage and (C) Surrounding damage. Significance between symbiont groups is indicated by the compact letter display system (CLD), i.e., those sharing the same letter are not significantly different. Corresponding p-values are provided in Table S2.

macro-invertebrate group and (c) differences in damage types within host-symbiont combinations, an ANOVA and Tukey's HSD post-hoc test were applied (package: "stats, function aov(), TukeyHSD()").

A linear regression analysis was conducted to examine the relationship between primary and surrounding damage. To improve visualization and interpretability, both primary damage and surrounding damage

were log-transformed (ln), surrounding damage was shifted with a constant of 0.1 to prevent taking the logarithm of zero. Regression lines were fitted using the least squares method (Legendre and Legendre, 2012), and Pearson correlation coefficients (R) (Lee Rodgers and Nicewander, 1988) were calculated for each symbiont group to assess the strength and direction of the relationship. The corresponding p-values indicate whether the observed correlations are statistically significant.

To quantify the relationship between log-transformed primary damage and log-transformed surrounding damage, linear regressions were performed separately for each symbiont group. The effect coefficient (slope) was extracted from each regression (package: "stats, function coef()"). To interpret the results on the original scale, an exponential back-transformation to the estimated effect coefficients was applied. To test whether the effect coefficients significantly differed between groups, a linear model was fitted to all symbiont groups including an interaction term (Crawley, 2012). Additionally, pairwise comparisons of the effect coefficients between symbiont groups were performed using estimated marginal trends (package: "emtrends, function emtrends()") and a Tukey-adjusted post-hoc test (package: "graphics, function pairs()"). All visualizations were created using the "ggplot2" package.

3. Results

3.1. Host coral species and symbiont groups

In total, 2,084 association records were documented across 29 coral species and six symbiont groups (Table 1). Since only host-symbiont combinations with 40 or more records were included, the analysis was limited to two host species for both *Anamobaea* and *Petaloconchus*, four host species for *Leiosolenus*, six host species for Pyrgomatidae and seven host species for both Cryptochiridae and *Spirobranchus*.

3.2. Damage categories

3.2.1. Total damage

Total damage, defined as the combined primary and surrounding damage, represents the total affected area of the host coral and differed significantly among symbiont groups (Fig. 4A). Symbiont groups can be broadly categorized into two clusters: those with smaller affected areas (*Leiosolenus*, Pyrgomatidae, and Cryptochiridae) and those with larger affected areas (*Anamobaea*, *Petaloconchus*, and *Spirobranchus*). Cryptochiridae, while having a median value comparable to *Leiosolenus* and Pyrgomatidae, exhibits greater variability, including some records with notably large, affected areas. This resulted in Cryptochiridae being statistically similar to *Anamobaea*, while showing significantly larger total damage than both *Leiosolenus* and Pyrgomatidae.

3.2.2. Primary damage

Primary damage showed a more distinct separation between symbiont groups, except for *Petaloconchus* and *Spirobranchus*, which did not differ significantly (Fig. 4B). The median values across groups followed a similar trend to total damage, except for *Leiosolenus*, which exhibited larger areas of primary damage than Pyrgomatidae.

3.2.3. Surrounding damage

Leiosolenus and Pyrgomatidae exhibited an opposite pattern for surrounding damage compared to primary damage (Fig. 4BC), i.e., levels of primary damage are higher for *Leiosolenus*, while Pyrgomatidae showed greater surrounding damage and vice versa. These differences were mutually counterposed and therefore no significant difference in total damage between these groups was visible. The trend observed for the other symbiont groups remained consistent, with median values for surrounding damage being higher than those for primary damage. An exception to this pattern occurred between *Petaloconchus*, *Spirobranchus* and *Anamobaea*, which did not differ significantly in their surrounding

Table 1
Records of coral-associated invertebrates per encountered host coral species and symbiont group. At least 40 and up to 50 records per host-symbiont combination (bold script) were selected for further analysis.

Coral species	Symbiont groups					
	Leiosolenus	Pyrgomatidae	Cryptochiridae	*Anamobaea*	*Spirobranchus*	*Petaloconchus*
Acropora palmata	2	0	3	0	0	0
Agaricia agaricites	8	**50**	**50**	3	**50**	9
Agaricia grahamae	0	2	0	0	0	0
Agaricia humilis	3	14	2	0	7	0
Agaricia lamarcki	2	**50**	**50**	13	0	3
Colpophyllia natans	2	0	19	6	9	5
Dichocoenia stokesii	0	2	1	0	3	0
Diploria labyrinthiformis	0	1	1	20	5	0
Eusmilia fastigiata	0	0	0	0	0	1
Favia fragum	4	0	6	0	3	0
Madracis auretenra	0	0	0	0	4	0
Madracis decactis	**43**	1	0	0	6	0
Madracis formosa	2	0	0	0	0	0
Madracis pharensis	**50**	9	1	2	18	1
Madracis senaria	37	5	0	13	10	7
Manicina areolata	0	0	1	0	0	0
Meandrina meandrites	1	0	3	7	0	0
Montastraea cavernosa	10	1	**48**	26	20	9
Mussa angulosa	0	0	0	0	0	1
Orbicella annularis	2	14	**50**	13	**50**	21
Orbicella faveolata	15	**50**	**50**	**50**	**50**	15
Orbicella franksi	2	**50**	**50**	30	**50**	14
Porites astreoides	**50**	**50**	1	14	**50**	**40**
Porites furcata	0	0	0	0	23	2
Porites porites	0	0	0	0	8	3
Pseudodiploria clivosa	0	2	1	0	1	0
Pseudodiploria strigosa	23	3	28	**46**	**50**	13
Siderastrea siderea	**50**	**50**	21	18	**50**	**41**
Stephanocoenia intersepta	14	**50**	3	25	27	6

damage.

3.3. Primary damage as a predictor variable for surrounding damage

The area size of surrounding damage showed a positive relationship with the area size of primary damage. All groups, except *Anamobaea*, demonstrated a significant positive correlation between these variables
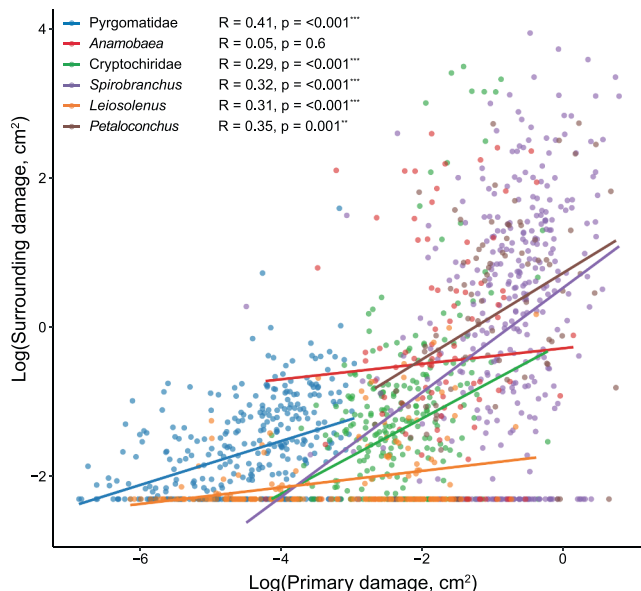
Fig. 5. Linear regression between primary and surrounding damage of six groups of coral-associated macroinvertebrates, with surrounding damage as dependent variable of primary damage, all data was logarithmically transformed. 'R' is the Pearson correlation coefficient. P-values are significant except for *Anamobaea*.

(Fig. 5). Despite the significant relationships, the R values (Pearson correlation coefficient) are relatively low, with Pyrgomatidae showing the highest value (R = 0.41).

The effect coefficients for each symbiont group were derived from the linear regression analysis, back-transformed and pairwise compared (Table 2). *Spirobranchus* exhibits the steepest trendline, significantly steeper than *Leiosolenus* and Pyrgomatidae. The effect coefficient of *Spirobranchus* is almost twice that of *Leiosolenus* and 1.5 times that of Pyrgomatidae. Also, the trendline of Cryptochiridae was significantly steeper than *Anamobaea*, with the effect coefficient being 1.5 times larger.

3.4. Primary and surrounding damage at host species level

Leiosolenus exhibited the second-least primary damage (Fig. 4B) in four coral species that were represented by at least 40 associations. The hosts clustered into two damage groups, *Madracis decactis* and *M. pharensis* showed significantly lower damage levels than *Porites*

Table 2
Effect coefficients per symbiont group, derived from the linear regression analysis (Fig. 5). The effect coefficient was both directly derived from the linear regression with log-transformed data (Effect coefficient (log)) and exponentially back transformed for a multiplicative effect on the original scale (Effect coefficient). Significance between symbiont groups is indicated by the compact letter display system (CLD), i.e., those sharing the same letter are not significantly different. Corresponding p-values are provided in Table S3.

Symbiont group	Significance (CLD)	Effect coefficient (log)	Effect coefficient
Anamobaea	NA	NA	NA
Leiosolenus	a	0.111	1.12
Pyrgomatidae	ab	0.295	1.34
Cryptochiridae	bc	0.506	1.66
Petaloconchus	abc	0.580	1.79
Spirobranchus	c	0.701	2.02

astreoides and *Siderastrea siderea* (Fig. 6A). Surrounding damage was low for this symbiont group (Fig. 4C), notwithstanding *P. astreoides* and *S. siderea* exhibited larger areas of surrounding damage than *M. decactis* (Fig. 6B).

