Coral Reefs
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RESEARCH

Pathological drivers of coral diseases across the Arabian Peninsula

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Abstract Increasing trends of coral mortality are a challenge to coral reef management worldwide, and a need exists to identify the causes and pathways involved. Pathology is useful to help decipher potential causes of mortality in animals, because it illuminates agents associated with lesions and gives insights on the nature of how a host responds to said agents. To better understand the nature of threats facing corals in the Arabian Peninsula, we performed gross and microscopic pathology on corals from Saudi Arabia, Qatar, and the United Arab Emirates. Among 321 coral fragments examined from 21 genera, tissue loss was the most common lesion seen in 31% of samples, reflecting its widespread presence on reefs from the Arabian Peninsula. Histologically, 68% of lesions exhibited necrosis, predominantly in the basal body wall and surface body wall. Endolithic filamentous microalgae and sponges, originating from the skeleton, were associated with 57% and 39% of lesions, respectively, and were often linked to necrosis and hyaline membrane formation. Cell-associated microbial aggregates and coccidia were detected mainly in *Acropora, Pocillopora*, and *Porites* but were not associated with adverse host response. Notably, 69–100% of fragments showing lesions were female likely reflecting the temporal reproductive life history of corals in the region. Our findings highlight endolithic organisms as major contributors to coral tissue degradation in the Arabian Peninsula. Future studies might focus on drivers of endolithic microalgal and sponge dynamics in the region and their role in coral reef health.

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Abstraite L'augmentation de la mortalité corallienne représente un défi majeur pour la gestion des récifs coralliens à l'échelle mondiale, et il est essentiel d'identifier les causes et les mécanismes impliqués. L'anatomopathologie est importante pour décrypter les causes potentielles de mortalité chez les animaux, car elle révèle des agents associés aux lésions et renseigne sur la manière dont l'hôte réagit à ces agents. Afin de mieux comprendre la nature des menaces qui pèsent sur les coraux de la péninsule Arabique, nous avons réalisé des analyses macroscopiques et microscopiques sur des coraux provenant d'Arabie saoudite, du Qatar et des Émirats arabes unis. Parmi les 321 fragments de coraux examinés, appartenant à 21 genres, la perte de tissu était la lésion la plus fréquente (31 % des échantillons), témoignant de sa large présence sur les récifs de la péninsule Arabique. Histologiquement, 68 % des lésions présentaient une nécrose, principalement au niveau de la paroi basale et de la paroi superficielle du corps. Les microalgues filamenteuses endolithiques et les éponges, issues du squelette, étaient associées respectivement à 57 % et 39 % des lésions, et étaient souvent liées à la nécrose et à la formation de membranes hyalines. Des agrégats microbiens associés aux cellules et des coccidies ont été principalement détectés chez les genres Acropora, Pocillopora et Porites, mais sans lien avec une réaction indésirable de l'hôte. Notamment, 69 à 100 % des fragments présentant des lésions provenaient de femelles, reflétant probablement le cycle de vie reproductif des coraux dans la région. Nos résultats mettent en évidence le rôle majeur des organismes endolithiques dans la dégradation des tissus coralliens de la péninsule Arabique. De futures études pourraient s'intéresser aux facteurs influençant la dynamique des microalgues et des éponges endolithiques dans la région et à leur rôle dans la santé des récifs coralliens.

Keywords Red Sea · Gulf of Oman · Arabian Gulf · Bacteria · Coccidia · Microalgae · Sponges · Endoliths · Host response

Introduction

The Red Sea is a mostly closed ancient ecosystem formed about 30 million years ago as a result of the northward movement of the Arabian tectonic plate (Bosworth 2015). It is characterized by a fringing shallow (average 35 m) shelf harboring over 190 species of corals that decrease in diversity from north to south following an increasing temperature (Rasul et al. 2015). The Red Sea's only connections to other bodies of water are through the Bab-al Mandab straits to the South and the man-made Suez Canal to the Northeast. In contrast to the Red Sea, the Persian/Arabian Gulf (PAG) is a much shallower (average 30 m), land-locked, and younger body of water having flooded completely only about 8,000 years ago (Vaughan et al. 2019); it is connected to the Gulf of Oman through the Strait of Hormuz to the east. Because of their shallow bathymetry, coral reefs in the PAG are subject to wide fluctuations in temperature (12–36 °C) and salinity (36–42 ppt) (Aeby et al. 2024) with water turnover being higher in the shallower PAG vs the deeper Red Sea (Sheppard et al. 1992). To the east of the PAG, the Gulf of Oman with greater depths and higher productivity supports a higher diversity of corals (Burt et al. 2016; Claereboudt 2019). This environmental variation between the three basins across the Arabian Peninsula has made these ecosystems of particular interest for studying corals' resilience to extreme conditions (Burt et al. 2020; Burt and Paparella 2024).

Coral reefs in the Arabian Peninsula are important for their intrinsic value and the economic services they provide. For example, in the Red Sea coral reefs provide economic benefits for tourism (Hilmi et al. 2012) and fisheries (Hoagland et al. 2013). However, like reefs elsewhere, corals in the Arabian Peninsula face threats such as dredging and land reclamation, development (Burt 2014), and ocean acidification (Fine et al. 2019) superimposed by higher than average warming rates (Raitsos et al. 2011; Alosairi et al. 2020). Disease is also becoming an increasingly recognized threat to coral reefs. For example, since 2014, stony coral tissue loss disease (SCTLD) killed vast numbers of corals over large areas of the Caribbean and led to local extinctions of some species (Papke et al. 2024). Although diseases have also been documented in the PAG (Tavakoli-Kolour et al. 2015; Howells et al. 2020; Hazraty-Kari et al. 2021; Aeby et al. 2024) and the Red Sea (Bruckner and Dempsey 2015; Aeby et al. 2021), the scale of animals affected and the effects of disease in the region are less severe than in the Caribbean. However, unexplained mortalities in reefs from the Arabian Peninsula (Bruckner and Dempsey 2015) along with unexplained secular declines in some previously common genera such as *Acropora* (Riegl 2002; Riegl et al. 2018) prompt the need for a greater understanding of potential causes of mortality in corals from the region. This is particularly true, as disease prevalence in this region has been shown to be strongly linked to temperatures, and marine heat waves are becoming increasingly frequent and severe (Howells et al. 2020; Hazraty-Kari et al. 2021; Burt 2024).

Most of our knowledge of disease in corals from the Arabian Peninsula stem from field observations (Riegl et al. 2012) that do not always allow for understanding of underlying causes of observed gross lesions. Histology surveys, involving microscopic examination of tissues, have proven useful elsewhere to help elucidate potential causes of lesions in corals. The benefits of incorporating histology in field surveys of disease in corals are two-fold. First, microscopy may show organisms associated with host cell pathology. For instance, seminal studies of black band disease and its association with cyanobacteria were revealed through careful microscopic examination of affected tissues (Rutzler and Santavy 1983). Second, microscopy can reveal how host response informs the genesis of gross lesions. For example, histology of SCTLD in the Caribbean showed corals were dying from primary pathology in endosymbionts leading to host cell death and gross manifestation of tissue loss (Landsberg et al. 2020).

We are aware of two studies in corals from the Arabian Peninsula where histology has been used. One of these described general histology of lesions but focused more on cell-associated microbial aggregates (Aeby et al. 2021), and another showed that fungi might be important contributors to lesions in *Acropora* (Howells et al. 2020). Here, we add to this limited information by systematically describing microscopic lesions in corals from four marine environments across the Arabian Peninsula: The Red Sea side of Saudi Arabia, Qatar, United Arab Emirates-Persian Arabian Gulf (UAE-PG), and UAE-Gulf of Oman (UAE-GO).

Methods

Corals were opportunistically sampled using standard methods (Work 2013) during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016, (Aeby et al. 2020, 2021; Howells et al. 2020). One of the samplings from the UAE occurred during a tissue loss disease (white syndrome) outbreak. Corals were sampled from two locations (39 samples from 22 colonies) from UAE-GO, six locations (130 samples from 65 colonies) from UAE-PG, nine locations (67 samples from 37 colonies) from Qatar, and 16 locations (85 samples from 42 colonies) from the Red Sea (Fig. 1). Reefs surveyed at UAE were dominated by *Porites*, *Acropora*, and Faviidae with about 50% coral cover and < 1% algal cover (Aeby et al. 2020). Reefs at Qatar had coral cover ranging from 3 to 39% with higher cover on deeper reefs and were dominated by Merulinidae and Poritidae (Bouwmeester et al. 2022). Reefs in the Red Sea Saudi Arabia had 40% coral cover dominated by

