FAUNA OF ARABIA **23**: 1–40 Date of publication: 15.07.2007

Reef-building corals and coral communities of the Yemen Red Sea

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Abstract: The types of reef forms and the composition, diversity, zoogeographic affinities and ecological status of coral communities of the Yemen Red Sea were assessed between 1996 and 1998. Contemporary coral growth occurs as true accreting reefs fringing the mainland coast and islands, submerged patch reefs, and in non-accreting coral assemblages typically associated with three forms of substrate: “red algal reefs”; relic Pleistocene to Holocene reefs; and lava flow terraces and volcanic rock pinnacles. Together these structures host a moderately diverse stony coral fauna of ca 221 scleractinian species (54 genera, 15 families), including Red Sea endemics and species previously unknown from Arabian seas. Zoogeographic affinities of the northern area of the Yemen Red Sea appear similar to the more adjacent Red Sea coast of Saudi Arabia (e.g. Farasan Islands). The southern area shares more similarities with the Gulf of Aden (Belhaf - Bir Ali area). Local coral populations are acclimated, and perhaps genetically adapted, to a harsh physico-chemical environment, surviving at high sea temperatures (average 31 °C, max. 35 °C) that typically kill conspecifics in other reef regions. Hierarchical cluster analysis derived six coral community types distributed in relation to prevailing environmental conditions: physical exposure, water clarity, sea temperature, substrate type, slope angle and depth. The communities exhibited high variability in condition, mostly related to the differential effects of coral bleaching and predation by crown-of-thorns seastars in the 1990 s, with living cover of hard corals, dead corals and macroalgae averaging 11 %, 29 % and 21 %, respectively. Because these communities occur near the tolerance limits for coral growth and reef development, any additional impacts may prove catastrophic. Management should focus on conserving the healthy reefs of the offshore islands (e.g. Hanish and Zubayr groups), as these may be the main source of coral recruits for the recovery of mainland coastal and nearshore coral populations, which have been severely damaged in the last decades. They may act as ‘stepping stones’ for gene flow connecting populations in the Red Sea more generally.

المرجان الباني للحيود البحرية ومجتمعات المرجان في الجزء اليمني من البحر الأحمر

ايمري توراكو وجون برودي وليندون ديفانتير

خلاصة: تم تحديد وتقييم اشكال الحيود البحرية المرجانية وتركيبها وتنوعها وصلاتها الجغرافية الحيوانية والحالة البيئية لمجتمعات المرجان في الجزء اليمني من البحر الأحمر خلال الفترة بين ١٩٩٦ و ١٩٩٨. يوجد النمو المرجاني حالياً على شكل حيود بحرية متنامية ومتصلة بشواطىء اليابسة والجزر وبحيود بحريه متجمعة تحت الماء وبحيود بحرية مرجانية غير متصلة مرتبطة بثلاثة أنماط من القيعان: حيود بحرية مرتبطة بالطحالب الحمراء وحيود بحرية متبقية من العصرين البلستوسيني والهلوسيني وحيود بحرية متكونة حول مجاريٍ الحمم البركانية وقمم الصخور البركانية. تستضيف جميع هذه التراكيبٍ أنواعاً من المرجان الصخري المتنوع نسبيا، حيث تضم ٢٢١ نوعاً ضمن ٥٤ جنساً و ١٥ عائلة، متضمنة أنواعاً متوطنة في البحر الأحمر وأنواعاً غير معروفة في البحارالعربية. وعلى ما يبدو، فإن الصلات الجغرافية الحيوانية للمناطق الشمالية من الجزء اليمني للبحر الأحمر تشبه تلك للجزء السعودي المجاور للبحر الأحمر (جزر فراسان

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على سبيل المثال). تشترك المنطقة الجنوبية بتشابهٍ أكبر مع تلك الموجودة في خليج عدن (منطقة بلحاف بير علي). تأقلمت جماعات المرجان المحلية وربما تكيفت وراثياً مع هذه البيئة القاسية من الناحية الفيزيائية الكيميائية، حيث تعيش على درجات حرارة مرتفعة (معدل ٣١ درجة مئوية وباقصى درجة تصل إلى ٣٥ درجة مئوية) والتي عادةً ما تكون كافية لقتل الأنواع المشابهة في مناطق حيود بحرية مرجانية أخرى. اشتق من التحليل الهرمي للمجموعات ٦ انماط من مجتمعات المرجان متوزعة حسب علاقتها بالظروف البيئية السائدة: التعرض الفيزيائي وصفاء المياه وحرارة البحر ونوع القاع وزاوية الميل والعمق. تبدي هذه المجتمعات تبايناً شديداً في حالتها وذلك على الأغلب مرتبط بالتأثير المتباين لإبيضاض المرجان والافتراس من نجوم البحر شوكية التاج في عام ١٩٩٠، وبوجود غطاء حي للمراجين الصلبة والمراجين الميته وبطحالب كبيرة بمعدل ١١% و ٢٩% و ٢١% على الترتيب. وحيث تعيش هذه المجتمعات على حدود الإحتمال من أجل النمو وتطور الحيود البحرية، فإن أي تأثيرات اضافية يمكن أن تتسبب في حدوث كارثة. يجب أن تركز جهود الإدارة البيئية على حماية الحيود البحرية الحيوية حول الجزر (مجموعة جزر حنيش والزبير على سبيل المثال)، حيث تمثل هذه المجتمعات المصدر الرئيسي لإمداد وتجديد المرجان من أجل استرداد جماعات المرجان للمناطق الساحلية والقريبة من الشاطىء، والتي أُلحق بها الأذى الشديد في العقود الماضية. ومن الممكن أن تقوم هذه الحيود البحرية بمصدر نشر للجينات الوراثية لتربط جماعات المرجان في البحر الأحمر بشكل عام.

INTRODUCTION

The Yemen Red Sea coast is ca 760 km in length (KRUPP et al. 2006), extending from the Saudi Arabian border in the north, at approximately 16°22' N to the entrance to the Red Sea at Bab al-Mandab in the south, at approximately 12°45' N (Fig. 1). The area is estimated to support ca 700 km^2 of coral reefs (SPALDING et al. 2001), including reefs fringing the mainland coast and continental islands at various distances from the mainland, some of which are of volcanic origin in deeper offshore waters. There are also extensive shallow reef patches, most less than 10 m in depth, on coastal shallow water deposits dominantly of terrigenous origin.

The coastal and island fringing reefs, patch reefs and coral pinnacles cover approximately 25 % of the coastline in total (KOTB et al. 2004). Reef development is generally reduced in comparison with the central and northern Red Sea, in part because of the different coastal topography characterized by extensive coastal shelves with shallow bathymetry, and also because of more 'marginal' environmental conditions for coral growth and reef-building (see e.g. GUINOTTE et al. 2003). Near Midi the 'continental' shelf extends 100 km offshore while in the south it is less than half this width. These areas are often dominated by soft substrates of thick alluvial sediments that may be unsuitable for coral settlement. Strong seasonal southerly winds and related water movements mobilise these sediments, resulting in high turbidity and related sediment stress to any corals present. The broad aerial extent and shallowness of the shelf also restricts water exchange and can result in comparatively high average and maximum water temperatures. Accordingly, "reef" structures often do not display classic form, but rather a reef flat and crest are barely developed and the slope is limited to a few metres in depth and length (TURAK & BRODIE 1999, KOTB et al. 2004).

The more than 100 islands support a variety of different coral communities, many of which had not been assessed, a major objective of this study. The island fringing reefs are based on fossil reef plateaus situated on the continental shelf (e.g. the Kamaran group or the southern Farasan) and offshore islands of volcanic origin situated away from the shore in clearer water (e.g. the Hanish, Zuqar and Zubayr groups). Beyond the shelf edge, the islands rise from 200 m to 1000 m depth.

Many Yemen Red Sea reefs are markedly different to their more northerly Red Sea counterparts, notably in geomorphology and species diversity (reviewed in SHEPPARD et al. 1992). The major defining characteristics of coral growth in the Yemen Red Sea are the extent of non-reefal coral communities and limited reef building by corals (SHEPPARD et al. 1992). Generally, the amount of reef development is dependent on the degree of reef building (net biogenic deposition or accretion rates by corals and other sessile benthos) versus reef destruction by bioerosion, physical destruction and chemical dissolution rates, and locality of growth (Davies 1982). These are in turn related to other locality-specific physical and biological parameters, such as water temperature, water movement in the form of tidal and wind driven currents, the organic and inorganic dissolved nutrients, and food particles such as phytoplankton, zooplankton and detritus. All of these factors have an influence on coral growth, reproduction, survival and general condition or 'health' of individual corals, and thus on the ability to build reefs. Assessment of the extent and degree of recent reef-building, and the governing or controlling factors, was one objective of the present study.

The ecological and physico-chemical controls of diversity and reef-building, operating on annual to decadal time-scales, are superimposed on the much longer-term geomorphological, paleo-climatic and paleo-zoological history of the region, as introduced briefly below.

Geological History and Paleo-zoogeography

The Yemen Red Sea has a relatively complex geomorphological history, related to tectonic movements and climatic regime, as briefly reviewed below. Episodes of volcanic activity, extensive evaporation, vast alluvial flows, marine sedimentation, uplift and subsidence associated with tectonic rifting shaped the foundations for today's reef development. Particularly during the Oligocene, intense volcanic activity created some of the large basaltic deposits in Yemen (reviewed in Bosworth et al. 2005), including a chain of volcanic remnant islands (Hanish and Az Zubayr groups, and At Tair Island).

"Plume related basaltic trap volcanism began in … SW Yemen at ~ 31 Ma, followed by rhyolitic volcanism at ~ 30 Ma. … By ~27.5-23.8 Ma a small rift basin was forming in the Eritrean Red Sea. At approximately the same time (~25 Ma), extension and rifting commenced within Afar itself. At ~24 Ma, a new phase of volcanism …appeared nearly synchronously throughout the entire Red Sea, from Afar and Yemen to northern Egypt. This second phase of magmatism was accompanied in the Red Sea by strong rift-normal extension and deposition of syn-tectonic sediments, mostly of marine and marginal marine affinity. … Throughout the Red Sea, the principal phase of rift shoulder uplift and rapid syn-rift subsidence followed shortly thereafter at ~20 Ma. Water depths increased dramatically…The local geometry of the Red Sea rift was strongly influenced by pre-existing basement structures, and as a consequence followed a complex path from Afar to Suez. …" (Bosworth et al. 2005).

Also commencing during this period was the formation of thick salt deposits, today an important area of uplift caused by weight of overtopping younger rocks (Behairy et al.1992, Sheppard et al. 1992). During the Miocene and Pliocene, episodes of closure of the connection with the Mediterranean and opening of the connection with the Indian Ocean, in part relating to the closure of the Tethys Seaway, introduced a new biota from the Indian Ocean to the Red Sea. This formed the basis for today's biota, as reef-associated species dispersed from the Indian Ocean through the newly formed strait at Bab al-Mandab.

The major glacial periods of the Pleistocene brought profound changes to the physico-chemical environment, including major fluctuations in sea level of the order of 120 m (Fairbanks 1989, Rohling et al. 1998), associated shifts in salinity and temperature, periods of extensive rain and associated terrigenous sediment deposits. The major drops in sea level, to the level of the shallow sill at the entrance at Bab al-Mandab, may have isolated the Red Sea from the Gulf of Aden and Indian Ocean for several thousand years, although this remains controversial (e.g. see Klausewitz 1989, Sheppard et al. 1992). The physico-chemical changes certainly had major impacts on the ecology of the Red Sea, and when climatic conditions were at their most extreme, some species may have become locally extinct and subsequently been replaced by new arrivals from the Indian Ocean when conditions improved. Also during the Pleistocene, significant periods of uplift raised reefs with 'uplifted margins', a common feature of the Red Sea including the Yemen coast (SHEPPARD et al. 1992). During the Eemian high stand ca. 125,000 years ago, sea levels were some 4-6 m above present levels. In the early part of the Holocene, sea level may also have been about one meter above today's level, and some low lying fossil reefs may be from these periods. During the early part of the Holocene, sea level may have rose about one metre above today's level, and some low lying fossil reefs may be from that period.

Marine Climate and Oceanography

Coral and reef growth in the southern Red Sea are strongly affected by several climatic influences. The region is dominated by the Asian weather system, though some intrusions from the Mediterranean or North African weather systems may affect the northern parts. The Yemen Red Sea is under the influence of the Indian Ocean monsoons (reviewed in SHEPPARD et al. 1992). During the winter months, winds from the east blow along the south of Arabia into the Gulf of Aden and are then channelled into the Red Sea, turning north and blowing along the coasts. During the summer months, when the monsoonal winds ease, winds from the northern Red Sea blow further to the south along the coast and generate significant longshore surface currents. In addition to the seasonal pattern, daily temperature-induced sea breezes, caused by the heating of the Tihama Plain, may build to considerable strength, generating high energy waves.

In the Red Sea tidal fluctuations are small. Diurnal (and semi-diurnal) tidal differences vary from virtually no movement at the centre of the Red Sea (tidal node) to a maximum of one metre in the north (Gulfs of Aqaba and Suez) and south (Bab al-Mandab). Another tidal node of minimum change has been reported from the Mukha area in Yemen (EDWARDS 1987, SHEPPARD et al. 1992). Annual tides related to the wind-driven water movement may add a variation of 0.5 to 1 m. In addition there are episodic tidal variations caused by severe weather conditions. Continuous onshore winds may pile up water nearshore, while offshore winds may push water off reef flats. High evaporation rates from the high temperatures and constant dry winds from the north can cause significant loss of surface water (EDWARDS 1987).

The waters of the Yemen Red Sea are hotter and more saline than most tropical waters. Water temperatures range between 30 °C offshore to 38 °C inshore in semi-enclosed bays during summer (April to October) with temperatures in winter about 5 °C cooler. Water from the Gulf of Aden upwells at Bab al-Mandab, providing cooler waters and sharper temperature gradients around Miyurn Island and the adjacent mainland. The northern Red Sea is highly saline, but Yemen's waters have only slightly elevated salinities. These range from about 36.5 ppt in the Bab al-Mandab to 38 ppt near Midi (Fig. 1).

Yemen lacks true river systems with regular discharge to the sea. While wadis may flow in periods of exceptional rainfall, discharge to the sea is uncommon, typically occurring only during flash floods (KRUPP et al. 2006). Thus no true estuarine systems exist with their complex and diverse mangrove communities. Instead, mangroves in Yemen form thin bands along the coast, dominated by *Avicennia marina*. However, wadis may influence coastal habitats through regular groundwater discharge and through sediment discharge in the rare flood events (KRUPP et al. 2006). Terrigenous sediments are also deposited on nearshore areas as a result of regular sand / dust storms, mostly in the late spring / early summer months. The storms are generated in the mountains, which run 50 to 100 km inland parallel to shore. The cooled air rushes down and across the Tihama plain, picking up dust and depositing it up to several kilometres out to sea. Inshore waters of the Yemen Red Sea are significantly hotter than most inshore tropical waters worldwide. As seagrass and coral communities have acclimated and perhaps adapted to the high temperatures (GATES & EDMUNDS 1999), these ecosystems may function differently from their counterparts in other regions of the world.