Primary damage for barnacles was smallest among all symbiont groups, and surrounding damage was second lowest (Fig. 4). Despite the small damage size, significant differences were observed among seven host coral species (Fig. 6C). Four of the seven host species—*Agaricia lamarcki*, *Orbicella faveolata*, *Orbicella franksi*, and *Stephanocoenia intersepta*—were clustered around a median primary damage of 0.02 cm². In

contrast, *Agaricia agaricites*, *Porites astreoides*, and *Siderastrea siderea* exhibited significantly smaller areas of primary damage. The pattern observed for surrounding damage resembled that of primary damage, albeit with greater variance and therefore with a slight change in significant differences between hosts (Fig. 6D). The most striking difference between primary and surrounding damage was shown by *S. intersepta*, which had less surrounding damage relative to its primary damage in comparison with the other host species of the high-level cluster, i.e., *A. lamarcki*, *O. faveolata*, and *O. franksi*. Other observations concerned *A. agaricites* showing lower values of surrounding damage than all the
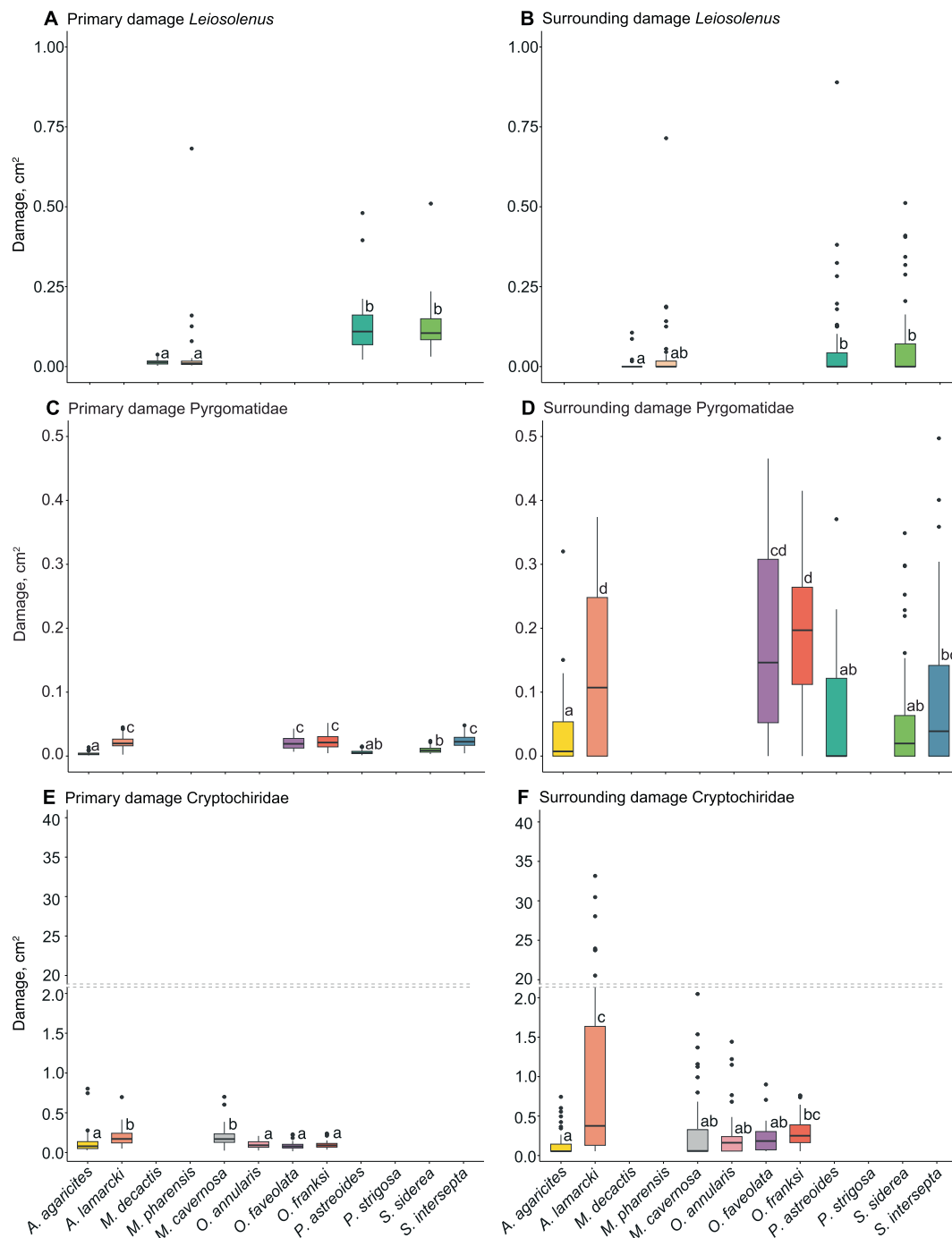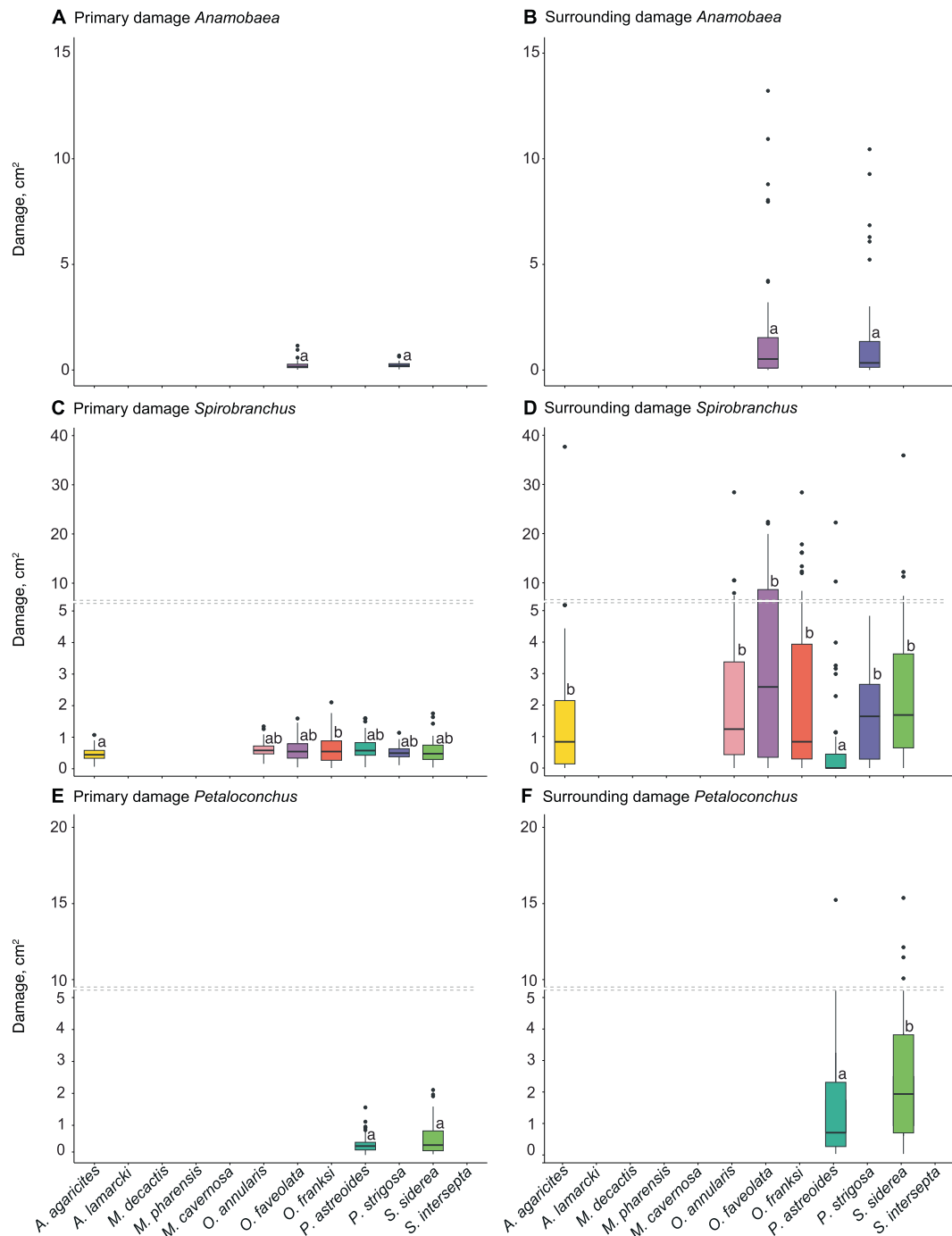

Fig. 6. Damage of host corals caused by the presence of *Leiosolenus* – (A) Primary damage and (B) Surrounding damage, Pyrgomatidae – (C) Primary damage and (D) Surrounding damage, Cryptochiridae – (E) Primary damage and (F) Surrounding damage. Host species not represented by at least 40 associations are not indicated. Significance between host species is indicated by the compact letter display system (CLD), i.e., those sharing the same letter are not significantly different. Corresponding p-values are provided in Tables S4–S6.

other host species, except for *P. astreoides* and *S. siderea*, whereas *A. lamarcki* and *O. franksi* showed significantly higher values than the other host species.

Cryptochiridae showed low-intermediate primary and surrounding damage relative to the other symbiont groups (Fig. 4). Significant differences were observed across the six included host coral species (Fig. 6E), i.e., *Agaricia lamarcki* and *Montastraea cavernosa* formed a cluster showing relatively large areas of primary damage, significantly higher than the other four host species, which were clustered around equally low levels. The surrounding damage showed a deviation from

the observed clusters in the primary damage (Fig. 6F), i.e., *A. lamarcki* had some exceptionally high damage records in this category, which was significantly more than that of the other host species, except for *O. franksi*. Another remarkable observation was *M. cavernosa*, which was in the high-level cluster for primary damage but in the lower-level cluster for surrounding damage.

Anamobaea exhibited intermediate primary and surrounding damage compared to the other symbiont groups (Fig. 4). Area sizes for primary and surrounding damage did not show differences between the two included coral species, i.e., *Orbicella faveolata* and *Pseudodiploria strigosa*.

Fig. 7. Damage of host corals caused by the presence of *Anamobaea* – (A) Primary damage and (B) Surrounding damage, *Spirobranchus* – (C) Primary damage and (D) Surrounding damage, *Petaloconchus* – (E) Primary damage and (F) Surrounding damage. Host species not represented by at least 40 associations are not indicated. Significance between host species is indicated by the compact letter display system (CLD), i.e., those sharing the same letter are not significantly different. Corresponding p-values are provided in Tables S7–S9.

For both host species, occasionally relatively much surrounding damage was recorded (Fig. 7AB).

Primary and surrounding damage levels for *Spirobranchus* were among the highest observed in this study (Fig. 4). Across its seven included host coral species, primary damage was largely consistent, except for *A. agaricites*, which exhibited significantly less damage than *O. franksi* (Fig. 7C). Surrounding damage was relatively much for all host species except for *P. astreoides*, which significantly showed the least damage of all host species for *Spirobranchus* sp. (Fig. 7D).

Primary and surrounding damage observed for *Petaloconchus* was relatively much (Fig. 4). Two host species were represented in sufficiently high numbers, *P. astreoides* and *S. siderea*, both exhibited similar levels of primary damage with no significant differences between them. Surrounding damage was significantly more in *S. siderea* than *P. astreoides* (Fig. 7AB).

3.5. Incidence and types of surrounding damage from the symbiont's perspective

Surrounding damage was observed around individuals of all six symbiont groups, though with notable variation in occurrence and damage types (Fig. 8). *Leiosolenus* exhibited the lowest occurrence of surrounding damage (31 %), while *Petaloconchus* showed the highest (91 %). Dead coral tissue was the least common around *Leiosolenus* (7 %) and the most around *Petaloconchus* (78 %). Both, *Anamobaea* and *Spirobranchus*, displayed surrounding damage in 78 % of their records. Dead coral tissue was observed in only 44 % of *Anamobaea* cases compared to 61 % of *Spirobranchus*. Similarly, surrounding damage was recorded around 66 % of Pyrgomatidae and 67 % of Cryptochiridae, while dead coral tissue was recorded around 18 % and 37 % of them, respectively.