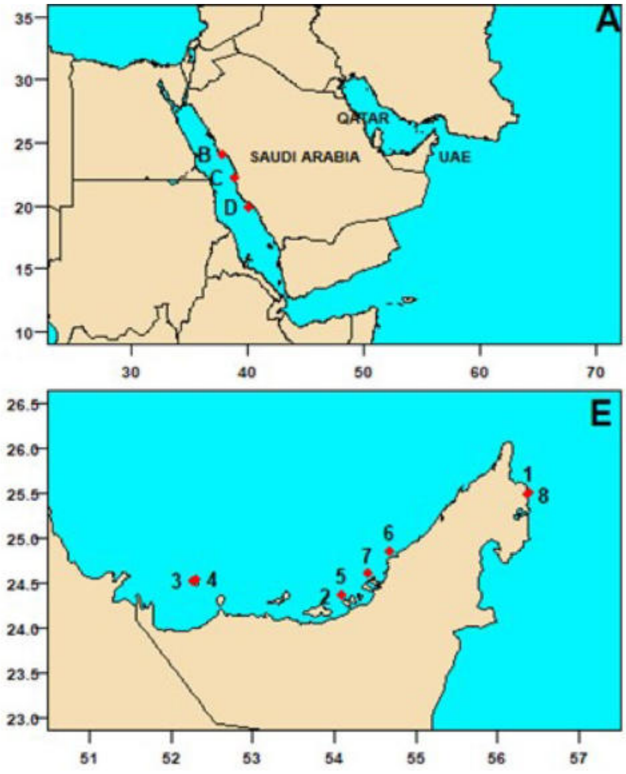
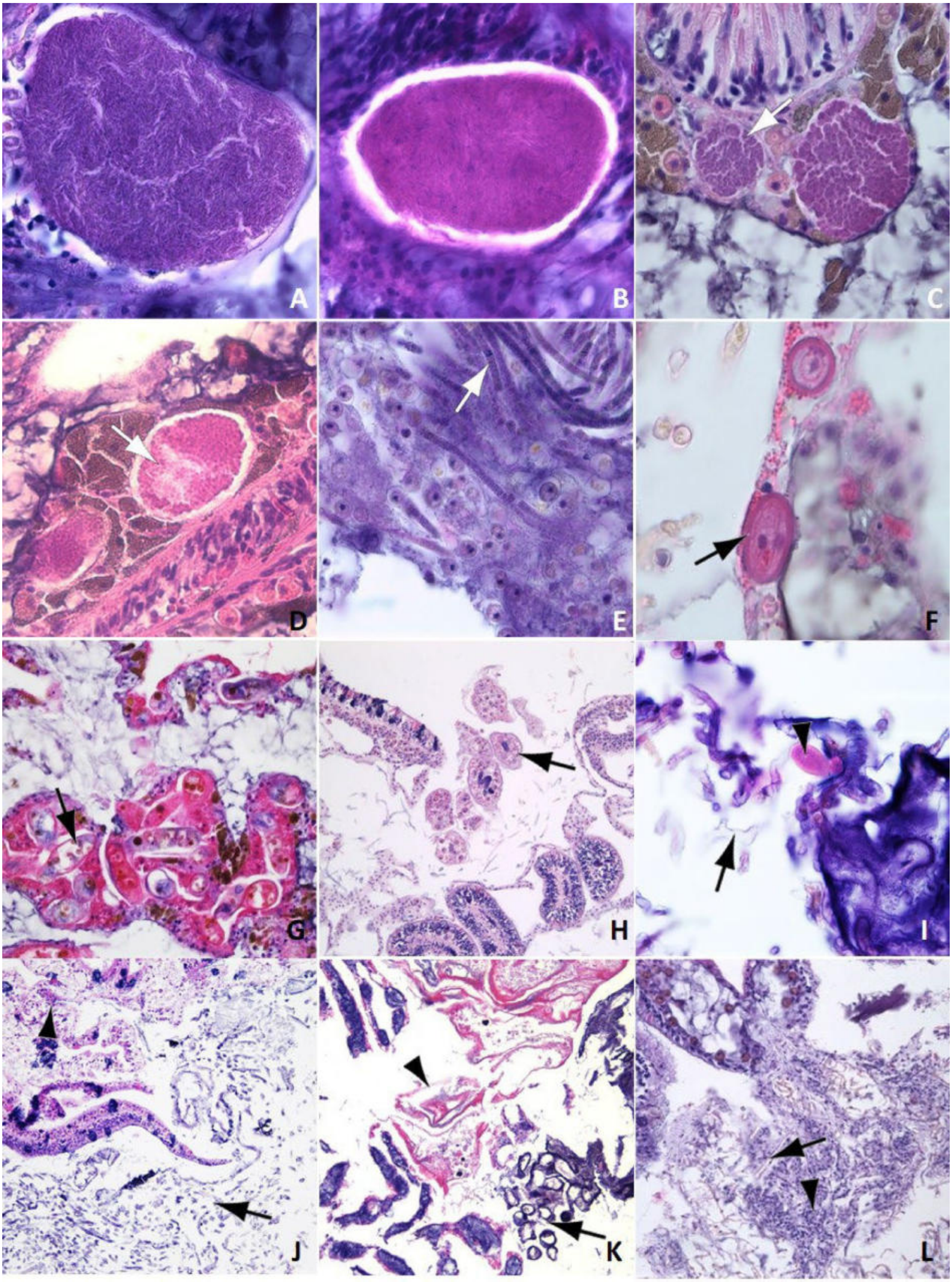


Fig. 1 Collection locations in Saudi Arabia (2015), Qatar (2018), and United Arab Emirates (UAE) (2015–2016). **A** Three countries with points B, C, and D corresponding to panels B–D to the right showing collection sites in the north, central, and south Red Sea coast of Saudi Arabia. **B** North Red Sea: Al Lith 1,2,3,4,5. **C** Central Red Sea: 1) Yanbu 4, Yanbu 5, Yanbu 6. **D** South Red Sea: 1) Abu Madafi 2) Al-Mashpah, 3) Inner Fsar, 4) La Plage, 5) Qita al Kirsh, 6) Shaab, 7) Tahlah. **E** United Arab Emirates: 1) Al Aqa, 2) Coral 85, 3) Delma West,4) Delma North, 5) Dhabiya, 6) Ras Ghanada, 7) Saadiyat, 8) Sharm Rocks; Al Aqa (1) and Sharm Rocks (8) comprise UAE-Gulf of Oman (UAE-GO) whereas the remaining sites comprise UAE-Persian Arabian Gulf (UAE-PG). **F** Qatar: 1) 20-sponge city, 2) Binzayan, 3) Bul Hanine 1, 4) Bul Hanine 2, 5) Bul Hanine 3, 6) Bul Hanine 4, 7) Fasht east Halul, 8) Fasht west Halul, 9) Umm al Arshan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◂**Fig. 2** Organisms seen on histology in corals from the Red Sea, Qatar, United Arab Emirates Persian Arabian Gulf (UAE-PG) and UAE-Gulf of Oman (UAE-GO). **A** Apparently normal *Platygyra* spp. from Qatar; basophilic rod cell-associated microbial aggregate (CAMA). **B** *Platygyra daedala* with bleaching from the Red Sea; eosinophilic rod CAMA. **C** Apparently normal massive *Porites* from the Red Sea; basophilic coccoid CAMA (arrow). **D** Apparently normal massive *Porites* from the Red Sea; eosinophilic coccoid CAMA (arrow). **E** *Psammocora* sp. with tissue loss from the Red Sea; note cyanobacteria (arrow) invading gastrodermis of the basal body wall. **F** Apparently normal massive *Porites* from the Red Sea; note small coccidia (arrow) within calicodermis with no host response. **G** Massive *Porites* with tissue loss from the Red Sea; note allantoid to elliptical large coccidia within gastrodermis of the basal body wall (arrow) with no evident host response. **H** *Acropora* spp. with tissue loss from the Red Sea; note ciliates (arrow) invading surface body wall and associated with necrosis. **I** *Psammocora* spp. with bleaching from the Red Sea; note fungal hyphae (arrow) with fruiting bodies (arrowhead) in the basal body wall. **J** *Cyphastrea* spp. with tissue loss from UAE-PG; note filamentous microalgae invading effacing surface and basal body wall with necrosis (arrowhead). **K** Massive *Porites* with discoloration from UAE-GO; note macroalgae with cell walls (arrow) effacing the basal body wall associated with necrosis and hyaline membrane formation (arrowhead). **L** Pillar *Porites* with tissue loss from UAE-PG; note sponge with choanocytes (arrowhead) and spicules (arrow) invading the basal body wall. Corals were sampled during baseline surveys of bleaching events at Qatar between March 25 and 29, 2018 and the United Arab Emirates between June 8, 2015 and August 9, 2016

Porites, *Pocillopora*, and Faviidae with 13% soft corals, and 7% crustose coralline algae (Aeby et al. 2021).

Sampling procedures involved photo-documenting gross lesions in situ both pan and close-up, and paired lesion and normal fragments from affected colonies were collected with rongeurs (for branching colonies) or hammer and chisel (for massive colonies), and fragments placed in seawater in prelabeled plastic bags. After the dive, fragments were photographed and fixed in 20% Z-Fix-raw seawater (Anatech, Battle Creek, Michigan, USA). Gross lesions were categorized as tissue loss, bleaching (white discoloration), discoloration (all other color anomalies), or growth anomalies (Work and Aeby 2006). Tissues were processed for histopathology as described (Work et al. 2014). Briefly, coral fragments were decalcified in formic acid, sectioned, embedded in paraffin, sectioned at 5 µm, and tissues stained with hematoxylin and eosin.

Tissues were examined and microscopic findings were coded as to anatomic location (topography), host response, and, if present, associated organisms (Topog_Host_Agent). Topography was classified as epidermis, mesoglea, gastrodermis, calicodermis, and mesentery. Host responses were classified as those changes deemed reversible such as metaplasia or hypertrophy or irreversible such as fragmentation or necrosis (Hawthorn et al. 2023). Organisms seen in tissue sections were categorized as cyanobacteria, fungi, sponges, filamentous and macroalgae, microcnidaria, small and large coccidia, ciliates, molluscs, crustacea, intragastrovascular multicellular structures, or unidentified metazoa (Work et al. 2011, 2015; Hawthorn et al. 2023). Cell-associated microbial aggregates or CAMA (Work and Aeby 2014; Singhakarn et al. 2025) were partitioned as eosinophilic or basophilic rods or cocci based on their appearance in tissue sections stained with hematoxylin and eosin (Fig. 2). We also documented the presence/absence of spermaries or oocytes within mesenteries.