History of coral research in the Yemen Red Sea

Several of the earliest European marine scientific explorations (e.g. FORSKÅL 1775) were conducted in Yemen (briefly reviewed in KRUPP et al. 2006). Many of the early scientists, including Forskål, Ehrenberg, Klunzinger, Botta and Rouseau, made substantial collections of marine fauna and flora, among them many coral specimens. Some of the earliest known coral species descriptions, by LINNAEUS (1767), FORSKÅL (1775), ELLIS & SOLANDER (1786), ESPER (1788-1830), LAMARCK (1816), EHRENBERG (1834), EDWARDS & HAIME (1860) and KLUNZINGER (1879), are of specimens collected from Yemen. Kamaran Island, a large low-lying nearshore island off the Ras Isa peninsula, is frequently cited as the origin for many coral type specimens. From around the turn of the 19th century, taxonomic studies continued (MARENZELLER 1907, GRAVIER 1911), although scientists also became interested in coral reefs as distinct habitats and the first ecological investigations began (GRAVIER 1911; CROSSLAND 1911, 1938).

After the two 20th century world wars, studies again resumed in the area (HASS 1952, ROGHI & BASCHIERI 1956), although most were carried out in the northern part of the Red Sea (Hurghada and Sinai Peninsula) and southern part of the west coast (Dahlak Archipelago of Eritrea and far northern Djibouti). Subsequently throughout the 1960 s and 1970 s many studies were carried out in the far northern Red Sea and Gulf of Aqaba (e.g. FISHELSON 1971, 1973, MERGNER 1971, LOYA 1972) and a few in the Dahlak Archipelago (FISHELSON 1971, HEAD 1980). At the same time, a resurgent interest in coral taxonomy (SCHEER 1971) produced the first modern systematic account of stony, reef-building corals of the Red Sea (SCHEER & PILLAI 1983, SHEPPARD & SHEPPARD 1991). In the last two decades of the 20th century, a large number of ecological and taxonomic studies of reef-building corals were carried out in the northern and central Red Sea, not reviewed herein. Corals of the more southerly areas, including the Yemen Red Sea, however, have received far less attention (e.g. BARRAT et al. 1987, ANTONIUS et al. 1990, SHEPPARD & SHEPPARD 1991, RUSHDI et al. 1994).

Ecological status

These earlier studies notwithstanding, comparatively little was known of the biodiversity or ecological status of Yemen's Red Sea reefs prior to the 1990 s, although a few sites have subsequently formed part of regular monitoring studies (KOTB et al. 2004). It is apparent that the condition of Yemen Red Sea reefs varies widely. Many reefs were badly damaged in the 1990 s by bleaching, predation by crown-of-thorns seastar (*Acanthaster planci)* outbreaks and trawling, with losses of up to 90 % of corals. Some reefs have recovered in the interim period (KOTB et al. 2004), although little to nothing is known for most areas.

The coastline is more heavily populated than many other areas of the Red Sea, and there are oil terminals at Ras Isa, Al Hodeidah and Al Mukha. Oil pollution, sewage and industrial development may be causing local impacts (BRODIE & TURAK 1999, SPALDING et al. 2001). Artisanal fishing provides the primary income for the majority of the coastal population. The reefs supply commercial quantities of reef fish and other products to Yemen, with overfishing in some areas, although previously (ca 1980 s) the reefs appeared to have lower commercial fish catches and lower fish productivity than other areas of the Red Sea (SHEPPARD et al. 1992). Nevertheless, fishing effort has continued to increase, and today is considered to be beyond sustainable levels for certain reef-associated species (KOTB et al. 2004), with steadily declining abundances.

The sea cucumber fishery has also expanded rapidly to supply international demand. Collection of aquarium fish around the Kamaran Islands reportedly uses destructive methods (KOTB et al. 2004). Fishing for shark-fin for the export market has decimated the local shark populations. Industrial and artisanal trawling for cuttlefish, coastal shrimp and inshore demersal fish is also damaging some reefs, while ship groundings have caused serious localized damage.

Objectives

The present study formed part of the GEF-UNDP project 'Protection of Marine Ecosystems of the Red Sea Coast of Yemen', and had four major objectives:

- To describe the extent, structure and distribution of coral reefs and coral communities
- To document coral species composition and community structure
- To document ecological status in terms of benthic cover, levels of damage and impacts of disturbances
- To provide ecological 'base-lines' for future management planning.

Abbreviations

CRA	Coralline red algae
GEF	Global Environment Facility
GPS	Global positioning system
REA	Rapid ecological assessment
SCUBA	Self contained underwater breathing apparatus
UNDP	United Nations Development Program

MATERIALS AND METHODS

Study area and site selection

Field surveys were conducted during three field trips in the Yemen spring season, in May 1996, 1997 and 1998. Site selection was based on references from previous work, topographic and hydrographic maps and aerial photographs, local information and personal observations from reconnaissance trips. Site names listed herein, for which well-recognized local names did not exist, were taken from hydrographical maps and charts. Criteria used in site selection included coverage of habitats types, areas of particular interest or uniqueness, areas of potential impact from industrial, tourism or urban development, potential special management areas and polluted/impacted areas.

Given the size of the study area and number and variety of reefs present, the surveys were neither extensive nor intensive, but rather represented our best attempt to assess the coral communities in a total field period of about 1.5 months. In practical terms, site selection was largely controlled by security, logistics, staffing and time constraints. Nevertheless, a representative selection of 51 sites in mainland, offshore and island reef habitats was assessed (Fig. 1), although some gaps

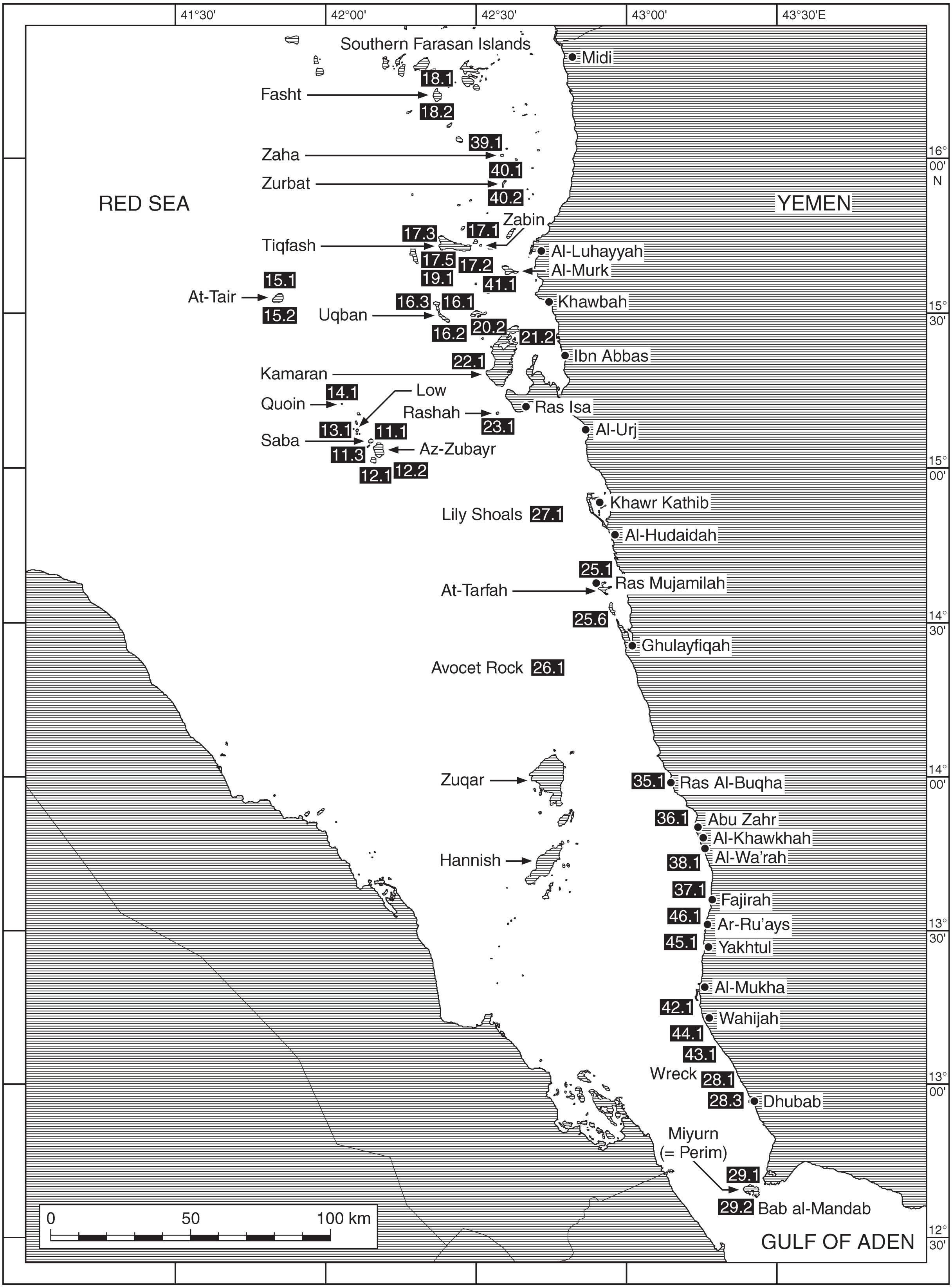

Fig. 1: Map of the study area showing locations of study sites.

Table 1. Categories of relative abundance, injury and sizes (maximum diameter) of each sessile benthic taxon in the biological inventories.

Rank	Relative abundance	Injury	Size frequency distribution
0	absent	0-1 in increments of 0.1	proportion of corals in each of 3 size classes: 1) 1-10 cm 2) 11-50 cm 3) > 50 cm
1	rare		
2	uncommon		
3	common		
4	abundant		
5	dominant		

remained, notably islands off the coast between Al Luhayah and Midi, from Ghulayfiqah to north of Al Khowkhasouth of Dhubab and the islands of the Hanish and Zuqar groups.

Field surveys

At each site, a standard method of rapid ecological assessment (REA) was employed, with information collected at three levels:

- Site identification characteristics (name, GPS, habitat type, date, site number)
- Physical characteristics, as maps and profiles, showing measured or estimated dimensions, zonation and other significant environmental characteristics
- Biological data with the addition of some environmental information (pollution and threats).

The field method for the biological surveys was similar to that employed in the central and northern Saudi Arabian Red Sea and Yemeni Socotra Archipelago (DeVantier et al. 2000, 2004). Thus these three papers provide a standard recent comparison of species composition, community structure and ecological status of corals in the eastern Red Sea and Arabian Sea. Sites were accessed by car (mainland fringing reefs), small boats (nearshore patch reefs) and dive boats (offshore island fringing reefs and patch reefs). At each site, the coral communities were surveyed using SCUBA. The vast majority of sites were shallow (less than 10 m depth) and were surveyed during one meandering swim across the entire depth range.

Each swim was of about 45 minutes duration. Generally the swims covered a distance of between 50 and 150 m along slope. Two types of information were assimilated and recorded on water-proof data-sheets during the survey swims:

- A detailed inventory of sessile benthic taxa, focused on the reef-building hermatypic Scleractinia
- An assessment of the relative percent cover of the substrate by the major benthic groups and amount of reef development (after Done 1982, Sheppard & Sheppard 1985, 1991).

Taxonomic inventories

Taxa were identified *in situ* to the following levels:

- Stony corals - species wherever possible (Veron & Pichon 1976, 1980, 1982; Veron et al. 1977; Veron & Wallace 1984; Veron 1986, 1993, 1995; Scheer & Pillai 1983; Hoeksema 1989, 1993; Sheppard & Sheppard 1991; Sheppard 1997), otherwise genus and growth form (e.g. *Porites* spp. of massive growth-form). Because of logistical limitations for deeper dives the

Table 2. Categories of benthic attributes and percentage cover categories.

Attribute		% cover category	
ecological	physical	Rank	%
Hard coral	Hard substrate	0	not present
Dead standing coral	Continuous pavement	1	1-10 %
Soft coral	Large blocks (diameter > 1 m)	2	11-30 %
Coralline algae	Small blocks (diameter < 1 m)	3	31-50 %
Turf algae	Rubble	4	51-75 %
Macro-algae	Sand	5	76-100 %

coral records and collection do not include deeper water corals, such as from the families Flabellidae, Caryophilliidae and Dendrophylliidae.

- Soft corals, zoanthids, corallimorpharians, anemones and some macroalgae - genus or family (Vine 1986, Allen & Steen 1995, Colin & Arneson 1995, Goslinger et al. 1996, Reinicke 1997).
- Other sessile macro-benthos, such as sponges, ascidians and most algae - higher taxonomic level, usually phylum plus growth-form (Vine 1986, Allen & Steen 1994, Colin & Arneson 1995, Goslinger et al. 1996).

At the end of each swim, the inventory was reviewed, and each taxon was categorized in terms of its relative abundance in the community (Table 1). These broad categories reflect relative numbers of individuals in each taxon at each site, rather than its contribution to benthic cover. These ordinal ranks are similar to those long employed in vegetation analysis (Barkman et al. 1964, Braun-Blanquet 1964). For each coral taxon present, a visual estimate of the total amount of injury present on colonies at each site was made, in increments of 0.1, where 0 = no injury and 1 = all colonies dead. The approximate proportion of colonies of each taxon in each of three size classes was also estimated. The size classes were 1 to 10 cm diameter, 11 to 50 cm diameter and greater than 50 cm diameter (Table 1).

Corals that could not be readily identified in the field were labelled with a sequentially numbered tag, photographed (Nikonos V with close-up kit and strobe flash unit), and representative samples of the colonies were collected for later identification using the taxonomic references cited above. The samples consisted of representative portions of colonies, entire colonies or individuals (e.g. for solitary fungiids). The specimens were bleached using household bleach and washed in fresh-water. A representative collection of specimens was left with project staff in Yemen. Corals that could not be identified were compared with the holotype and other specimens housed in the Australian Institute of Marine Science and Museum of Tropical Queensland (both in Townsville, Australia) and Muséum National d'Histoire Naturelle (Paris, France). Provisional identifications and corals that remained unidentified were referred to taxonomic experts (Dr. J.E.N. Veron, Australian Institute of Marine Science, Dr. C.C. Wallace, Museum of Tropical Queensland, Australia) for further appraisal (Wallace 1999; Veron 2000, 2002). The Yemen collection, with complementary collections from the central-northern Saudi Arabian Red Sea and Socotra Archipelago (DeVantier et al. 2000, 2004), are now housed at the Museum of Tropical Queensland.

Categorization of benthic cover and reef development

At completion of each swim, six ecological and six substratum attributes (Table 2) were assigned to one of six standard categories, based on an assessment integrated over the length of the swim.

Table 3. Physico-chemical parameters of 51 reef sites, Yemen Red Sea.

	Underwater visibility (m)	Salinity (ppt)	Water Temperature (°C)
Mean	8.5	36.3	31.4
Median	8	36.5	32
Mode	10	36.5	32
Standard Deviation	5.3	1.36	1.5
Range	24	5.8	6.7
Minimum	1	31.6	28.3
Maximum	25	37.4	35

These broad categories have been shown to be relatively insensitive to biases among different observers (MILLER & DE'ATH 1996, also see VOGT et al. 1997, MILLER & MULLER 1999) and capable of discriminating among contrasting benthic assemblages (DONE 1982, DEVANTIER et al. 1998).