Bleached areas were recorded concerning all symbiont groups, albeit infrequently around *Spirobranchus*, *Petaloconchus* and *Anamobaea*

individuals. Coral tissue around Pyrgomatidae showed the highest incidence of bleaching (33 %). Pigmented areas were present in four of the six groups, although with relatively low frequency (11–15 %). Algae-covered areas were exclusively observed in *Anamobaea* (31 %) and *Petaloconchus* (9 %), which notably lacked pigmented areas.

3.6. Incidence and types of surrounding damage from the host perspective

3.6.1. Boring mussels of the genus Leiosolenus

Both in terms of incidence and area size, surrounding damage in host coral species of *Leiosolenus* was low. Its mean area size was significantly lower than for the other symbiont groups (Fig. 4C). *Madracis decactis* had the lowest incidence of affected tissue, only 9 % of *Leiosolenus* in this host species was surrounded by damage, all consisting of pigmentation (Fig. 9A).

Both dead and bleached coral tissue was observed in three of the four host species i.e., *M. pharensis*, *P. astreoides* and *S. siderea*. Bleached area sizes around *Leiosolenus* on *M. pharensis* were significantly smaller than both the other host species and the area size of dead coral tissue on *M. pharensis* itself. Pigmentation was present in all host species and was divided into two species pairs, *M. decactis* – *M. pharensis,* and *P. astreoides* – *S. siderea*. the latter of which had significantly larger area sizes for this damage type than the other.

3.6.2. Coral barnacles of the family Pyrgomatidae

Seven host coral species of Pyrgomatidae were analyzed for differences in surrounding damage. A high variation in incidence was observed. Notably, surrounding damage was relatively infrequent in *Porites astreoides* and *Agaricia agaricites*, while *Siderastrea siderea* and *Stephanocoenia intersepta* exhibited intermediate levels. *Agaricia lamarcki* and *Orbicella faveolata* showed high occurrences, and nearly all barnacles in *Orbicella franksi* had surrounding damage (Fig. 9B).

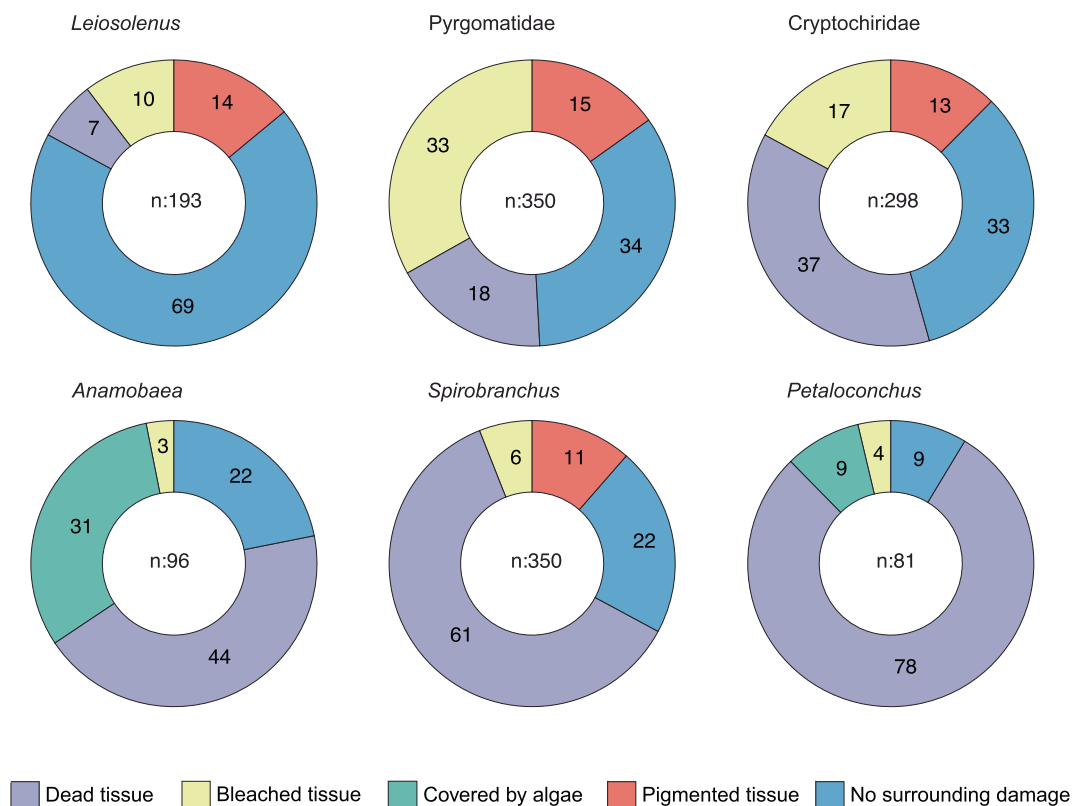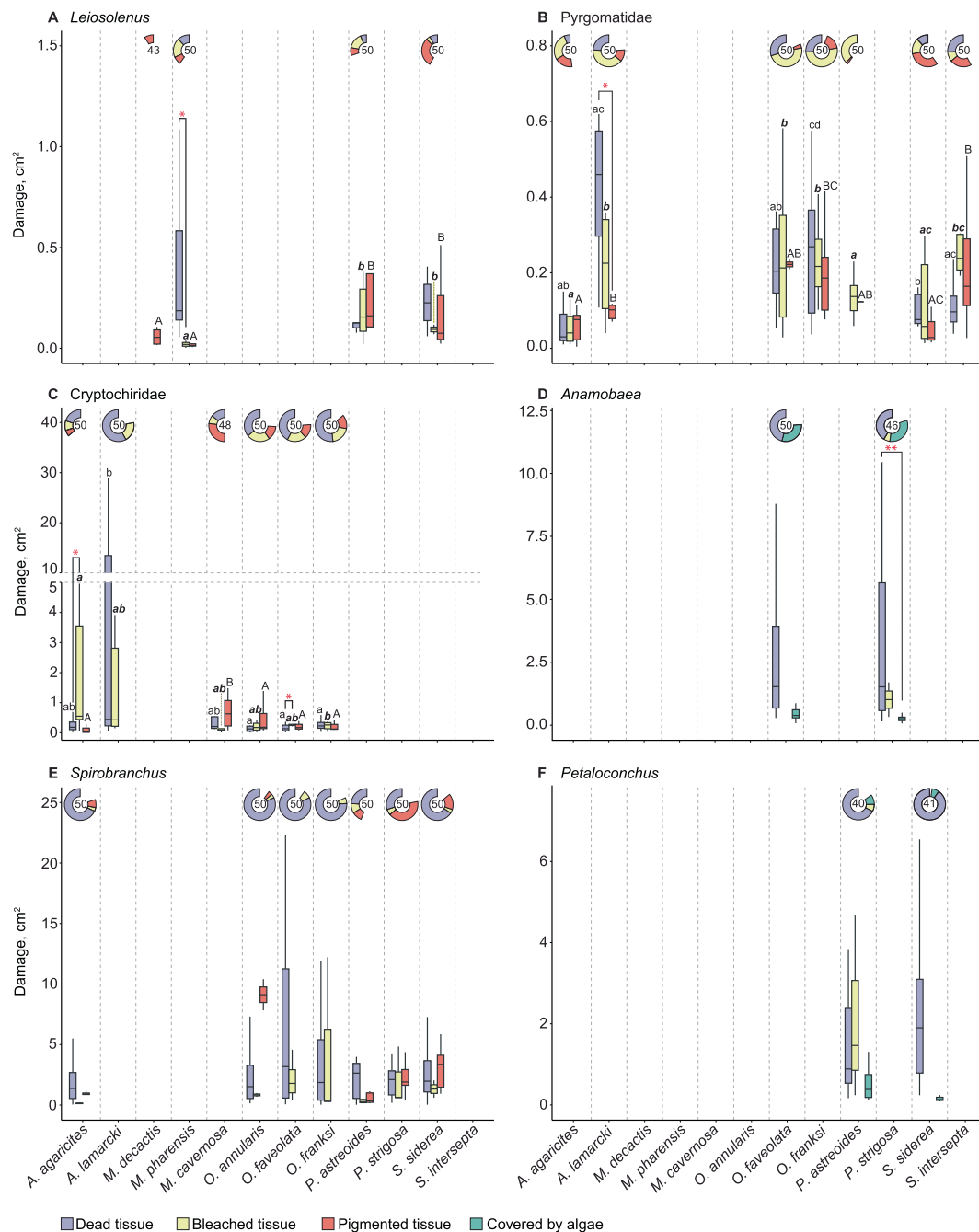Considering dead coral tissue, the most notable finding was the high

Fig. 8. Coral injuries around associated fauna. Relative incidence of damage types of six groups of coral-associated macroinvertebrates, relative part sizes are indicated with percentages.

Fig. 9. Surrounding damage per host coral and symbiont group. Significant differences between damage types within host species are marked with red asterisks (*p < 0.05, **p < 0.01, ***p < 0.001), significant differences per damage type between host species within one symbiont group are indicated by the compact letter display system (CLD), those sharing the same letter are not significantly different. To indicate differences between damage types, variations of typeface—regular (Dead tissue), bold and italic (Bleached tissue), and uppercase (Pigmented tissue)—were used. Damage types for which no differences between host species were found were not assigned any letter to improve readability. The relative incidence of damage types per host species is shown in the doughnut diagram above the corresponding host species, blank parts indicate no presence of surrounding damage. The n-value for the host-symbiont combination is presented inside each doughnut diagram. Corresponding p-values are provided in Tables S10–S19. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mean damaged area size in *O. franksi*, which was significantly larger than in *S. siderea* and *A. agaricites*. Conversely, *S. siderea* showed significantly smaller dead tissue areas than *S. intersepta*, *O. franksi*, and *A. lamarcki*. While the median value of dead tissue for *A. lamarcki* was relatively high, it only differed significantly from *S. siderea*.

Coral species clustered into two groups based on the area of bleached tissue: (a) *A. lamarcki*, *O. faveolata*, *O. franksi*, and *S. intersepta* (large, bleached area) and (b) *A. agaricites*, *P. astreoides*, and *S. siderea* (small, bleached area). An exception was *S. siderea*, which did not differ

significantly from *S. intersepta*.

The clustering pattern for pigmented areas mirrored that of bleached tissue. *A. lamarcki*, *O. faveolata*, *O. franksi*, and *S. intersepta* exhibited significantly larger pigmented areas than *A. agaricites* and *S. siderea*. Exceptions included *O. faveolata*, which was not significantly different from *A. agaricites*, and *O. franksi*, which was not significantly different from *S. siderea*. The most striking results were the significantly larger pigmented areas in *S. intersepta* and *A. lamarcki* compared to *A. agaricites* and *S. siderea*.

