The Status, Threats, and Resilience of Reef-Building Corals of the Saudi Arabian Red Sea

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Abstract

The Saudi Arabian Red Sea (SARS) contains diverse shallow water coral reef systems that include attached (fringing and dendritic reefs) and detached (platform, patch, tower, ribbon, and barrier reefs) reef systems extending up to 90 km offshore. To better understand the current status of coral reefs in SARS, the Living Oceans Foundation conducted assessments of representative reef environments in the Farasan Islands (2006), Ras Al-Qasabah (2007), Al Wajh and Yanbu (2008), and the Farasan Banks (2009). A combination of belt transects and quadrats was used to assess the diversity, size structure, partial mortality, condition, and recruitment of the dominant reef-building corals. Most sites had high structural complexity, with up to 52 genera of scleractinian corals recorded from a single region. Living corals varied in abundance and cover by region, habitat, and depth, with the highest species richness documented in the south (Farasan Banks), followed by Al Wajh and Yanbu and lowest at Ras Al-Qasabah. On most reefs, a single species was dominant. The reef architecture was constructed by massive and columnar *Porites*, with unusually large (1–4 m diameter) colonies in shallow water (up to 80 % live cover in 2–10 m depth) and a deeper reef *Porites* framework that was mostly dead. *Porites lutea* was the single most abundant coral throughout SARS, and the dominant species on leeward reef crests and slopes, while reef slopes and deeper coral carpets were predominantly *Porites columnaris* and *P. rus*. Faviids (*Goniastrea* and *Echinopora*) were the next most abundant corals, especially in areas that had experienced a disturbance, although these were small (most <15 cm diameter) and made up a small fraction of the total live coral cover. Multi-specific *Acropora* assemblages often formed large thickets, but these were restricted in distribution. *Pocillopora* was the dominant taxon in Yanbu, widespread in Al Wajh, and much less common in northern and southern sites. Coral cover throughout the region averaged about 20 %, with higher cover (often >50 %) in shallow water and rapid decline with increasing depth. In each region, many reefs (15–36 %) showed signs of damage and had less than 5 % live coral cover. These degraded sites were characterized by extensive dead skeletons in growth position, substrates colonized by thick mats of turf algae and soft corals (*Xenia*), and surviving massive and plating corals that were subdivided by partial mortality into numerous small (<10 cm) ramets. Mortality was attributed to bleaching events, disease, and outbreaks of corallivores occurring over the last 10–15 years. Several sites also exhibited signs of recent mortality from crown of thorns sea stars (*Acanthaster*), coral-eating snails, and coral disease. In many cases, the *Porites* framework had been recolonized by

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faviids, acroporids, and other corals and these had subsequently died. Most degraded areas appeared to be rebounding, as substrates had high cover of crustose coralline algae (CCA), little macroalgae, and high numbers of coral recruits and juvenile corals.

Introduction

The Red Sea contains unique, biologically diverse coral reefs that exhibit striking contrasts in their biology, environmental attributes, and degree of human influence. The reefs form part of the greater Indo-Pacific region and are the most biologically diverse reef communities outside of the southeast Asia coral triangle. Coral species overlap with Indian Ocean fauna and also contain about 10 % endemic species, with over 260 reported coral species in 68 genera and 16 families (Sheppard et al. 1992). The small geographic range of several species suggests long periods of isolation, its extreme environment, and the limited exchange that occurs through the Bab-al-Mandab Strait (Persga 2006). Red Sea coral reefs are some of the most northerly reef communities and are subjected to harsh climatic conditions including temperature and salinity extremes and high solar radiation (DeVantier and Pilcher 2000). Inflowing surface currents and winds vary seasonally, affecting water temperature, salinity, upwelling, and wave action and exchange with the Indian Ocean (Behairy et al. 1992). The Red Sea is also unique for having unusually warm temperatures that extend throughout the water column.

Most of the Red Sea is characterized by fringing coral reefs that extend nearly 2,000 km from the Gulfs of Suez and Aqaba in the north to Bab-al-Mandab and Gulf of Aden in the south (Persga 2006). Fringing reefs form a narrow border a few kilometers wide along the shoreline and surrounding islands, dropping steeply into the depths of the Red Sea. Fringing reefs are 5,000–7,000 years old (Behairy et al. 1992) and largely formed by a framework of *Acropora* and *Porites* corals.

Off much of Saudi Arabia, the coastal shelf is wider and it supports extensive sea grass, coral reef, and mangrove habitats, with shallow reef communities found from the shoreline to distances of up to 50–100 km offshore (Bruckner et al. 2011a). These areas support a wide range of reef morphologies, including barrier reefs, platform reefs, patch reefs, and atoll-like tower reefs. The offshore reef formations are unusual in that they defy classic (i.e., Darwinian) coral reef classification schemes. Their development is attributed to (1) the high levels of tectonic activity that characterize the area, (2) salt diapirs, (3) hyper-arid climate punctuated by extreme rainfall events during low sea-level stands, and (4) sediment delivery through wadis and other drainage basins (Bruckner et al. 2011a; Rowlands et al. 2014). The wide range of environmental conditions, latitudinal gradient, and the underlying geologic structure all contribute to the development and persistence of these highly variable coral habitats (Bosence 2005). Their future survival may be integrally linked to the degree of anthropogenic influences.

Human pressures associated with two centuries of rapid industrialization and precipitous economic growth increasingly threaten the fragile coral reef environments of the Red Sea. According to the 2011, *Status of Coral Reefs of the World*, the Red Sea is extremely vulnerable to environmental threats posed by large coastal populations, overfishing, pollution, and coastal development (Burke et al. 2011). Nearly 60 % of the reefs in the Red Sea are at risk from landfilling and dredging, port activities, sewage and other pollution, and tourism (Burke et al. 2011). Global stressors associated with climate change are also predicted to have major compounding impacts on Red Sea coral reefs. Mass coral mortality occurred due to bleaching in the central to northern Saudi Arabian Red Sea in late 1998 (DeVantier and Pilcher 2000), but most showed promising signs of recovery a decade later (Wilkinson 2008). In 2005, coral reefs were reported to be generally in good condition, with 30–50 % live coral cover at most locations and more than 50 % total cover on average at 5 m depth (Persga 2006). While no bleaching was noted between 2006 and 2009, a mass bleaching event occurred in central Saudi Arabia in 2010 (Riegl et al. 2013). Thermal stress and ocean acidification are projected to increase threat levels up to nearly 90 % by 2030; by 2050, these climate change impacts, combined with current local impacts, will push all reefs in the Middle East to threatened status, with 65 % at high, very high, or critical risk (Burke et al. 2011).

This chapter provides an overview of the current status of reef-building corals on different reef systems throughout the Saudi Arabian Red Sea, with emphasis on five regions with prominent offshore reef systems. The distribution, abundance, cover, population structure, and condition of corals are compared within and among these five regions. A detailed description of the major biotic threats affecting the coral communities is also presented. The data included in this report represent a collaborative effort of multiple scientists that participated in a four-year research mission conducted by the Khaled bin Sultan Living Oceans Foundation.

Methods

Coral community structure was examined on 129 reefs in five regions (Fig. 1) including Ras Al-Qasabah ($n = 19$), Al Wajh ($n = 21$), Yanbu ($n = 11$), the Farasan Banks ($n = 56$),

