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## Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE)

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**Abstract** Two positive sea-surface temperature anomalies occurred in the Arabian Gulf in short sequence. Between May and August 1996 and 1998, sea-surface temperatures in the southern Arabian Gulf were elevated by 2°C above average. The consequences for coral fauna, coral diseases and coral regeneration were studied in Dubai (United Arab Emirates) between Jebel Ali and Ras Hasyan. In 1996, coral death was widespread, affecting primarily the genus *Acropora*. In *Acropora*-dominated areas, live coral cover was reduced from 90% to about 26% in 1996, while in 1998 only a reduction from 26% to 22% of the remaining coral cover occurred. In the study area, all six *Acropora* species suffered total mortality in 1996, thus the coral fauna was reduced from 34 species to 27. The nearest areas with surviving *Acropora* were 30 km to the east (Deira) and 20 km to the west (Al Jazira). Massive coral species suffered negligible mortality, and slowly increased in space cover. The *Acropora* overkill turned 7.9 km<sup>2</sup> (19.7% of total coral-covered area) of previously lush coral gardens into a dead framework that was increasingly bioeroded. *Acropora* recruitment only started in 1998, average recruit size in 1999 was 7 ± 3 cm, and recruits were rare. Prior to the mass mortality event, coral diseases were common and seasonal (14 ± 5% of corals, mainly *Acropora*, affected in summer, in winter 7 ± 6%, mainly massives), after the mortality event seasonality

was lost and infection remained below winter levels (6 ± 5%, only massives infected). In fish, overall species richness decreased from 95 to 64 species in point counts, but frequency only decreased in one species (*Pseudochromis persicus*). Guild structure changed inasmuch as herbivores and planktivores increased, and invertivores decreased, although differences were not statistically significant. The most abundant family, both prior to and after the coral mass mortality, was Lutjanidae. It appears that even though much of the coral was dead, the maintenance of structural complexity allowed the fish assemblage to avoid a similar catastrophic change to that experienced by the coral assemblage.

### Introduction

It is generally accepted that the 1998 sea-surface temperature (SST) anomaly and bleaching event caused widespread perturbations in Indo-Pacific coral systems, and it is considered by many to have been the most important bleaching event documented so far (Wilkinson 1998, 2000; Goreau et al. 2000). However, some peripheral areas of the Indo-Pacific, like the Arabian Gulf, did not experience comparable bleaching and coral mortality in 1998, but were already hit by an SST anomaly in 1996 that caused widespread coral death (Wilkinson 1998; Riegl 1999). Interestingly, mainly *Acropora* species were affected, with less damage to other taxa. Since, in the Arabian Gulf, *Acropora* are the dominant corals, which cover most space in many dense coral assemblages and build most of the carbonate structure, one would expect modifications of the system's functioning, also with regard to the fish fauna.

Worldwide, *Acropora* appear to be among the first corals to experience heavy losses in times of crisis (Coles and Fadlallah 1991; Gleason 1993; Wilkinson 1998; Marshall and Baird 2000) and in some areas are in serious decline (Aronson and Precht 1997). It is therefore of interest to study the effects of *Acropora* loss in a