Among the host species, only *A. lamarcki* showed significant differences between damage types, with dead tissue areas being significantly larger than pigmented areas.

3.6.3. Gall crabs of the family Cryptochiridae

Damage surrounding Cryptochiridae showed high variability among host species, both in terms of area size and damage type (Fig. 9C). While *Agaricia agaricites* generally showed a low occurrence of surrounding damage, it displayed the largest bleached areas recorded among all host species of Cryptochiridae and was significantly higher than *O. franksi*. The other host species showed no significant differences considering this damage type.

Dead coral tissue was most prevalent in *Agaricia lamarcki*, in some cases extremely large dead areas were recorded and it also showed the largest mean area size of this damage type. The dead patches in *A. lamarcki* were significantly larger than those observed for the three *Orbicella* species (*O. annularis, O. faveolata,* and *O. franksi*), which formed a cluster with smaller dead areas. Pigmented areas were absent in *A. lamarcki*. In contrast, *Montastraea cavernosa* exhibited significantly larger pigmented areas compared to the other host species and had the highest number of records (13 out of 48) for this damage type.

Significant differences between damage types were observed in two host species i.e., in both *A. agaricites* and *O. faveolata*, bleached areas were significantly larger than dead areas.

3.6.4. Feather duster worms of the genus Anamobaea

Surrounding damage was observed in 75–80 % of all *Anamobaea* records across the two included host species (*Pseudodiploria strigosa* and *Orbicella faveolata*) (Fig. 9D). No significant differences between host species were found. Pigmented areas surrounding the worms were absent, and bleached tissue was rare, as it was observed in only three cases on *P. strigosa* and none on *O. faveolata*.

Dead coral tissue accounted for most of the surrounding damage, both in terms of incidence and area size. On *P. strigosa*, the mean area size of dead coral tissue was significantly larger than the area size covered by algae.

The damage type 'covered by algae' was unique to records of *Anamobaea* and *Petaloconchus*. It was observed in 25–30 % of the epibionts on both host species, though the area size remained relatively small.

3.6.5. Christmas tree worms of the genus Spirobranchus

Surrounding damage in all host species was high, significantly larger than the observed surrounding damage in the host species of *Leiosolenus*, Pyrgomatidae and Cryptochiridae (Fig. 4C). Significant differences were neither observed among host species for the same damage type, nor within the same host species for different damage types (Fig. 9E). The presence of surrounding damage was relatively high in all host species (> 75 %) except *Porites astreoides*, which was relatively infrequently recorded with surrounding damage (<50 %). Among damage types, pigmentation showed the highest variability, being absent in two out of seven host species i.e., *Orbicella faveolata* and *O. franksi*. The incidence of surrounding damage was high in *Pseudodiploria strigosa* (> 40 %), intermediate in *Siderastrea siderea* (16 %) and low (< 10 %) in the other host species.

3.6.6. Worm snails of the genus Petaloconchus

The damaged area around worm snails was relatively large in comparison to three other symbiont species, *Leiosolenus*, Pyrgomatidae and Cryptochiridae (Fig. 4C). Only two host species could be included for this symbiont i.e., *Porites astreoides* and *Siderastrea siderea*, showing both a relatively high incidence of surrounding damage, which was significantly lower in *P. astreoides* than in *S. siderea* (Fig. 7F). The same pattern for these host species was also observed for *Spirobranchus* (Fig. 7D). The type of damage surrounding *Petaloconchus* consisted primarily of dead tissue with a relatively large area size (Fig. 9F). In *P. astreoides* dead and bleached tissue and areas covered by algae were observed, showing no

significant differences in area size. *Siderastrea siderea* predominantly showed larger dead-coral areas, whereas areas covered by algae (< 8 %) and absent surrounding damage (< 3 %) were rarely recorded.

4. Discussion

4.1. Host coral diversity

A total of 29 coral species were recorded as hosts for six symbiont groups. Considering *Spirobranchus,* 21 host coral species were found in this study, which is similar to those earlier described from Curaçao (Hoeksema et al., 2019c). Exceptions to this were *Millepora* spp. which was not included in this study and coral species which are only recorded rarely as a host for *Spirobranchus* e.g., *Agaricia lamarcki, A. humilis, Dichocoenia stokesii, Eusmilia fastigiata, Favia fragum, Madracis senaria, Meandrina meandrites* and *Porites furcata* (Hoeksema et al., 2019c). Most of these coral species were infrequently encountered in the transects, except for *Agaricia lamarcki*, which was abundant and much recorded as hosts for both Cryptochiridae and Pyrgomatidae which can be explained by a certain degree of host specificity of *Spirobranchus* (Idris et al., 2022; van der Schoot and Hoeksema, 2024).

A few coral species in the investigated depth range were not observed as hosts, either because they were not encountered in the belt transects or because they did not show associated fauna in the present study (*Cladopsammia manuelensis. Dendrogyra cilindrica, Helioseris cucullata, Isophyllia* spp*., Mycetophyllia* spp*., Scolymia cubensis, S. lacera,* and *Tubastraea coccinea*). One of them, *H. cucullata* is suffering a decline in abundance at Curaçao (Vermeij et al., 2011) and known as a possible host for barnacles, serpulid worms, feather duster worms and gall crabs (Hoeksema et al., 2017, 2022c), whereas *C. manuelensis, D. cylindrica,* and *T. coccinea* have been reported as hosts for serpulid worms (Hoeksema and ten Hove, 2017a; van der Schoot and Hoeksema, 2024), and *T. coccinea* also for worm snails (Hoeksema et al., 2025), but not for the other associated fauna of the present study. The other species may be too rare for finding associated fauna (Kobluk and Lysenko, 1987; Moulding and Ladd, 2022), and of these *Mycetophyllia* spp. and *Scolymia* spp. may be the least suitable as hosts because of their thick, fleshy polyps, similar to *Mussa angulosa*. Moreover, several coral species, not observed as hosts in this study, are known for high interspecific aggression, which they exert by deploying extruded mesenterial filaments to dissolve adjacent tissues through extracoelenteric digestion (Lang, 1971, 1973; Logan, 1984). This defensive response was also observed during the settlement of barnacle larvae but was tolerated and even thought to facilitate the settlement process (Liu et al., 2016; Yap et al., 2023). The specific cause for the absence of the above-mentioned coral species as hosts remains a subject of future study.

4.2. Damage categories in the host corals

Strong variation was observed between the included symbiont groups in this study, both in terms of primary and surrounding damage differences were obvious. These findings are consistent with qualitative studies on multiple groups of coral-associated invertebrates, which reported both high symbiont diversity and varying effects on their hosts, ranging from positive to negative, thereby complicating conclusions about the overall nature of the symbiosis (Stella et al., 2011; Barton et al., 2020). Individuals of *Petaloconchus*, *Spirobranchus* and *Anamobaea* occupied much space on the coral tissue and showed the largest surrounding wounds. Interestingly the group occupying the least space (Pyrgomatidae), showed large affected surrounding areas relative to its primary damage, while individuals of *Leiosolenus*, although occupying larger areas, were surrounded by significantly less damaged area, which is in apparent contrast to its known adverse effects (Owada, 2007; Schönberg et al., 2017; Tortolero-Langarica et al., 2022). Considering the median values, the same pattern is possibly present between *Petaloconchus* and *Spirobranchus*, the latter showing a larger affected

surrounding area relative to the occupied area (primary damage).

4.3. Relationship between primary damage and surrounding damage

An increase in primary damage corresponds with an increase in surrounding damage for most symbiont groups. All symbiont groups, except *Anamobaea*, demonstrated a significant positive association between these variables (Fig. 5). Interestingly, the two groups with the highest median values for both primary and surrounding damage, the worm snails (*Petaloconchus*) and the Christmas tree worms (*Spirobranchus*), exhibited the steepest trendlines. This observation suggests that symbionts causing greater primary damage may contribute disproportionately more to the surrounding damage. This is supported by the effect coefficients of each symbiont group, which were significantly higher for *Spirobranchus*—showing substantial primary damage—than for *Leiosolenus* and Pyrgomatidae, where little primary damage was observed. These findings are in consonance with the observed variety in epibiont related lesions between Pacific host taxa (Dirgantara et al., 2023) and the variety in host damage between Atlantic corallivorous snails and worm snails (Hoeksema et al., 2022a; Verboom and Hoeksema, 2023).

Despite the significant relationships, the R-values are relatively low, with Pyrgomatidae showing the highest value (0.41). This indicates that, while primary damage is a contributing factor, surrounding damage is likely influenced by other variables as well, such as eutrophication (Le Grand and Fabricius, 2011; Rice et al., 2020; van der Schoot and Hoeksema, 2022) and sedimentation (Scaps and Denis, 2008; Harty, 2011). This is in line with the observed variability between primary and surrounding damage in the present study (Sections 3.4–3.6).

4.4. Incidence and type of surrounding damage

To adequately assess the impact of a group of coral-associated macroinvertebrates on its host coral, it is important to consider the area size, the incidence rate and the type of damage altogether. The damage types can be ranked in a hierarchical order based on severity, from most to least severe, as follows: (a) dead tissue, (b) bleached tissue, (c) tissue covered by algae, and (d) pigmented tissue. When considering these aspects, *Spirobranchus* and *Petaloconchus* appear to be the associated species that are most hazardous for their hosts. Regarding incidence, *Spirobranchus* and *Petalonchus* exhibit the strongest adverse effect on their host, the damage incidence for these species was highest (78 % and 91 %, respectively), and the highest percentage of dead tissue in the area surrounding these symbiont species was observed (61 % and 78 % respectively). In contrast, the boring mussels (*Leiosolenus*), which are well-known for the adverse effects on their host corals (Owada, 2007; Schönberg et al., 2017; Tortolero-Langarica et al., 2022) showed the least damage on the host's surface. This apparent dispute might be related to the contribution of ammonium from the bivalve to its host which potentially benefits the host's tissue, as was observed for *Lithophaga simplex* in the host species *Astreopora myriophthalma* (Mokady et al., 1998). Moreover, most damage caused by *Leiosolenus* is not on the coral's surface but inside its skeleton, which is more severe than in the other symbiont groups. The high damage observed around *Spirobranchus* and *Petaloconchus* might be related to an amplifying effect caused by algae growing on the tube or, in the case of *Spirobranchus*, on its tube and operculum (Hoeksema et al., 2019c). As nutrients stimulate algal growth in general and specifically of turf algae on the operculum of *Spirobranchus* (Isdianto et al., 2024), this might contribute to the adverse effect on their hosts (Hoeksema et al., 2018b, 2019b, 2019c).