The reef was classified into one of four categories based on the amount of reef development (after HOPLEY 1982, HOPLEY et al. 1989, SHEPPARD & SHEPPARD 1991, DEVANTIER et al. 1998), where:

- Reefs with extensive reef flats (greater than 50 m wide)
- Reefs with moderate flats (less than 50 m wide)
- Reefs with no flats but with some carbonate accretion (incipient reefs)
- Coral assemblages developed on rock, sand or rubble.

The sites were also classified into one of four categories based on the degree of exposure to wave energy:

- Sheltered
- Semi-sheltered
- Semi-exposed
- Exposed

Sea temperatures were recorded in degrees Celsius with a thermometer mounted on a SCUBA regulator and STD meter. Salinity was recorded with a STD meter. The depths of the sites (maximum and minimum), average angle of reef slope to the horizontal (nearest 10 %), and underwater visibility (in meters) were also recorded. The presence of any unique or outstanding biological or ecological features, such as particularly large corals or unusual community compositions, bleached corals (partial or total loss of pigments on living corals, see BROWN 1997 for review), coral predators such as the crown-of-thorns seastar and *Drupella* snails, and other causes of coral mortality were also recorded.

Data analysis

Descriptive summary statistics of the physico-chemical and ecological and environmental site descriptor variables were generated in EXCEL. The different types of coral reefs and non-accreting coral assemblages present were characterized into major groups of sites, based on their location (mainland or island fringing reef and submerged reef patches), degree of biogenic accretion and type of underlying non-reefal substrate (for non-accreting coral assemblages). The non-accreting coral areas are also known typically as coral communities (see e.g. HOPLEY 1982, HOPLEY et al. 1989, DEVANTIER et al. 1998, RIEGL & PILLER 1999), however herein we use the term 'assemblages', as the term 'community' is used to describe groups of sites sharing particular suites of coral species composition and abundance. These coral community types were generated by hierarchical cluster analysis using rank abundance scores of all coral (scleractinian) taxa in the inventories. The species per site data were analysed using Squared Euclidian distance and Ward's method amalgamation schedule. The species that best characterized each community group (key indicator taxa) were determined, based on relative abundance and fidelity. Summary statistics of the major ecological and environmental characteristics of the communities were generated. Red Sea biogeographic comparisons are based on the coral species lists published in Scheer & Pillai (1983), Antonius et al. (1990), Sheppard & Sheppard (1991) and Veron (2000).

RESULTS

Physico-chemical setting

During the survey period in the springs of 1996 to 1998, there was substantial variability in the three physico-chemical parameters; with underwater visibility ranging from 1 to 25 m, salinity ranging from 31.6 to 37.4 ppt and sea surface temperature ranging from 28.3 to 35.0 °C (Table 3). The ranges of all three parameters are similar to other reef areas of similar size, although the minimum value for visibility (1 m) and maximum value for sea temperature are approaching the tolerance limits for coral growth and reef development (Coles 1988, Kleypas et al. 1999, Guinotte et al. 2003). Sea temperature measurements during earlier reconnaissance surveys in 1996 were substantially higher, typically around 34 °C and as high as 37 °C notably at Al Salif. Miyurn Island, at the mouth of the straits of Bab al-Mandab, was atypical of the region in being subjected to periodic nutrient rich cool water upwelling from the Gulf of Aden, with sea temperatures as low as 28.3 °C. Occasional rushes of even cooler water were felt during diving in the South Miyurn area.

Reef forms, distribution and development

Coral growth was widespread along most of the ca 760 km mainland coastline and all islands (Fig. 1). As introduced above, the areas of exclusion for coral formations correspond to mouths of ancient rivers that are now only noticeable in the form of wide dry wadis. Because of the varied topographic conditions and the relatively harsh physico-chemical environment, Yemen's reefs have several special characteristics, including a general lack of inter-tidal corals and lack of typical reef zonation patterns, lack of typical 'spur and groove' structures and the presence of 'red algal' reefs, as described below.

Absence of typical intertidal corals and reef flat zonation

Most reefs either did not have intertidal reef flat development, or when developed, the flats were essentially devoid of live corals. With the exception of Miyurn Island, the reefs typically lacked an intertidal zone, consistent with the limited tidal movement, with the potential maximum change typically of less than 0.5 m. On the Yemen coast, the seasonal tide cycle may add another 0.5 m to that range. On a longer time scale, episodic high and low tides which may happen over a period of a decade or more have been reported (Edwards 1987, Sheppard et al. 1992). The minimum diurnal tide movement allows coral growth to near the sea surface during the high season. However during the low annual tide or extreme episodic lows, any reef flats will be exposed for extended periods, resulting in extensive mortality of corals (see e.g. LOYA 1976). This differs dramatically from most reefs in other parts of the Indo-Pacific where, because of the more substantial tidal range, important intertidal coral communities with distinct zonation patterns are developed (see e.g. GOREAU 1959, GEISTER 1977, DONE 1982, SHEPPARD 1982). In the Yemen Red Sea, coral growth is limited to the outer edge of the reef margin, and the limited water depth means that in general there are no major zonation patterns, even on the reef slopes.

Dearth of "spur and groove" systems

Only at one site, on the west coast of Kamaran Island facing south-west into the prevailing weather, was a typical 'spur and groove' structure present, and this may well be relict rather than of contemporary development. The main characteristic of the site was the constant open water surge, even at periods of relative calm, a feature common to other 'spur and groove' systems. Here, the 'spurs' were formed predominantly by dead stands of long and thin branched *Stylophora pistillata*[1] which were covered with a 10-20 cm deposit of crustose coralline red algae (CRA). Live *S. pistillata* with this type of growth form was not present elsewhere at this site, and the status of preservation of the dead branches suggested this might be a reef that was rapidly exposed, then resubmerged. At the bases of the steep sided 'grooves', small faviid colonies were present.

Red algal reefs

From the shallow coastal waters of southern Saudi Arabia, SHEPPARD (1985) described reef formations built essentially of crustose red algae and named them "Algal reefs". Such reef formations also occur along the north coast of Yemen, notably in the shallow nearshore waters north of Al Hodeidah, and as far south as Al Urj. These reefs are essentially built by red coralline algae of the genera *Hydrolithon* and *Lithothamnion*, though they may at present, as in the past, support coral growth and limited coral reef development. They occur generally in semi-sheltered, low energy environments with high temperature, salinity and sedimentation levels where coral growth is limited. These algal reefs are usually covered by dense macro-algal growth, and are also typically surrounded by seagrass beds. Associated biota usually includes sea urchins, and fish diversity and abundance are generally low (BRODIE & TURAK 1999).

In the far north, near the border of Saudi Arabia, islands 10 to 20 km offshore are formed by fossil reefs 2 to 3 m above sea level with alternating layers of coral (ca 0.5 m thick) and CRA (1.5 to 2 m thick). This indicates that historically the reefs were mainly formed by CRA, with short periods, when conditions were more favourable, of coral growth. During our surveys, seawater temperatures in this area were typically 32 to 34 °C and occasionally up to 35 °C, which is well above the upper tolerance limits for most corals in most reef regions world-wide (COLES 1988, JOKIEL & COLES 1990, SHEPPARD et al. 1992, GUINOTTE et al. 2003).

For example, the reef near Al Urj (Fig. 1) had most characteristics of a typical algal reef (as described by SHEPPARD et al. 1992), but lacked dense *Sargassum* growth, possibly a seasonal (spring) sampling artefact. There were striking biotic contrasts between two adjacent reef patches at Al Urj. The CRA reef had a highly depauperate fauna, yet it was developed in close proximity, across a 20 m channel, to a more typical coral reef with moderate cover of live coral and a rich variety of plant, invertebrate and fish life. In this case the CRA growth may have colonized a dead coral reef base at some considerable time in the past, although it was not possible to find coral skeletons under the CRA.

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[1] Authors of coral species mentioned in text are listed in the Appendix.

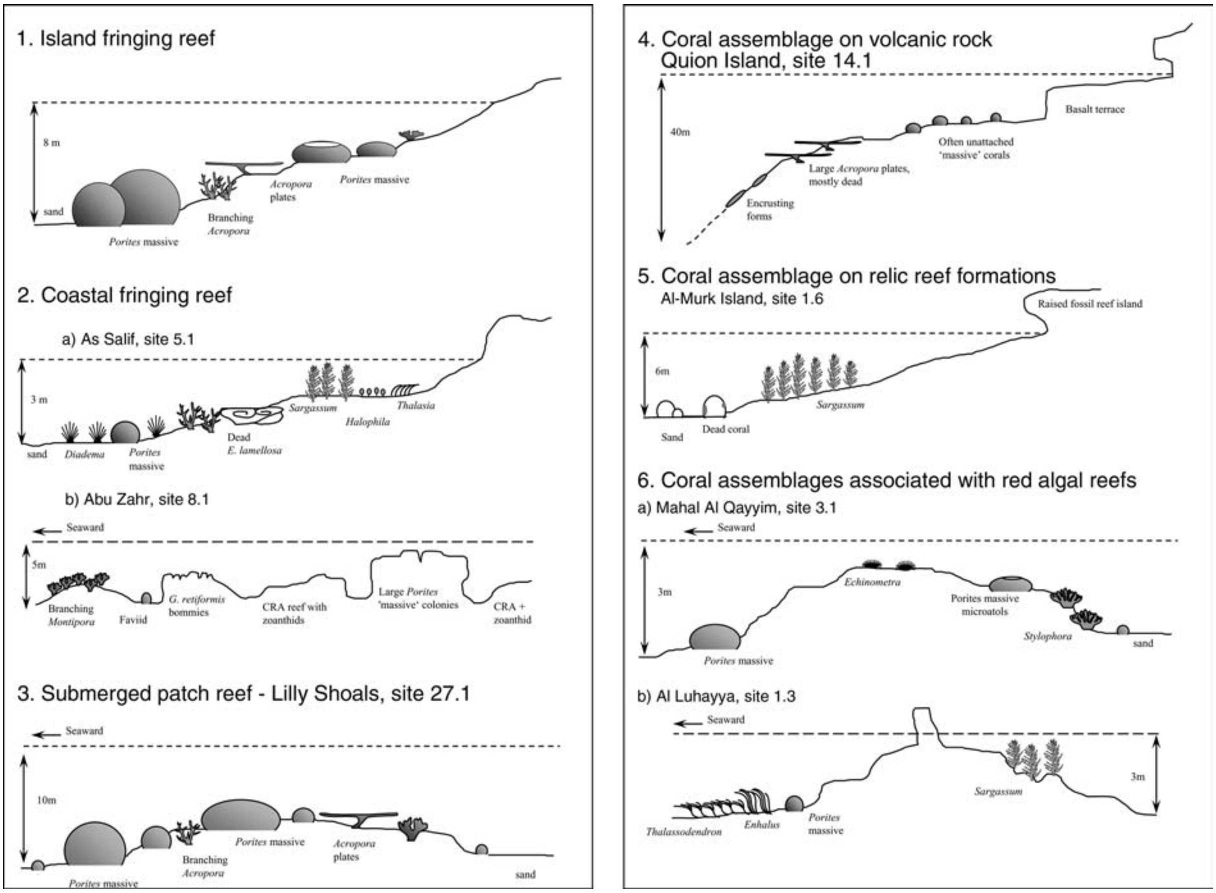


Fig. 2: Profiles of different types of reefs and coral assemblages, Yemen Red Sea.

CRA clearly plays an important role in reef building in the Yemeni Red Sea, with other forms of CRA reef accretion also occurring. These include: deposition on coral reef crests; as shallow algal reefs; or as the alternating coral and CRA 'layered' reefs. CRA reef crests were present at many sites where the upward growing margin of the outer reef flat reached to just below the water surface. On extreme diurnal or seasonal low tides these areas are likely to be exposed for considerable periods. This exposure, combined with heating of the very shallow waters, is likely to provide conditions inimical to coral survival, and foster replacement by the more tolerant CRA. In some areas the CRA deposits are 10 to 20 m wide and appear to be up to 50 cm thick. Typically, various species of macroalgae grew among the bulbous columns of CRA, most commonly *Caulerpa racemosa* and other species of *Caulerpa* and *Halimeda*. The bulbous CRA columns also provide an ideal habitat for one of the most common sea urchins *Echinometra mathaei*. These various CRA reef formations were restricted to near-shore environments where environmental conditions are most severe, and were not present on reefs around offshore islands and deep water pinnacles.

Coral reefs and coral assemblages

Contemporary coral growth occurs both as accreting reefs and non-accreting coral assemblages growing on a variety of substrates. The coral reefs show three types of development: fringing reefs of offshore islands; fringing reefs of the southern coast; and patch reefs. Coral assemblages are typically associated with three forms of substrate: relic Pleistocene to Holocene reef deposits; volcanic rock pinnacles and lava flow terraces; and the red algal reefs. Clear-water, steep reef slopes and major spur and groove structures more typical of the northern to central regions of the Red Sea (Sheppard et al. 1992, Behairy et al. 1992, Riegl & Piller 1999, DeVantier et al. 2000) are not present.

Coral reefs

Island fringing reefs

These are true coral reefs with substantial biogenic carbonate accretion by corals. Biogenically accreting reefs occur at the southern part of Saba Island of the Az Zubayr group and Miyurn Island in the straits of Bab al-Mandab (Fig. 1). There is also likely to be similar coral reef formation around islands of the Hanish group, notably Zugar Island. Island fringing reefs typically had extensive flats, with gradual slopes of broken-up reef patches and intermittent sand areas. Benthic topographical relief or 'rugosity' was generally high, varying from 1 to 3 m height. Some of the coral patches and ridges were formed by coral rubble accumulations from storms. These rubble ridges were often covered with thick mats of the brown alga *Dictyota*. Water clarity and coral species diversity were among the highest (Fig. 2, profile 1). Live coral cover was generally higher (ca 10 %) in the southern and offshore areas than at most of the northern and central areas, and there were stands of large massive coral colonies (2 to 4 m diameter), likely of the order of one to several centuries old.

Miyurn Island had distinct coral formations of both accreting reefs and non-accreting coral assemblages. The island is of volcanic origin and reef growth is on basal volcanic rock, in some places reaching several metres in thickness. On the northern side of the island, extensive reef flats with diverse coral growth were developed. Both the eastern and western sides supported mainly monospecific beds of *Stylophora pistillata* on volcanic rock, with limited biogenic accretion. Bays on the southern side were dominated by large *Porites* colonies up to 5 m in diameter. Although this area appears to be subjected to sporadic bleaching related to cool water intrusions from the Gulf of Aden, the corals had survived such events and continued to proliferate at the time of this study.

Coastal fringing reefs

Coastal fringing reefs are well developed along the southern coast. A long reef fringes the coast, with only a few small gaps, from just north of Al Khawkhah at latitude 13°55' N south, to opposite Miyurn Island, and appears to continue in patches around the rocky headland into the Gulf of Aden coast. The reef's width varies from less than 100 m up to 1 km and often has a shallow (0.2-1.5 m depth) sand and rubble lagoon on the leeward side with small patches of seagrass among boulders with some coral growth around the edges. This is one of the most important coastal features in the southern Red Sea.

Coastal fringing reefs usually have a CRA or coral rubble crest, typically supporting macro-algal growth, the most common being species of *Padina*, *Sargassum*, *Caulerpa* and *Halimeda*. In places, the shoreward lagoon or sand and rubble flat supports seagrass beds of *Thalassodendron ciliatum*, *Cymodecea rotundata* and *Halodule uninervis*. Among the algae and seagrass some small, usually unattached coral colonies of *Porites*, *Stylophora pistillata*, *Montipora* and faviids occur (Fig. 2, profile 2, a and b).