To calculate an overall health score for a coral fragment, we assigned a numerical score for host response and for topography for each histology finding. Reversible and irreversible host responses got a score of 2 and 3, respectively (Fig. 3). Each topography affected (epidermis, mesoglea, gastrodermis, calicodermis, mesentery) received a score of 1 (Table 1). For example, if we saw the presence of necrosis of the basal body wall, the host response got a score of 3 and the topography a score of 4 (sum of calicodermis, gastrodermis, mesoglea, mesenteries) arriving at a histology score of 12 ($3 * 4$) for that particular finding. Histology scores were summed across a fragment to arrive at an overall health score with a higher score indicating a less healthy coral fragment.

Data were assessed for normality and equal variance using the Shapiro–Wilk test. Because data did not fit assumptions of normality and/or equal variance, histology lesion scores were compared between gross lesions categories using Kruskal–Wallis ANOVA with post hoc analyses done with Dunn's post hoc comparisons. Chi-square test was used to assess the relationship between hyaline membrane deposition and necrosis. Data were visualized with modified rainfall plots (Domanska et al. 2017), heat maps, or line plots. Locations were binned into four regions deemed ecologically relevant to the Arabian Peninsula (Bruckner and Dempsey 2015; Burt and Paparella 2024): 1) Red Sea comprised samples from Saudi Arabia, 2) Qatar comprised samples from Qatar, 3) United Arab Emirates-Persian Arabian Gulf (UAE-PG) comprised samples from the Persian Arabian Gulf side of the United Arab Emirates (UAE), and 4) UAE-Gulf of Oman (UAE-GO) comprised samples from the Gulf of Oman side of the UAE. Percentages of corals with and without gonads and their relationships were tabulated (Fig. 4). All data analyses were done with R (R Core Team 2021).

Results

The distribution of corals sampled differed between regions. The three most abundant taxa sampled for each region were *Pavona explanulata*, *Porites* massive, and *Platygyra daedala* for UAE-GO; *Porites* pillar, *Platygyra daedala*, *Acropora downingi* for UAE-PG; *Porites* massive, *Pocillopora* spp.,

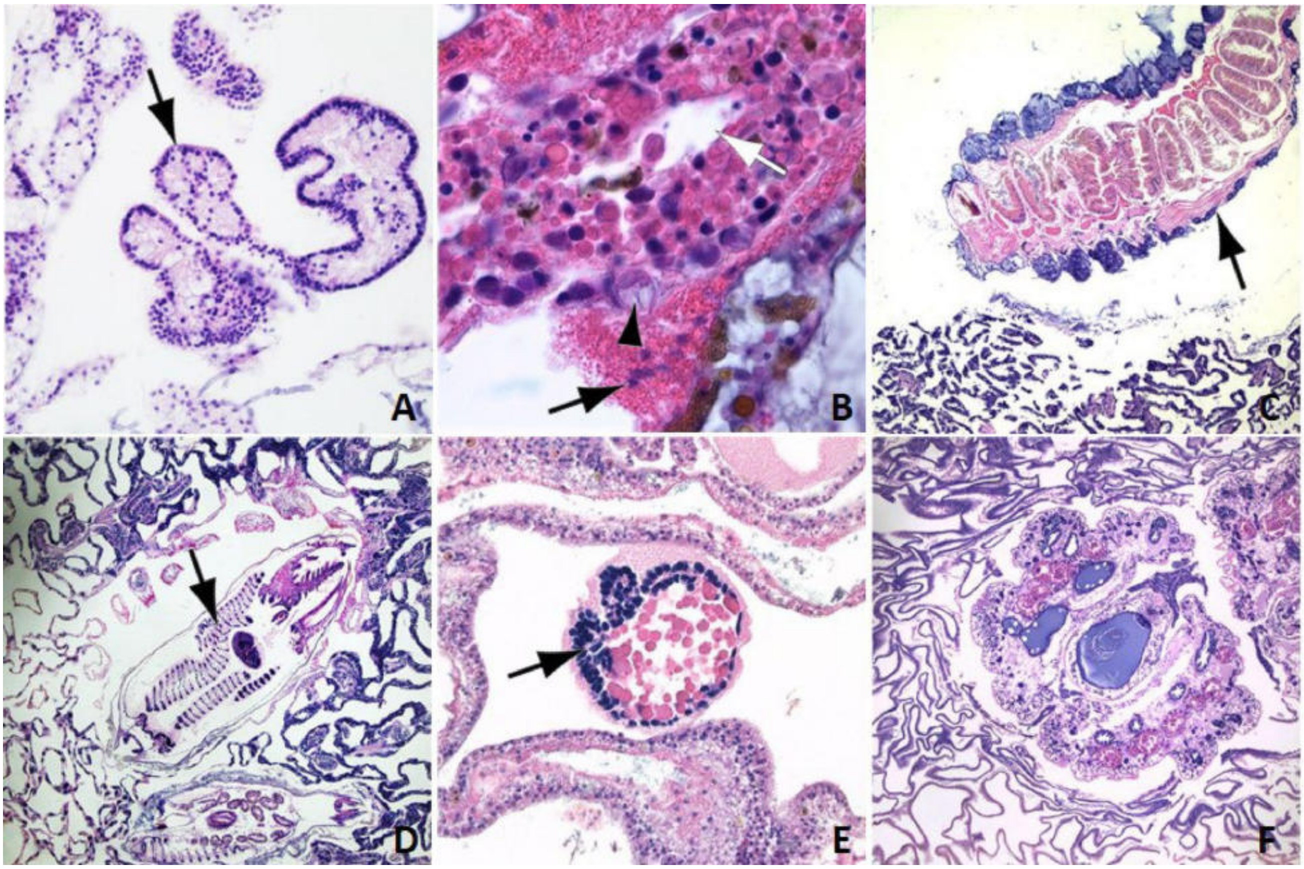


Fig. 3 **A**-**F** Organisms seen on histology (Continued) in corals from the Red Sea, Qatar, and United Arab Emirates–Gulf of Oman (UAE-GO). **A** *Acropora* spp. with tissue loss from the Red Sea; note intra-gastrovascular multicellular structures (arrow). **B** Massive *Porites* with tissue loss from the Red Sea; note microcnidarian with lumen (white arrow) and cnidae (arrowhead) with mild hyperplasia (black arrow) of adjacent calicodermis. **C** Massive *Porites* with discoloration from UAE-GO; note helminth (arrow) effacing basal body wall. **D** Massive *Porites* with discoloration from Qatar; note crustacea (barnacles) with cuticle and gills (arrow) within basal body wall with little to no host response. **E** *Turbinaria* spp. with bleaching from Qatar; note unidentified metazoan within gastrovascular canals. **F** *Turbinaria* spp. with tissue loss from Qatar; note large unidentified metazoan effacing basal body wall. Corals were sampled during baseline surveys of bleaching events at Qatar between March 25 and 29, 2018 and the United Arab Emirates between June 8, 2015, and August 9, 2016

Stylophora spp. for Red Sea; and *Platygyra* spp., *Dipsastraea* spp., and *Porites* massive for Qatar. Tissue loss was the most commonly sampled gross lesion for all regions except for Qatar where discoloration dominated (Table S1). Of 321 fragments examined on histology, 130 (40%) came from the United Arab Emirates side of the PAG, 67 (21%) came from Qatar, 39 (12%) came from the Gulf of Oman, and 85 (26%) came from the Red Sea (Table S2).