Furthermore, the damage types "covered by algae" and "pigmented" were observed complementary i.e., the first only occurs adjacent to *Anamobaea* and *Petaloconchus* while the latter is observed only in the host corals of the other four symbiont groups. This is possibly explained by the inability to evaluate the tissue below the algal coverage, which was possibly pigmented but was not recorded as such.

4.5. Variation in primary damage among the host groups

Two clusters of primary damage were observed for Pyrgomatidae, which for this group is equal to their orifice size. Pyrgomatidae species are known for their host-specificity (Tsang et al., 2014; van der Schoot and Hoeksema, 2024) and the orifice morphology of coral barnacles is known to be species-specific (Anderson, 1992). This might easily lead to the assumption that equal primary damage means the predominance of certain barnacle-host combinations. For example, the small-sized primary damage observed around barnacles in *A. agaricites* and *P. astreoides*, suggests that the same barnacle species for these hosts are recorded in this study. However, *P. astreoides* is only inhabited by *Ceratoconcha* sp. and *A. agaricites* only by *Megatrema* sp. (van der Schoot and Hoeksema, 2024). The similar limited damage shown by both coral-barnacle combinations appears to be coincidental, and not taxonomically related.

Although *Agaricia agaricites* and *S. intersepta* are both inhabited by *Megatrema* barnacles, presumably *M. madreporarum* (Ross and Pitombo, 2002), they significantly differ in primary (and surrounding) damage. Therefore, the orifice size may not only depend on the barnacle but also on its host species. Since barnacles keep their orifice free from coral overgrowth (Anderson, 1992), the resulting orifice size could be related to the overgrowth capability of the host coral.

A similar observation was made for Cryptochiridae, *Agararicia lamarcki* and *Montastraea cavernosa* form a high-level cluster of primary damage but are presumably not inhabited by the same gall crab species (van der Schoot and Hoeksema, 2024). *Montastraea cavernosa* is likely to be inhabited by the same gall crab species as *Orbicella* spp., i.e., *Troglocarcinus corallicola*, while *A. lamarcki* is likely inhabited by *Opecarcinus hypostegus*. Also, both *Agaricia* species are likely to be inhabited by the same gall crab species, *O. hypostegus*, while primary damage of *A. lamarcki* was significantly higher than that of *A. agaricites*. Therefore, it seems likely that the observed difference in primary damage for both Cryptochiridae and Pyrgomatidae, is caused by a different responsiveness of the host species for the associated species.

For *Spirobranchus* and *Petaloconchus*, the observed primary damage was constant among host species. *Spirobranchus* sp. is known to be a relatively generalist coral symbiont (van der Schoot and Hoeksema, 2024), and the most dominant species in all Caribbean host species is *Spirobranchus giganteus* (Hoeksema et al., 2019c). The *Petaloconchus* records in this study are also expected to consist of only one species (Hoeksema et al., 2022a, 2025). Based on these findings both species appear to cause a certain, substantial degree of primary damage which is independent of the host coral species.

Despite the low primary damage of *Leiosolenus* sp., two clusters were distinguished for the corresponding host species, i.e., (a) *Madracis decactis* and *Madracis pharensis* and (b) *P. astreoides* and *S. siderea*. *Madracis decactis* is likely to be predominantly inhabited by *L. dixonae* and *S. siderea* by *L. bisulcatus* (van der Schoot and Hoeksema, 2024). If the primary damage is mainly caused by characteristics of the *Leiosolenus* sp., it is likely that all host species in a cluster are inhabited by the same species of *Leiosolenus*. As no records to species level are known for *P. astreoides* and *M. pharensis*, no conclusions can be drawn on this matter.

The records for *Anamobaea* potentially consist of two species. Both host species show the same area size of primary damage (Fig. 9A). No information about host specificity and distribution in the Caribbean for *Anamobaea* is known at species level, although a first inventory reported on 25 scleractinian host species for this genus (Hoeksema et al., 2022c).

Based on the findings in this study, in combination with the known host ranges of the associated groups, the observed differences in area size of primary damage are likely related to specific characteristics of the symbiont species, the host coral species or both. Further research is needed to examine the relationship between primary damage and the sensitivity of the host coral, as this may indicate its susceptibility to coral-associated damage. It is possible that the thick, fleshy tissue, and

relative high aggression shown by *Isophyllia* spp. *Mussa angulosa*, *Mycetophyllia* spp. and *Scolymia* spp. (all family Faviidae, subfamily Mussinae) offers them protection against harmful symbionts.

4.6. Surrounding damage and damage type at host species level

Surrounding damage caused by pyrgomatid barnacles is generally little but varies between host species. The area size of surrounding damage follows the pattern of primary damage, which is in line with the observed positive association between primary and surrounding damage (Fig. 5). Both the incidence and the area size of surrounding damage is lower in *Agaricia agaricites* and *Porites astreoides*, which either indicates a difference in tolerance of the host species for the same barnacle species, or a difference in impact on the host coral between different barnacle species. Based on the findings in this study, the first explanation appears plausible. For example, *A. agaricites* an *S. intersepta* are both expected to be inhabited by *Megatrema madreporarum* (Ross and Pitombo, 2002), while the surrounding damage is significantly higher in *S. intersepta*.

Agaricia lamarcki, *Orbicella faveolata* and *O. franksi* exhibit a high incidence of surrounding damage, which mainly consists of bleached and dead areas. In *A. lamarcki* the dead areas are significantly larger than the pigmented areas. *Agaricia lamarcki* is known to be associated with two barnacle species, i.e., *Ceratoconcha* sp. and *Megatrema* sp., but barnacle species associated with *O. faveolata* and *O. franksi* are unidentified (van der Schoot and Hoeksema, 2024). Therefore, it cannot be determined whether this damage is caused by specific barnacle species.

Feather duster worms show large areas of surrounding damage for both examined host species. The damage type "dead tissue" is predominantly present and in *Pseudodiploria strigosa* significantly larger than areas of the damage type "covered by algae". These findings indicate a large and indiscriminate adverse effect of *Anamobaea* on its host corals.

The surrounding damage for Cryptochiridae is low for most host species, with an exception for *A. lamarcki,* which is significantly higher than the other host species with the exception of *O. franksi*. Given that *A. agaricites* and *A. lamarcki* are most probably inhabited by the same gall crab species, *Opecarcinus hypostegus* (van der Schoot and Hoeksema, 2024), it may be concluded that *A. lamarcki* is more susceptible for cryptochirid-related damage than *A. agaricites*, and that this susceptibility is reflected by the primary damage. The large difference in surrounding damage between the *Agaricia* host species is mainly explained by the difference in incidence of surrounding damage, which is higher in *A. lamarcki*. Area sizes of the different damage types are not significantly different between these species. Furthermore, pigmented areas are present in almost all host species of Cryptochiridae. Considering that surrounding damage is particularly high in *A. lamarcki* and pigmentation is absent in this host, it is plausible that pigmentation reflects resistance of the host species against expansion activities of the cryptochirid associate (Ramesh et al., 2023).

The surrounding damage of *Leiosolenus* is the least among all groups, which is principally explained by a low incidence of surrounding damage in general. In case it was present, the areas were small. This may give a distorted picture, as studies describing damage caused by boring bivalves are widespread (Scott and Risk, 1988; Owada, 2007; Schönberg et al., 2017; Hoeksema et al., 2022b). The findings in this study demonstrate that the structural damage, which is present beneath the surface, is very well hidden, giving a false healthy appearance of the host coral from the outside.

Pigmentated areas were observed in all host species of *Leiosolenus* but were significantly larger in *P. astreoides* and *S. siderea,* which may depend on the species identity of *Leiosolenus*, which requires further investigation.

Primary coral damage caused by both *Spirobranchus* and *Petaloconchus* was relatively similar for all host species, but the surrounding damage in *P. astreoides* was significantly smaller than in the other host species. For *Spirobranchus* this was mainly caused by a relative low incidence of surrounding damage. In case surrounding damage was present, the area size and damage type were not significantly different from the other host species. For *Petaloconchus* sp. the low surrounding damage in *P. astreoides* was principally caused by smaller lesions, and to a lesser extent by a slightly lower incidence of surrounding damage. Also, the damage type "dead tissue" was uncommon in *P. astreoides*. These findings show that *P. astreoides* is less prone to surrounding damage from both Christmas tree worms and worm snails than the other host species of these symbionts. This result is in line with the resilient character of *P. astreoides*, which may explain its expanding dominant position on Caribbean coral reefs during the past decades of coral reef decline (Green et al., 2008). It was also observed to be less affected by interactions with algae than, for example, the coral *Montastraea cavernosa* (Morrow et al., 2013). Considering *P. astreoides*, colonies showed much variation in damage surrounding *Spirobranchus*, it is possible that the resistance to *Spirobranchus* symbionts is genetically determined. The resistance could be related to a relatively high antioxidant capacity and simultaneously a high level of superoxide, which is a reactive oxygen species, at the coral surface (Claquin et al., 2021; Zhang et al., 2016). Superoxide is associated with increased cell viability and proliferation in algae and cyanobacteria (Hansel et al., 2016) and therefore might have a beneficial influence on the regeneration capacity of the coral tissue as well, which is possibly reflected by pigmented areas surrounding Christmas tree worms.

5. Conclusions – Bioindicator potential of coral-associated fauna

The symbiont groups assessed in this study show large variation in visible damage on their host corals, however, five out of six symbiont groups showed a positive relationship between primary and surrounding damage, all with an effect coefficient > 1, and significantly larger for *Spirobranchus* than for *Leiosolenus* and Pyrgomatidae. These findings open opportunities for the use of coral symbionts as bioindicators of coral health. Until now, most studies orienting on the use of coral-associated invertebrates as bioindicators focused on density of coral associates as a measure of reef health (Risk et al., 1994; Scaps and Denis, 2008) or water quality in terms of sedimentation (Fonseca et al., 2006; Harty, 2011) and eutrophication (Le Grand and Fabricius, 2011; van der Schoot and Hoeksema, 2022). The present study shows that the presence of coral symbionts likely may cause coral injuries and therefore indicates a decreased health of the host coral, which is in consonance with similar conclusions from the Indo-Pacific (Tortolero-Langarica et al., 2022; Afkar et al., 2024).

The present study shows that certain groups of coral symbionts pose a larger threat to their hosts than others, and that some hosts appear substantially more resistant to symbiont stress than others. Therefore, information on symbiont fauna in relation to specific host coral species can be used to more precisely indicate the stress a host coral may face, which is usually not taken into account in studies concerning reef health (e.g., Lirman et al., 2014; Castro-Sanguino et al., 2021). Future research is encouraged to focus on specific combinations of host corals and their associates, and to determine whether the symbiont is predominantly aggressive or the host particularly susceptible, and to place this in the context of environmental conditions. As coral reef ecosystems are undergoing an existential crisis, it is crucially important to understand the role of harmful coral associates, allowing to use this knowledge for effective coral reef management.