The seaward reef margin typically descends to around 3 to 4 m depth, although south of Al Mukha massive *Platygyra* colonies occurred on a sandy bottom of 5 to 6 m depth in relatively clear water. In places, the cross reef profile shows a different structure with a more distinct lagoon and crest area. A fringing reef formed exclusively by *Galaxea fascicularis* was reported to stretch for several kilometers south of Al Mukha (Barrat et al. 1987). This, the largest single-species reef structure yet reported, was not found during the present study, despite considerable searching, and hence may have died and become overgrown by algae and other benthic organisms.

Submerged patch reefs

In terms of surface and volume of contemporary coral reef accretion, these reefs are the most important in the Yemen Red Sea. Large patches occur west of Al Hodeidah (Fig. 2, profile 3), south of Ras Isa peninsula and scattered in the southern Farasan Islands in inter-island waters. The shallower parts generally are 6 to 8 m below sea surface. However some patches in the southern Farasan group grow close to the sea surface and may be exposed at extreme low tides. Several large patches were not marked on current hydrographic charts, and because these patches are mostly developed below 6 m depth in relatively turbid waters they do not appear on satellite photographs. It is possible that much of the inter-island waters in the southern Farasan area may support such reef growth. These patch reefs support a moderately diverse coral fauna, dominated by *Porites* and other small corals of 'massive' form.

Coral Assemblages

Three major forms of coral assemblages, with minimal or no carbonate accretion, are present.

Coral assemblages on volcanic rock

Offshore islands of the Hanish and Az Zubayr groups and At Tair Island are situated along the mid Red Sea fault line and hence are of volcanic origin. These assemblages rise from a relatively deep sea floor (40-70 m) in clear water. Typically the best coral growth was on the eastern to southern sides, where the profile descended more gradually to a terrace from 15 to 20 m depth, then plunged down steeply to 40 m or more (Plate 1). In contrast, the exposed north and north-west sides of the pinnacles usually dropped steeply to the bottom, with only sparse coral growth (Fig. 2, profile 4). Despite the lack of extensive reef accretion around the pinnacles, hard coral diversity was generally high, as at Six Foot Rocks south of Tiqfash Island and Avocet Rock south of Al Hodeidah (Plates 2, 3).

With the exception of a wide patch of reef extending south of Saba Island of the Az Zubayr group, the rest of the islands in that group and At Tair Island supported coral assemblages on volcanic rock along a mid depth line of about 6 m. On the lava flow terraces of At Tair and islands of the Az Zubayr group, small coral colonies of massive growth form, frequently *Porites*, grew unattached to the flat volcanic rock (Plate 4), their colony shape minimising the possibility of being turned over, rolled around and damaged. Under the volcanic ash cliffs of At Tair Island, where fine sediments occur nearshore, large *Siderastrea savignyana* colonies reached several m in diameter, among the largest known (Sheppard & Sheppard 1991, Veron 2000), many part-buried, yet surviving, beneath the sediments (Plate 5). At Quoin Island, large plating *Acropora* colonies to greater than 4 m in diameter covered areas of several hundred square metres at depths between 8 and 20 m. These were recently killed, and although covered by algal growth some colonies were so recently dead that they could be identified to species level (Plate 1). Mortality was attributed to predation by the crown-of-thorns seastar, with several large seastars feeding on remaining live corals (see below).

Coral assemblages on relic reefs

The majority of coral growth along the northern coast and nearshore islands occurs on relic Pleistocene or Holocene reef formations. In this area shallow waters typically limit coastal reefs to less than

Table 4. Diversity of hard coral taxa from southern Red Sea (not including deep water and small cryptic forms).

Author	SCHEER & PILLAI 1983	HEAD 1987	SHEPPARD & SHEPPARD 1991	This study
Families	16	14	14	14
Genera	52	31	59	54
Species	163	74	115	221

6 m depth. Reef growth reached sea level long ago, hence main growth is outward, being restricted in places by fine mobile sediments. The reef edge usually dropped abruptly from 0.5 to 1 m depth to a sandy bottom at about 4 m, or had a gradual broken slope with blocks of reef that had rolled down onto the sand flat below. Behind the relic fringing reef front, a sand or sand/rubble flat and semi-lagoon extended towards the shoreline, occasionally supporting extensive macroalgae or patches of seagrass. The typically small sizes of corals, including dead colonies, suggest that there may not have been long periods of sustained coral growth. Virtually all the corals in this area had suffered mortality from a recent widespread event (see later), and hence, it was difficult to assess the real extent of recent reef growth. Dead corals were covered by prolific growth of fleshy macroalgae including *Sargassum*, *Padina* and *Dictyota* (Fig. 2, profile 5). Most of the live corals were growing remnants from the latest wide spread mortality. Small colonies, in particular those from larval settlement, were scarce, indicating limited recent recruitment. The apparent lack of larval recruitment and proliferation of macroalgae suggest that in these assemblages recovery will be very slow, perhaps further exacerbated by bioerosion. The long-spined, black sea urchin *Diadema setosum* was very common and was particularly prevalent on reef edges around Tiqfash, Uqban, Fasht Islands and other islands off Al Luhayyah.

Coral assemblages associated with red algal reefs

As noted above, red algal reefs occur in shallow coastal waters from the Saudi Arabian border to south of Ras Isa Peninsula and around many nearshore islands along this coastline, in waters that are never deeper than 6 m and typically of 2 to 4 m depth (Fig. 2, profiles 6 a, b). On these CRA reefs, coral growth may range from a few small colonies of some hardy species to extensive assemblages with high cover. These were dominated by species which are most tolerant of harsh environmental conditions, or rapid recruiters following disturbance, notably pocilloporids and massive and encrusting poritids and siderastreids (also see SHEPPARD et al. 1992). On algal reefs further offshore coral growth is more extensive and diversity higher, including tabular, massive and foliaceous forms. Here, coral cover may be so extensive that these may superficially resemble reefs built by corals. However the corals never attain great size, reaching a maximum diameter of about 50 cm, suggesting episodic mortality on a decadal time-scale, supported by the presence of many small (less than 50 cm in diameter) dead corals. Fleshy macroalgae *Caulerpa*, *Sargassum* and *Padina* were also common. Dense *Sargassum* mats with fronds greater than 2 m tall occasionally totally obscured the underlying coralline red algal growth.

SPECIES COMPOSITION AND DIVERSITY

Previous studies have suggested that the Yemen Red Sea supported low coral diversity (SHEPPARD et al. 1992, HEAD 1987, BARRAT et al. 1987). The area does however support a moderately high regional diversity of reef-building corals of around 221 species (Table 4, Appendix).

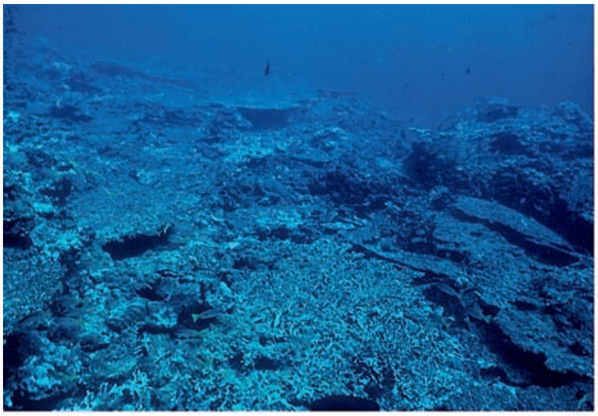
Local (site) diversity ranged from one to 76 species, with an average of 35 species. Approximately half the sites had more than 40 species and six sites had more than 50 species. The higher

Table 5. List of new coral records for Yemen and the Red Sea. The lists of records for the southern Red Sea and Red Sea are based on Scheer & Pillai (1983), Head (1987), Antonius et al. (1990) and Sheppard & Sheppard (1991). Authors of species are listed in Appendix 1.

	South Red Sea	Whole Red Sea	New species
Stylophora mamillata	♦		
Montipora echinata			♦
Montipora foliosa	♦		
M. hispida	♦		
M. nodosa		♦	
Montipora pachytuberculata			♦
Montipora saudii			♦
M. spumosa	♦		
M. stilosa	♦		
M. tuberculosa	♦		
M. venosa	♦		
Acropora abrotanoides	♦		
A. acuminata	♦		
A. austera	♦		
A. downingi			♦
A. elseyi		♦	
A. eurystoma	♦		
A. grandis	♦		
A. horrida	♦		
A. intermedia (A. nobilis)	♦		
A. latistella	♦		
A. loripes		♦	
A. microphthalma		♦	
A. millepora		♦	
A. pharaonis	♦		
A. polystoma	♦		
A. robusta	♦		
A. samoensis	♦		
A. secale	♦		
A. selago		♦	
A. spicifera	♦		
A. squarrosa	♦		
A. subulata		♦	
A. valenciennesi	♦		
A. valida	♦		
Astreopora expansa	♦		
Astreopora myriophthalma	♦		
Euphyllia glabrescens	♦		
Galaxea astreata	♦		
Gyrosmilia interrupta	♦		
Anomastraea irregularis		♦	
Coscinaraea columna	♦		
Coscinaraea monile	♦		
Psammocora explanulata	♦		
Psammocora profundacella	♦		
Psammocora superficialis	♦		
Siderastrea savignyana	♦		
Gardineroseris planulata	♦		
Leptoseris explanata	♦		
Cycloseris costulata	♦		
Fungia danai	♦		
Pectinia africanus			♦
Micromussa amakusensis		♦	
Acanthastrea lordhowensis		♦	
Lobophyllia hataii	♦		
Symphyllia radians		♦	
Caulastrea tumida	♦		
Favia lizardensis	♦		
F. matthaii	♦		
F. rotundata	♦		
Favites complanata	♦		
Goniastrea retiformis	♦		
Platygyra crosslandi	♦		
Oulophyllia bennettae		♦	
Montastrea magnistellata	♦		
Cyphastrea hexasepta			♦
Porites monticulosa		♦	
Porites rus	♦		
Goniopora ciliatus			♦
Goniopora djiboutiensis		♦	
Goniopora minor	♦		
Total	50	14	7

diversity sites generally occurred in waters of higher clarity and with deeper surrounding waters. Highest local diversity occurred at a non-reefal coral community on "Six Foot Rocks" (Plate 2), comparable in richness to reefs in other areas of the Red Sea and Arabian Sea (e.g. Kemp & Benzoni 2000, DeVantier et al. 2000, 2004).

This study identified 71 species previously not recorded from the southern Red Sea, of which 14 were new distribution records for the Red Sea more generally (Table 5). Another 7 species were undescribed prior to this study: *Montipora echinata, M. pachytuberculata, M. saudii, Acropora down-*



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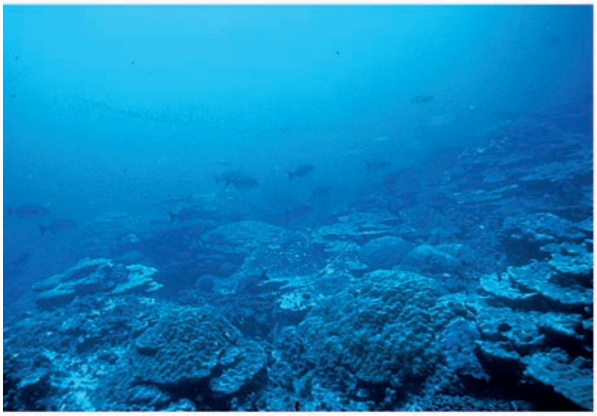

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Plate 1: On Quion Island extensive areas of very large *Acropora* table colonies were killed most probably by crown-of-thorns seastars. **Plate 2:** Rich coral communities at "Six Foot Rocks", where the highest diversity of hard corals was found. **Plate 3:** Lower slope communities at Avocet Rock; at this depth the normally massive *Porites* colonies become flattened and plate like. **Plate 4:** Coral communities on volcanic rock at Az Zubayr Island; on the right is an upper lava flow terrace.

ingi, Pectinia africanus, Cyphastrea hexasepta and *Goniopora ciliatus* (WALLACE 1999, VERON 2000, 2002). Notably, both site and regional richness may have been adversely affected by the extent of recent damage to corals in large parts of the survey area (see later). Further studies, particularly around the offshore Hanish Island group, will likely increase the coral species tally considerably.

Zoogeographic affinities of the northern area appeared most similar to the adjacent Farasan Islands of southern Saudi Arabia (ANTONIUS et al. 1990, SHEPPARD & SHEPPARD 1991, SHEPPARD et al. 1992), and to the more northern Saudi Arabian Red Sea coast (DEVANTIER et al. 2000), with the presence of some characteristic Red Sea endemics, such as *Montipora saudii* and *Symphyllia erythraea*, although with others, such as *Erythrastrea flabellata* Scheer & Pillai, 1983, apparently absent. The southern area appears to share more faunal similarities with the Yemen Gulf of Aden coast (Belhaf - Bir Ali area) and Arabian Sea (KEMP & BENZONI 2000, DEVANTIER & HARIRI 2005), with the occurrence of typical Arabian Sea species such as *Acropora downingi*. Subsequent to this study, *S. erythraea* and several other Red Sea 'endemics' were also discovered at the Socotra Islands in the Arabian Sea (DEVANTIER et al. 2004), suggesting that the Yemen Red Sea may provide an important connection in their populations.

There was high uniformity in species' distributions among sites, similar to the central and northern Red Sea (SHEPPARD & SHEPPARD 1991, DEVANTIER et al. 2000). Most species present have wide Indo-Pacific distribution ranges and also occur in a broad range of habitats. Most sites were dominated by three to four species, the remaining species present typically being represented by

Table 6. Physical characteristics of the coral community and sub-community types, Yemen Red Sea. All numbers, except for site numbers, are mean values.

	High diversity			Low diversity		
Community type	A	B		C	D	
Sub type		B1	B2		D1	D2
Number of sites	11	7	4	6	9	6
Max. depth (m)	9	6	6	4	4	3
Min. depth (m)	3	3	2	1	1	1
Visibility (m)	14	12	7	8	6	3
Water temp. (°C)	30.3	31.3	31.3	30.4	32.2	31.7
Substratum						
Continuous pavement (%)	40	41	5	0	11	7
Large blocks (%)	22	11	30	18	27	28
Small blocks (%)	17	24	30	33	32	33
Rubble (%)	4	10	10	35	16	13
Sand (%)	17	13	25	13	15	20

one or a few colonies, thus making only minor contributions to benthic cover and reef framework. Massive species of *Porites* were the most common and widespread corals, occurring at all sites. These are the main framework builders of contemporary coral reefs in this area (also see Riegl & Piller 1999 and references therein). The other two most common corals were the branching pocilloporid *Stylophora pistillata* and massive faviid *Platygyra daedalea*.

Coral community structure

Of the 221 species recorded, approximately one quarter occurred in half or more of the sites, and changes in species' composition and dominance proved useful in defining types of coral communities. Four main coral communities, two of which were sub-divisible into two sub-communities each (Fig. 3), were broadly distributed in relation to environmental characteristics (Table 6), particularly water clarity and depth.