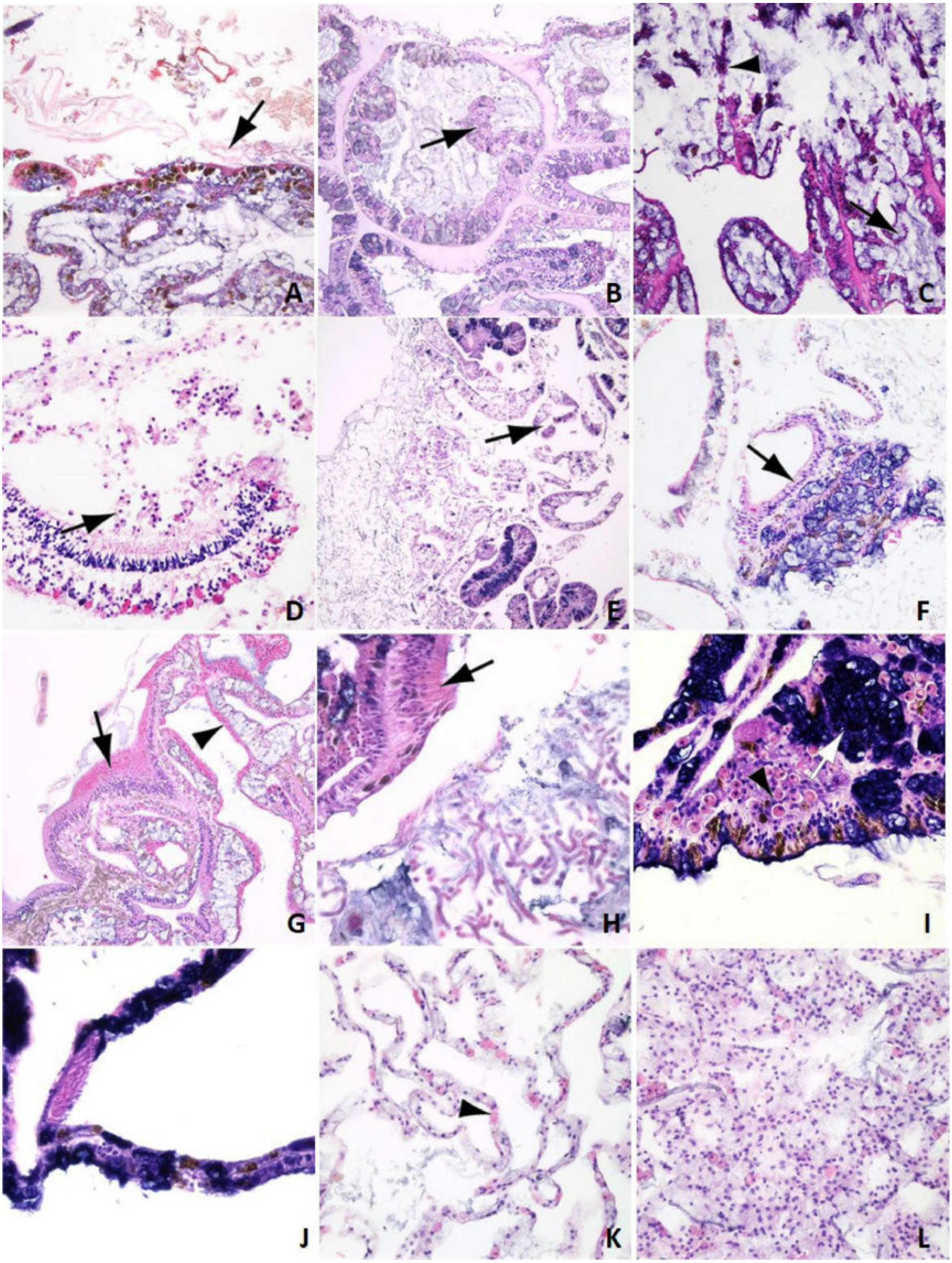
Of 101 fragments with tissue loss the top three host responses and topographies were necrosis of basal body wall (49%), necrosis of surface body wall (34%), and hyaline membrane deposition in basal body wall (18%). Of 31 fragments with discoloration the top three topographies and host responses were necrosis of surface body wall (48%), necrosis of basal body wall (29%), hyaline membrane deposition in surface body wall (23%). Of 12 fragments with growth anomalies, the top three topographies and host responses were necrosis of basal body wall (42%), hyperplasia of basal body wall (25%), and hyaline membrane deposition in basal body wall (17%). Of 13 fragments with bleaching, the top three topographies and host responses were atrophy of surface body wall (46%), necrosis of basal body wall (31%), and necrosis of surface body wall (23%). Of 126 apparently normal fragments, the top three topographies and host responses were necrosis of surface body wall (25%), necrosis of basal body wall (18%), and atrophy of surface body wall (10%) (Table S3). When the most common genera (*Acropora, Platygyra, and Porites*) and gross lesion combinations were compared to host response, irreversible changes dominated (necrosis and hyaline membrane deposition) with basal and surface body wall most often affected (Fig. 5).

Cell-associated microbial aggregates (CAMA) were frequently observed in corals but not associated with any host pathological response. Of 321 fragments examined,

Table 1 Categories of topography, host response, and organisms used to classify histology lesions of coral diseases in corals from Qatar (2018), United Arab Emirates (2015–2016) and Saudi Arabia (2015)

Code	Description	Score	Description
Cell-associated microbial aggregates			
BABR	Basophilic rod bacterial aggregate		Figure 2A
BAER	Eosinophilic rod bacterial aggregate		Figure 2B
BABC	Basophilic coccoid bacterial aggregate		Figure 2C
BAEC	Eosinophilic Coccoid bacterial aggregate		Figure 2D
Other organisms			
CYAN	Cyanobacteria		Figure 2E
COCC	Coccidia small		Figure 2F
COCL	Coccidia large		Figure 2G
CILI	Ciliate		Figure 2H
FUNG	Fungi		Figure 2I
FILA	Filamentous algae		Figure 2J
MACR	Macroalgae		Figure 2K
COCL	Sponge		Figure 2L
IGMS	Intragastrovascular multicellular structures		Figure 3A
MICN	Microcnidaria		Figure 3B
HELM	Helminth		Figure 3C
CRUS	Crustacea		Figure 3D
META	Unidentified Metazoa		Figures 3E-F
MOLL	Mollusc		(Raymundo et al. 2016)
Irreversible host response			
NECR	Necrosis	3	Figures 4A-C
HYAL	Hyaline membranes	2	Figure 4A
GRBR	Granular brown cell	2	Figure 4A
DISS	Dissociation	3	Figure 4D
FRAG	Fragmentation	3	Figure 4E
Reversible host response			
EPIM	Epidermal metaplasia	2	Figure 4F
CAME	Calicodermal metaplasia	2	Figure 4G
COLU	Columnar metaplasia	2	Figure 4H
MUCU	Mucus cell hypertrophy	2	Figure 4I
HYPT	Hypertrophy	2	Figure 4C,I
ATRO	Atrophy	2	Figure 4J
EOGR	Eosinophilic granular cells	2	Figure 4K
HYPP	Hyperplasia	2	Figure 4L
DEPO	Pigment deposition	2	Deposition of pink granular pigment
PINK	Pink protein deposition	2	Deposition of homogenous pink material within gastrovascular canals
Topography			
CALI	Calicodermis	1	(Hawthorn et al. 2023)
EPID	Epidermis	1	
GBBW	Gastrodermis basal body wall	1	
GSBW	Gastrodermis surface body wall	1	
MBBW	Mesoglea basal body wall	1	
MF	Mesenteries	1	
SK	Skeleton	1	
SBW	Surface body wall	3	
BBW	Basal body wall	4	
GVC	Gastrovascular canals	NA	

Scores apply only to coral tissues or host response and were used to calculate histology scores for fragments (refer to methods). Descriptions are in either Figs. 2–4 or in literature cited. NA means not applicable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◂**Fig. 4** Irreversible (**A**-**E**) and reversible (**J**-**L**) host response of corals from the Red Sea and United Arab Emirates–Persian Arabian Gulf (UAE-PG). **A** Massive *Porites* spp. with tissue loss from the Red Sea; note necrosis of the surface body wall with hyaline membrane formation (arrow) subsumed by infiltrates of granular brown cells. **B** Apparently normal pillar *Porites* from UAE-PG; note localized necrosis and lifting off of the gastrodermis of the basal body wall (arrow). **C** Apparently normal pillar *Porites* from UAE-PG; note mucus cell hypertrophy (arrow) and necrosis (arrowhead). **D** *Acropora downingi* with tissue loss from UAE-PG; note dissociation of the gastrodermis of the surface body wall (arrow). **E** Apparently normal *Cyphastrea microphthlama* from UAE-PG; note invasion by filamentous microalgae associated with necrosis and fragmentation of tissues (arrow). **F** Massive *Porites* with tissue loss from UAE-PG; note epidermal metaplasia of the calicodermis (arrow). **G** Pillar *Porites* with tissue loss from UAE-PG; note calicodermal metaplasia of the epidermis (arrow) with normal calicodermis as comparative (arrowhead). **H** Massive *Porites* with tissue loss from the Red Sea; note filamentous algae (right) and columnar metaplasia of the calicodermis (arrow). **I** *Cyphastrea chalcidicum* with bleaching from UAE-PG; normal surface body wall with columnar epidermis (bottom), gastrodermis replete with endosymbionts (arrowhead), and mucus cell hypertrophy (white arrow). **J** Same as I except bleached portion; note flattened atrophied gastrodermis and epidermis with the absence of endosymbionts. **K** *Montipora* spp. with growth anomaly from the Red Sea; apparently normal tissue with the basal body wall and gastrodermis with occasional eosinophilic granular cells. **L** Same as K but with a growth anomaly; note hyperplasia of the basal body wall. Corals were sampled during baseline surveys of bleaching events at Qatar between March 25 and 29, 2018 and the United Arab Emirates between June 8, 2015 and August 9, 2016

61 (19%) contained CAMA. The majority originated from *Porites* (56%), followed by *Acropora* (22%), *Pocillopora* (8%), *Platygyra* (7%), and *Stylophora* (7%). The composition of bacteria in CAMA differed between genera of corals. Coccoid bacteria were observed only in *Porites*, eosinophilic rods dominated in *Platygyra*, *Pocillopora*, and *Stylophora*, whereas basophilic rods dominated in *Acropora*. All but *Stylophora* had mixed populations of bacterial morphologies (Table 2).

Aside from CAMA, of 321 fragments examined, the most commonly observed organisms on microscopy were filamentous microalgae (33%), sponges (24%), unidentified metazoa (7%), macroalgae (6%), crustacea (6%), microhelminths (6%), cyanobacteria (5%), fungi (4%), ciliates, microcnidaria, small and large coccidia (1% each), intragastrovascular multicellular structures (IGMS), and molluscs (< 1% each).

When organisms were classified to tissue compartment, CAMA were mainly in gastrodermis of surface and basal body wall, filamentous microalgae were mainly in basal body wall, and sponges were mainly in basal and surface body wall. Microcnidaria and coccidia were exclusively in calicodermis, IGMS and crustacea were only in gastrovascular canals, and molluscs were only in surface body wall. Remaining organisms were in multiple tissue compartments (Fig. 6). Filamentous algae and sponges were more abundant in skeleton (endolithic) than in tissues (Fig. 7).