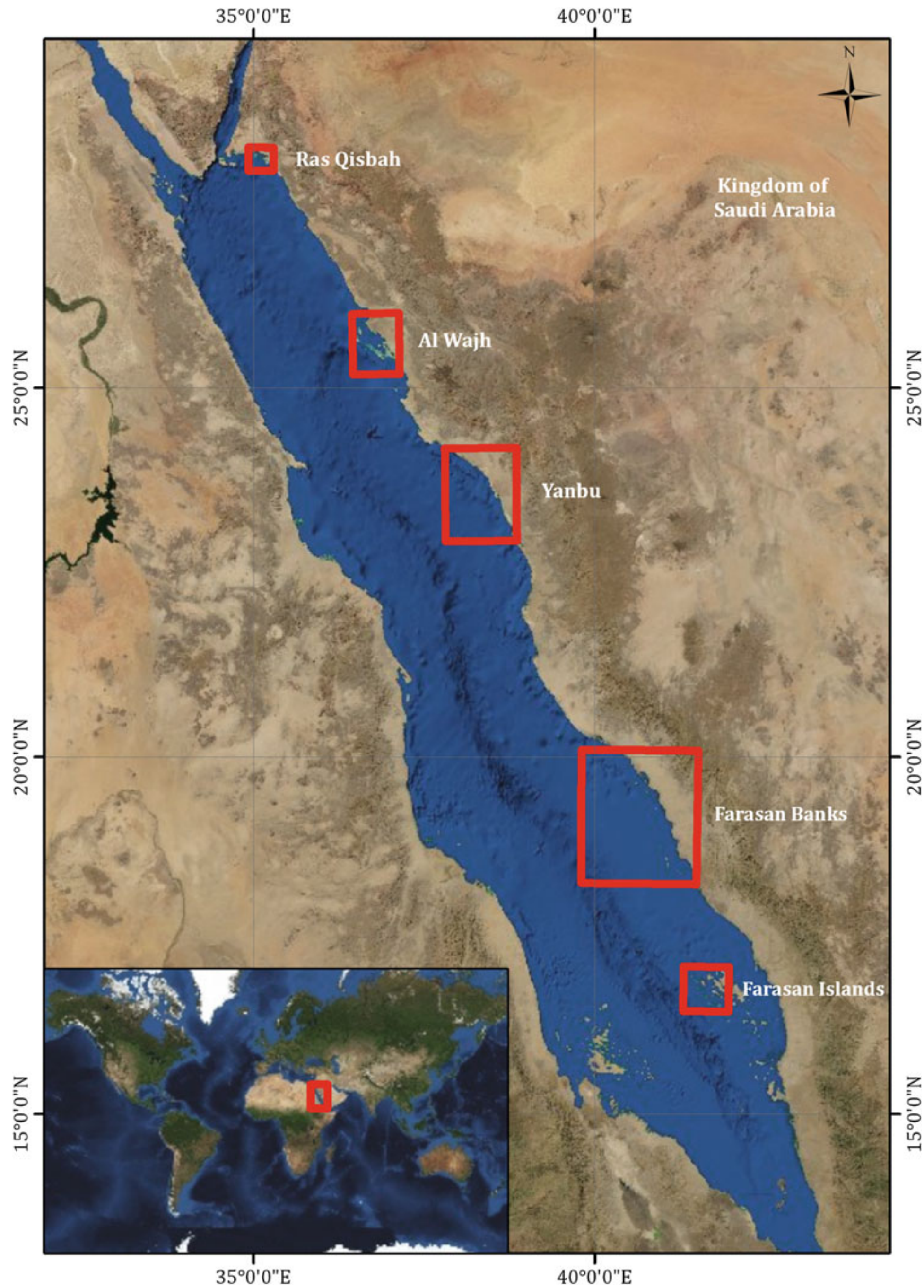

Fig. 1 Five major areas examined by the Khaled bin Sultan Living Oceans Foundation during the four-year research mission. Base image provided by Google

and the Farasan Islands (n = 22) (Fig. 2). On each reef, depth-stratified surveys (3–5, 10–12, and 15–20 m) were conducted using photographic transects, belt transects, and quadrats. Four measures were recorded for corals: (1) coral cover; (2) coral taxa (to genus) and growth form; (3) coral size class distributions; and (4) coral condition (extent of mortality and cause of mortality) (Table 1). The abundance, size, and amount of partial mortality (subdivided into recent and old mortality) of all corals 4 cm or larger in size (recorded to genus) were assessed along either 10 m by 1 m or 25 m by 1 m belt transects using a 1-m bar marked in 1-cm intervals for scale. Sampling for corals smaller than 4 cm was done using a minimum of six 25 by 25 cm quadrats per transect, with each quadrat located at predetermined intervals (e.g., at 0, 5, 10, 15, 20, and 25 m). Measurements varied slightly among sites, depending on the observer. Coral size was measured to the nearest cm on reefs examined in Ras Al-Qasabah, Farasan Islands, and Farasan Banks, while corals assessed in Al Wajh and Yanbu were lumped into six size classes. Coral abundance is presented for each taxon as a percent of all corals recorded within transects and the total planar surface area occupied by that

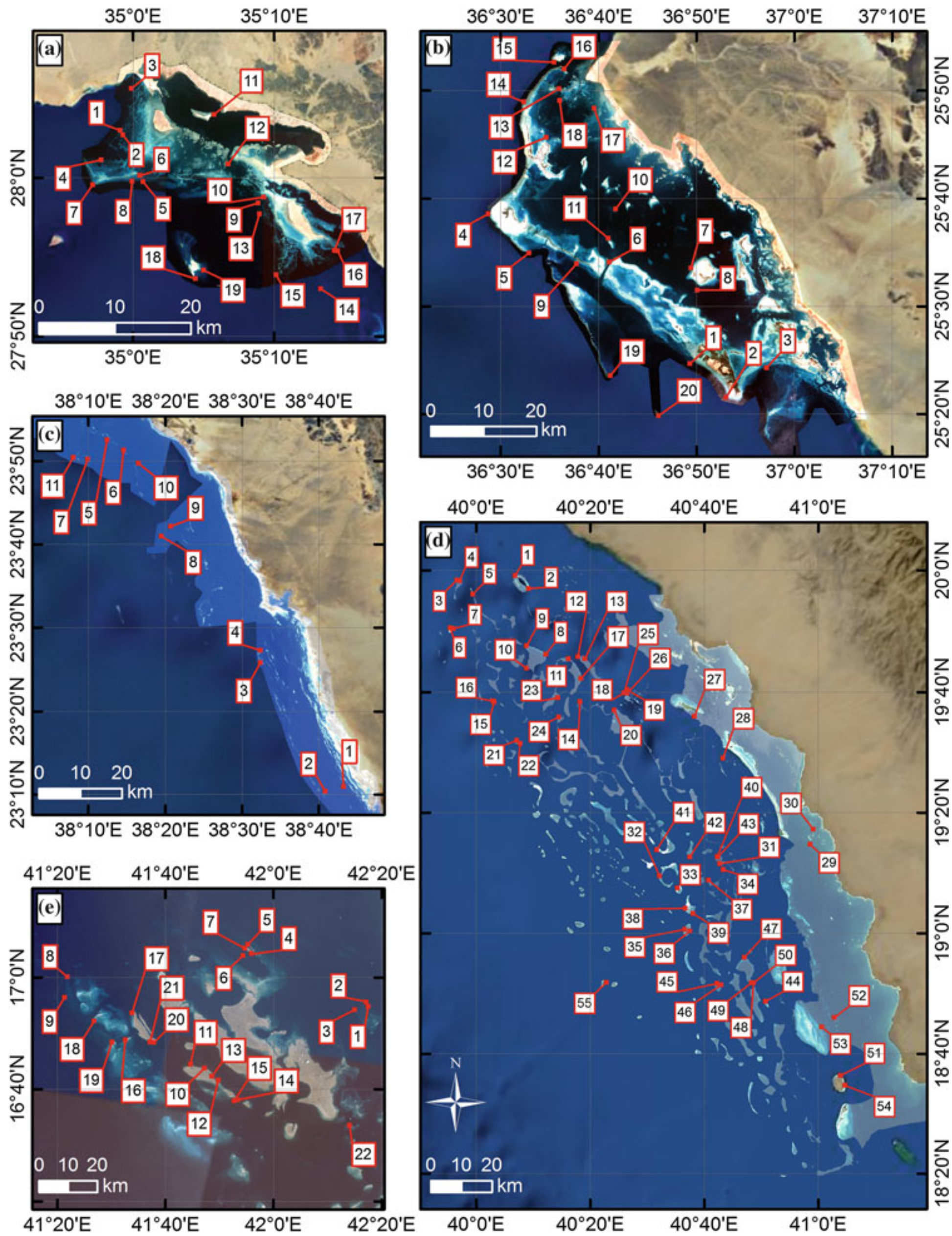

Fig. 2 Location of study sites within each of the five regions. **a** Ras Al-Qasabah; **b** Al Wajh; **c** Yanbu; **d** Farasan Banks; **e** Farasan Islands. For GPS coordinates of sites, see Bruckner (2011b)

taxa. Planar surface area was calculated by multiplying the square of the radius by pi.

For all phototransects, benthic community composition, including cover and size (planar surface area) of corals, cover of other animals (subdivided into soft corals, sponges, and other invertebrates), cover of algae subdivided by functional group (turf, macroalgae, crustose coralline algae, erect coralline algae, and cyanobacteria), and substrate type (rubble, sand, and uncolonized pavement) were assessed using coral point count (CPCE) software developed by the National Coral Reef Institute (NCRI). Cover was determined by recording the benthic attribute located directly below a random point, with 30–50 points per photograph (depending on the size of the image; for example, 30 points for a 0.5-m^2 photograph and 50 points for a 1-m^2 photograph). This software also allowed tracing of the outline of individual corals to determine their planar surface area and size of live versus dead portions of the colony.