CRediT authorship contribution statement

Roeland J. van der Schoot: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Conceptualization. **Bert W. Hoeksema:** Writing – review & editing, Writing – original draft, Supervision.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114015.

Data availability

Data will be made available on request.

References

Afkar, Barus, T.A., John, A.H., Sarong, M.A., 2024. Christmas tree worm *Spirobranchus* spp. (Annelida: Serpulidae) as indicators of coral health at Weh Island, Aceh Province, Indonesia. Biodiversitas J. Biol. Divers. 25, 1743–1753. https://doi.org/10.13057/biodiv/d250445.

Anderson, D.T., 1992. Structure, function and phylogeny of coral-inhabiting barnacles (Cirripedia, Balanoidea). Zool. J. Linn. 106, 277–339. https://doi.org/10.1111/j.1096-3642.1992.tb01249.x.

Bähr, S., van der Meij, S.E.T, Santoro, E.P., Benzoni, F., 2025. Imaging PAM fluorometry reveals stable photosynthetic efficiency in multibiont symbioses on coral reefs. Front. Mar. Sci. 12, 1568287. https://doi.org/10.3389/fmars.2025.1568287.

Barton, J.A., Bourne, D.G., Humphrey, C., Hutson, K.S., 2020. Parasites and coral-associated invertebrates that impact coral health. Rev. Aquacult. 12, 22842303. https://doi.org/10.1111/raq.12434.

Becking, L.E., Martinez, S.J., Aji, L.P., Ahmad, A., Alzate, A., Folkers, M., Lestari, D.F., Subhan, B., Hoeksema, B.W., 2024. Stony corals and their associated fauna residing in marine lakes under extreme environmental conditions. Diversity 16, 295. https://doi.org/10.3390/d16050295.

Ben-Tzvi, O., Einbinder, S., Brokovich, E., 2006. A beneficial association between a polychaete worm and a scleractinian coral? Coral Reefs 25, 98. https://doi.org/10.1007/s00338-005-0084-3.

Borger, J.L., 2005. Dark spot syndrome: a scleractinian coral disease or a general stress response? Coral Reefs 24, 139–144. https://doi.org/10.1007/s00338-004-0434-6.

Box, G.E., Cox, D.R., 1964. An analysis of transformations. J. R. Stat. Soc. Ser. B Stat. Methodol. 26, 211–243. https://doi.org/10.1111/j.2517-6161.1964.tb00553.x.

Bravo, H., Dromard, C.R., van der Meer, M.T.J., Schleimer, A., van der Meij, S.E.T., 2024. Dining on corals: stable isotope evidence for close trophic connection between gall crabs (Cryptochiridae) and their stony coral hosts. Symbiosis 92, 51–62. https://doi.org/10.1007/s13199-023-00968-y.

Breves, A., Széchy, M.T.M.D., Lavrado, H.P., Junqueira, A.O., 2017. Abundance of the reef-building *Petaloconchus varians* (Gastropoda: Vermetidae) on intertidal rocky shores at Ilha Grande Bay, southeastern Brazil. Anais Da Academia Brasileira De Ciências 89, 907–918. https://doi.org/10.1590/0001-3765201720160433.

Carricart-Ganivet, J.P., Carrera-Parra, L.F., Quan-Young, L.I., García-Madrigal, M.S., 2004. Ecological note on *Troglocarcinus corallicola* (Brachyura: Cryptochiridae) living in symbiosis with *Manicina areolata* (Cnidaria: Scleractinia) in the Mexican Caribbean. Coral Reefs 23, 215–217. https://doi.org/10.1007/s00338-004-0381-2.

Castro, P., 1976. Brachyuran crabs symbiotic with scleractinian corals: a review of their biology. Micronesica 12, 99–110.

Castro-Sanguino, C., Ortiz, J.C., Thompson, A., Wolff, N.H., Ferrari, R., Robson, B., Magno-Canto, M.M., Puotinen, M., Fabricius, K.E., Uthicke, S., 2021. Reef state and performance as indicators of cumulative impacts on coral reefs. Ecol. Ind. 123, 107335. https://doi.org/10.1016/j.ecolind.2020.107335.

Chan, B.K.K., Wong, K.J., Cheng, Y.R., Thiel, M., Poore, G., 2020. Biogeography and host usage of coral-associated crustaceans: barnacles, copepods, and gall crabs as model organisms. In: Thiel, M., Poore, G. (Eds.), The Natural History of the Crustacea: Evolution and Biogeography of the Crustacea, 8. Oxford University Press, Oxford, UK, pp. 183–215. https://doi.org/10.1093/oso/9780190637842.003.0008.

Claquin, P., Rene-Trouillefou, M., Lopez, P.J., Japaud, A., Bouchon-Navaro, Y., Cordonnier, S., Bouchon, C., 2021. Singular physiological behavior of the scleractinian coral *Porites astreoides* in the dark phase. Coral Reefs 40, 139–150. https://doi.org/10.1007/s00338-020-02023-4.

Cleary, D.F.R., Suharsono, Hoeksema, B.W., 2006. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. Biodivers. Conserv. 15, 3653–3674. https://doi.org/10.1007/s10531-004-4692-y.

Crawley, M.J., 2012. The R Book. John Wiley & Sons Ltd, USA. https://doi.org/10.1002/9781118448908.

DeVantier, L.M., Reichelt, R.E., Bradbury, R.H., 1986. Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: predator pressure as a mechanism of coevolution. Mar. Ecol. Prog. Ser. 32, 307–310. https://doi.org/10.3354/meps032307.

Dirgantara, D., Afzal, M.S., Nakamura, T., 2023. Distinct patterns of coral lesion composition from national/quasi-national marine parks of Kerama and Yoron Islands, Ryukyu Archipelago. Deep Sea Res. II 210, 105309. https://doi.org/10.1016/j.dsr2.2023.105309.

Fonseca, E.A.C., Dean, H.K., Cortés, J., 2006. Non-colonial coral macro-borers as indicators of coral reef status in the south Pacific of Costa Rica. Rev. Biol. Trop. 54, 101–115. https://doi.org/10.15517/rbt.v54i1.13977.

Fordyce, A.J., Ainsworth, T.D., Leggat, W., 2020. Microalgae, a boring bivalve and a coral—a newly described association between two coral reef bioeroders within their coral host. Integr. Org. Biol. 2, obaa035. https://doi.org/10.1093/iob/obaa035.

García-Hernández, J.E., de Gier, W., van Moorsel, G.W.N.M., Hoeksema, B.W., 2020. The scleractinian *Agaricia undata* as a new host for the coral-gall crab *Opecarcinus hypostegus* at Bonaire, southern Caribbean. Symbiosis 81, 303–311. https://doi.org/10.1007/s13199-020-00706-8.

Gittenberger, A., Gittenberger, E., 2011. Cryptic, adaptive radiation of endoparasitic snails: sibling species of *Leptoconchus* (Gastropoda: Coralliophilidae) in corals. Org. Divers. Evol. 11, 21–41. https://doi.org/10.1007/s13127-011-0039-1.

Goulet, T.L., Goulet, D., 2021. Climate change leads to a reduction in symbiotic derived cnidarian biodiversity on coral reefs. Front. Ecol. Evol. 9, 636279. https://doi.org/10.3389/fevo.2021.636279.

Green, D.H., Edmunds, P.J., Carpenter, R.C., 2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. Mar. Ecol. Prog. Ser. 359, 1–10. https://doi.org/10.3354/meps07454.

Hadfield, M.G., Kay, E.A., Gillette, M.U., Lloyd, M.C., 1972. The Vermetidae (Mollusca: Gastropoda) of the hawaiian Islands. Mar. Biol. 12, 81–98. https://doi.org/10.1007/BF00347431.

Hansel, C.M., Buchwald, C., Diaz, J.M., Ossolinski, J.E., Dyhrman, S.T., Van Mooy, B.A. S., Polyviou, D., 2016. Dynamics of extracellular superoxide production by *Trichodesmium* colonies from the Sargasso Sea. Limnol. Oceanogr. 61, 1188–1200. https://doi.org/10.1002/lno.10266.

Harty, M., 2011. Christmas tree worms (*Spirobranchus giganteus*) as a potential bioindicator species of sedimentation stress in coral reef environments of Bonaire, Dutch Caribbean. Physis J. Mar. Sci. 9, 20–30.

Hoeksema, B.W., ten Hove, H.A., 2017a. The invasive sun coral *Tubastraea coccinea* hosting a native Christmas tree worm at Curaçao, Dutch Caribbean. Mar. Biodivers. 47, 59–65. https://doi.org/10.1007/s12526-016-0472-7.

Hoeksema, B.W., ten Hove, H.A., 2017b. Attack on a Christmas tree worm by a Caribbean sharpnose pufferfish at St. Eustatius, Dutch Caribbean. Bull. Mar. Sci. 93, 1023–1024. https://doi.org/10.5343/bms.2017.1059.

Hoeksema, B.W., van Beusekom, M., ten Hove, H.A., Ivanenko, V.N., van der Meij, S.E.T., van Moorsel, G.W.N.M., 2017. *Helioseris cucullata* as a host coral at St. Eustatius, Dutch Caribbean. Mar. Biodivers. 47, 71–78. https://doi.org/10.1007/s12526-016-0599-6.

Hoeksema, B.W., Butôt, R., García-Hernández, J.E., 2018a. A new host and range record for the gall crab *Fungicola fagei* as symbiont of the mushroom coral *Lobactis scutaria* at Hawaii. Pac. Sci. 72, 251–261. https://doi.org/10.2984/72.2.7.

Hoeksema, B.W., ten Hove, H.A., Berumen, M.I., 2018b. A three-way association causing coral injuries in the Red Sea. Bull. Mar. Sci. 94, 1525–1526. https://doi.org/10.5343/bms.2018.0006.

Hoeksema, B.W., Giyanto, Suharsono, 2019. The role of maximum shelf depth versus distance from shore in explaining a diversity gradient of mushroom corals (Fungiidae) off Jakarta. Diversity 11, 46. https://doi.org/10.3390/d11030046.

Hoeksema, B.W., van der Schoot, R.J., Wels, D., Scott, C.M., ten Hove, H.A., 2019a. Filamentous turf algae on tube worms intensify damage in massive *Porites* corals. Ecology 100, e02668. https://doi.org/10.1002/ecy.2668.

Hoeksema, B.W., Wels, D., van der Schoot, R.J., ten Hove, H.A., 2019b. Coral injuries caused by *Spirobranchus* opercula with and without epibiotic turf algae at Curaçao. Mar. Biol. 166, 60. https://doi.org/10.1007/s00227-019-3504-6.