Communities A, B1 and B2 were of relatively high richness, occurring on pinnacles, offshore islands and the south sides of mid to outer shelf islands (Fig. 4). With the exception of Miyurn Island, sites in this group were present in the north and offshore area in waters of higher clarity (Table 6, Fig. 4). Communities C, D1 and D2 were of relatively low richness and occurred in relatively shallow and turbid environments along the exposed south coast or protected island reefs. High diversity communities had overall higher hard substrate and live hard coral cover, with dead coral cover only marginally higher than their low diversity counterparts, whereas low diversity communities had higher rubble and coralline algae cover (Table 6, Fig. 4).

High diversity communities

Community A: *Platygyra - Acropora humilis* community of clear water facing open sea: This community occurred around offshore islands of the northern Az Zubayr group, At Tair and Uqban Islands in the north and Miyurn Island in the south, volcanic rock pinnacles rising from relatively deeper, clearer water and submerged patch reefs (Fig. 4). Offshore islands of the Hanish Island group probably also support this, and other, community types. This community extended into

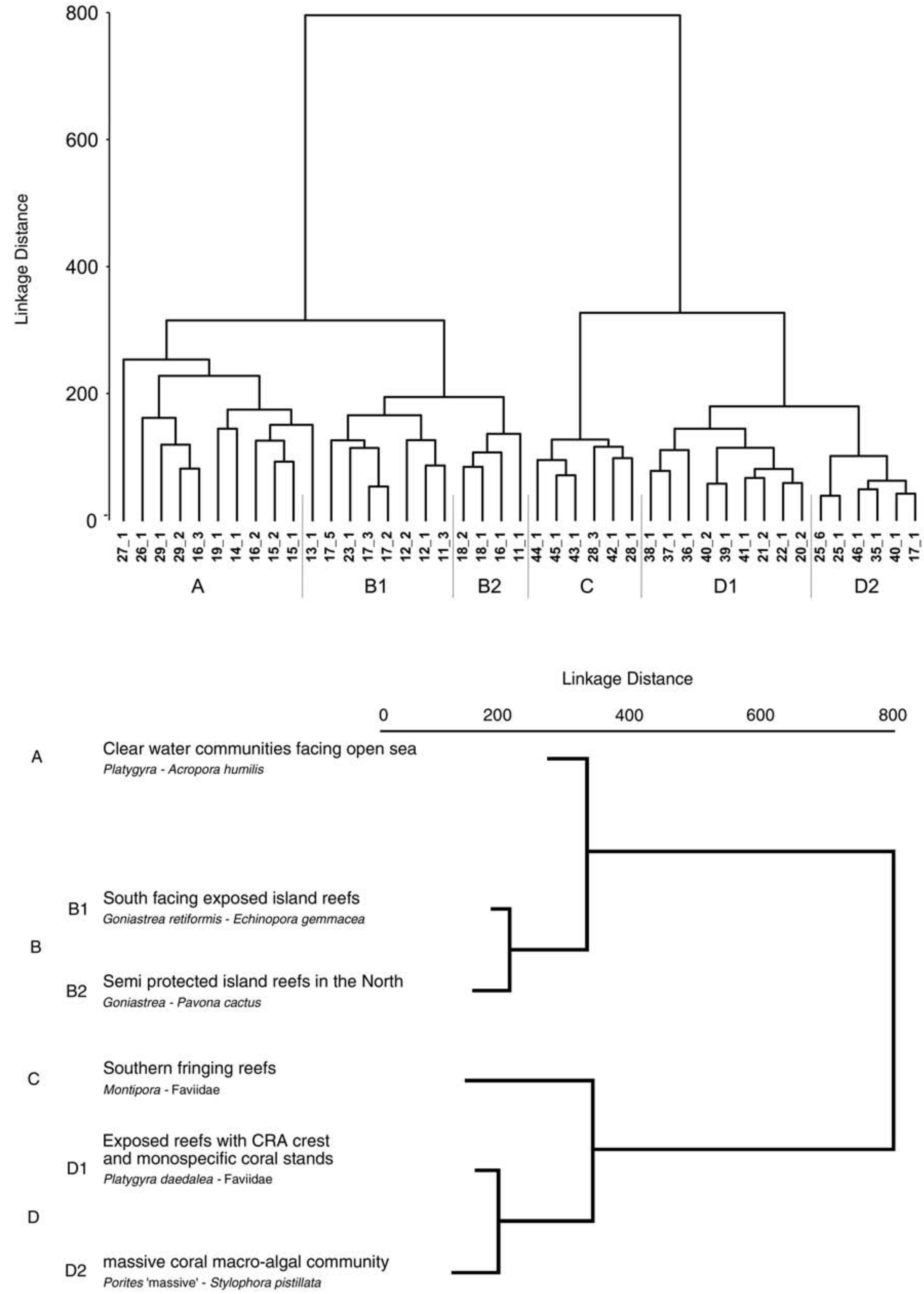


Fig. 3: Results of a cluster analysis defining six coral reef community types. The total number of species in each community was: A – 127, B1 – 92; B2 – 85; C – 64; D1 – 85; D2 – 16 species. There are two main clusters of high (A and B) and low (C and D) diversity communities. Subsequently each dived into two clusters, with clusters B and D formed of two sub-community types each.

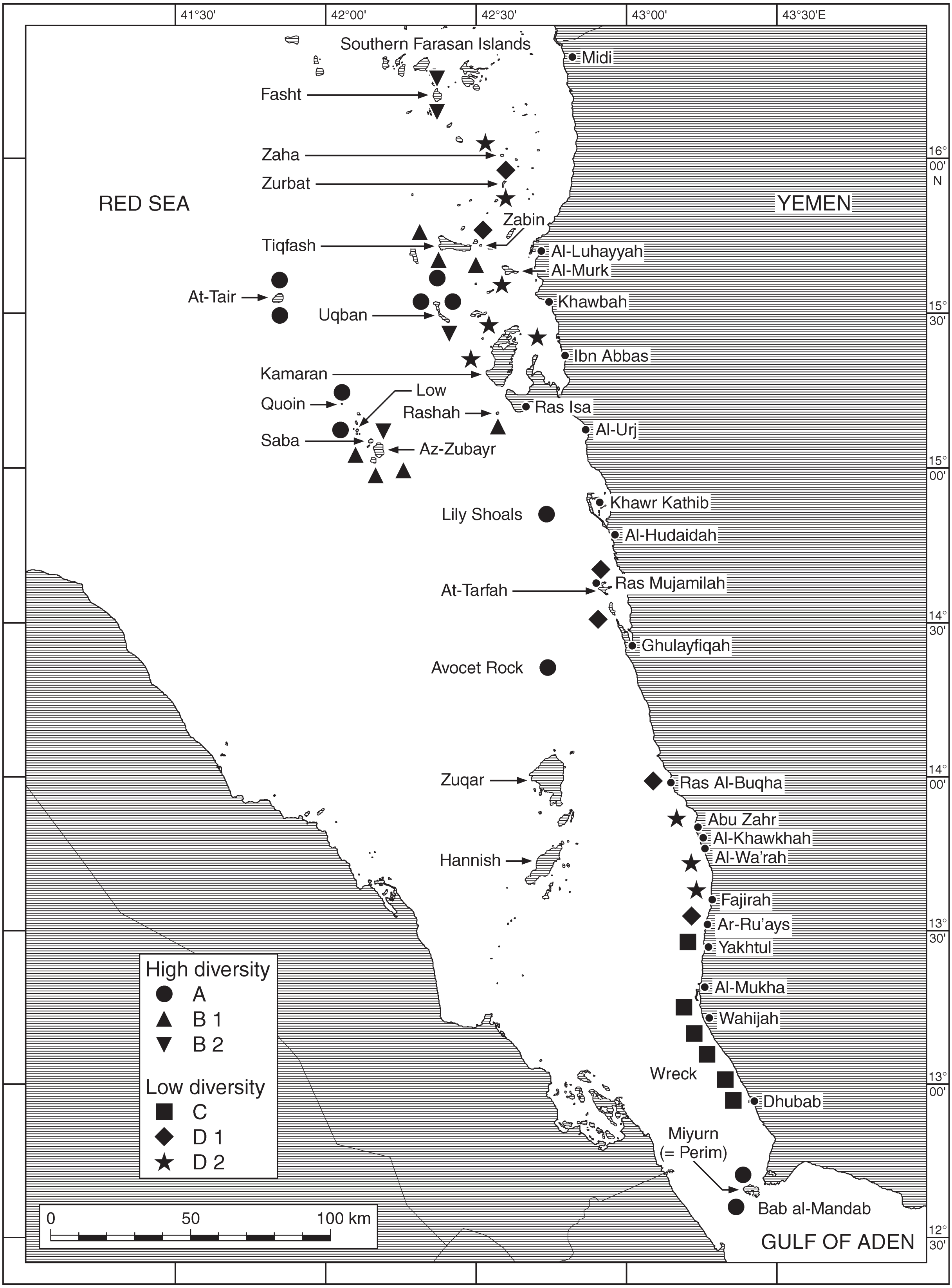
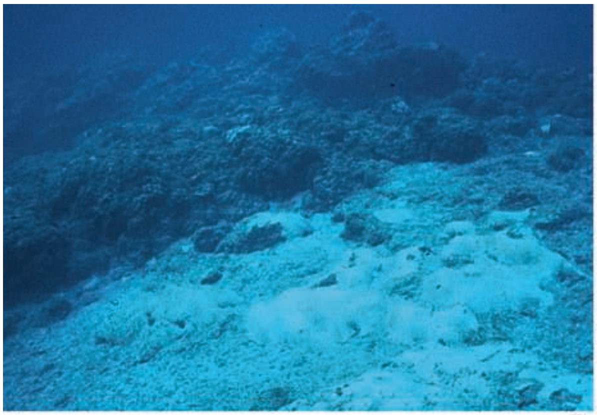


Fig. 4: Map of the study area showing distribution of coral community types.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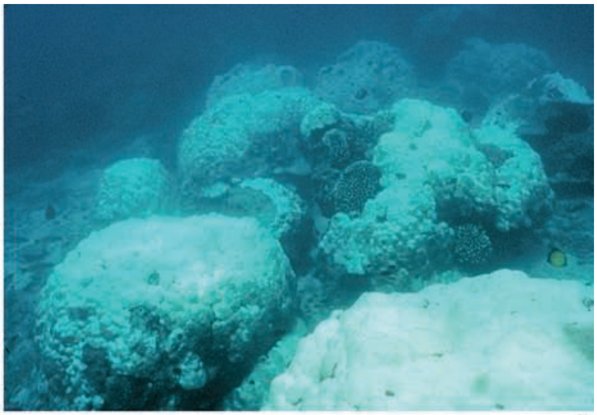
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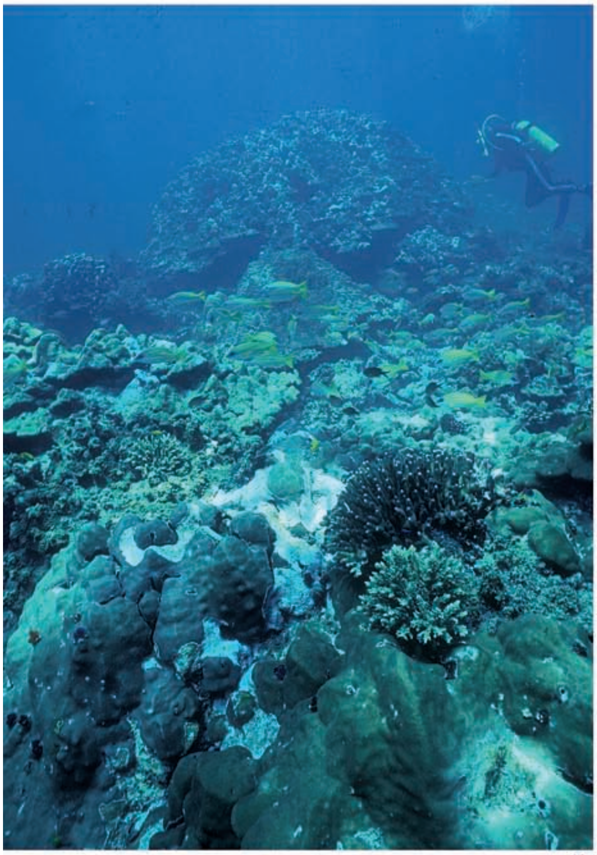
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deeper water, up to 40 m depth. Reef building ranged from minimal or absent to some of the most extensive reef accretions at Miyurn Island and the patch reef extending south of Saba Island. On the offshore islands, coral communities were growing on volcanic base rock. In these areas fine sediment levels were low and many colonies of massive growth form were unattached to the underlying substrate. On the south of Miyurn Island, some corals showed evidence of recent bleaching, possibly due to cool water upwelling (Plate 6). This is likely a regular occurrence at that site, and the corals did not appear adversely affected. The most common distinguishing characteristics were the high coral species richness (mean: 49 species), highest hard coral cover (mean: 22 %) and some of the largest (and probably oldest) coral colonies present in Yemen Red Sea waters (Plate 7). Algal growth was among the lowest of all communities (Fig. 5). Most scleractinian coral families from the Red Sea were represented, with Faviidae being the most common and having the highest number of species (Table 7). As in most other communities, massive *Porites* were the most abundant and at Avocet rock accounted for over 80 % of live coral cover. This community also had some of the largest areas of *Acropora* corals, although most of them were recently dead (e.g. Quoin Island).

Sub-community B1: *Goniastrea retiformis - Echinopora gemmacea* community of south facing exposed island reefs: This community occurred mainly around the south facing sides of the southern Zubayr Island group, Tiqfash and Rashah Islands. Usually reef accretion was limited, particularly at the southern Zubayr group. Rashah Island had higher accretion. Fine sediment levels were low. This community had relatively high coral species richness (mean 39 species), relatively low live coral cover (mean: 8 %) and highest dead coral cover (mean: 40 %). Macro algae cover was also among the highest (mean: 28 %). Most scleractinian coral families from the Red Sea were represented, with Faviidae being the most common and having the highest number of species present. *Styplophora pistillata, Galaxea fascicularis* and *Lobophyllia hemprichii* were also common (Table 7).

Sub-community B2: *Goniastrea - Pavona cactus* community of semi protected island reefs in the North: This community occurred around islands near the shelf edge of the southern Farasan Islands and semi-protected reefs in the Zubayr Island group. This community occurred in relatively shallow water depths of less than 6 m, with low underwater visibility (mean: 7 m) and higher seawater temperatures (mean: 31.3 °C). Hard coral species richness (mean: 46 species) and live coral cover (mean: 19 %) were high. Cover of macroalgae (mean: 18 %) was close to average while cover of dead standing coral was high (mean: 33 %). Some dead coral surfaces and beds of dead branching corals were covered with thick mats of *Dictyota* on the upper slopes and thick dense fronds of *Halimeda* further down. The universally dominant corals, *Porites* and *Stylophora pistillata* aside, the most common corals were *Pavona cactus*, *Goniastrea* spp. and *Echinopora gemmacea* (Table 7). Small branching *Acropora* thickets also occurred on the sand floor, suggesting that strong water movement and shifting sediment may be limited. This may be one of the reasons why higher coral cover and diversity occurred around islands of the southern Farasan group (Plate 8).