When organisms were classified to host response, necrosis was commonly associated with cyanobacteria, ciliates, fungi, filamentous algae, sponges, and molluscs. Hypertrophy was commonly associated with coccidia and microcnidaria. Cell-associated microbial aggregates, intragastrovascular multicellular structures (IGMS), and crustacea did not induce any detectable host response (Fig. 8). When the presence of the top two organisms (filamentous microalgae and sponges) was compared between apparently normal and lesion fragments (all coral species) by region, they had a tropism for the skeleton and basal body wall regardless of health status with prevalence highest for Gulf of Oman and Qatar (Fig. 9).

Histology scores did not fit assumptions of normality/equal variance ($W = 0.88916$, p-value = 5.466e−12). Histology scores differed significantly between gross lesion categories (Kruskal–Wallis ANOVA = 18.139, $df = 4$, p-value = 0.001159) with histology scores for normal significantly lower than for the remaining categories ($p = 0.000342$) (Fig. 10). Hyaline membrane formation was 20 times more likely to occur with necrosis (p-value = 1.106e−12, odds ratio 20.61 (95% confidence interval (CI): 6.4–106).

Gender of corals could be determined from 75 of 321 (23%) fragments examined. Corals were sampled between March and November with a percent of both:female:male as follows: March (F-88%:M-12%; $N = 26$), June (F-25%;M-75%; $N = 4$); August (B-4%:F-74%:M-22%; $N = 27$), October (B-41%:F-41%:M-18%; $N = 17$), and November (F-100%; $N = 1$). A female bias was also seen when corals were partitioned by gross lesion type (Table 3).

Discussion

We used a simplified nomenclature to classify gross lesions in corals into four categories (bleaching, discoloration, tissue loss, and growth anomalies) for two reasons: First, these categories are unambiguous and less prone to subjective interpretations (Work and Aeby 2006). Second, this simplified scheme allowed for more meaningful interpretation of biological patterns given the necessarily haphazard and opportunistic sampling scheme with a lack of balanced design between countries, lesions, and genera of corals. That said, the assortment of gross lesions sampled here broadly reflected the distribution of gross lesions and host distribution present in corals from the Arabian Peninsula. For instance, in surveys of lesions in corals from the Persian/Arabian Gulf, Aeby et al. (2020, 2021) found tissue loss diseases (black band, white syndromes) on

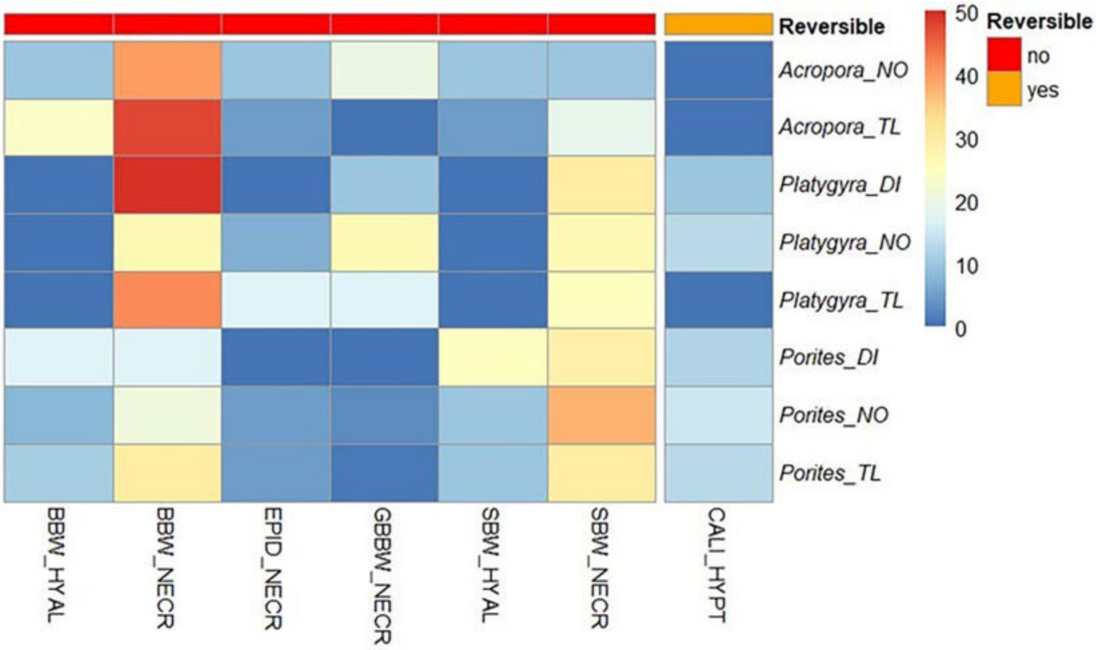

Fig. 5 Heatmap of histology vs gross lesion in three abundant genera of corals from the Arabian Peninsula manifesting gross lesions where $N > 20$ for genus_gross lesions and $N > 10$ for histology. Color scale to right shows the percent of microscopic lesions (topography_host response x-axis) for a given genus_gross lesion (y-axis). Reversible bar on the top color codes histologic lesions as reversible or not. Letter codes for gross lesions are DI-Discoloration, NO-apparently normal, TL-tissue loss. Letter codes for topography (x-axis) are BBW-basal body wall, CALI-calicodermis, EPID-epidermis, GBBW-gastrodermis of basal body wall, SBW-surface body wall. Letter codes for host response are NECR-necrosis, HYAL-hyaline membrane deposition, HYPT-hypertrophy. Sample sizes for x-axis: BBW_HYAL = 24, BBW_NECR = 69, CALI_HYPT = 25, EPID_NECR = 12, GBBW_NECR = 11, SBW_HYAL = 22, SBW_NECR = 66. Sample sizes for y-axis: Acropora_NO = 10, Acropora_TL = 21, Platygyra_DI = 10, Platygyra_NO = 15, Platygyra_TL = 12, Porites_DI = 24, Porites_NO = 39, Porites_TL = 98. Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015 and August 9, 2016

Porites, *Platygyra*, and *Acropora* and yellow banded tissue loss in *Porites*. Howells et al. (2020) also found tissue loss to be common in multiple species of corals with *Acropora* particularly susceptible. Along the Saudi Arabian side of the Red Sea, the most commonly encountered diseases in corals were tissue loss (white syndrome) in *Acropora* and *Porites* and growth anomalies in *Porites* (Aeby et al. 2021). Bruckner and Dempsey (2015) found a variety of lesions in Red Sea corals including growth anomalies in *Acropora*, white syndromes on *Acropora* and *Dipsastraea*, and black band on *Favites* among others. Hazraty-Kari et al. (2021) found all four lesion types in the northern Persian Gulf. All these lesion types (tissue loss, growth anomalies, and black band) were sampled for this analysis.

Table 2 Number (percent) of each morphology of cell-associated microbial aggregates partitioned by genera

	BABC	BABR	BAEC	BAER
Porites	22 (100%)	0 (0%)	12 (100%)	0 (0%)
Acropora	0 (0%)	13 (86.7%)	0 (0%)	1 (8.3%)
Pocillopora	0 (0%)	1 (6.7%)	0 (0%)	4 (33.3%)
Stylophora	0 (0%)	0 (0%)	0 (0%)	4 (33.3%)
Platygyra	0 (0%)	1 (6.7%)	0 (0%)	3 (25%)
Total	22	15	12	12

Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

Basophilic coccoid (BABC), basophilic rod (BABR), eosinophilic coccoid (BAEC), eosinophilic rod (BAER)

For the commonly sampled genera (*Acropora, Platygyra, and Porites*), some patterns were evident when relating histology to gross lesions. Irreversible changes such as necrosis were most common for all lesion types, aside from bleaching where atrophy was prominent. The common presence of necrosis in tissue loss would account for the relatively higher histology score relative to other lesion types and explain the pathophysiology of this process in the manifestation of gross lesions; recall that higher histology scores indicate less healthy corals. Scoring of lesions has been used