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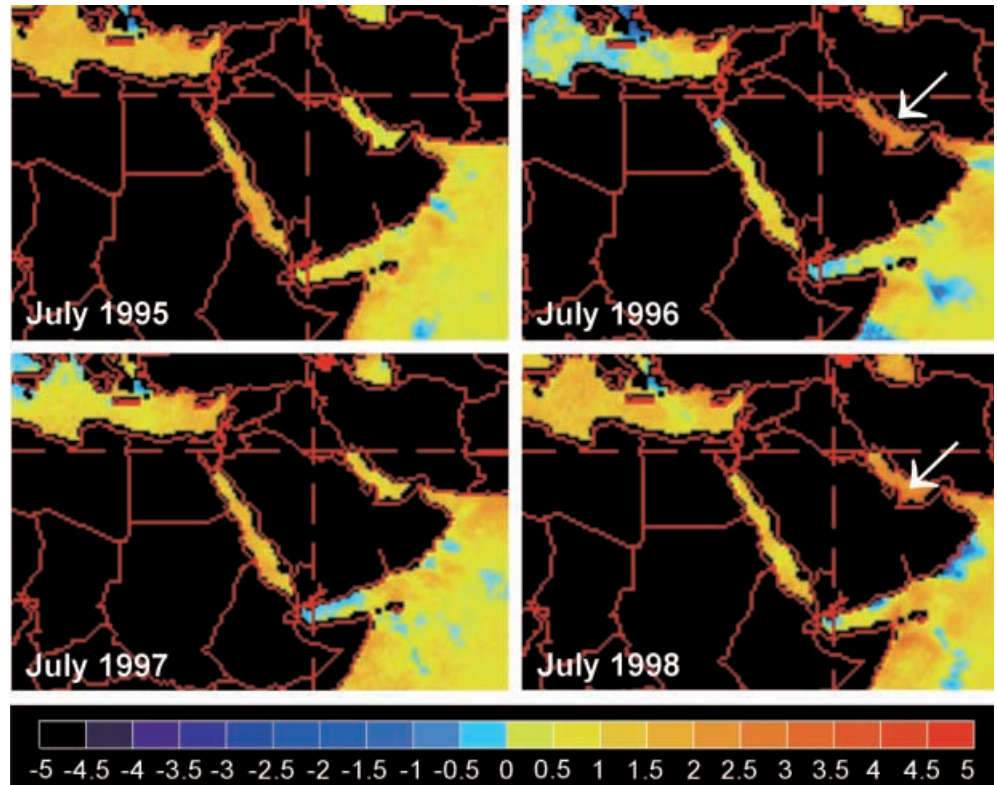
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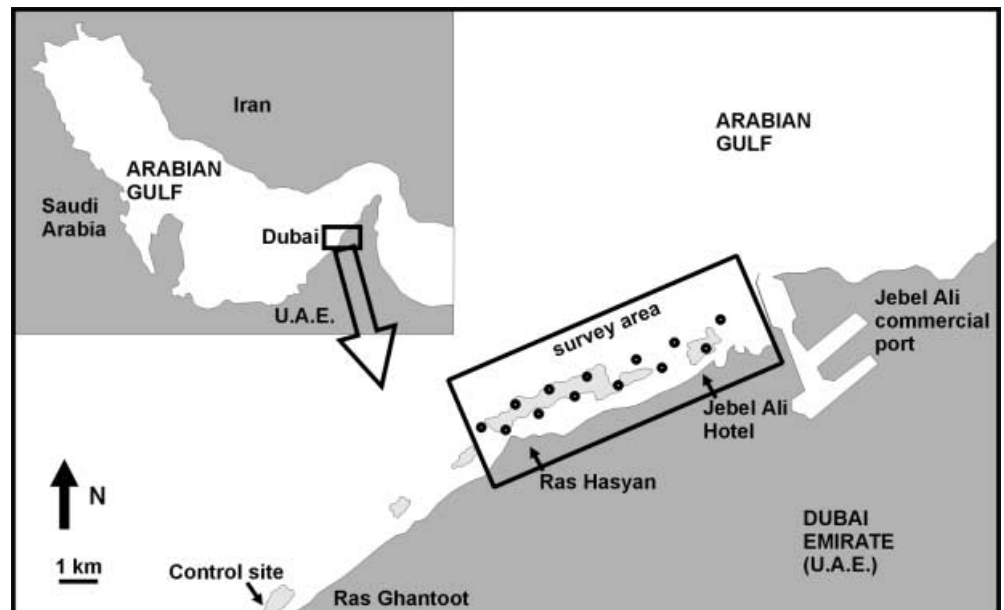
system previously dominated by this genus. In particular, system components which appear to depend on high density of a particular coral species, like coral diseases or certain fish assemblages, could be expected to change after such a significant mass mortality event.