Plate 5: Large *Siderastrea savignyana* colonies part-buried in sediment at At Tair Island. **Plate 6:** Trails of recently bleached coral colonies at south Miyurn where cold water upwelling was present. **Plate 7:** Lower reef slopes of clear water Community A had the occasional large *Porites* colony. **Plate 8:** Branching *Acropora* and good coral growth in Community B2 on southern Fasht reef. **Plate 9:** Branching *Acropora* and *Porites* on lower slopes of southern fringing reefs Coomunity C. **Plate 10:** Coral and coralline red algae fringing reefs on the west end of Tiqfash Island. **Plate 11:** Numerous *Platygyra daedalea* colonies on lower slopes of southern fringing reefs.

Table 7. Top ten coral species at each community and sub-community type in terms of occurrence and abundance. Species used in community type descriptions are in bold. **Site:** number of sites where taxon was recorded, **abn:** total abundance of taxon in all sites where it was recorded (i.e. the sum of the relative abundance rank (Table 1) in each site).

High diversity			Low diversity		
	A	11		C	6
Taxa	site	abn	Taxa	site	abn
Porites massive	11	34	*Porites* massive	6	14
Stylophora pistillata	11	25	*Stylophora pistillata*	6	14
Platygyra daedalea	11	24	***Montipora monasteriata***	6	12
Leptastrea purpurea	11	21	***Favites pentagona***	6	11
Echinopora gemmacea	11	19	*Platygyra daedalea*	6	10
Acropora humilis	11	17	*Echinopora gemmacea*	6	8
Lobophyllia hemprichii	11	16	*Porites nodifera*	6	8
Pocillopora damicornis	10	19	*Goniasatrea retiformis*	5	9
Galaxea fascicularis	10	15	*Favia favus*	5	6
Platygyra lamellina	10	15	*Montipora stellata*	4	11
	B1	7		D1	9
Taxa	site	abn	Taxa	site	abn
Porites massive	7	20	*Porites* massive	9	24
Goniastrea retiformis	7	18	***Platygyra daedalea***	9	21
Stylophora pistillata	7	15	***Favia favus***	8	13
Echinopora gemmacea	7	14	*Goniastrea retiformis*	6	12
Galaxea fascicularis	7	14	*Leptastrea purpurea*	6	11
Platygyra daedalea	7	13	*Echinopora lamellosa*	6	10
Cyphastrea microphthalma	7	10	*Porites nodifera*	6	9
Leptastrea purpurea	7	10	*Stylophora pistillata*	6	7
Lobophyllia hemprichii	7	9	*Cyphastrea serailia*	6	6
Platygyra lamellina	6	8	*Favites complanata*	5	7
	B2	4		D2	6
Taxa	site	abn	Taxa	site	abn
Porites massive	4	12	***Porites*** **massive**	6	8
Pavona cactus	4	10	*Platygyra daedalea*	3	4
Stylophora pistillata	4	10	***Stylophora pistillata***	3	4
Echinopora gemmacea	4	9	*Fungia fungites*	2	6
Galaxea fascicularis	4	9	*Siderastrea savignyana*	2	4
Goniastrea retiformis	4	8	*Goniastrea retiformis*	1	2
Favia favus	4	7	*Acropora nasuta*	1	1
Goniastrea australensis	4	7	*Echinopora gemmacea*	1	1
Goniastrea edwardsi	4	7	*Favia pallida*	1	1
Platygyra daedalea	4	7	*Favites abdita*	1	1

Low Diversity Communities

Community C: *Montipora* - Faviidae community of southern fringing reefs: This community was found exclusively between Yakhtul and Dhubab (Fig. 4). Hard substrate was sparse (the lowest of the communities) and cover of rubble was the highest. Live hard coral cover (mean: 13 %) was similar to that of macroalgae, and was slightly above the overall coral average. Dead coral cover (mean: 25 %) was slightly below average (Fig. 5). Active coral growth was limited to the outer flat, crest and slope where water depths reached 1 m or more. *Montipora monasteriata* and *Favites pentago-*

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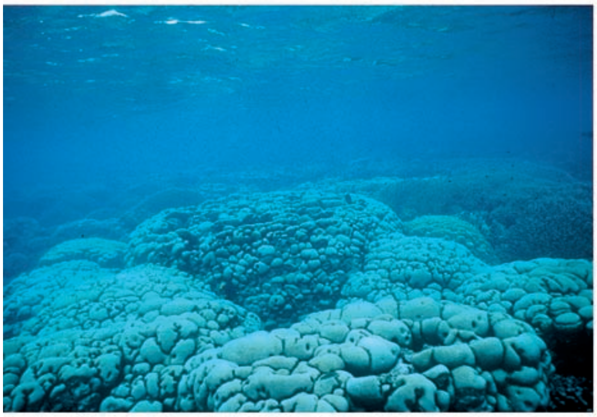

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Plate 12: *Fungia fungites* beds at At Toufa Island where lush branching *Acropora* growth was reported in 1985. **Plate 13:** *Sargassum* in community D2 off Kamaran Island. **Plates 14, 15:** Large colonies of *Goniastrea retiformis* colonies near Khowkha, which were live and healthy in 1996, but were killed, probably by bleaching, in 1998 (Plate 15).

na were the most common corals and typical of this community (Table 7). Other characteristic corals included occasional large colonies of massive *Porites* among beds of staghorn *Acropora* (Plate 9).

Sub-community D1: *Platygyra daedalea* - Faviidae community on exposed reefs with coralline algal crest and mono-specific coral stands: This community was widespread along the mainland coast and some nearshore islands (Fig. 4). Facing the prevailing wave action, many of these sites had developed coralline algae crests (Plate 10). This community had a high average hard coral cover (mean: 44 %), although it was mostly dead standing coral (mean: 37 %, Fig. 5), with mounds or ridges of branching coral rubble, dead massive corals and tabular *Acropora*. Other sites had large live mono-specific stands of *Goniastrea retiformis*, *Montipora saudii*, *Platygyra daedalea* (Plate 11) and *Stylophora pistillata* (Table 7).

Sub-community D2: *Porites* “massive” - *Stylophora pistillata*, massive coral - macro-algal community: This community was also widespread along the mainland coast and nearshore islands, particularly around Al Luhayyah and Kamaran Island in the north and Yahktul in the south. This was the lowest diversity community (mean: 5 species), characterized by massive *Porites*. *Stylophora pistillata* and *Platygyra daedalea* were also present at most sites (Table 7), although never in high abundance. *Siderastrea savignyana* occurred in the shallowest areas, often hidden among the long fronds of *Sargassum*. The mushroom coral *Fungia fungites* was the most abundant coral at one site. This community also had low live coral cover (mean: 1 %, Fig. 5). In most sites, however, dead

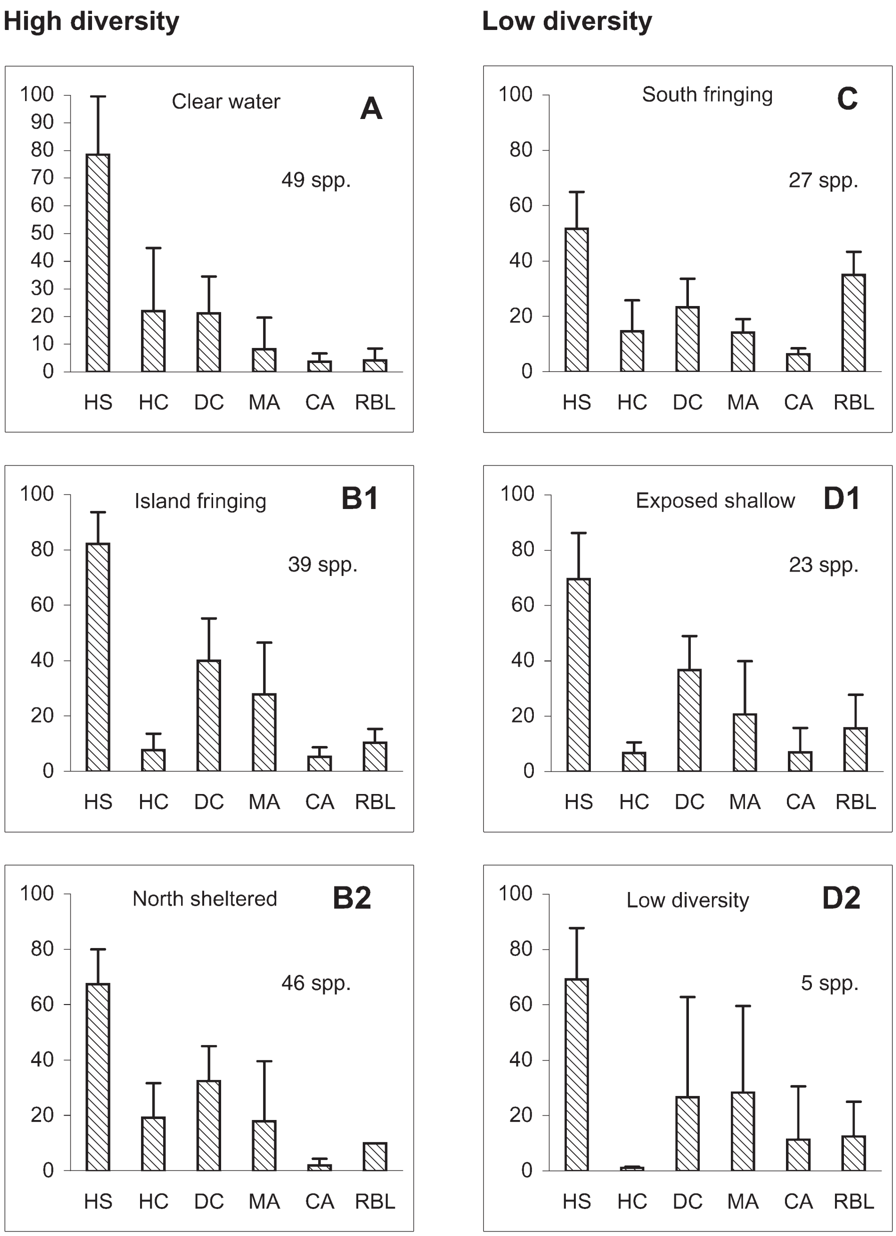

Fig. 5: Average values (error bars are stdev) of some significant bottom cover attributes for the community types. HS: Hard Substrate, HC: Hard Coral, DC: Dead Coral, MA: Macro Algae, CA: Coralline Algae, RBL: Rubble. Number of sp. is average number of species.

standing coral cover was high (mean: 27 %), indicating severe recent disturbance, notably at Zabin Island of the Tiqfash group and NW Zurbat Island. Taufa (Ras Mujamilah) Island in the bay of Ghulayfiqah also had good coral growth in the 1980 s (Barrat et al. 1987). An apparent shift in coral community composition had occurred on the south side of At Taufa Island, as the branching *Acropora* stands present in 1985 (Barrat et al. 1987), were no longer present, and the substrate was covered with the mushroom coral *Fungia fungites* (Plate 12). Many sites had very thick macro algal growth (mean: 35 %), with *Sargassum*, *Turbinaria*, *Padina* and *Dictyota* dominant (Plate 13). Shallow areas near wadi mouths of mainland coastal sites between Ghulayfiqah and Al Khawkhah had small patches of hard substrate on coarse and fine sediments. A few corals clung to the boulders or larger patches, but no appreciable reef accretion was evident. Algal growth was sparse with a general appearance of degradation of hard substrate.

Ecological status

Many reefs, particularly of the nearshore areas, exhibited extensive coral mortality, with cover of dead corals exceeding that of live corals. Overall, living cover of hard corals, dead corals and macroalgae averaged 11 %, 29 % and 21 % respectively. Reefs in best ecological condition were those of the offshore islands. Extensive recent coral death (since the mid-1980 s) had occurred in the northern nearshore area, with even more recent mortality (1990 s) in the southern region. Some sites with near total mortality had healthy coral growth 10 years earlier (Barrat et al. 1987). However the size distribution of living and dead colonies suggests that extensive episodic coral mortality at short (decadal) intervals may be 'normal'. The richness of small mobile invertebrate benthos and abundance of medium size predatory fish that feed on them, and the abundance of herbivorous fish also suggest that the usual situation on these reefs is one of less coral and more algae. Several major forms of disturbance were implicated.

Bleaching

The nearshore reefs have been subjected to a number of intense bleaching episodes (the expulsion of the symbiotic micro-algae, zooxanthellae; see Brown 1997 for review) in recent decades. If bleaching is of sufficient intensity and / or duration, it can lead to partial or near complete mortality of the species affected (Glynn 1993, Brown 1997). On the nearshore Yemen reefs, the pattern of coral mortality (and survival) was consistent with both temperature and high irradiance, the latter implicated by the presence of a typical 'shading' pattern on surviving corals. These reefs are typically bathed by very high seawater temperatures (measured at up to 35 °C and likely occasionally exceeding this) and irradiance. Mortality had happened at the same time (early 1990 s) over most of the area, affecting most if not all coral taxa present. Based on changes in coral cover, another episode of high, if perhaps more localized, mortality occurred in 1996-97. In 1996, a relatively high hard coral cover of monospecific stands of *Goniastrea retiformis*, branching *Montipora* and massive *Porites* was present near Al Khawkhah (Fig. 1, Plate 14). The following year most corals in the area were dead (Plate 15), the most parsimonious explanation being a severe bleaching event.

And yet again in 1998 there was extensive coral bleaching in the Arabian region and elsewhere, causing high coral mortality world wide (Wilkinson et al. 1999, Sheppard 1999, 2003, Wilkinson 2000, Abuzinada et al. 2005, DeVantier & Hariri 2005, DeVantier et al. 2005 a, b). With such repeated bleaching events, and in view of the extent of damage and lack of reproductive stocks of corals of reproductive age, opportunities for recovery are being regularly set back.

Crown-of-thorns seastars

Recent extensive coral mortality had also occurred on offshore reefs, there attributable to predation by crown-of-thorns seastars. Residual populations of seastars (density greater than 10 ha^{-1}), and evidence in the form of characteristic feeding scars on corals, were still present in some sites. The remaining seastars were feeding during the day, typical behaviour exhibited during a population 'outbreak'. When in non-outbreak abundance (< 1 ha^{-1}) the seastars are usually cryptic during daylight, emerging to feed on coral at dusk (see e.g. Endean 1976, Moran 1986, Keesing 1992). Outbreaks of the seastars have been reported previously from other parts of the Red Sea, and the level of damage to corals appears comparable to that caused by *A. planci* in Sudan in the late 1960 s and Saudi Arabia and Egypt more recently (Ormond & Campbell 1971, 1974, Moore 1990, DeVantier et al. 2000).

On these reefs, most acroporid corals, preferred prey of *A. planci* (De'ath & Moran 1998), were dead. These included very large (4 to 5 m diameter) colonies of tabular *Acropora* (Plate 1) and stands of branching *Acropora*. The remaining live coral cover was mainly comprised of massive species and others generally not preferred by *A. planci*. Some of the affected sites had healthy coral growth, including terraces of large tabular *Acropora*, in the early 1990 s, and hence the likely time of the main *A. planci* outbreaks was 1994-1996, an estimate supported by the recent bioerosion and amount of algal growth on the dead corals.