Results

Coral Community Structure

A total of 55 genera were recorded in the 5 regions. The Farasan Banks exhibited the highest diversity (54 genera), followed by Al Wajh (52), Yanbu (49), Farasan Islands (46), and Ras Al-Qasabah (44). The spatial distribution of the

Table 1 Resilience assessments for stony corals included in SARS surveys

Measure	Description
Stony coral	Genus-level identification of the composition, abundance, cover, size structure, condition, and level of recruitment within representative habitats
Taxa and growth form	The diversity and structural complexity of a site. Communities with higher numbers of functional groups (e.g., acroporids, faviids, pocilloporids, and poritids) and growth forms (e.g., branching, plating, massive corals), and redundancy of these groups may support more associated species and be more resilient
Cover	Measure of amount of living coral. Small changes in cover are difficult to document, but abrupt changes may reflect a major disturbance
Size structure	Maturity and ecological state of the taxa. Dominance of large corals may be a sign of stable environmental conditions and long-term persistence of the community; a dominance by small corals suggests frequent disturbance or recovery from a recent disturbance
Recruitment	Abundance of recruits reflects the reef's potential for growth and recovery after major disturbances and the influx of genetic diversity
Fragmentation	Level of physical disturbance and potential for asexual propagation. Locations of fragments (accumulations in sand channels or on reef) and fragment condition (no tissue loss; fusion to the substrate; presence of new growth) reflects the potential survival and contribution of fragments to recovery
Dead standing coral	Amount of dead standing coral can be used to hindcast past disturbance events up to a decade or more
Old mortality	Presence of dead areas on corals that are colonized by other biotic agents (e.g., skeleton is not white). Species-specific differences reflect the life history strategies, population dynamics and susceptibility to various physical and biological factors. Old mortality may increase with colony size
Recent mortality	Extent of recent mortality (white skeleton) reflects the severity, timing, and duration of a stressor. Large white areas indicate rapid ongoing tissue loss, while a thin band of white skeleton and a wide band of green, algal-colonized skeleton suggests the event is near its end
Bleaching	Reef-wide bleaching may be associated with recent or ongoing temperature anomalies; extent of recent mortality indicates the duration and severity of the temperature stress
Disease	Spatial patterns of disease reflect potential for spread and level of contagion. Distinction between background mortality (chronic stressors) and of disease outbreaks (acute mortality)
Corallivores	Abundance of coral predators (*Drupella* and *Coralliophila* snails, *Acanthaster* sea stars) indicative of the amount of recent mortality and possible changes to coral community structure and species diversity due to chronic high-level infestations or outbreaks
Competition and overgrowth	Negative factors inhibiting the growth and recovery of corals and causes of chronic mortality (e.g., algal competition) and bioerosion (e.g., sponges). Extent and composition of competitor may reflect status of fish communities (herbivores), nutrient loading, and sedimentation
Coral associates	Obligate corallivores (butterflyfish) provide an indication of the health of the coral community or a particular taxa
	Abundance and diversity of fishes and invertebrates within coral branches are indicative of the topographic complexity and health of the site
	An abundance of territorial damselfish within branches and large algal lawns indicate possible overfishing of piscivores
	High densities of sea urchins may be associated with extensive bioerosion of reef substrates and low recruitment and survival of newly settled corals; macroalgae may increase in with the absence of sea urchins, especially sites with few herbivorous fishes

dominant coral species varied by region, site, and habitat/depth. The dominant genera throughout all sites were *Porites* and *Acropora*, with *P. lutea* being the single most common species (Fig. 3). On offshore habitats in the central Red Sea, the three consistently dominant coral genera over all pooled sites were *Acropora* (average cover over all transects 3 %), *Porites* (2.75 %), and *Pocillopora* (1.3 %). Large mono-specific assemblages of *Pocillopora* were found on shallow fore-reefs in Yanbu; this genus was present but not among the five most dominant species in Al Wajh and Farasan Banks and was rare in Ras Al-Qasabah and Farasan Islands. In Al Wajh, *Montipora* was the second most abundant genera, primarily on offshore reefs, while branching and table acroporids were most common on inshore and turbid reefs. Acroporids were only rarely seen on offshore sites of Al Wajh, with the exception of small digitate acroporids and tightly branched, low-lying colonies in reef crests and shallow fore-reefs (Fig. 3b).

Tabular acroporids formed dense thickets in shallow water (<8 m) on offshore sites at the northern and northwestern end of the bank system in the Farasan Islands, while dense *Acropora* communities were found throughout nearshore and

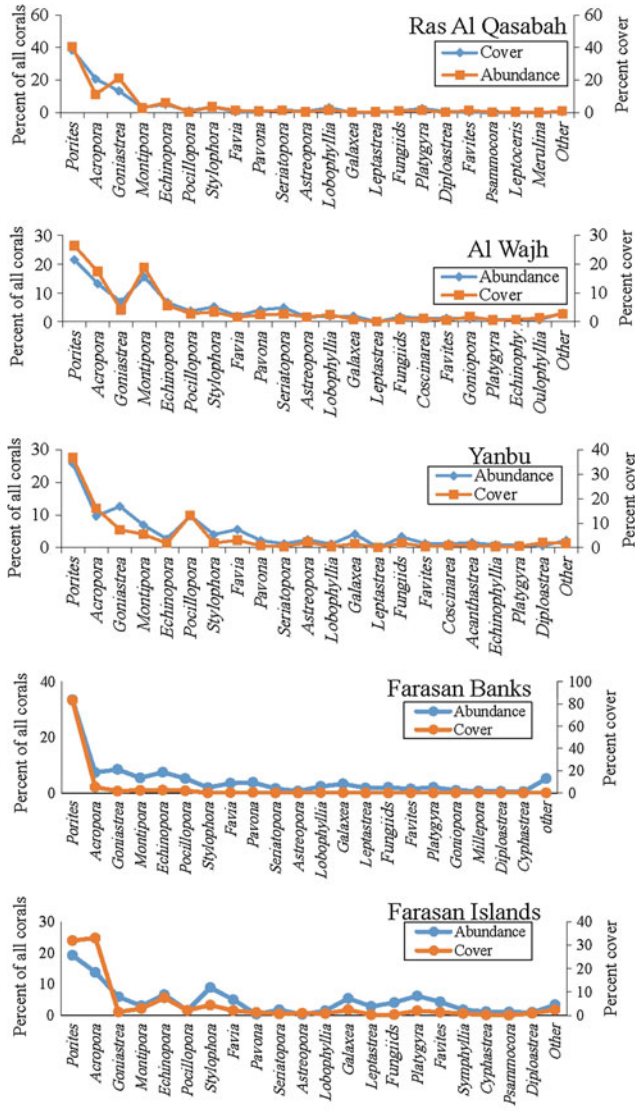

Fig. 3 Relative abundance and area occupied by all of the coral genera identified within belt transects. Each genus is illustrated as a percent of all genera recorded and the total estimated planar surface area of all corals in that genera. **a** Ras Al-Qasabah; **b** Al Wajh; **c** Yanbu; **d** Farasan Banks; **e** Farasan Islands

midshelf locations in the Farasan Banks; *Acropora* was rare overall in Ras Al-Qasabah. Coral assemblages on offshore vertical walls either formed encrusting, foliaceous, and plate-like colonies of *Montipora*, *Echinopora*, *Pavona*, *Turbinaria*, *Leptoseris*, and *Pachyseris*, or small submassive colonies, such as *Stylophora marmorata*; 22 % of offshore locations had large dead stands of foliaceous corals still in growth position. Small *Goniastrea* colonies (recruits and remnants) were the most abundant coral in lagoonal areas of Al Wajh and throughout Ras Al-Qasabah, especially where most of the *Porites* colonies had died.

Coral Cover

The benthic environment in most locations was dominated by scleractinian corals, which were highest at the Farasan Banks (mean cover = 29.4 % ± 13.4 SE; range across sites = 4–60 %) and was lowest at Ras Al-Qasabah (mean cover = 20.4 % ± 10.4 SE; range = 2–40.1 %) (Fig. 4). Dead standing corals also comprised a significant portion of the total cover (mean cover = 10.4 % across all sites). Between 15 and 36 % of sites in each region showed signs of damage and had significantly less living coral cover (1–5 %) and higher cover of dead standing skeletons (14–20 %). This included all of Ras Al-Qasabah, most lagoonal reefs in Al Wajh, and several remote midshelf and offshore locations in Yanbu, the Farasan Banks, and the Farasan Islands.