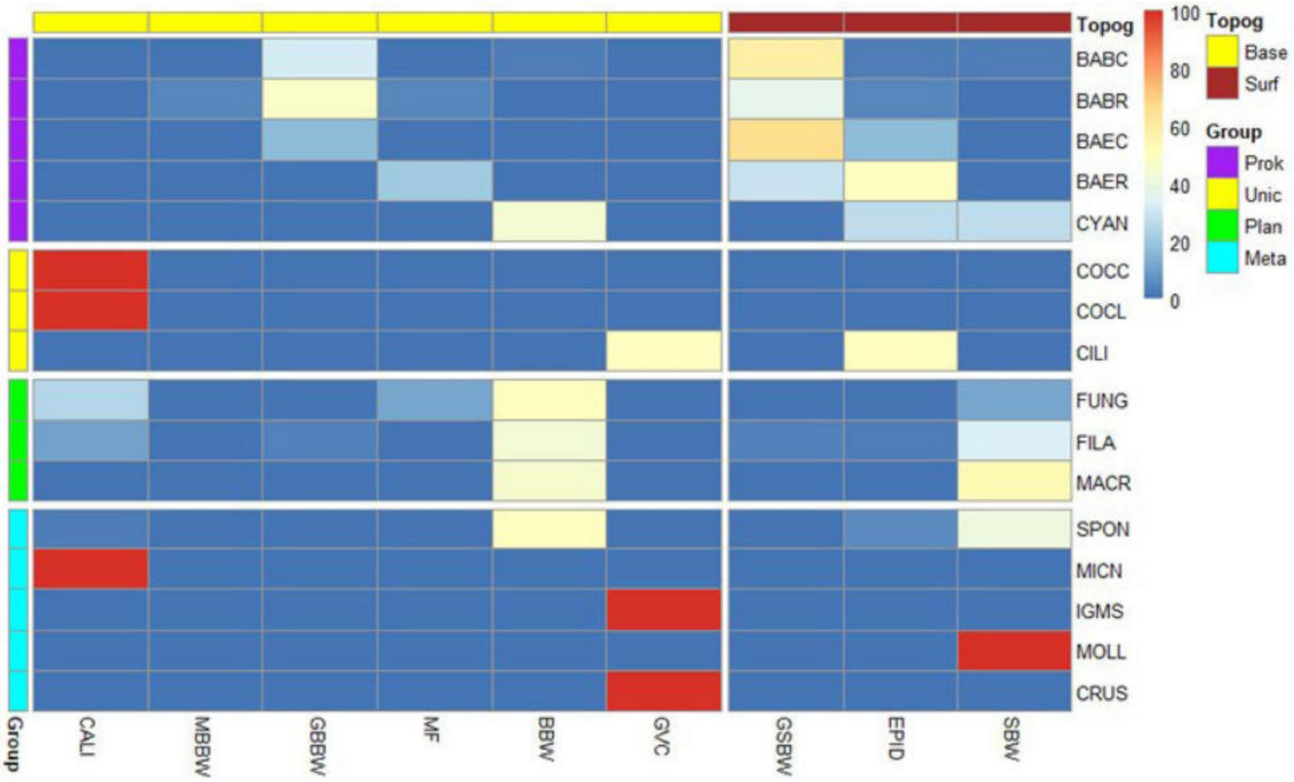

Fig. 6 Heatmap of host topography vs organisms seen on the histology of corals from the Arabian peninsula. Color scale to right shows the percent of topographical locations (*x*-axis) occupied in tissues for a given organism (*y* -axis). Topog bar on the top color codes host topography as surface (Surf) or basal (Base) body wall recognizing that gastrovascular canals can be in both but coded as basal for clarity of presentation. Group bar to left color codes organisms as prokaryotes (Prok), unicellular eukaryotes (Unic), plants/fungi (Plant) and metazoan (Meta). Letter codes for organisms (y-axis) are BABC-basophilic coccoid bacteria, BABR-Basophilic rod bacteria, BAEC-Eosinophilic coccoid bacteria, BAER-Eosinophilic rod bacteria, CYAN-cyanobacteria, COCC-small coccidia, COCL-large coccidia, CILI-ciliates, CRUS-crustacea, FUNG-fungi, FILA-filamentous algae, IGMS-intragastrovascular multicellular structures, MACR-macroalgae, MICN-microcnidaria, MOLL-molluscs, SPON-sponge. Letter codes for topography (*x*-axis) are BBW-basal body wall, CALI-Calicodermis, EPID-epidermis, GBBW-gastrodermis basal body wall, GSBW-gastrodermis surface body wall, GVC-gastrovascular canals, MBBW-Mesoglea basal body wall, MF-mesenteries, SBW-surface body wall. Sample sizes for x-axis: BBW = 91, CALI = 21, EPID = 23, GBBW = 26, GSBW = 43, GVC = 22, MBBW = 1, MF = 5, SBW = 62 Sample sizes for y-axis: BABC = 34, BABR = 21, BAEC = 12, BAER = 14, CILI = 4, COCC = 2, COCL = 2, CRUS = 18, CYAN = 22, FILA = 70, FUNG = 8, HELM = 5, IGMS = 1, MACR = 26, META = 19, MICN = 3, MOLL = 1, SPON = 3. Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

in other animals to provide a summary health index allowing for more systematic analyses of pathologic findings. For example, Bernet et al. (1999) developed a detailed scoring system for lesions in fish that was then successfully used to differentiate the health of fish upstream and downstream of wastewater sites (Bernet et al. 2000). The scoring system used here for corals coupled with a more systematic and balanced sampling design, controlling for genus location and gross lesion type, could prove useful to compare coral health between different regions for a given genus.

The types of host responses seen here mirrored those observed in corals elsewhere. For example, necrosis associated with hyaline membrane formation has been found in *Acropora* with growth anomalies in Samoa (Work et al. 2008a), discoloration in *Porites* from Micronesia (Work et al. 2015), and tissue loss in *Siderastrea* from the US Virgin Islands (USVI) (Work et al. 2024). Atrophy is a common host response in bleached corals that has been observed in *Mycedium* from Micronesia (Work et al. 2015) and *Agaricia* from the USVI (Work et al. 2024). The statistically significant association between necrosis and hyaline membrane formation suggests a strong link between these two host responses. The origin of this membrane deposition is unclear, but their pink color on hematoxylin and eosin indicates a strong acidic protein component (Chan 2014). Corals are known to produce acid proteins generally associated with calcification (Constantz and Weiner 1988), and using immunohistochemistry tools to localize these proteins (Mass

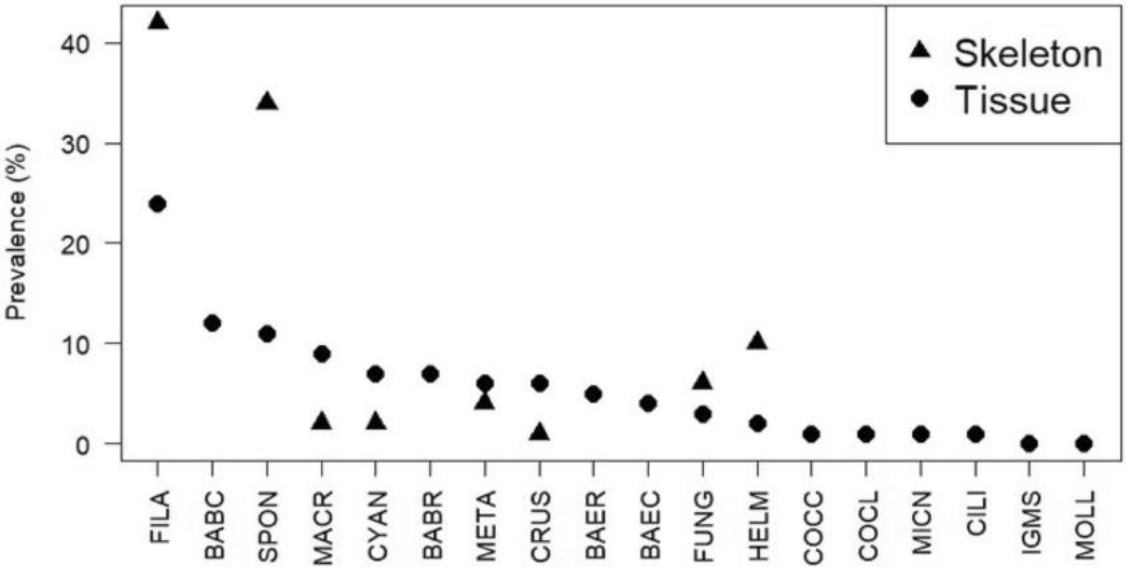

Fig. 7 Prevalence of different agents seen in the tissue and skeleton of corals from the Arabian peninsula. Letter codes for organisms (*x*-axis) are FILA-filamentous algae, BABC-basophilic coccoid bacteria, SPON - sponge, MACR - macroalgae, CYAN - cyanobacteria, BABR - Basophilic rod bacteria, META-Unidentified metazoan, CRUS - crustacea, BAER - Eosinophilic rod bacteria, BAEC-Eosinophilic coccoid bacteria, FUNG - fungi; HELM - Helminths, COCC - small coccidia, COCL-large coccidia, CILI - ciliates, IGMS - intragastrovascular multicellular structures, MOLL-molluscs. Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

et al. 2014) to lesions might shed additional light on their origin. Hyaline membrane formation in corals is particularly prominent with host response of the calicodermal layer (Hawthorn et al. 2023) which would accord with findings here showing that insults to corals appear to originate from skeleton. The basal body wall in corals seems particularly susceptible to necrosis, a phenomenon seen in corals from the Caribbean. For instance, SCTLD appears to start in the basal body wall in multiple coral species (Landsberg et al. 2020). Understanding what it is about cell types in those tissue layers that makes them so susceptible to mortality might be arenas of useful research in the future. Tools such as single cell RNA-Seq have been applied to corals to provide greater granularity as to cell types in corals (Levy et al. 2021), and such approaches might help understand susceptibility of certain coral cell types to mortality.

Our results reinforce previous findings that CAMAs, despite their frequent occurrence across multiple coral genera, are histologically benign. The absence of detectable host response across both healthy and diseased tissue fragments suggests that CAMAs likely represent a stable component of the coral holobiont, rather than opportunistic pathogens. Cell-associated microbial aggregates were first described in Caribbean *Acropora* where they were thought to be associated with tissue loss disease (Peters et al. 1983). Subsequent work in the Pacific showed CAMA to be widespread in corals mainly in *Acropora*, *Porites*, and *Pocillopora;* there they were considered a potential symbiont based on the lack of significant host response (Work and Aeby 2014). Consistent with corals from the Pacific, CAMA in corals from the Arabian Peninsula are most common in *Acropora*, *Porites,* and *Pocilloporidae* (*Stylophora*). Molecular studies in the Pacific have identified CAMAs as being comprised of *Endozoicomonas* both by molecular (Neave et al. 2017; Pogoreutz and Ziegler 2024) and microscopic methods (Wada et al. 2019). However, the variety of morphologies of bacteria seen here and in the Pacific (Wada et al. 2022; Singhakarn et al. 2025) suggests that other types of bacteria may be involved. Future studies might consider using special stains such as Gram stains (Popescu and Doyle 1996) or metagenomics (Neave et al. 2017) to better characterize such aggregates.