Drupella

Additional coral mortality was caused by the coral-feeding muricid gastropods *Drupella*, one of a number of corallivorous gastropod genera reported from the Red Sea (Schuhmacher 1992), and the only one present in the areas surveyed. *Drupella* outbreaks can cause coral mortality comparable in extent to *A. planci* in other parts of the Indo-Pacific (Moyer et al. 1982; Turner 1994 a, b). Previously in the Red Sea, coral predation by snails has been reported from Sudan, Saudi Arabia and the Gulf of Aqaba (Schuhmacher 1992, Antonius & Riegl 1997, DeVantier et al. 2000), though the impact was not major (affecting less than 1 % cover). In the Yemen Red Sea, *Drupella* were present in varying abundance at most sites surveyed. These typically were most common on compact branching corals, such as corymbose, caespitose and tabular *Acropora* and less commonly on pocilloporids, although also present on most other types of corals, including massive *Porites*, *Galaxea* and encrusting forms. Generally coral predation by the snails was at a sub-lethal level, with most infected corals showing partial mortality ranging from 10 to 70 % of the colony. In summary, many reefs were affected to greater or lesser degree by these three main forms of disturbance, and in the shorter term (less than one decade) recovery of coral communities in the Yemen Red Sea will likely be slow and hampered because of a lack of new recruitment.

DISCUSSION

It has been noted previously (Behairy et al. 1992, Sheppard et al. 1992) that coral reef development in the southern Red Sea is limited. To quote from Behairy et al. (1992), in the "south (of the Red Sea), the different, highly sedimentary regime mostly excludes any reefs, especially fringing reefs. The south is more a province for soft substrate, mangroves and seagrass beds with occasional reefs in locations which are favorable to corals".

While supporting this conclusion, the present study has also shown that Yemen Red Sea waters do contain numerous areas of coral reef and coral communities fringing the coast and islands and in patches in open water (Figs 1, 4). Typically most shallow areas (less than 30 m depth) contain coral communities of some type, with species richness, cover and degree of accretion limited to greater or lesser degree by the physico-chemical environment and bioerosion, particularly high water temperatures and / or levels of irradiance and / or unstable substrate, and the presence of large numbers of urchins and other bioeroding organisms.

The communities shared a high degree of uniformity in species composition, with depauperate sites typically formed by a sub-set of species from the richer areas (also see SHEPPARD & SHEPPARD 1991, SHEPPARD et al. 1992, DEVANTIER et al. 2000). The relatively high sea water temperatures in the region are likely to be the most important factor limiting species richness, coral growth and reef development, although bathymetry, sediment and turbidity characteristics of coastal waters, and episodic disturbances, are also likely to be important. During the period of this study, seawater temperatures were typically high throughout the survey area (greater than 31 °C and up to 35 °C), and salinity varied by a maximum of 2 ppt (from 36 to 38 ppt, May to June). Turbidity was usually very high inshore, with underwater visibility in the range of 2 to 6 m. However, in offshore waters, turbidity was lower, with visibility in the range of 5 to 15 m. Seasonal variations in environmental conditions may increase the range of variability in turbidity among areas and have a strong influence on community structure.

The combined stresses to corals reach their maximum in the north of Yemen. There seawater temperatures in shallow waters typically reached 34 °C in spring and may occasionally rise above the tolerance limits for corals (COLES 1988, JOKIEL & COLES 1990, KLEYPAS et al. 1999, GUINOTTE et al. 2003). Nevertheless, the moderately high diversity, with 221 hermatypic species in total and three-quarters of these species occurring in the northern area, indicates that many corals are capable of living under the 'normal conditions' for the area. Although no genetic studies have been conducted to date, these are likely to be locally-acclimated and / or adapted populations surviving in a temperature regime inimical to their conspecific counterparts in many reef regions globally (JOKIEL & COLES 1990, BUDDEMEIER & SMITH 1999, KLEYPAS et al. 1999).

Apparent high temperature tolerances notwithstanding, growth and survival appear to be episodically interrupted by extreme temperatures causing extensive mortality through bleaching. Under conditions that become more favourable to macroalgal growth and the proliferation of bioeroding species, carbonate accretion by corals can rapidly be reduced to rubble and finer sediments (GLYNN 1988). Thus the extent and degree of disturbance (primarily from bleaching and seastar predation) are also perhaps contributing to the lack of recent reef accretion. These disturbances have been growing steadily in recent years, the former increasingly linked with a trend of global warming (HOEGH-GULDBERG 1999, WILKINSON 2004), the latter with loss of seastar predatory fishes from over-fishing and nutrient enrichment (reviewed in MORAN 1986, BIRKELAND & LUCAS 1990, DEVANTIER & DONE 2007). Fishing pressure in the Yemen Red Sea is increasing rapidly on reef fishes, invertebrates including lobsters and sea cucumbers, and sharks (KOTB et al. 2004, KRUPP et al. 2006).

Several other forms of local human impact also threaten these reefs. Despite the typically low rainfall, episodic flood events can transport large amounts of sediments and nutrients to coastal waters. Elsewhere, discharge of increased amounts of sediments from rivers, following large-scale catchment modification for agriculture or urban development, has led to degradation or destruction of coastal ecosystems. Sediment smothering and/or loss of light from increased turbidity (ROGERS 1990) can seriously affect coral reefs and seagrass beds, with well documented examples in Central America (CORTES & RISK 1985), the Philippines (HODGSON 1989), Indonesia (EDINGER et al. 1998) and Australia (PREEN et al. 1995). With the export of labour from Yemen to the Gulf region in recent decades some of the very old and elaborate terrace systems on the major wadis (VOGEL 1987) have ceased to be maintained and have deteriorated (VOGEL 1993). This has been exacerbated on some wadis by the construction, under donor programmes, of irrigation systems that do not maintain the terrace system. In addition, extensive cutting of timber for firewood has deforested some upper catchment areas (Shidiwan & Adin 1991). On Wadi Zabid, for example, damage to the terrace system and deforestation has caused massive erosion in the uplands and extensive sedimentation in the lowlands (Varisco et al. 1992). It is possible that greatly increased amounts of sediment, from the collapse of the terrace systems, will discharge to coastal areas near the mouths of wadis. This sediment has been accumulating in the terrace systems for over one thousand years and the amounts involved may be very large.

Ephemeral desert rivers can have high rates of bedload sediment transport (Laronne & Reid 1993). In the northern Red Sea, sediment from ephemeral rivers has little effect on coastal reefs because of adjacent deep water. Most sediment is quickly transported down the continental slope out of range of reef growth and hence re-suspension of sediment is minimal (Hawkins & Roberts 1994). On Yemen's Red Sea coast, however, the relatively wide shelf is likely to facilitate deposition of sediments in shallow water in the range of depths suitable for coral growth. The strong winds common in the area resuspend sediment, contributing to turbid inshore waters and creation of conditions difficult for coral growth. Unstable bottom sediments also prevent coral colonization and some of the existing distribution of reefs along the Yemen Red Sea coast appears to be governed by bottom sediment type and wadi discharge. Estimates of the wadi fluxes of sediment and possible changes in recent times are needed to evaluate the risks to inshore habitats (also see Buddemeier & Fautin 2002).

Another potential risk is increases in wastewater discharge containing nutrients and pesticides from coastal towns and agricultural areas. This is another of the most serious threats facing coral reefs and tropical seagrass areas around the world, implicated in reef and seagrass degradation in the Caribbean (Rawlins et al. 1998), the Great Barrier Reef (Bell & Elmetri 1995) and Indonesia (Edinger et al. 1998). In Yemen, pesticides are used in agriculture in both the Tihama and the upland terrace systems but the total quantities used are relatively low (DouAbal & Haddad 1996). In Yemen, marine organisms appear to contain only low levels of pesticide residues and PCBs (DouAbal & Haddad 1996). Nevertheless, some localized sewage pollution has already occurred in the vicinity of coastal towns (Krupp et al. 2006).

The role of dust storms in transporting sediment, pesticides and nutrients to the Red Sea also needs quantification. Dust storms occur frequently between April and August. They originate in the mountains and sweep across the Tihama picking up dust and litter and then dissipate over the sea. These dust storms may be a major source of sediment to coastal and oceanic waters (Folger 1970) and also transport soil contaminants such as pesticides, nutrients and toxic metals. In Saudi Arabia, near Jeddah, dust in dust storms was shown to contain high concentrations of cadmium (Behairy et al. 1985). It was suggested that the cadmium had originated from cement manufacture and oil combustion in the area inland from Jeddah.

Many buildings in the coastal villages on the Yemen Red Sea coast are built from coral blocks. DHV consultants (1990) reported that coral has been widely used in construction for many years in small quantities. More recently they report coral in use for road construction, which is having a devastating impact on some reefs. Anecdotal reports of coral block export were also noted. However mining of coral from living sub-tidal reefs was not observed. Most of the coral buildings inspected appeared to be built of fossil coral. Another potential risk to nearshore reefs is the future development and expansion of tourism. In Yemen, the present level of visitor damage to the reefs is minimal. However plans are being developed for future large-scale coastal tourism (Burns & Cooper 1997). With insufficient planning and environmental safeguards, such developments have adversely affected reefs in other areas of the Red Sea, notably along sections of the Egyptian coast (Kotb et al. 2004), and it is hoped that these will provide salutary lessons for future tourism and infrastructure development along Yemen's Red Sea coast.

CONCLUSIONS

The substantial increase in the number of species documented to around 221 species, and potential for further additions, particularly on the offshore islands, suggests that the southern Red Sea may approach more northerly areas of the Red Sea in terms of overall coral species richness (Sheppard & Sheppard 1991, DeVantier et al. 2000, Veron 2000). Considering the geological history, paleo-climatology and oceanography of the area (Klausewitz 1989, Sheppard et al. 1992), the biogeographic position of the southern Red Sea may be very important. Located between the Gulf of Aden (providing a degree of connectivity to the Indian Ocean fauna) and the northern Red Sea, the southern Red Sea is a transition zone which likely receives recruits from both areas, as demonstrated by the occurrence of characteristic regional endemics (e.g. *Acropora downingi, Montipora saudii* among others, Table 5 and Appendix). The southern Red Sea is subjected to reversing monsoonal winds which blow from the north in the summer, pushing a coastal current to the south; and south in the winter, pushing water up through the strait at Bab al-Mandeb from the Gulf of Aden (Morley 1975, Edwards 1987). These seasonal wind-driven surface current reversals may provide a mixed supply of propagules from two different regions of marine fauna, depending on the relevant spawning periodicity (Harrison & Wallace 1990). In particular, coral and other reef-associated populations on the volcanic islands along the central area, including the Hanish and Zuqar islands, Zubayr Islands and At Tair Island, are likely vital as 'stepping stones' for dispersal, promoting gene flow connecting reef populations in the Red Sea more generally. Any permanent or longterm damage to coral populations on these islands would likely have severe biogeographical consequences, and it is highly recommended that these receive conservation priority. Indeed, because of its outstanding tropical marine biodiversity and likely endemism, the larger southern Red Sea area was identified as a priority site for consideration for inclusion on the World Heritage Register (Hillary et al. 2003), and these islands are likely to be key locations in sustaining this biodiversity.

The unexpected amount of coral growth and level of species richness notwithstanding, parts of the area, particularly nearshore, are to varying degree clearly 'marginal' for coral survival and reef-growth, in the senses of definitions 2 and 3 of Guinotte et al. (2003):

2. "On the basis of proximity to an environmental condition known or reasonably assumed, based on physiological or biogeographic evidence, to place an absolute limit on the occurrence of reef communities or key classes of reef organisms.
3. In terms of organism and community condition (cover, composition, diversity, health) or metabolism".

Predictions of increasing marginality of reef systems world-wide, because of local impacts and global change via warming and changing ocean chemistry (Smith & Buddemeier 1992, Guinotte et al. 2003, Sheppard 2003) do not auger well for these already marginal communities (also see Harriott & Banks 2002). Yet coincidentally, the likely high degree of local acclimation and perhaps adaptation of corals and other reef species to the marginal conditions of some parts of the Yemen Red Sea present unique opportunities for research crucial to improved understanding of future reef vulnerability (Buddemeier & Fautin 2002). In light of these predictions, every effort should be made to minimize impacts and the trend to increasing ecological marginality of Yemen's Red Sea reefs (Kotb et al. 2004). In this respect, considerable progress has been made in developing appropriate strategies and action plans (PERSGA 1998, PERSGA/GEF 2003), yet major challenges remain in effective implementation.

ACKNOWLEDGEMENTS

This study was part of the UNDP/GEF Protection of Marine Habitats of the Red Sea Coast of Yemen Project. The authors would like to thank those organisations and individuals who assisted in providing environmental information for this paper or logistical support for field trips while in Yemen. Specifically these include the Ministry of Fish Wealth, Environmental Protection Council (now Authority), Oceanography Department of the University of Sana'a, Public Corporation for Maritime Affairs, Yemen Hunt Oil, Murtada Alwan, Ali Douabul, Hassan Hebba, Rifaat Hanna, David Medio and Captain Rafiq. We also acknowledge the help in the field, and in all other aspects, of our participating Yemeni colleagues in this project. We thank Charles Sheppard and Bernard Riegl and the editors for their reviews and Friedhelm Krupp for his consistent encouragement towards publishing these results.

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Manuscript submitted: 16 May 2006
Manuscript accepted: 17 December 2006

APPENDIX

Inventory of species recorded during the present study (1996-1998, 221 species) in Yemen and previously recorded in Southern Red Sea (prior to 1996, 100 species). X= Recorded during the present study (215 species; 54 genera); P= Previous record (100 species); U= Unconfirmed (6 species). All records from this study are from visual observations, photographic records and specimens collected. Unconfirmed species are of specimens deposited and waiting confirmation on their species status pending further investigation.