In all regions except Ras Al-Qasabah, coral cover was usually the highest in the shallow reef crest and fore-reef on outer fore-reef locations (1–5 m depth; 30–70 %). Coral cover declined with depth, with 20–30 % cover at middepths (7–12 m depth), and <5–30 % at the base of the reef slope (15–30 m), especially on midshelf and outer sites. Throughout the Saudi Arabian Red Sea (SARS), *Porites* made up 25 % or more of the living coral cover and over 80 % of the coral cover in the Farasan Banks. The cover of *Acropora* exceeded *Porites* only in the Farasan Islands, mainly due to the dominance of large colonies on offshore locations (Fig. 7b). In all locations, the substrate and dead skeletons were carpeted in soft corals (predominantly *Xenia*;14–20 % cover), encrusting sponges, and other non-coral invertebrates, especially in degraded areas and on deeper reefs (>20 m depth), and these were often competing with hard corals for space and overgrowing surviving remnants. Deep (>20 m) offshore reefs in the Farasan Banks also had low cover of scleractinian corals and large assemblages (30–50 % cover) of organ pipe coral (*Tubipora musica*). Shallow locations in the Farasan Islands, nearshore reef flat communities in Farasan Banks, and areas in Ras Al-Qasabah had high cover of macroalgae and moderate cover of turf algae and crustose coralline algae, while macroalgae were rare elsewhere (Fig. 4).

Coral Size Structure

Corals in all locations were mostly small in size (over 90 % <20 cm diameter), with medium-sized corals (20–40 cm) making up most of the cover (Fig. 5). These differences are due to the non-linear relationship between coral size and surface area as a result of a very high numerical abundance of recruits, juvenile corals, and tissue remnants. Recruits and juvenile corals (<5 cm diameter) were more

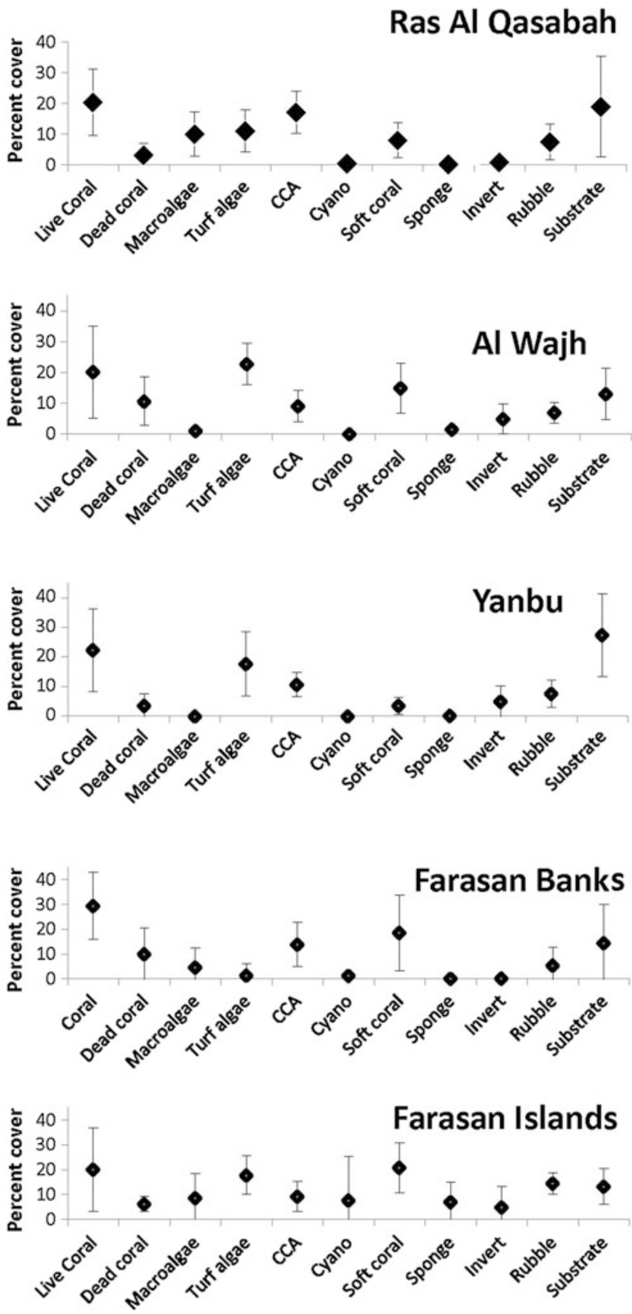

Fig. 4 Benthic cover subdivided into live coral cover, dead coral, algal functional groups (macroalgae, turf algae, crustose coralline algae, and cyanobacteria), benthic invertebrates (soft coral, sponges, and all other invertebrates, pooled), and rubble and uncolonized substrate (sand and pavement). **a** Ras Al-Qasabah; **b** Al Wajh; **c** Yanbu; **d** Farasan Banks; **e** Farasan Islands

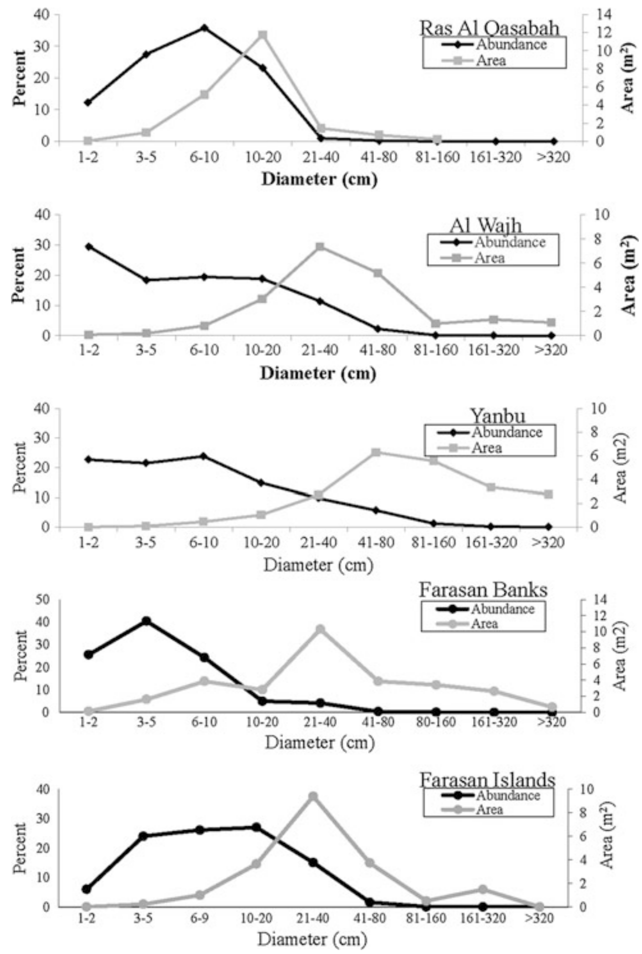

Fig. 5 The total abundance of corals per size class and the total colony area for all scleractinian corals (pooled species). **a** Ras Al-Qasabah; **b** Al Wajh; **c** Yanbu; **d** Farasan Banks; **e** Farasan Islands

abundant than all other size classes at Al Wajh (48 % of all corals; Fig. 5b), Yanbu (44 %; Fig. 5c), and Farasan Banks (38 %; Fig. 5d). Although small corals dominated numerically in these locations, most of the cover consisted of 30–40 cm diameter colonies at the Farasan Banks and 21–80 cm at Al Wajh, while much larger corals (40–160 cm) made up most of the cover at Yanbu. Ras Al-Qasabah (Fig. 5a) and the Farasan Islands (Fig. 5e) had much lower numbers of recruits and juveniles. Even though Ras Al-Qasabah was dominated by small corals (most corals were 6–9 cm diameter with 10–20 cm colonies making up most of the cover), these tended to be surviving tissue remnants on much larger skeletons. While 3–20 cm colonies were most numerous in the Farasan Islands, the bulk of the cover consisted of colonies that were 30–75 cm. The mean colony size also varied greatly between taxa. The largest corals overall were *Porites* and *Acropora*, with low numbers of very large (>1 m) *Diploastrea*, *Galaxea*, and *Montipora* colonies seen in some locations, while faviids (*Favia*, *Favites*, *Platygyra*, *Leptastrea*, *and Cyphastrea*) tended to be small (<10 cm). The size structures for the four most abundant genera (*Porites*, *Acropora*, *Goniastrea*, and *Echinopora*) are shown in Fig. 6.