Since the Gulf was not only affected by a single temperature anomaly in 1996 but also by a subsequent one in 1998 (Wilkinson 1998; Goreau et al. 2000; Fig. 1), comparison is possible of the effects of two potentially catastrophic events in short succession.

**Fig. 1** Satellite-derived sea surface temperature data from the Arabian region showing the anomalies of 1996 and 1998, in comparison to the normal years 1995 and 1997. Only data for July are shown. The 1996 anomaly lasted from April to September, that of 1998 from May to September. The 1996 and 1998 images show a 2°C positive anomaly for July. Further (propriety) data confirming these temperature excursions were obtained from thermographs but could not be shown in this paper (Dubai municipality, unpublished)



**Fig. 2** Study area in the southern Arabian Gulf, Dubai Emirate, United Arab Emirates. Sample sites are indicated by circles



This study examines pre- and post-mass mortality and SST anomaly event characteristics of: (1) the coral assemblage structure, (2) the frequency and nature of coral diseases and (3) the fish assemblage.

## Materials and methods

In the Dubai study area (between Jebel Ali port and Ras Hasyan, Fig. 2), 26 evenly distributed, equidistant sample points were se-

lected within the known area of dense coral growth where two line-transect sampling methods were utilized because of variable coral cover. Sampling in 1995–1996 employed continuous-intercept recording on 10-m line transects and line-point-intercept recording in 1 m intervals on 50-m line transects (Loya 1978; Weinberg 1981; English et al. 1994). Details and rationale for the sampling method can be found in Riegl (1999). After the 1996 coral mass mortality, the area was revisited and re-sampled in April 1998 (prior to the onset of the 1998 SST anomaly), October/November 1999 and July 2000 (no sampling). This time, only random transects were used in the same areas where sampling was performed in previous years (as recorded by d-GPS). The random-sampling approach relied on overall statistical differences within the sampled assemblage rather than on repetitive measurements of the same colonies. Skeleton breakdown and renewed recruitment were documented. All coral recruits were identified to species and measured. Also areas that were known to have been affected by man-made disturbances (similar mortality due to dredging plumes in nearby Al Jazira close to Ras Ghantoot, Abu Dhabi) 15 years prior to the 1996 temperature anomaly were visited to obtain a time series of framework-breakdown or -regeneration processes.

Data processing for classification and ordination used a square matrix of coral cover; data were fourth root transformed for the production of a similarity matrix. Agglomerative, hierarchical cluster analysis used the Bray–Curtis quantitative similarity coefficient and group average sorting (Warwick and Clarke 1993) for 10-m transects. Although the Bray–Curtis similarity coefficient is superior to Euclidean distance as a measure (Bloom 1981), the latter was nevertheless used for the 50-m transects since the clusters obtained with this algorithm were better interpretable from a biological viewpoint. Multidimensional scaling was used to provide an alternative to view the processes of change within assemblages (Clarke and Warwick 1998).

Coral taxonomy follows Wallace (1999) and Veron (2000). Therefore, some well-established species names from the area were changed. For example, *Acropora clathrata* according to Wallace (1999) is now *A. downingi*. According to Veron (2000) both species names, *A. downingi* and *A. clathrata*, are valid. The latter opinion is followed in this paper. Also *Porites compressa* has been renamed *P. harrisoni* (Veron 2000). The taxonomy in the present paper therefore differs from that used in a previous paper from the same study area (Riegl 1999).

Sea surface temperature was obtained by in situ measurements provided by the Dubai Municipality, and satellite-derived data were obtained from the website [http://psbgi1.nesdis.noaa.gov:8080/PSB/SST/climo\\_archive](http://psbgi1.nesdis.noaa.gov:8080/PSB/SST/climo_archive).