Zooxanthellate Scleractinia	Records
Family Astrocoeniidae Koby, 1890	
Genus ***Stylocoeniella*** Yabe and Sugiyama, 1935	
Stylocoeniella armata (Ehrenberg, 1834)	X
Stylocoeniella guentheri Bassett-Smith, 1890	X, P
Genus ***Madracis*** Milne Edwards and Haime, 1849	
Madracis kirbyi Veron and Pichon, 1976	U
Family Pocilloporidae Gray, 1842	
Genus ***Pocillopora*** Lamarck, 1816	
Pocillopora damicornis (Linnaeus, 1758)	X, P
Pocillopora verrucosa (Ellis and Solander, 1786)	X, P
Genus ***Seriatopora*** Lamarck, 1816	
Seriatopora caliendrum Ehrenberg, 1834	X, P
Seriatopora hystrix Dana, 1846	X, P
Genus ***Stylophora*** Schweigger, 1819	
Stylophora mamillata Scheer and Pillai, 1983	X, P
Stylophora pistillata Esper, 1797	X, P
Stylophora wellsi Scheer, 1964	X, P
Family Acroporidae Verrill, 1902	
Genus ***Montipora*** Blainville, 1830	
Montipora aequituberculata Bernard, 1897	X, P
Montipora circumvallata (Ehrenberg, 1834)	X
Montipora danae (Milne Edwards and Haime, 1851)	X, P
Montipora echinata Veron, DeVantier and Turak, 2002	X
Montipora floweri Wells, 1954	X, P
Montipora foliosa (Pallas, 1766)	X
Montipora grisea Bernard, 1897	X
Montipora hispida (Dana, 1846)	X
Montipora informis Bernard, 1897	X
Montipora monasteriata (Forskål, 1775)	X
Montipora nodosa (Dana, 1846)	X
Montipora pachytuberculata Veron, DeVantier and Turak, 2002	X
Montipora peltiformis Bernard, 1897	U
Montipora saudii Turak, DeVantier and Veron, 2002	X
Montipora spongiosa (Ehrenberg, 1834)	X
Montipora spumosa (Lamarck, 1816)	X
Montipora stellata Bernard, 1897	X, P
Montipora stilosa (Ehrenberg, 1834)	X
Montipora tuberculosa (Lamarck, 1816)	X
Montipora venosa (Ehrenberg, 1834)	X
Montipora verrucosa (Lamarck, 1816)	X, P
Genus ***Acropora*** Oken, 1815	
Acropora abrotanoides (Lamarck, 1816)	X, P
Acropora aculeus (Dana, 1846)	
Acropora acuminata (Verrill, 1864)	X
Acropora austera (Dana, 1846)	X, P
Acropora cerealis (Dana, 1846)	X
Acropora clathrata (Brook, 1891)	X, P
Acropora cytherea (Dana, 1846)	X, P
Acropora digitifera (Dana, 1846)	X, P
Acropora divaricata (Dana, 1846)	X
Acropora donei Veron and Wallace, 1984	X
Acropora downingi Wallace, 1999	X
Acropora elseyi (Brook, 1892)	X
Acropora eurystoma (Klunzinger, 1879)	X
Acropora gemmifera (Brook, 1892)	X
Acropora grandis (Brook, 1892)	X, P
Acropora granulosa (Milne Edwards and Haime, 1860)	U
Acropora haimei (Milne Edwards and Haime, 1860)	X, P
Acropora hemprichii (Ehrenberg, 1834)	X, P
Acropora horrida (Dana, 1846)	X
Acropora humilis (Dana, 1846)	X, P
Acropora hyacinthus (Dana, 1846)	P
Acropora intermedia (Brook, 1891)*	X, P
Acropora latistella (Brook, 1891)	X
Acropora loripes (Brook, 1892)	X
Acropora microphthalma (Verrill, 1859)	X
Acropora millepora (Ehrenberg, 1834)	X
Acropora muricata (Linneaus, 1758)*	X, P
Acropora nasuta (Dana, 1846)	X
Acropora pharaonis (Milne Edwards and Haime, 1860)	X
Acropora polystoma (Brook, 1891)	X

Zooxanthellate Scleractinia	Records
Acropora robusta (Dana, 1846)	X
Acropora samoensis (Brook, 1891)	X
Acropora secale (Studer, 1878)	X
Acropora selago (Studer, 1878)	X
Acropora spicifera (Dana, 1846)	X
Acropora squarrosa (Ehrenberg, 1834)	X
Acropora subulata (Dana, 1846)	X
Acropora valenciennesi (Milne Edwards and Haime, 1860)	X, P
Acropora valida (Dana, 1846)	X, P
Acropora vaughani Wells, 1954	X
Acropora yongei Veron and Wallace, 1984	U, P
Genus ***Astreopora*** Blainville, 1830	
Astreopora expansa Brüggemann, 1877	X, P
Astreopora myriophthalma (Lamarck, 1816)	X, P
Family Euphilliidae Veron, 2000	
Genus ***Euphyllia*** Dana, 1846	
Euphyllia glabrescens (Chamisso and Eysenhardt, 1821)	X
Genus ***Plerogyra*** Milne Edwards and Haime, 1848	
Plerogyra sinuosa (Dana, 1846)	X, P
Family Oculinidae Gray, 1847	
Genus ***Galaxea*** Oken, 1815	
Galaxea astreata (Lamarck, 1816)	X
Galaxea fascicularis (Linnaeus, 1767)	X, P
Family Meandrinidae Gray, 1847	
Genus ***Gyrosmilia*** Milne Edwards and Haime, 1851	
Gyrosmilia interrupta (Ehrenberg, 1834)	X, P
Family Siderasteridae Vaughan and Wells, 1943	
Genus ***Anomastraea*** Marenzeller, 1901	
Anomastraea irregularis Marenzeller, 1901	X
Genus ***Coscinaraea*** Milne Edwards and Haime, 1848	
Coscinaraea columna (Dana, 1846)	X
Coscinaraea monile (Forskål, 1775)	X
Genus ***Psammocora*** Dana, 1846	
Psammocora contigua (Esper, 1797)	X, P
Psammocora explanulata Horst, 1922	X, P
Psammocora haimeana Milne Edwards and Haime, 1851	X, P
Psammocora profundacella Gardiner, 1898	X
Psammocora superficialis Gardiner, 1898	X
Genus ***Siderastrea*** Blainville, 1830	
Siderastrea savignyana Milne Edwards and Haime, 1850	X, P
Family Agariciidae Gray, 1847	
Genus ***Gardineroseris*** Scheer and Pillai, 1974	
Gardineroseris planulata Dana, 1846	X, P
Genus ***Leptoseris*** Milne Edwards and Haime, 1849	
Leptoseris explanata Yabe and Sugiyama, 1941	X
Leptoseris foliosa Dineson, 1980	X
Leptoseris hawaiiensis Vaughan, 1907	X, P
Leptoseris mycetoseroides Wells, 1954	X, P
Leptoseris scabra Vaughan, 1907	X, P
Leptoseris yabei (Pillai and Scheer, 1976)	X, P
Genus ***Pachyseris*** Milne Edwards and Haime, 1849	
Pachyseris speciosa (Dana, 1846)	X, P
Genus ***Pavona*** Lamarck, 1801	
Pavona cactus (Forskål, 1775)	X, P
Pavona decussata (Dana, 1846)	X
Pavona duerdeni Vaughan, 1907	X, P
Pavona explanulata (Lamarck, 1816)	X, P
Pavona frondifera (Lamarck, 1816)	X, P
Pavona maldivensis (Gardiner, 1905)	X, P
Pavona varians Verrill, 1864	X, P
Pavona venosa (Ehrenberg, 1834)	X
Family Fungiidae Dana, 1846	
Genus ***Cycloseris*** Milne Edwards and Haime, 1849	
Cycloseris costulata (Ortmann, 1889)	X
Cycloseris cyclolites Lamarck, 1801	X
Cycloseris patelliformis (Boschma, 1923)	X
Cycloseris vaughani (Boschma, 1923)	X, P
Genus ***Diaseris*** Milne Edwards and Haime, 1849	
Diaseris distorta (Michelin, 1843)	X
Genus ***Fungia*** Lamarck, 1801	
Fungia concinna Verrill, 1864	X
Fungia corona Döderlein, 1901	X
Fungia danai Milne Edwards and Haime, 1851	X
Fungia fungites (Linneaus, 1758)	X, P
Fungia granulosa Klunzinger, 1879	X
Fungia horrida Dana, 1846	X
Fungia klunzingeri Döderlein, 1901	X
Fungia moluccensis Horst, 1919	X
Fungia paumotensis Stutchbury, 1833	X
Fungia repanda Dana, 1846	X, P
Fungia scruposa Klunzinger, 1879	X
Fungia scutaria Lamarck, 1801	X, P
Genus ***Ctenactis*** Verrill, 1864	
Ctenactis crassa (Dana, 1846)	X, P
Ctenactis echinata (Pallas, 1766)	X, P
Genus ***Herpolitha*** Eschscholtz, 1825	
Herpolitha limax (Houttuyn, 1772)	X, P
Genus ***Podabacia*** Milne Edwards and Haime, 1849	
Podabacia crustacea (Pallas, 1766)	X, P

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Family Pectinidae Vaughan and Wells, 1943	
Genus ***Echinophyllia*** Klunzinger, 1879	
Echinophyllia aspera (Ellis and Solander, 1788)	X, P
Echinophyllia echinata (Saville-Kent, 1871)	X, P
Genus ***Mycedium*** Oken, 1815	
Mycedium elephantotus (Pallas, 1766)	X, P
Genus ***Oxypora*** Saville-Kent, 1871	
Oxypora lacera Verrill, 1864	X, P
Genus ***Pectinia*** Oken, 1815	
Pectinia africanus Veron, 2002	X
Family Merulinidae Verrill, 1866	
Genus ***Hydnophora*** Fischer de Waldheim, 1807	
Hydnophora exesa (Pallas, 1766)	X, P
Hydnophora microconos (Lamarck, 1816)	X, P
Genus ***Merulina*** Ehrenberg, 1834	
Merulina ampliata (Ellis and Solander, 1786)	X, P
Merulina scheeri Head, 1983	X
Family Dendrophylliidae Gray, 1847	
Genus ***Turbinaria*** Oken, 1815	
Turbinaria mesenterina (Lamarck, 1816)	X
Turbinaria reniformis Bernard, 1896	X
Turbinaria stellulata (Lamarck, 1816)	X
Family Mussidae Ortmann, 1890	
Genus ***Blastomussa*** Wells, 1961	
Blastomussa merleti Wells, 1961	X, P
Genus ***Micromussa*** Veron, 2000	
Micromussa amakusensis (Veron, 1990)	X
Genus ***Acanthastrea*** Milne Edwards and Haime, 1848	
Acanthastrea echinata (Dana, 1846)	X, P
Acanthastrea lordhowensis Veron and Pichon, 1982	X
Genus ***Lobophyllia*** Blainville, 1830	
Lobophyllia corymbosa (Forskål, 1775)	X, P
Lobophyllia hataii Yabe and Sugiyama, 1936	X
Lobophyllia hemprichii (Ehrenberg, 1834)	X, P
Lobophyllia robusta Yabe and Sugiyama, 1936	X
Genus ***Symphyllia*** Milne Edwards and Haime, 1848	
Symphyllia agaricia Milne Edwards and Haime, 1849	X
Symphyllia erythraea (Klunzinger, 1879)	X
Symphyllia radians Milne Edwards and Haime, 1849	X
Symphyllia recta (Dana, 1846)	X
Family Faviidae Gregory, 1900	
Genus ***Caulastrea*** Dana, 1846	
Caulastrea connata (Ortmann, 1892)	U
Caulastrea tumida Matthai, 1928	X
Genus ***Favia*** Oken, 1815	
Favia danae Verrill, 1872	X
Favia favus (Forskål, 1775)	X, P
Favia laxa (Klunzinger, 1879)	X
Favia lizardensis Veron and Pichon, 1977	X
Favia matthaii Vaughan, 1918	X
Favia pallida (Dana, 1846)	X, P
Favia speciosa Dana, 1846	X
Favia stelligera (Dana, 1846)	X, P
Genus ***Favites*** Link, 1807	
Favites abdita (Ellis and Solander, 1786)	X, P
Favites chinensis (Verrill, 1866)	X, P
Favites complanata (Ehrenberg, 1834)	X
Favites flexuosa (Dana, 1846)	X, P
Favites halicora (Ehrenberg, 1834)	X, P
Favites pentagona (Esper, 1794)	X, P
Favites russelli (Wells, 1954)	X
Genus ***Goniastrea*** Milne Edwards and Haime, 1848	
Goniastrea aspera Verrill, 1905	X
Goniastrea australensis (Milne Edwards and Haime, 1857)	X
Goniastrea edwardsi Chevalier, 1971	X, P
Goniastrea pectinata (Ehrenberg, 1834)	X, P
Goniastrea peresi (Faure and Pichon, 1978)	X, P
Goniastrea retiformis (Lamarck, 1816)	X
Genus ***Platygyra*** Ehrenberg, 1834	
Platygyra crosslandi Matthai, 1928	X
Platygyra daedalea (Ellis and Solander, 1786)	X, P
Platygyra lamellina (Ehrenberg, 1834)	X, P
Platygyra sinensis (Milne Edwards and Haime, 1849)	X
Genus ***Oulophyllia*** Milne Edwards and Haime, 1848	
Oulophyllia bennettae (Veron, Pichon, 1977)	X
Oulophyllia crispa (Lamarck, 1816)	X, P
Genus ***Leptoria*** Milne Edwards and Haime, 1848	
Leptoria phrygia (Ellis and Solander, 1786)	X, P
Genus ***Montastrea*** Blainville, 1830	
Montastrea curta (Dana, 1846)	X, P
Montastrea magnistellata Chevalier, 1971	X
Genus ***Plesiastrea*** Milne Edwards and Haime, 1848	
Plesiastrea versipora (Lamarck, 1816)	X, P
Genus ***Leptastrea*** Milne Edwards and Haime, 1848	
Leptastrea inaequalis Klunzinger, 1879	X, P
Leptastrea pruinosa Crossland, 1952	X
Leptastrea purpurea (Dana, 1846)	X, P
Leptastrea transversa Klunzinger, 1879	X, P
Genus ***Cyphastrea*** Milne Edwards and Haime, 1848	
Cyphastrea chalcidium (Forskål, 1775)	X, P
Cyphastrea microphthalma (Lamarck, 1816)	X, P

Zooxanthellate Scleractinia	Records
Cyphastrea serailia (Forskål, 1775)	X, P
Cyphastrea hexasepta Veron, Turak and DeVantier, 2002	X
Genus ***Diploastrea*** Matthai, 1914	
Diploastrea heliopora (Lamarck, 1816)	X, P
Genus ***Echinopora*** Lamarck, 1816	
Echinopora forskaliana (Milne Edwards and Haime, 1850)	U
Echinopora fruticulosa (Ehrenberg, 1834)	X
Echinopora gemmacea Lamarck, 1816	X, P
Echinopora hirsutissima Milne Edwards and Haime, 1849	X
Echinopora lamellosa (Esper, 1795)	X, P
Family Poritidae Gray, 1842	
Genus ***Alveopora*** Blainville, 1830	
Alveopora allingi Hoffmeister, 1925	X
Alveopora daedalea (Forskål, 1775)	X
Alveopora ocellata Wells, 1954	X
Alveopora spongiosa Dana, 1846	X
Alveopora tizardi Bassett-Smith, 1890	X
Alveopora viridis Quoy and Gaimard, 1833	X
Genus ***Goniopora*** Blainville, 1830	
Goniopora ciliatus Veron, 2002	X
Goniopora columna Dana, 1846	X
Goniopora djiboutiensis Vaughan, 1907	X
Goniopora lobata Milne Edwards and Haime, 1860	X, P
Goniopora minor Crossland, 1952	X
Goniopora savignyi Dana, 1846	X
Goniopora somaliensis Vaughan, 1907	X
Goniopora stokesi Milne Edwards and Haime, 1851	X
Goniopora tenella (Quelch, 1886)	X
Goniopora tenuidens (Quelch, 1886)	X
Genus ***Porites*** Link, 1807	
Porites annae Crossland, 1952	P
Porites columnaris Klunzinger, 1879	X
Porites echinulata Klungzinger, 1879	X
Porites lichen Dana, 1846	X, P
Porites lobata Dana, 1846	X
Porites lutea Milne Edwards and Haime, 1851	X, P
Porites monticulosa Dana, 1846	X
Porites nigrescens Dana, 1846	X, P
Porites nodifera Klunzinger, 1879	X, P
Porites profundus Rehberg, 1892	X
Porites rus (Forskål, 1775)	X
Porites solida (Forskål, 1775)	X

* The status of some species names is currently disputed: e.g. *Acropora intermedia* (Brook, 1891) – *Acropora nobilis* (Dana, 1846) and *Acropora muricata* (Linnaeus, 1758) – *Acropora formosa* (Dana, 1846). See Wallace 1999, Veron 2000 for discussion.