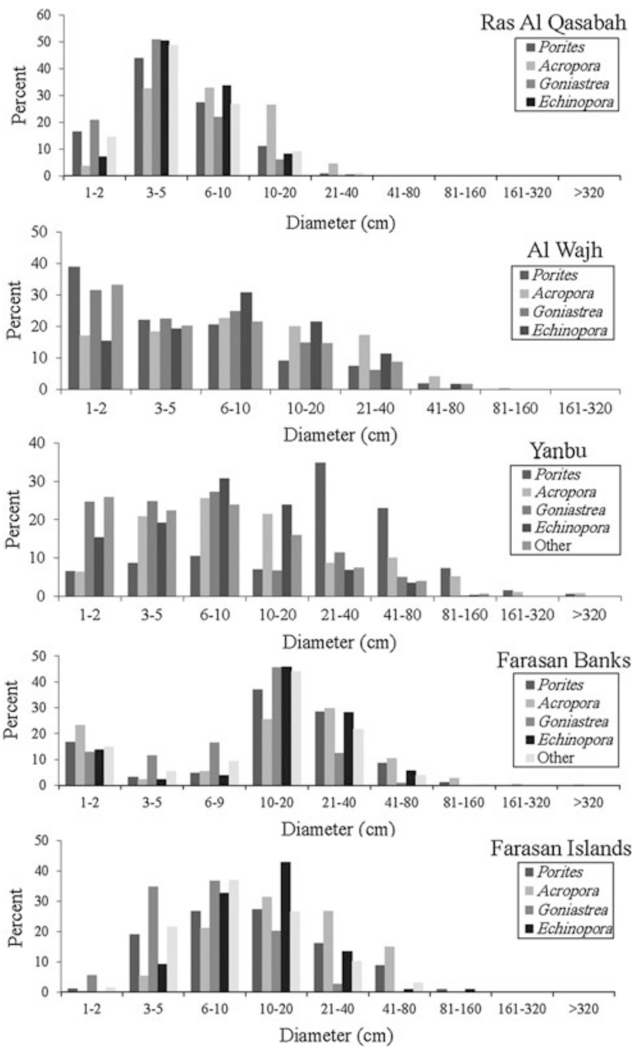

Fig. 6 Size frequency distribution of the four dominant genera of corals and all other species pooled. **a** Ras Al-Qasabah; **b** Al Wajh; **c** Yanbu; **d** Farasan Banks; **e** Farasan Islands

Coral Recruitment

Coral recruitment was lowest at Ras Al-Qasabah and the Farasan Islands, with moderate levels of recruitment documented at fore-reef sites in Yanbu and both barrier reef and lagoonal sites at Al Wajh. The Farasan Banks had the highest recruitment overall, especially in degraded sites; an average density of 3.3 ± 1.7 juvenile corals (<4 cm diameter) per quadrat and ∼13 juvenile corals (>4 cm diameter) per m^2 was documented. Poritids were the most common recruiters (26 %), followed by the faviids (20 %), *Pavona* (12 %), and the acroporids (11 %). Seven genera made up three quarters of all recruits (74.7 %). The distribution of recruitment frequency reflected the dominance of large corals: *Porites* recruited more commonly than *Acropora* and also covered more space on the reefs. The commonly recruiting faviids, which have comparable growth rates to *Porites*, nevertheless covered less space on the reef. Almost the entire encountered *Leptastrea* population consisted of small colonies. Although *Montipora* recruited more frequently than *Acropora* and also has a high growth rate, it was found to cover far less space on the reefs.

Coral Condition

The three major factors responsible for coral mortality identified in SARS are coral bleaching, coral disease, and corallivory. Coral bleaching was rare during the assessments with exception of mild bleaching in 2006, at Ras Al-Qasabah. Coral diseases were identified in all locations, although prevalence was generally low. The most common coral diseases reported for the Indo-Pacific were observed in this study, including white syndrome, brown band, yellow band, skeletal eroding band, and black band disease. Several colonies had sustained extensive partial mortality from diseases, suggesting that diseases play a key role in reef degradation (Fig. 7).

Coral predation appeared to be the most significant chronic source of mortality affecting these reefs (Fig. 8). In particular, localized outbreaks of *Drupella* snails and crown of thorns starfish (COTS) were noted. Active COTS outbreaks were observed in the Farasan Islands, Al Wajh (lagoonal sites only), and the Farasan Banks, but not in Ras Al-Qasabah. COTS counts ranged from 10 to 498 animals per 100 m^2, with highest densities and the highest number of affected reefs at the Farasan Banks. In the Farasan Banks, nearly 20 % of the sites had sustained near total mortality of adult corals prior to these surveys, and extensive recent mortality at other sites was attributed to ongoing COTS outbreaks. At low density, COTS preferred acroporid corals as a food source and fed only occasionally on poritids. In areas with high densities (Farasan Banks), no prey preference was observed and most taxa were equally affected. At sites that were subjected to intensive COTS depredation in the past, *Diploastrea heliopora* was the only large coral (diameter ∼1 m) that had survived, with high numbers of small (10–20 cm diameter) massive colonies of *Echinopora* and isolated tissue remnants of *Goniastrea.* Several sites that had been damaged prior to these surveys also exhibited extensive mortality on the deeper parts of the fore-reef (>5 m) while healthy coral communities remained in shallow water (2–5 m), suggesting that damage was not due to past bleaching events. Lesions from coral-eating snails (*Drupella*) were observed frequently on *Pocillopora*, followed by *Acropora*, while *Porites* and faviids were mostly affected by *Coralliophila*. In general, *Drupella* caused large patches of tissue loss that expanded across the corals in a band-like manner while *Coralliophila* typically inhabited depressions

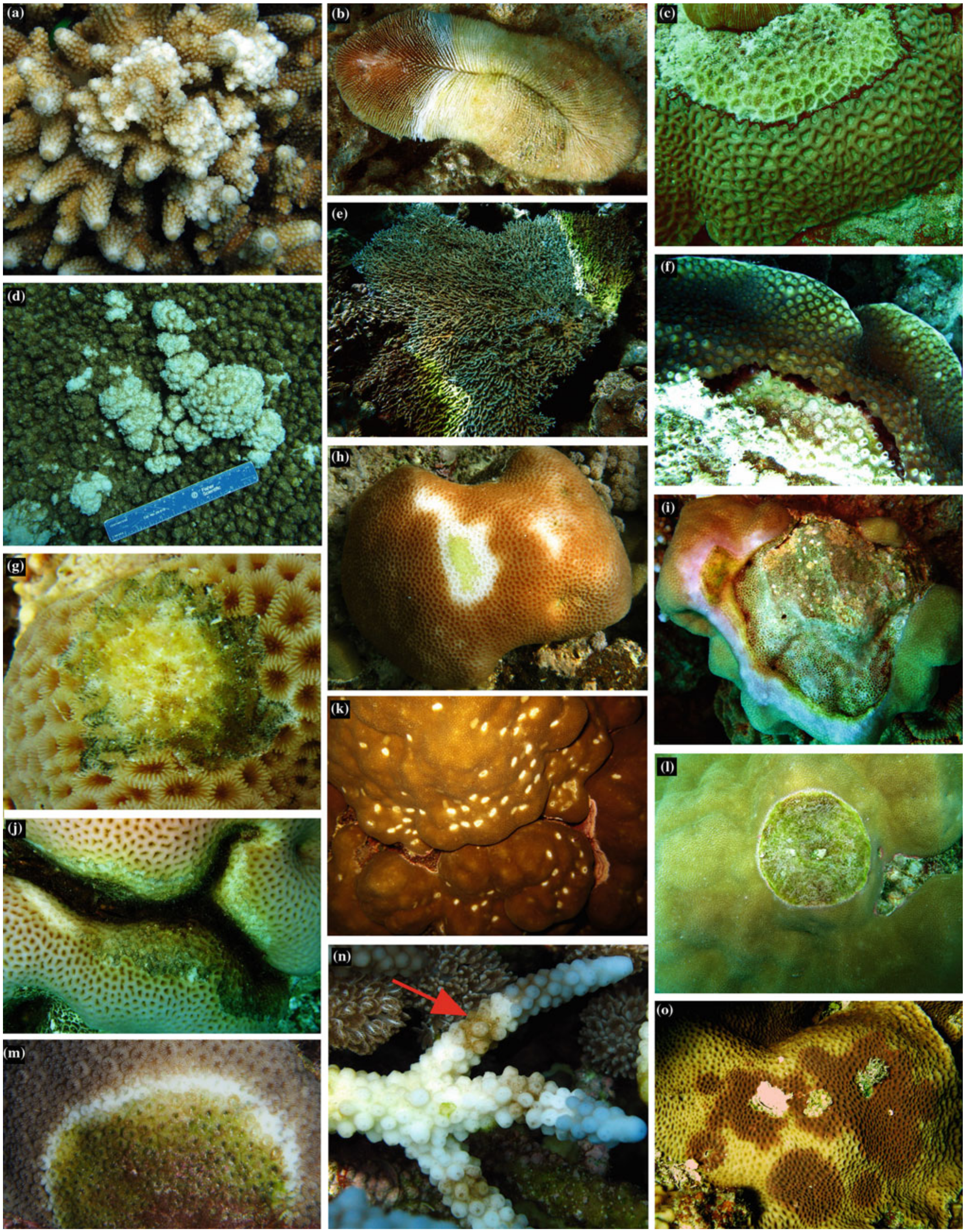

Fig. 7 Coral diseases observed in the Red Sea. **a** Growth anomaly (hyperplasia) on *Acropora gemmifera*. **b** White syndrome on *Ctenactis echinata*. **c** Black band disease on *Favites* spp. **d** Tumors (neoplasia) on a table *Acropora*. **e** White syndrome on *Acropora hyacinthus*. **f** Black band disease on *Echinopora*. **g** Skeletal eroding band on *Goniastrea*. **h** Undescribed multifocal lesion on *Goniastrea*. **i** Pink line disease on *Porites lutea*. **j** Skeletal eroding band on *Goniastrea*. **k** Ulcerative white spots (PUWS) on *Porites*. **l** Pink line disease on *Porites*. **m** White syndrome on *Favia*. **n** Brown band disease on *Acropora*. **o** Dark spots disease on *Goniastrea*