For the estimation of spatial cover of coral frameworks, maps produced by Riegl et al., (in press) were imported into a Zeiss KS 400 3.0 image analysis program which allowed the determination of total space covered by corals in the surveyed area, versus areas covered by bare sand and seagrass. Thus, the total area of framework formation potential could be calculated both in square kilometers and percentage of total mapped area. This calculation

ignored assemblage-specific space cover by corals within the categories used since it only focussed on the total area covered by coral growth (total square meters covered by the dense *Acropora* assemblage, dense *P. harrisoni* assemblage, sparse *P. lutea* assemblage, etc.).

The same transects as used for coral assemblage analysis were used for disease counts. If any part of an intercepted colony was diseased, even if not directly under the transect line, it was recorded. This allowed detection of areas with high disease frequency and quantification of affected colonies in the population as well as species-specific frequency. Transplantation experiments were made with white band disease and yellow band disease. Diseased parts of colonies were broken off and tied to healthy branches within the same colony, in order to avoid immunoincompatibility reactions, and to other colonies using cable ties (Antonius 1985, 1988). Infection rate was checked every third day.

Fish counts were performed using the Bohnsack visual fish census technique (Bohnsack and Bannerot 1986) at various randomly chosen locations during the last 2 weeks of October 1995 and 1999, to avoid any seasonal effects. Due to the patchy distribution of corals (or coral skeletons) fish counts were limited to a distance of 4 m from the diver and were only performed in areas of at least 80% coral cover.

## Results

In both 1996 and 1998 positive temperature excursions of almost the same magnitude occurred in the study area. In both years, the SST anomaly started in April and lasted until September. June, July and August of both years showed a positive 1.5–2.5°C anomaly (Table 1), which is generally considered to be above the bleaching threshold. Maximum in situ measured temperatures in the study area were 35°C, which is about 2°C above the usually recorded maxima and thus supports the satellite-derived data.

Prior to the 1996 mass mortality, five well-separable coral assemblages (designated A–E) of highly variable substratum coverage were differentiated by both 10- and 50-m transects (Fig. 3; Table 2). The following characteristics were determined for each assemblage:

A Large, widely spaced *Porites lutea* and other *Porites* with additional, mainly massive, species. This coral assemblage had the highest spatial extension and did not suffer during either the 1996 or the 1998 SST anomaly (Tables 2, 3).

**Table 1** Temperature anomaly in the Arabian Gulf in 1996 and 1998 as calculated from the NOAA website ([http://psbgi1.nesdis.noaa.gov:8080/PSB/SST/climo\\_archive](http://psbgi1.nesdis.noaa.gov:8080/PSB/SST/climo_archive))