Filamentous microalgae and sponges dominated in tissues whereas filamentous microalgae, sponges, and microhelminths dominated in the skeleton. Endoliths, organisms that grow in the coral skeleton, are common and can be important to coral health and carbonate cycling on coral reefs (Tribollet 2008). In some cases, endoliths can overgrow the skeleton and invade overlying tissue. An example of this is dark spots disease where endolithic fungi overgrowth of the skeleton led to lesions in overlying tissues (Work et al. 2008b). A similar process might be occurring with filamentous algae and sponges in corals from the Arabian Peninsula. Host response to these endolithic organisms was dominated by necrosis suggesting that they are having adverse effects

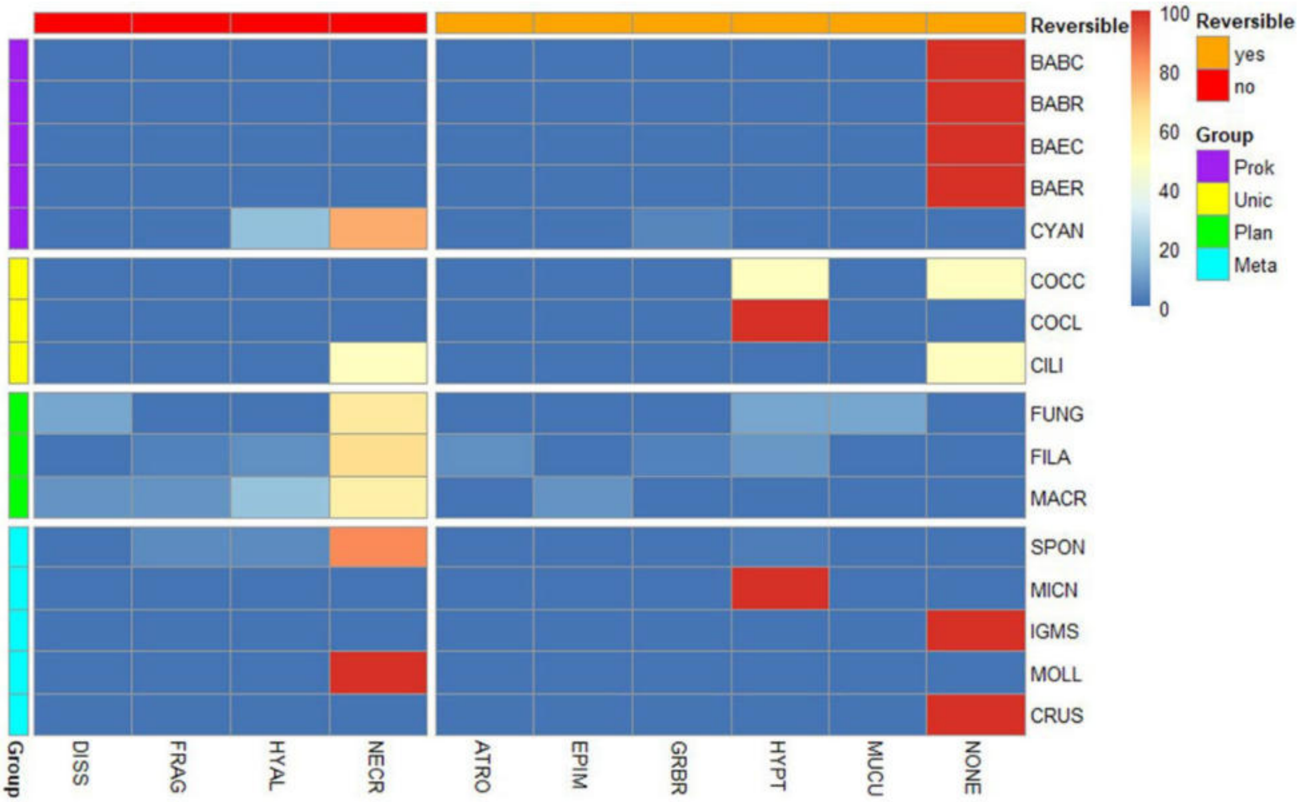

Fig. 8 Heat map of coral host response vs Organisms seen on histology. Color scale to the right shows the percent of host response types (*x*-axis) for a given organism (*y* -axis) seen associated with the response on histology. Reverse bar on the top color codes host responses as reversible or not. Group bar to the left color codes organisms as prokaryotes (Pro), unicellular eukaryotes (Unic), plants/fungi (Plan) and metazoan (Met). Letter codes for organisms (y-axis) are BABC-basophilic coccoid bacteria, BABR-Basophilic rod bacteria, BAEC-Eosinophilic coccoid bacteria, BAER-Eosinophilic rod bacteria, CYAN-cyanobacteria, COCC-small coccidia, COCL-large coccidia, CILI-ciliates, CRUS-crustacea, FUNG-fungi, FILA-filamentous algae, IGMS-intragastrovascular multicellular structures, MACR-macroalgae, MICN-microcnidaria, MOLL-molluscs, SPON-sponge. Letter codes for host response (*x*-axis) are ATRO-Atrophy, DISS-dissociation, EPIM-epidermal metaplasia, FRAG-fragmentation, GRBR-granular brown cell infiltrates, HYAL-Hyaline membranes, HYPT-hypertrophy, MUCU-Mucus cell hyperplasia, NECR-Necrosis, NONE-No host response. Sample sizes for the x-axis: DISS = 4, FRAG = 7, HYAL = 16, NECR = 114, ATRO = 5, EPIM = 2, GRBR = 4, HYPT = 14, MUCU = 1, NONE = 103 Sample sizes for the y-axis: BABC = 34, BABR = 21, BAEC = 12, BAER = 14, CYAN = 22, COCC = 2, COCL = 2, CILI = 4, FUNG = 8, FILA = 70, MACR = 26, SPON = 32, MICN = 3, IGMS = 1, MOLL = 1, CRUS = 18. Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

on the animal. The higher percentage of skeletons populated by filamentous algae and sponges relative to tissues suggests that under certain circumstances, endoliths can grow into and invade overlying tissues prompting a host response. As an example, endolithic algae can become more abundant with increased light availability such as when bleached corals lose their endosymbiotic Symbiodiniaceae (Carilli et al. 2010). Moreover, Al-Mansoori et al. (2020) found higher levels of bioerosion in coral skeletons from the PAG and GO coasts of the UAE compared with other regions, and in two of three species, erosion was highest in reefs with more extreme environmental conditions and stronger bleaching histories.

Thus, it appears that environmental conditions within the waters of the Arabian Peninsula, especially around Qatar, are conducive to the overgrowth of endolithic filamentous microalgae and sponges in corals. Confirming this would require temporal observations of lesion development. Overgrowth of corals by sponges is a known threat to corals in the region. For instance, *Cliona* and *Clathria* are known surface invaders of corals in the Arabian Gulf (George 2012). Bioeroding sponges are also a well-known phenomenon examined mainly in the context of carbonate cycling (Schönberg et al. 2017) and not as potential primary causes of mortality in corals. The growth of sponges (Wulff 2017) and algae (Littler et al. 2006) on reefs is regulated by top-down processes such as predation and bottom-up processes such as

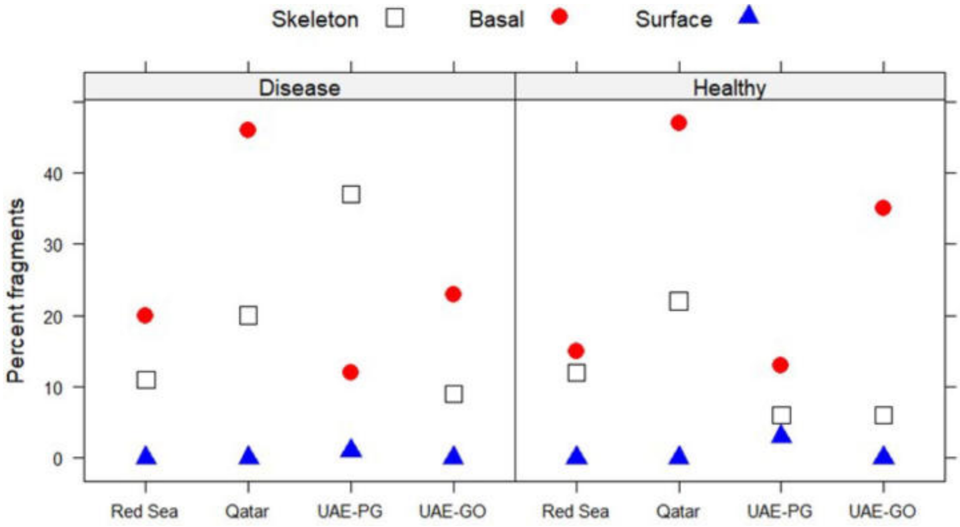

Fig. 9 Percent of coral fragments (disease lesion and apparently healthy) with filamentous algae or sponges in skeleton, basal or surface body wall partitioned by region. UAE is United Arab Emirates, PG is Persian Arabian Gulf, and GO is Gulf of Oman. Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between 20 October and 9 November 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