Hoeksema, B.W., García-Hernández, J.E., van Moorsel, G.W.N.M., Olthof, G., ten Hove, H.A., 2020. Extension of the recorded host range of Caribbean Christmas tree worms (*Spirobranchus* spp.) with two scleractinians, a zoantharian, and an ascidian. Diversity 12, 115. https://doi.org/10.3390/d12030115.

Hoeksema, B.W., Harper, C.E., Langdon-Down, S.J., van der Schoot, R.J., Smith-Moorhouse, A., Spaargaren, R., Timmerman, R.F., 2022a. Host range of the coral-associated worm snail *Petaloconchus* sp. (Gastropoda: Vermetidae), a newly discovered cryptogenic pest species in the southern Caribbean. Diversity 14, 196. https://doi.org/10.3390/d14030196.

Hoeksema, B.W., Smith-Moorhouse, A., Harper, C.E., van der Schoot, R.J., Timmerman, R.F., Spaargaren, R., Langdon-Down, S.J., 2022b. Black mantle tissue of endolithic mussels (*Leiosolenus* spp.) is cloaking borehole orifices in Caribbean reef corals. Diversity 14, 401. https://doi.org/10.3390/d14050401.

Hoeksema, B.W., Timmerman, R.F., Spaargaren, R., Smith-Moorhouse, A., van der Schoot, R.J., Langdon-Down, S.J., Harper, C.E., 2022c. Morphological modifications and injuries of corals caused by symbiotic feather duster worms (Sabellidae) in the Caribbean. Diversity 14, 332. https://doi.org/10.3390/d14050332.

Hoeksema, B.W., van der Loos, L.M., van Moorsel, G.W.N.M., 2022d. Coral diversity matches marine park zonation but not economic value of coral reef sites at St. Eustatius, eastern Caribbean. J. Environ. Manage. 320, 115829. https://doi.org/10.1016/j.jenvman.2022.115829.

Hoeksema, B.W., Samimi-Namin, K., McFadden, C.S., Rocha, R.M., van Ofwegen, L.P., Hiemstra, A.F., Vermeij, M.J.A., 2023. Non-native coral species dominate the fouling community on a semi-submersible platform in the southern Caribbean. Mar. Pollut. Bull. 194, 115354. https://doi.org/10.1016/j.marpolbul.2023.115354.

Hoeksema, B.W., Taekema, W., Samimi-Namin, K., 2025. Dead non-native corals (*Tubastraea coccinea*) and their associated fauna trawled from the North Sea provide evidence for long-distance transport by hull fouling. Mar. Pollut. Bull. 215, 117839. https://doi.org/10.1016/j.marpolbul.2025.117839.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Hu, J., Zhang, Y., Yiu, S.K.F., Xie, J.Y., Qiu, J.W., 2020. A new species of predatory nudibranch (Gastropoda: Trinchesiidae) of the scleractinian coral *Goniopora*. Zool. Stud. 59, e62.

Humann, P., Deloach, N., 2013. Reef Coral Identification: Florida, Caribbean. Bahamas, third ed. New World Publications, Jacksonville, Florida.

Humann, P., Deloach, N., Wilk, L., 2013. Reef Creature Identification: Florida, Caribbean, Bahamas, third ed. New World Publications, Jacksonville, Florida, USA.

Hutchings, P., 2008. Role of polychaetes in bioerosion of coral substrates. In: Wisshak, M., Tapanila, L. (Eds.), Current Developments in Bioerosion. Springer, Berlin, pp. 249–264. https://doi.org/10.1007/978-3-540-77598-0_13.

Idris, I., Mohd-Salleh, N.A., Ahmad Fadzil, N.D.N., 2022. Host preferences and colouration of Christmas tree worms, *Spirobranchus corniculatus* (Grube, 1862) from Bidong Island, South China Sea. In: Chuan, O.M., Martin, M.B., Nurulnadia, M.Y., Afzan Azmi, W. (Eds.), Bidong Island. Geography of the Physical Environment. Springer, Cham. https://doi.org/10.1007/978-3-030-91924-5_15.

Isdianto, A., Amanda, S.S., Yamindago, A., Dewi, C.S.U., Aliviyanti, D., Luthfi, O.M., Fathah, A.L., Atikawati, D., Putri, B.M., Puspitasari, I.D., 2024. Water quality impact christmas tree worms (*Spirobranchus* spp.) distribution and community structure on hard corals at Sempu Island Nature Reserve, Malang, Indonesia. J. Ecol. Eng. 25, 175–186. https://doi.org/10.12911/22998993/186161.

Jia, Z., Tian, P., Wang, W., Cao, B., Xu, Z., Xiao, J., Niu, W., 2023. First record of corallivorous nudibranch *Pinufius* (Gastropoda: Nudibranchia) in the South China Sea: a suspected new species of *Pinufius*. Diversity 15, 226. https://doi.org/10.3390/d15020226.

Jones, B., Pemberton, S.G., 1988. *Lithophaga* borings and their influence on the diagenesis of corals in the Pleistocene Ironshore Formation of Grand Cayman Island, British West Indies. PALAIOS 3, 3–21. https://doi.org/10.2307/3514541.

Kleemann, K.H., 1980. Boring bivalves and their host corals from the Great Barrier Reef. J. Moll. Stud. 46, 13–54. https://doi.org/10.1093/oxfordjournals.mollus.a065519.

Kleemann, K., 1996. Biocorrosion by bivalves. Mar. Ecol. 17, 145–158. https://doi.org/10.1111/j.1439-0485.1996.tb00496.x.

Klöppel, A., Brümmer, F., Schwabe, D., Morlock, G., 2013. Detection of bioactive compounds in the mucus nets of *Dendropoma maxima*, Sowerby 1825 (Prosobranch Gastropod Vermetidae, Mollusca). J. Mar. Sci. 283506. https://doi.org/10.1155/2013/283506.

Kobluk, D.R., Lysenko, M.A., 1987. Southern Caribbean cryptic scleractinian reef corals from Bonaire, N.A. PALAIOS 2, 205–218. https://doi.org/10.2307/3514671.

Kolbasov, G.A., Tsao, Y.-F., Chan, B.K.K., 2025. Unveiling a hitherto monotypic crustacean coral endoparasite: Diversity and morphology of the genus *Zibrowia* Grygier, 1995 (Thecostraca: Ascothoracida) through integrative taxonomy. Mar. Biodivers. 55, 41. https://doi.org/10.1007/s12526-025-01516-1.

Kramer, J., Amit, T., Gavrieli, N., Gross, M., Wangpraseurt, D., Loya, Y., 2024. Quantifying attributes of boring bivalve populations in corals using micro-computed tomography. Front. Mar. Sci. 11, 1407537. https://doi.org/10.3389/fmars.2024.1407537.

Lang, J., 1971. Interspecific aggression by scleractinian corals. 1. the rediscovery of *Scolymia cubensis* (Milne Edwards & Haime). Bull. Mar. Sci. 21, 952–959.

Lang, J., 1973. Interspecific aggression by scleractinian corals. 2. why the race is not only to the swift. Bull. Mar. Sci. 23, 260–279.

Le Grand, H.M., Fabricius, K.E., 2011. Relationship of internal macrobioeroder densities in living massive *Porites* to turbidity and chlorophyll on the Australian Great Barrier Reef. Coral Reefs 30, 97–107. https://doi.org/10.1007/s00338-010-0670-x.

Lee Rodgers, J., Nicewander, W.A., 1988. Thirteen ways to look at the correlation coefficient. Am. Stat. 42, 59–66. https://doi.org/10.1080/00031305.1988.10475524.

Legendre, P., Legendre, L., 2012. Numerical Ecology, 3rd ed. Elsevier, Amsterdam.

Lirman, D., Formel, N., Schopmeyer, S., Ault, J.S., Smith, S.G., Gilliam, D., Riegl, B., 2014. Percent recent mortality (PRM) of stony corals as an ecological indicator of coral reef condition. Ecol. Ind. 44, 120–127. https://doi.org/10.1016/j.ecolind.2013.10.021.

Liu, J.C.W., Høeg, J.T., Chan, B.K.K., 2016. How do coral barnacles start their life in their hosts? Biol. Lett. 12, 20160124. https://doi.org/10.1098/rsbl.2016.0124.

Logan, A., 1984. Interspecific aggression in hermatypic corals from Bermuda. Coral Reefs 3, 131–138. https://doi.org/10.1007/BF00301957.

Lymperaki, M.M., Hill, C.E.L., Hoeksema, B.W., 2022. The effects of wave exposure and host cover on coral-associated fauna of a centuries-old artificial reef in the Caribbean. Ecol. Eng. 176, 106536. https://doi.org/10.1016/j.ecoleng.2021.106536.

Maggioni, D., Arrigoni, R., Seveso, D., Galli, P., Berumen, M.L., Denis, V., Hoeksema, B.W., Huang, D., Manca, F., Pica, D., Puce, S., Reimer, J.D., Montano, S., 2022. Evolution and biogeography of the *Zanclea*-Scleractinia symbiosis. Coral Reefs 41, 779–795. https://doi.org/10.1007/s00338-020-02010-9.

Mehrotra, R., Arnold, S., Wang, A., Chavanich, S., Hoeksema, B.W., Caballer Gutierrez, M., 2020. A new species of coral-feeding nudibranch (Mollusca: Gastropoda) from the Gulf of Thailand. Mar. Biodivers. 50, 36. https://doi.org/10.1007/s12526-020-01050-2.

Mehrotra, R., Caballer, M., Kaullysing, D., Jualaong, S., Hoeksema, B.W., 2024. Parasites or predators? Gastropod ectoparasites and their scleractinian host corals at Koh Tao, Gulf of Thailand, with the description of a new species. Symbiosis 92, 209–230. https://doi.org/10.1007/s13199-023-00967-z.

Mizrahi, D., Duarte, R.C., Kitahara, M.V., Flores, A.A.V., 2023. Interactions between invaders: facilitation of boring bivalves leads to reduced adhesive strength of sun corals. Coral Reefs 42, 473–481. https://doi.org/10.1007/s00338-023-02358-8.

Mokady, O., Loya, Y., Lazar, B., 1998. Ammonium contribution from boring bivalves to their coral host–a mutualistic symbiosis? Mar. Ecol. Prog. Ser. 169, 295–301 https://doi.org/-10.3354/meps169295.

Montano, S., 2020. The extraordinary importance of coral-associated fauna. Diversity 12, 357. https://doi.org/10.3390/d12090357.

Montano, S., 2022. Diversity of coral-associated fauna: an urgent call for research. Diversity 14, 765. https://doi.org/10.3390/d14090765.

Montano, S., Fattorini, S., Parravicini, V., Berumen, M.L., Galli, P., Maggioni, D., Arrigoni, R., Seveso, D., Strona, G., 2017. Corals hosting symbiotic hydrozoans are less susceptible to predation and disease. Proc. R. Soc. B Biol. Sci. 284, 20172405. https://doi.org/10.1098/rspb.2017.2405.