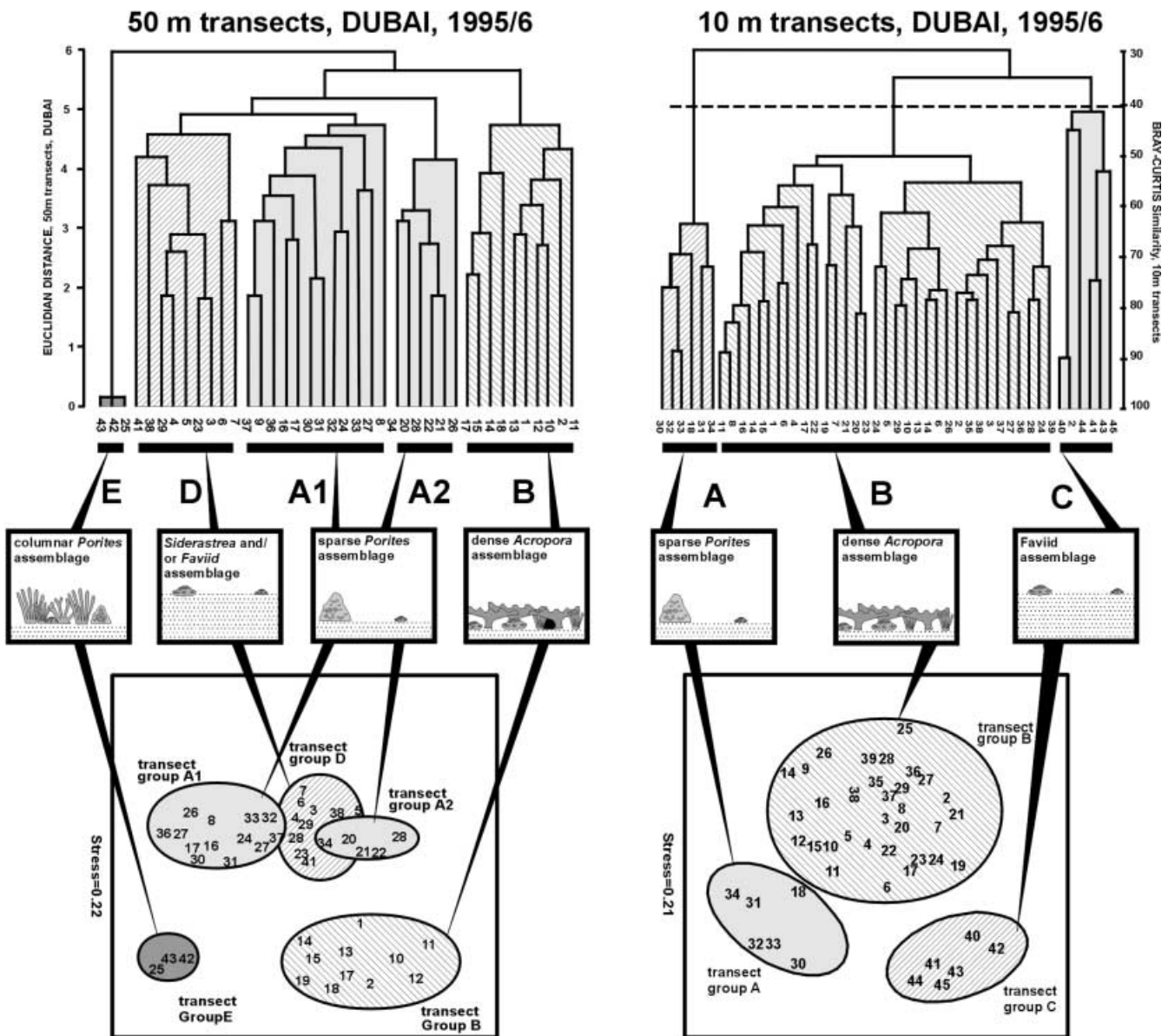
Year	Month	Positive temperature excursion (°C)	Remarks
1996	Apr	1.5	Southeastern Gulf only
	May	1.5	
	Jun	2	
	Jul	2.5	
	Aug	2	
	Sep	1	
1998	Apr	1	Warmest in southeastern Gulf
	May	1.5	
	Jun	2–2.5	
	Jul	1.5–2	
	Aug	2	
	Sep	1–1.5	

B Mainly tabular colonies of *Acropora clathrata* and *A. downingi* and six other, generally subordinate, *Acropora* species with high (40–90%) coral cover of available substratum. Frequent overtopping of competitively subordinate massive corals, like *Porites* spp., *Cyphastrea* spp. and *Platygyra* spp. Towards its periphery, cover by other *Acropora* species (such as *A. pharaonis*) and massive corals of the genera *Porites*, *Cyphastrea*, *Favia* and *Platygyra* increased. Heavy mortality in the 1996 mass mortality event (Fig. 4, cf. Fig. 6a, b; Tables 2, 3), not in 1998.

- C Widely spaced patches of faviid colonies that were not affected either in 1996 or 1998.
- D Widely spaced *Siderastrea savignyana* colonies that were also not affected either in 1996 or 1998.
- E Densely spaced (80% coral cover), columnar *Porites harrisoni* colonies intermingled with massive colonies, mainly faviids (*Favia* sp., *Platygyra* sp.) with patchy distribution. Low mortality in 1996 and 1998.