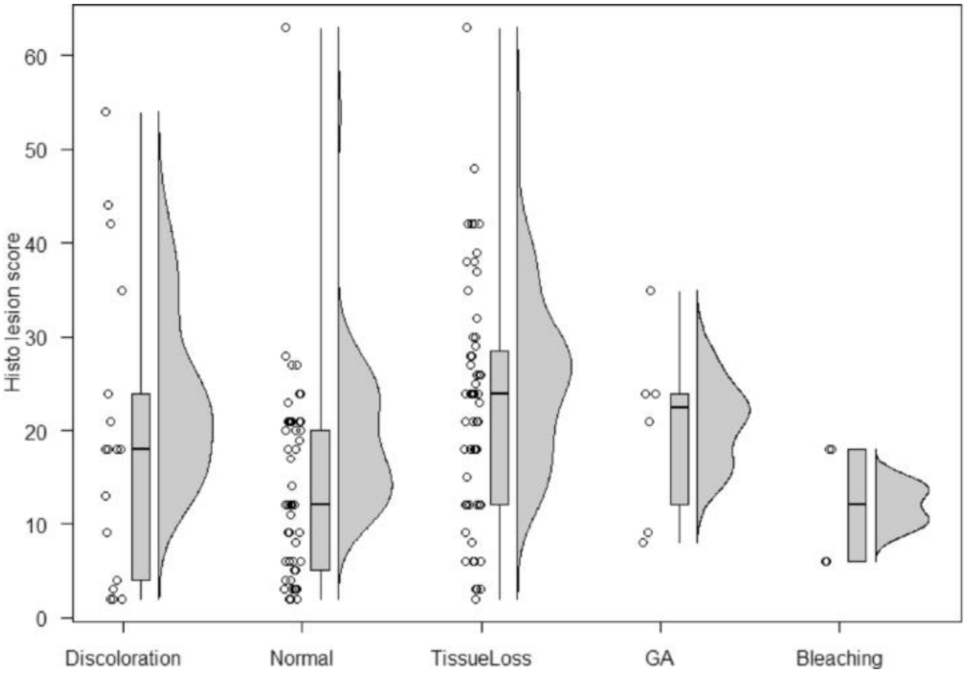

Fig. 10 Rainfall plots of histology scores for corals partitioned by gross lesion type. For each gross lesion, the following are depicted left to right: raw data points horizontally jittered to enhance clarity; box plot showing median (bold horizontal line), 25 and 75 percentiles (vertical box boundaries), and 1.5*interquartile range (whiskers); density plot of data points. GA-growth anomaly. Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March 25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

Table 3 Number (percent) of total corals fragments (all genera) where sex could be determined partitioned among gross lesion types

	Bleaching	Discoloration	GA	Normal	TissueLoss
Both	0 (0%)	1 (11%)	0 (0%)	5 (12%)	2 (12%)
Female	2 (67%)	8 (89%)	6 (100%)	25 (61%)	11 (69%)
Male	1 (33%)	0 (0%)	0 (0%)	11 (27%)	3 (19%)
Total	3	9	6	41	16

Corals were opportunistically sampled during baseline surveys of bleaching events at the Red Sea side of Saudi Arabia between October 20 and November 9, 2015, Qatar between March25 and 29, 2018, and the United Arab Emirates (UAE) between June 8, 2015, and August 9, 2016

GA-growth anomaly

nutrition driving growth. Investigating the seasonality of filamentous microalgae, their identity, and their environmental drivers might explain some of the patterns of gross lesions seen on corals from the Arabian Peninsula. Given the apparent role of endolithic organisms in coral mortality, management strategies that limit sedimentation, nutrient enrichment, and overfishing (which can favor algae) may help preserve coral health in corals from the region.

Cyanobacteria were the only prokaryotes associated with an irreversible host response (necrosis) suggesting them to be pathogenic to corals with most distributed on the surface body wall suggesting a top-down invasion. Filamentous cyanobacteria are the visually dominant component of black band disease (BBD) which is a well-studied disease in corals. BBD is caused by a microbial consortium (sulfide-oxidizing bacteria, sulfate-reducing bacteria and numerous heterotrophic bacteria), enmeshed in the cyanobacteria band on the coral (Richardson 2004). The sulfate-reducing bacteria are responsible for a highly concentrated sulfide and anoxic conditions underneath the BBD mat that are lethal to coral tissue (Carlton and Richardson 1995; Richardson et al. 2009). Black band disease has been documented in corals from the Arabian Peninsula (Riegl 2002; Bruckner and Dempsey 2015; Aeby et al. 2021). Long-term studies of Arabian reefs also show that cyanobacteria increase markedly after bleaching events suggesting that they may be opportunists (Riegl et al. 2024). Future studies might focus on identifying the organisms associated with this lesion to see if it is similar to that observed in other regions. For example, cyanobacteria have been isolated from black band lesions in corals and identified as *Phormidium corallyticum* in the Caribbean (Richardson and Kuta 2003), *Pseudoscillatoria coralii* in the Red Sea (Rasoulouniriana et al. 2009), *Oscillatoria* sp. RMS2 from Palau (Sussman et al. 2006) and in Hawaii, the cyanobacteria in BBD was 99% similar to the Red Sea and Palau strains (Aeby et al. 2015). Developing a better understanding of coral immunity and defenses (Mydlarz et al. 2010) against such organisms might also aid in longer-term management.

Coccidia are unicellular eukaryotes often associated with disease in animals (Fayer 1980). In corals, coccidia were first documented histologically in mesenteries of 6 species of *Acropora* from Jamaica, St. Croix, and Puerto Rico (Upton and Peters 1986). The presence of similar organisms in mesenteries of corals has since been confirmed in Florida (Landsberg et al. 2020) and the US Virgin Islands (Work et al. 2024). Notably, in no case have these coccidia been associated with host cell pathology on microscopic examination suggesting they could be some sort of endosymbiont. Molecular studies have shown widespread presence of non-zooxanthellate apicomplexa in Caribbean corals (Kwong et al. 2019) lending further credence to the hypothesis that they may be symbiotic (Keeling et al. 2021). Our findings of coccidia in corals from the Arabian Peninsula expand the geographic range of these organisms and confirm existing patterns that they are not likely pathogens. We base this on the mild and reversible host response (calicodermal hypertrophy) found associated with these organisms. In contrast to coccidia of Caribbean corals that were seen in mesenteries of at least six different coral species (Upton and Peters 1986), coccidia in corals from the Arabian Peninsula were uncommon and limited to the calicodermis of *Porites* from the Red Sea only. Future studies using molecular methods could show whether they are similar to those documented elsewhere (Kwong et al. 2019).

Sex ratios of corals from colonies manifesting lesions were skewed toward females regardless of the type of gross lesion or month sampled. In the United Arab Emirates, Bauman et al. (2011) looked at gross evidence of oocytes in polyps of *Acropora*, *Dipsastraea*, *Platygyra*, and *Cyphastrea* and found peak reproduction in April with 60–70% colonies with oocytes. Using histology in *Acropora*, *Cyphastrea*, *Platygyra*, and *Porites* from the same region, Hashmi et al. (2012) found peak reproduction between March and May with oogenesis lasting for 6–8 months, while spermatogenesis lasted for 2 months. Given that a temporal bias exists for females, at least in the UAE, the skewed sex ratio may reflect the reproductive history of corals in the region and the fact that all taxa listed here except *Porites* are simultaneous hermaphrodites. Corals in this study were sampled in October–November from the Red Sea, March in Qatar, and June–August in the UAE with a female bias in all regions. More systematic sampling controlling for genera and seasons along with lesion type might reveal whether a true sex bias exists for the development of lesions in corals. Sex predilection occurs in some diseases of other animals. For example, lupus erythematosus, an autoimmune disease in humans, affects mainly females (Nusbaum et al. 2020). Seeing if similar sex predilection occurs for disease in corals elsewhere might be a future avenue of investigations.

In summary, although corals in the Arabian peninsula have lower diversity compared to the Pacific (Coles 2003), they manifest some similar microscopic patterns. Like corals from the Pacific, host response is dependent on associated organisms (Work et al. 2012; Raymundo et al. 2016) and cell-associated microbial aggregates are most prominent in *Porites*, *Pocilloporidae,* and *Acropora* (Work and Aeby 2014). In contrast to corals in the Pacific, overgrowth by endolithic sponges and microalgae appears to play a more important role in tissue pathology akin to some diseases in the Caribbean like dark spots in *Siderastrea* where fungal overgrowth can kill corals (Work and Weil 2015). Investigating how these organisms modulate coral health and carbonate cycling (Lange et al. 2020) on reefs from the Arabian Peninsula might aid in their longer-term preservation.

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Author contribution Conceived the study done by TMW, GSA, DA, JB, EH, PR, MZ, TJ, AS, GV, JB, CRV, and RB. Collected samples done by TMW, GSA, DA, JB, EH, PR, MZ, TJ, AS, and GV. Analyzed data done by TMW and GSA. Wrote MS by TMW, GSA, DA, JB, EH, PR, MZ, TJ, AS, GV, JB, CRV, and RB. All authors reviewed the manuscript.

Data availability Data generated in this study are available in a U.S. Geological Survey data release [https://doi.org/10.5066/P14KHGVH] (https:/doi.org/https://doi.org/10.5066/P14KHGVH).

Declarations

Conflict of interest The authors declare no competing interests.

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