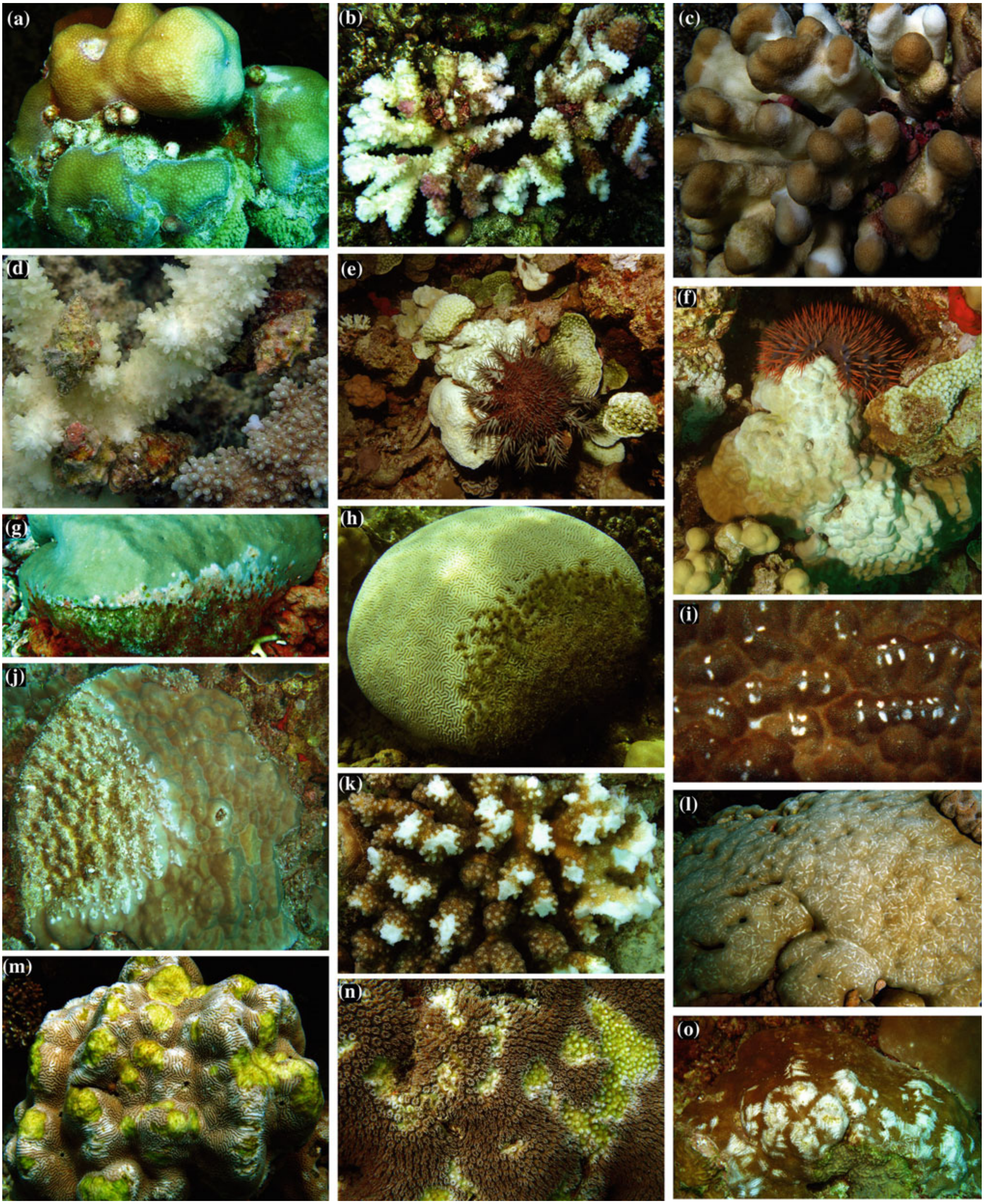

Fig. 8 Characteristic signs of predation observed in the Red Sea. **a** *Coralliophila* gastropods feeding on *Porites*. **b** *Drupella* gastropods feeding on *Pocillopora verrucosa*. **c** *Stylophora* with gastropod predation. **d** Close-up of *Drupella* snails on *Acropora*. **e** *Acanthaster* (crown of thorns starfish) feeding on *Echinopora*. **f** COTS feeding on *Porites*. **g**, **h**, and **j** Damselfish algal lawns on *Porites* and *Platygyra*. **i** Spot biting by parrotfish on *Porites*. **k** *Pocillopora* with branch ends bitten off by parrotfish. **l**, **m**, **n**, and **o** Focused biting by parrotfish on *Leptoria*, *Galaxea*, and *Porites*