Morrow, K.M., Liles, M.R., Paul, V.J., Moss, A.G., Chadwick, N.E., 2013. Bacterial shifts associated with coral–macroalgal competition in the Caribbean Sea. Mar. Ecol. Prog. Ser. 488, 103–117. https://doi.org/10.3354/meps10394.

Moulding, A., Ladd, M., 2022. Staghorn coral (*Acropora cervicornis*), elkhorn coral (*Acropora palmata*), lobed star coral (*Orbicella annularis*), mountainous star coral (*Orbicella faveolata*), boulder star coral (*Orbicella franksi*), rough cactus coral (*Mycetophyllia ferox*), and pillar coral (*Dendrogyra cylindrus*) 5-year review. United States. National Marine Fisheries Service, Southeast Region https://doi.org/10.25923/jyer-dv55.

Nogueira, M.M., Menezes, N.M., Johnsson, R., Neves, E., 2014. The adverse effects of cryptochirid crabs (Decapoda: Brachyura) on *Siderastrea stellata* Verril, 1868 (Anthozoa: Scleractinia): causes and consequences of cavity establishment. Cah. Biol. Mar. 55, 155–162.

Nugues, M.M., Bak, R.P.M., 2007. Dark spot syndrome: recent or old? Coral Reefs 26, 359. https://doi.org/10.1007/s00338-007-0201-6.

Owada, M., 2007. Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia: Mytilidae): a third functional clade. Mar. Biol. 150, 853–860. https://doi.org/10.1007/s00227-006-0409-y.

Pezner, A.K., Lim, A.R., Kang, J.J., Armenta, T.C., Blumstein, D.T., 2017. Hiding behavior in Christmas tree worms on different time scales. Behav. Ecol. 28, 154–163 https://doi.org/-10.1093/beheco/arw140.

Pratchett, M.S., 2001. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. Mar. Ecol. Prog. Ser. 214, 111–119. https://doi.org/10.3354/meps214111.

Pratte, Z.A., Longo, G.O., Burns, A.S., Hay, M.E., Stewart, F.J., 2018. Contact with turf algae alters the coral microbiome: contact versus systemic impacts. Coral Reefs 37, 1–13. https://doi.org/10.1007/s00338-017-1615-4.

R Core Team, 2024. _R: a Language and Environment for Statistical computing_. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org.

Ramesh, C., Shunmugaraj, T., Koushik, S., Murthy, M.V.R., 2023. *Porites* sp. deposits pink pigmentation to limit the propagation of vermitid gastropods and rhodoliths at coral surface interfaces. Discov. Environ. 1, 20. https://doi.org/10.1007/s44274-023-00017-x.

Rauch, C., Hoeksema, B.W., Hermanto, B., Fransen, C.H.J.M., 2019. Shrimps of the genus *Periclimenes* (Crustacea, Decapoda, Palaemonidae) associated with mushroom corals (Scleractinia, Fungiidae): linking DNA barcodes to morphology. Contrib. Zool. 88, 201–235. https://doi.org/10.1163/18759866-20191357.

Ray, G.C., Grassle, J.F., 1991. Marine biological diversity. Bioscience 41, 453–457. https://doi.org/10.2307/1311799.

Risk, M.J., Dunn, J.J., Allison, W.R., Horrill, C., 1994. Reef monitoring in Maldives and Zanzibar: low-tech and high-tech science. In: Ginsberg, R.N. (Ed.), Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, 1993. Rosenstiel School of Marine and Atmospheric Science, University of Miami, pp. 66–72.

Risk, M.J., Heikoop, J.M., Edinger, E.N., Erdmann, M.V., 2001. The assessment 'toolbox': community-based reef evaluation methods coupled with geochemical techniques to identify sources of stress. Bull. Mar. Sci. 69, 443–458.

Rice, M.M., Maher, R.L., Correa, A.M., Moeller, H.V., Lemoine, N.P., Shantz, A.A., Burkepile, D.E., Silbiger, N.J., 2020. Macroborer presence on corals increases with nutrient input and promotes parrotfish bioerosion. Coral Reefs 39, 409–418. https://doi.org/10.1007/s00338-020-01904-y.

Ross, A., Newman, W.A., 1969. A coral-eating barnacle. Pac. Sci. 23, 252–256.

Ross, A., Newman, W.A., 1995. A coral-eating barnacle, revisited (Cirripedia, Pyrgomatidae). Bijdr. Dierk. 65, 129–175. https://doi.org/10.1163/26660644-06503001.

Ross, A., Newman, W.A., 2000. A new coral-eating barnacle: the first record from the Great Barrier Reef. Australia. Mem. Queensl. Mus. 45, 585–591.

Ross, A., Pitombo, F.B., 2002. Notes on the coral-inhabiting Megatrematinae and the description of a new tribe, new genus and three new species (Cirripedia: Sessilia: Pyrgomatidae). Sess. Org. 19, 57–68. https://doi.org/10.4282/sosj.19.57.

Ruppert, E.E., Fox, R.S., Barnes, R.D., 2004. Invertebrate Zoology. a Functional Evolutionary Approach, 7th ed. Thomson Brooks/Cole, Belmont, California.

Samimi-Namin, K., Risk, M.J., Hoeksema, B.W., Zohari, Z., Rezai, H., 2010. Coral mortality and serpulid infestations associated with red tide, in the Persian Gulf. Coral Reefs 29, 509. https://doi.org/10.1007/s00338-010-0601-x.

Scaps, P., Denis, V., 2008. Can organisms associated with live scleractinian corals be used as indicators of coral reef status? Atoll Res. Bull. 566, 1–21. https://doi.org/10.5479/si.00775630.566.1.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675. https://doi.org/10.1038/nmeth.2089.

Schönberg, C.H.L., Fang, J.K.H., Carreiro-Silva, M., Tribollet, A., Wisshak, M., 2017. Bioerosion: the other ocean acidification problem. ICES J. Mar. Sci. 74, 895–925 https://doi.org-/10.1093/icesjms/fsw254.

Scott, P.J.B., Risk, M.J., 1988. The effect of *Lithophaga* (Bivalvia: Mytilidae) boreholes on the strength of the coral *Porites lobata*. Coral Reefs 7, 145–151. https://doi.org/10.1007/BF00300974.

Sommer, B., Chang, Y.Y., Beger, M., Pandolfi, J.M., 2024. Does high parasite load contribute to limitation of the poleward range of *Acropora* corals? Coral Reefs 43, 1139–1144. https://doi.org/10.1007/s00338-024-02518-4.

Stella, J.S., Pratchett, M.S., Hutchings, P.A., Jones, G.P., 2011. Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. Oceanogr. Mar. Biol. Annu. Rev. 49, 43–104.

Stewart, H.L., Holbrook, S.J., Schmitt, R.J., Brooks, A.J., 2006. Symbiotic crabs maintain coral health by clearing sediments. Coral Reefs 25, 609–615. https://doi.org/10.1007/s00338-006-0132-7.

Strathmann, R.R., Cameron, R.A., Strathmann, M.F., 1984. *Spirobranchus giganteus* (Pallas) breaks a rule for suspension-feeders. J. Exp. Mar. Biol. Ecol. 79, 245–249. https://doi.org/10.1016/0022-0981(84)90198-9.

Tan, K.S., Tan, S.H.M., 2024. Tussles with mussels: mytiloidean phylogeny revisited (Bivalvia: Pteriomorphia). J. Moll. Stud. 90, eyae039. https://doi.org/10.1093/mollus/eyae039.

Tortolero-Langarica, J.J.A., Salazar-Silva, P., Morales-Ruiz, E., Curiel-Vizcarra, Y., Carricart-Ganivet, J.P., 2022. The effect of polychaetes infestation on calcification rates and morphological changes in reef-building coral *Porites lobata*. Symbiosis 86, 337–344. https://doi.org/10.1007/s13199-022-00840-5.

Tovar-Hernández, M.A., Salazar-Vallejo, S.I., 2006. Sabellids (Polychaeta: Sabellidae) from the Grand Caribbean. Zool. Stud. 45, 24–66.

Tsang, L.M., Chu, K.H., Nozawa, Y., Chan, B.K.K., 2014. Morphological and host specificity evolution in coral symbiont barnacles (Balanomorpha: Pyrgomatidae) inferred from a multi-locus phylogeny. Mol. Phylogenet. Evol. 77, 11–22. https://doi.org/10.1016/j.ympev.2014.03.002.

van der Meij, S.E.T., 2014. Host species, range extensions, and an observation of the mating system of Atlantic shallow-water gall crabs (Decapoda: Cryptochiridae). Bull. Mar. Sci. 90, 1001–1010. https://doi.org/10.5343/bms.2014.1017.

van der Schoot, R.J., Hoeksema, B.W., 2022. Abundance of coral-associated fauna in relation to depth and eutrophication along the leeward side of Curaçao, southern Caribbean. Mar. Environ. Res. 181, 105738. https://doi.org/10.1016/j.marenvres.2022.105738.

van der Schoot, R.J., Hoeksema, B.W., 2024. Host specificity of coral-associated fauna and its relevance for coral reef biodiversity. Int. J. Parasitol. 54, 65–88. https://doi.org/10.1016/j.ijpara.2023.09.002.

Verboom, L., Hoeksema, B.W., 2023. Resource partitioning by corallivorous snails on Bonaire (Southern Caribbean). Diversity 15, 34. https://doi.org/10.3390/d15010034.

Vermeij, M.J.A., Bakker, J., van der Hal, N., Bak, R.P.M., 2011. Juvenile coral abundance has decreased by more than 50% in only three decades on a small Caribbean island. Diversity 3, 296–307. https://doi.org/10.3390/d3030296.

Vinagre, C., Silva, R., Mendonça, V., Flores, A.A., Baeta, A., Marques, J.C., 2018. Food web organization following the invasion of habitat-modifying *Tubastraea* spp. corals appears to favour the invasive borer bivalve *Leiosolenus aristatus*. Ecol. Ind. 85, 1204–1209. https://doi.org/10.1016/j.ecolind.2017.11.056.

Yap, F.C., Chen, H.N., Chan, B.K.K., 2023. Host specificity and adaptive evolution in settlement behaviour of coral-associated barnacle larvae (Cirripedia: Pyrgomatidae). Sci. Rep. 13, 9668. https://doi.org/10.1038/s41598-023-33738-3.

Zhang, T., Diaz, J.M., Brighi, C., Parsons, R.J., McNally, S., Apprill, A., Hansel, C.M., 2016. Dark production of extracellular superoxide by the coral *Porites astreoides* and representative symbionts. Front. Mar. Sci. 3, 232. https://doi.org/10.3389/fmars.2016.00232.