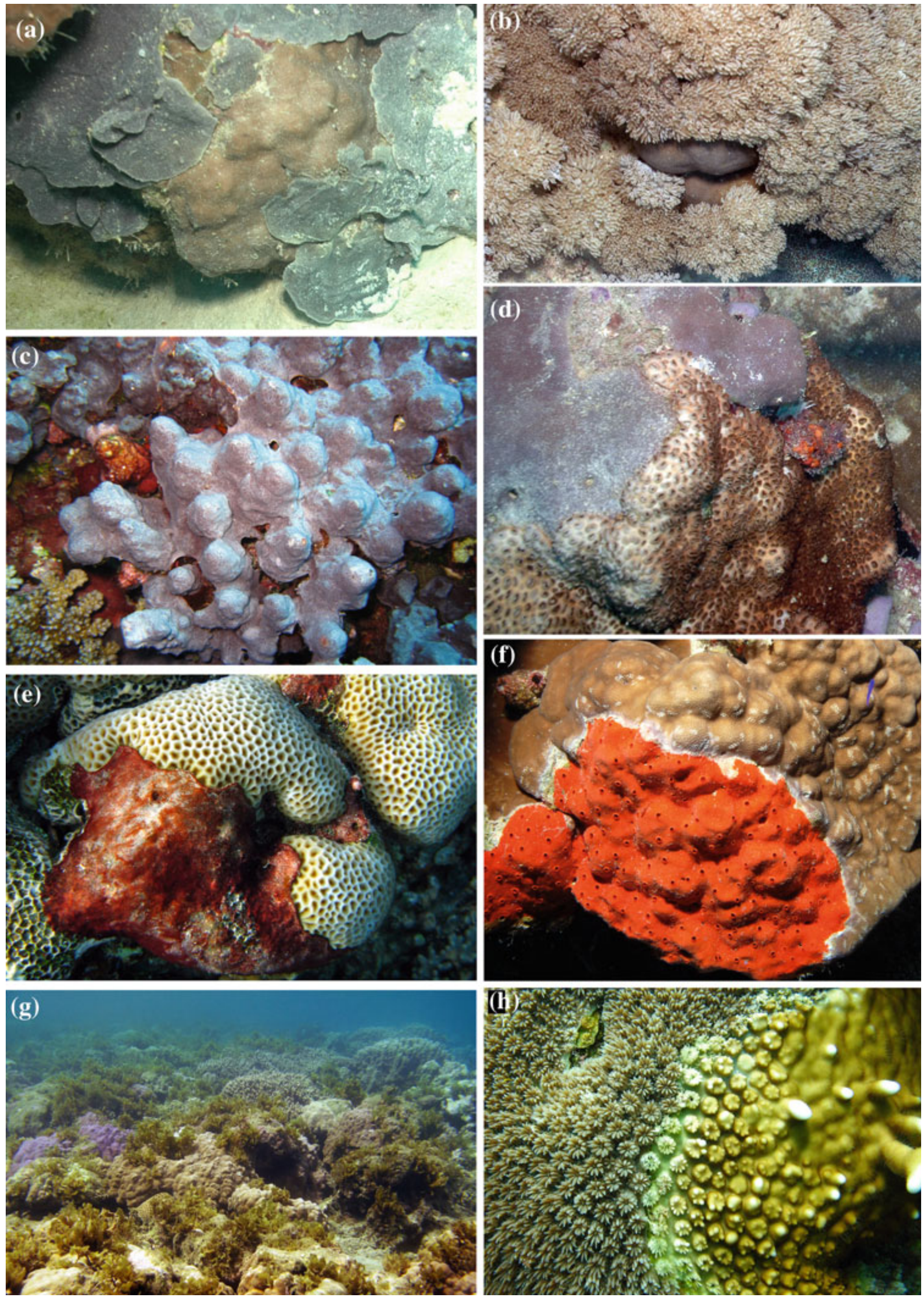

Fig. 9 Nuisance species. **a** Fan sponge (possibly *Phyllospongia*) that commonly overgrows corals in the Farasan Islands and Farasan Banks, shown here covering a *Porites lutea*. **b** *Xenia*, a soft coral that monopolizes substrate, overgrows corals, and inhibits recruitment. *Xenia* was a dominant constituent of deeper reef communities throughout the SARS and is seen here overgrowing a *Porites lutea* in the Farasan Islands. **c** Unidentified encrusting sponge that covered large areas of reef and overgrew corals in deeper locations in the Farasan Banks. **d** Mat of *Palythoa* (colonial zoanthids) overgrowing *Porites lutea*. **e** Cyanobacterial mat on a colony of *Goniastrea*. **f** Encrusting/bioeroding sponge killing a *Porites lobata* colony. **g** Brown macroalgae covered large portions of reef flat communities in nearshore and southern localities. **h** *Millepora* hydrozoan coral overgrowing *Galaxea*

in a colony, especially between lobes, and only rarely caused visible tissue loss. *Drupella* appeared to control the upper size limit of *Pocillopora* colonies in Yanbu, as most corals over 10 cm were infested with snails and few intact colonies over 20 cm were found.

A number of nuisance species (e.g., *Xenia*, clionid sponges, encrusting sponges, leather coral, *Millepora*, zoanthids, and *Peyssonnelia* brown algae) competed and overgrew corals and monopolized substrates. Throughout SARS, the deeper *Porites* framework was largely dead and most of the skeletons were carpeted in mats of *Xenia*. In the Farasan Banks and Farasan Islands, encrusting sponges often formed large mats on open substrates and they were frequently observed overgrowing and bioeroding corals. Macroalgae were generally uncommon, but in parts of Ras Al-Qasabah, shallow nearshore sites in the Farasan Banks, and throughout the Farasan Islands, a substantial amount of substrate was colonized by macroalgae. Damselfish algal lawns were especially common in areas with few predatory fishes (Fig. 9).

Discussion

The assessments conducted in the Saudi Arabian Red Sea, including measures of coral diversity, size structure, condition, causes of mortality, and other benthic attributes present a first indication of the status, vulnerability, and resilience of these reefs. Knowledge of the demographic structure of a coral population can provide insight into the effects of disturbance and resilience of reefs. Coral populations are normally highly positively skewed, with dominance by the smallest size classes and an exponential decrease with increasing colony size (Bak and Meesters 1998, 1999). Larger colonies typically become rarer in a population, but they have a decreased probability of total colony mortality relative to smaller colonies (Hughes and Jackson 1985; Soong and Lang 1992). One consequence of this is that smaller colonies suffer total mortality more frequently than larger colonies, while larger colonies sustain higher levels of partial mortality over multiple disturbances, but have a greater chance of survival (Babcock and Mundy 1996; Hall and Hughes 1996). Thus, size frequency distributions of coral populations are key indicators for categorizing changes in coral communities in response to acute and chronic disturbances and may help identify differences between populations exposed to differing degrees of environmental stressors.

In addition to differences in survival, colony size is an indicator of the reproductive potential of the population. Corals show a positive relationship between colony size and fecundity, with smaller colonies allocating more energy to growth and maintenance and focusing on reproduction only after achieving a critical threshold size (Szmant-Froelich 1985; Harrison and Wallace 1990). Reproductively mature colonies may also regress in size below that minimum threshold, becoming non-reproductive (Szmant 1991). Competitive abilities and regenerative potential also increase with size (Meesters et al. 1994). By combining size structure with estimates of mortality, it is possible to predict whether a population is more likely to continue to contribute to recruitment. A reef consisting of healthy, larger, older colonies with low levels of partial mortality is likely to produce higher numbers of gametes than a reef dominated by juveniles or older colonies with high levels of partial mortality. A population dominated by small size classes may indicate high mortality in intermediate and larger corals (Nyström et al. 2008). Large colonies that have been reduced into tissue isolates that are below the minimum size needed for reproduction may expend more energy on growth and maintenance and less on reproduction (Bruckner 2012).

In SARS, knowledge of the extent of partial and whole colony mortality provided an indication of the severity of past disturbances, resistance of the corals, how much recovery has occurred, and the likelihood that the reef will survive future disturbances. For instance, several offshore reefs in Al Wajh were dominated by large, massive *Porites* colonies with few juveniles; these areas likely have not experienced a recent large-scale disturbance. This suggests that, despite what appears to be a fairly stable community, these reefs may lack resilience to future disturbances, as new corals are not settling or replacing older colonies. Most reefs in Ras Al-Qasabah and lagoonal reefs in Al Wajh had few large corals, several canopy layers of dead corals in growth position, and a high abundance of small tissue remnants, suggesting these reefs have been perturbed very frequently. In contrast, a large number of midshelf and offshore reefs in the Farasan Banks had few large corals, high numbers of skeletons in growth position, and an unusually high number of recruits, indicating a mass die-off from a previous disturbance, with signs of rapid recovery.

Ras Al-Qasabah

Reefs throughout the region showed evidence of a past (10–15 years) mortality event that affected 50–75 % of the corals and was responsible for the loss of most of the columnar *Porites* colonies. The *Porites* framework was subsequently colonized by acroporids, faviids, and *Lobophyllia* in shallow water, and foliose and plating *Echinopora* and *Turbinaria* colonies in deeper water but most of these corals had 3–9 years before these surveys, and skeletons remained in growth position. Living coral cover is now lower than in all other regions; surviving corals include highly fragmented remnants of large *Porites* colonies, small massive faviid corals (*Goniastrea* and *Echinopora)* and encrusting *Montipora* and branching corals (primarily *Stylophora* and *Seriatopora).* There were also high cover of *Millepora*, *Xenia*, and *Peyssonnelia*, large areas of uncolonized reef framework, and considerable amounts of rubble.

Coral bleaching events appear to be the major stress responsible for extensive losses of coral at Ras Al-Qasabah. First, extensive mortality was apparent in all sites and depths including shallow water, unlike other regions examined in this study which had prolific coral growth in shallow water (1–5 m) and mortality restricted to middepth and deep sites. Furthermore, during the four-year mission, bleaching was only documented in Ras Al-Qasabah. One contributing factor is that the region is exposed to temperature extremes and it lacks the protective buffering afforded by the upwelling of cooler waters because the eastern boundary current that flows northwards up the Saudi coastline may suppress wind-driven upwelling of deep water. Mortality will therefore be higher than expected during periods of unusual thermal anomalies and more severe than the relatively more healthy neighboring Tiran area (Ras Qisbah) off the Sinai Peninsula. Sites at the edge of the platform along the extensive bank and reticulate reef systems were also affected by pooling of water over shallow reefs, and high outflows of sediment and super-heated water may prevent recovery of these sites and exacerbate the impacts of future bleaching events. The richest coral cover and diversity remain in areas near channels, as tide-driven flow through restricted channels promotes flushing

Al Wajh and Yanbu

The coral community structure at Yanbu and Al Wajh was dominated by small tissue remnants of *Porites columnaris* and high numbers of recruits and juveniles of *Acropora*, *Montipora*, *Goniastrea*, *Favia*, and *Pocillopora.* Although the sites show evidence of a past mortality event, they appear to have stabilized and are now recovering. While many of these reefs are vulnerable to future perturbations, they also show high resilience. Al Wajh has an extensive bank and barrier reef system, and an unusually large lagoonal system with a high number of shallow and differentiated habitats (e.g., grassbed, mangrove, patch reef, and fringing reef). The highest coral cover occurred on the barrier reef and on reefs located near channels, while most lagoonal patch reefs exhibited low cover. The lagoonal reefs appear to have experienced a mass mortality event 6–9 years before these surveys were completed, with coral communities dominated by small, fragmented tissue remnants along with a moderate number of faviid, poritid, and acroporid colonies. These disturbances appear to have affected many of the important framework corals, as evidenced by the extensive amount of dead coral and bioerosion of these colonies. Lagoonal habitats are likely to experience more highly fluctuating temperatures in the shallows, higher sediment transport, lower visibility, stronger/more variable currents, a greater degree of ponding of waters, and moderate to high levels of turbidity. The reefs at Yanbu include extensive shallow coastal marine habitats with large stands of mangroves, submerged grass beds, and a complex offshore barrier reef system consisting of a string of linear reef complexes parallel to the coast and separated by a major shipping channel. Water temperatures are likely to be cooler on offshore sites due to the steeper linear slopes, and thus, bleaching impacts will be less severe. Shading by the reef structure was pronounced; the linear reef system runs north/south, with a high degree of shading on vertical faces and slopes, particularly for the steeper west-facing slopes in the morning. Yanbu's reefs as well as the outer barrier reef sites of Al Wajh are both likely to be exposed to high wave energy and have few sheltered locations.

Farasan Banks

The Farasan Banks contain the most extensive and diverse reef environments in SARS, with fringing reefs along the mainland coast, nearshore algal reefs, circular or elongated patch and platform reefs, barrier reefs, coral pinnacles, and emergent or submerged atoll-like structures. Shallow and deeper reef habitats were dominated by a high cover of living *Porites.* These taxa was both numerically dominant and often the largest corals in the population, although nearly one-third of the sites examined contained large areas of dead *Porites* framework as well as signs of recent mortality from disease and predation. Nevertheless, most mortality was patchy and restricted to middepth and deeper locations, while shallow sites often had 50–70 % living coral cover, suggesting bleaching played a minor role in disturbances. The site experiences large latitudinal and seasonal extremes in temperature, and above-average salinities, two factors that would typically contribute to high mortality of corals. Still, the presence of flourishing coral communities in many of the sites suggests local populations are well adapted to temperature-induced stress, with local environmental extremes likely to be close to their physiological tolerance maxima. In this case, local coral populations may be particularly vulnerable to climate change.

On a positive note, the midshelf and offshore reefs in most sites were surrounded by deep water and strong currents (seasonally changing direction) and exhibited numerous physical attributes (such as steep vertical walls and overhangs) that are likely to moderate temperature extremes. Furthermore, turbid conditions on nearshore reefs reduce UV penetration, also mitigating the potential for coral bleaching. Although many sites appeared degraded, with a near total loss of adult colonies, the region exhibited numerous additional factors that confer resilience. First, the number of coral recruits was 2–10 times higher than that observed elsewhere in the Red Sea and up to 100 times higher than that reported from adjacent areas in the Indian Ocean. Secondly, substrate quality was high and conducive to coral settlement, with low amounts of unstable rubble, very low macroalgal cover, relatively low cover of soft corals, and higher amounts of crustose coralline algae than observed in other areas along the Saudi Arabian Red Sea coastline.

Farasan Islands

Coral communities in the Farasan Islands were largely restricted to windward and leeward coral crests, located seaward of the major islands, while nearshore habitats were largely algae-covered pavements, sand flat communities, seagrass meadows, mangroves, patch reefs, and macroalgal-dominated fringing reefs. Live corals typically formed small patches in shallow water (<8 m) surrounded by rubble fields and sediment covered algal pavements, with low cover of living corals in deeper water, except for offshore locations. Most of the sites with the highest living coral cover were located to the west and northwest of Farasan Kabir, especially those sites on Al Baghlah Bank, Massad Island, Shuma, and Lajhan. Located far offshore, they have much less siltation than nearshore habitats. In contrast, reefs off the main islands, including Zufaf Island and Dushuk Island, were much more degraded. These sites had higher abundances of soft corals, encrusting and bioeroding sponges, macroalgae, and cyanobacteria. This community shift may be the result of a number of stressors, namely land-based nutrient loading and/or reduced herbivory. While many sites showed signs of previous disturbance events evidenced by extensive rubble, dead coral, and colonization by early recruiting soft corals, the high proportion of small colonies throughout these disturbed sites is indicative of the success of recent successful recruitment events and progressive regeneration.

Conclusion

Like elsewhere, SARS coral reefs have been subjected to serious disturbances over the past few decades including the 1998 bleaching event (DeVantier and Pilcher 2000). Sites examined during these surveys had been impacted by ongoing COTS outbreaks and had clearly suffered from past bleaching. Causes of coral mortality could be clearly identified in most cases; in other cases, low coral cover and high numbers of dead and mostly dead colonies in growth position bore testimony of disturbances that had occurred in the recent past (10–15 years). Impacts to these sites occurred in all habitats and reef zones although the severity of damage was highly variable. Many reefs appeared to have been disturbed, undergone recovery, and then damaged again, while others showed few signs of degradation. The variability between sites and within individual reefs, coupled with the number of degraded reefs, suggests that local disturbances acting on individual reefs (e.g., COTs and disease outbreaks) have been more common than region-wide (e.g., mass bleaching) events.

While diversity remained fairly high, the occurrence of completely denuded reefs and low remaining species diversity on these sites suggests that some of the rarer coral species identified from the region during earlier studies are likely to disappear (Sheppard 1985; Sheppard and Sheppard 1985, 1991; Devantier et al. 2000). Although coral community differentiation with regards to zone-forming genera was still apparent throughout SARS, there appears to be a loss of the largest colonies, especially some of the slower growing taxa that were reported in previous studies (Kleemann 1992; Riegl and Piller 1997, 1999; Devantier et al. 2000). While numerous unusually large skeletons were encountered, in degraded areas, surviving colonies consisted largely of small tissue remnants. Further, there has been a general shift from *Acropora* and *Porites* in shallow water to faster growing *Stylophora* and *Pocillopora*, and from large *Porites* to smaller faviid colonies in deep water (Riegl et al. 2013). These factors highlight an increase in community homogenization and decline in average size of coral colonies, as reported for other parts of the Red Sea (Riegl et al. 2012).

Although these reefs have undergone extensive degradation over the last several decades, most reefs show a promising trajectory of recovery. The dominant reef frame builders are massive and submassive colonies of *Porites.* This taxon is more tolerant to thermal stress than most other genera and also less susceptible to mortality from disease. Coral diseases were present, but relatively uncommon, with exception of a disease affecting massive *Porites* colonies. Several outbreaks of *Acanthaster planci* (crown of thorns) were noted in midshelf reefs, and these sea stars were negatively impacting sites with the highest live cover of branching acroporid corals.

Nevertheless, their target species are among the fastest growing corals and they exhibited very high levels of recruitment. A high diversity of reef-building corals exists, including multiple growth forms and resistant taxa, many functional groups, and a wide size range extending from the small (juvenile and recruits) to large-sized colonies. In areas with widespread mortality of adult corals, the dead colony structure remained largely intact, and substrate quality was high, with high cover of crustose coralline algae. Further, the presence of unusually high numbers of juvenile corals and recruitment levels that often exceeded those reported from other locations in the Red Sea and Indian Ocean suggests these reefs are undergoing rapid recovery. Reefs also exhibited a number of environmental and physical factors that confer resilience. In general, reefs in central and southern SARS had relatively high structural complexity, several canopy layers (which helps shade corals), low amounts of loose rubble (which makes the substrate unstable and reduces the settlement of corals), and little macroalgae (which overgrows and smothers slower growing corals).

Although most damaged areas were showing promising signs of recovery during these surveys, many areas are at a critical threshold and could fail to recover from future disturbances. Firstly, the region is under increasing pressure from artisanal and subsistence fisheries (Bruckner 2011a; Bruckner et al. 2011b) and most of the fishing occurs within the lagoon and nearshore sites, where corals are under the greatest stress from temperature perturbations and land-based stresses. As populations continue to expand in coastal areas, the consequences of human threats are likely to worsen. The presence of cyanobacterial mats, a rarity of detritivores (e.g., sea cucumbers), a scarcity of large herbivores, coupled with high cover of *Xenia* (carpeting much of the *Porites* framework), increases in other nuisance species (encrusting and bioeroding sponges, damselfish algal lawns) provide strong evidence that substrate quality may be declining. The five regions examined in this study contain the most unique and extensive coral reef ecosystems found in the Red Sea, and they support extensive associated nursery habitats (e.g., mangroves and seagrass beds). As climate-related stressors in the Red Sea continue to increase (Cantin et al. 2010), it is critical that human impacts to these areas are reduced and more consideration is given for the inclusion of these areas in a network of marine protected areas.

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