The SST anomaly in 1996 affected primarily *Acropora* species and had negligible effects on other taxa (Table 3; Fig. 4). The total coral fauna was reduced from 34 species to 27 species (all *Acropora* removed, fauna checklist in Riegl 1999). Since *Acropora* had the highest framebuilding capacity (high population density, interlocking and rapid skeletal growth), the living component of virtually the entire framework-producing area (with the exception of the dense *P. harrisoni* assemblage) was

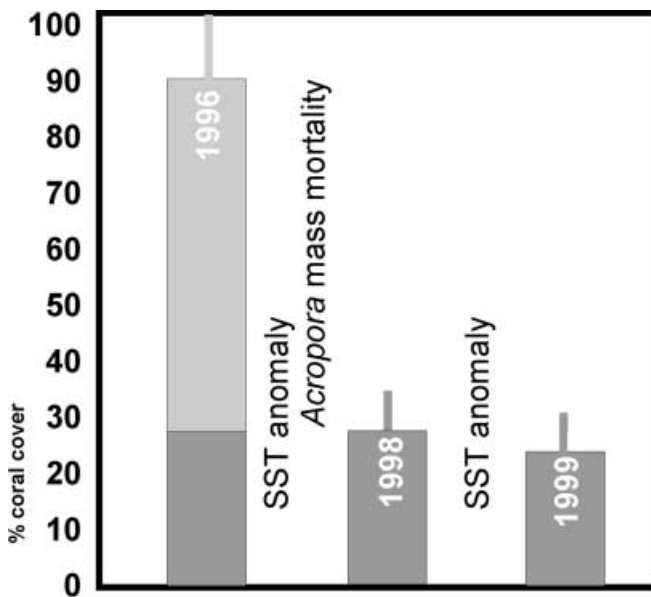
**Fig. 3** Coral assemblage analyses by agglomerative, hierarchical cluster analysis and multidimensional scaling in the Arabian Gulf in winter 1995/1996 using 50-m point-intercept and 10-m continuous-intercept line transects. Assemblages are further characterized in Table 2



**Table 2** Biological characteristics of coral assemblages in the Arabian Gulf study area between Jebel Ali and Ras Ghantoot. Assemblage code refers to Fig. 3. Dominant species are those that cover the most space within each assemblage (i.e. ecologically and visually dominant). Not all assemblages were sampled by both transect methods (*n.s.* not sampled). Dominant typology refers to

Assemblage code	Dominant species (alive) in 1996	Living coral cover of substratum, all species (10-m transects)	Living coral cover of substratum, all species (50-m transects)	Dominant typology of corals
A	<i>Porites lutea</i>	36 ± 15	21 ± 11	Big massive
B	<i>Acropora clathrata</i> and <i>A. downingi</i>	62 ± 24	54 ± 22	Tabular, branching
C	<i>Favia</i> spp.	16 ± 4	n.s.	Small massive
D	<i>Siderastrea savignyana</i>	n.s.	14 ± 7	Small massive
E	<i>Porites harrisoni</i>	n.s.	51 ± 2	Columnar

the growth-form type found in most constituent corals of the respective assemblage (*big massive* corals usually attained sizes up to and > 50–100 cm diameter; *small massive* corals were usually < 10 cm in diameter). Values are means and standard deviation of percentages of total transect (sample) area covered by each assemblage (all species)



**Fig. 4** Live coral coverage of the substratum in Dubai, Arabian Gulf, in response to the 1996 and 1998 sea-surface temperature (SST) anomalies. Only the 1996 SST anomaly led to a significant reduction of live cover (see also Table 3). The light gray part of the column (1996) is coverage by *Acropora*

lost in this mass mortality event. Prior to the mortality event, 7.9 km<sup>2</sup> of the 37.7 km<sup>2</sup> study area had framework-building potential. After the event, this was reduced to 0.1 km<sup>2</sup> – a loss of 98.7% of the framework-building

coral area (Fig. 5). The 1998 SST anomaly had only minor effects on the assemblage and triggered neither mass bleaching nor strong mortality (Fig. 4). This was most likely because all susceptible species had already been removed from the coral assemblage. The SST anomaly was as strong as that of 1996 (Fig. 1).

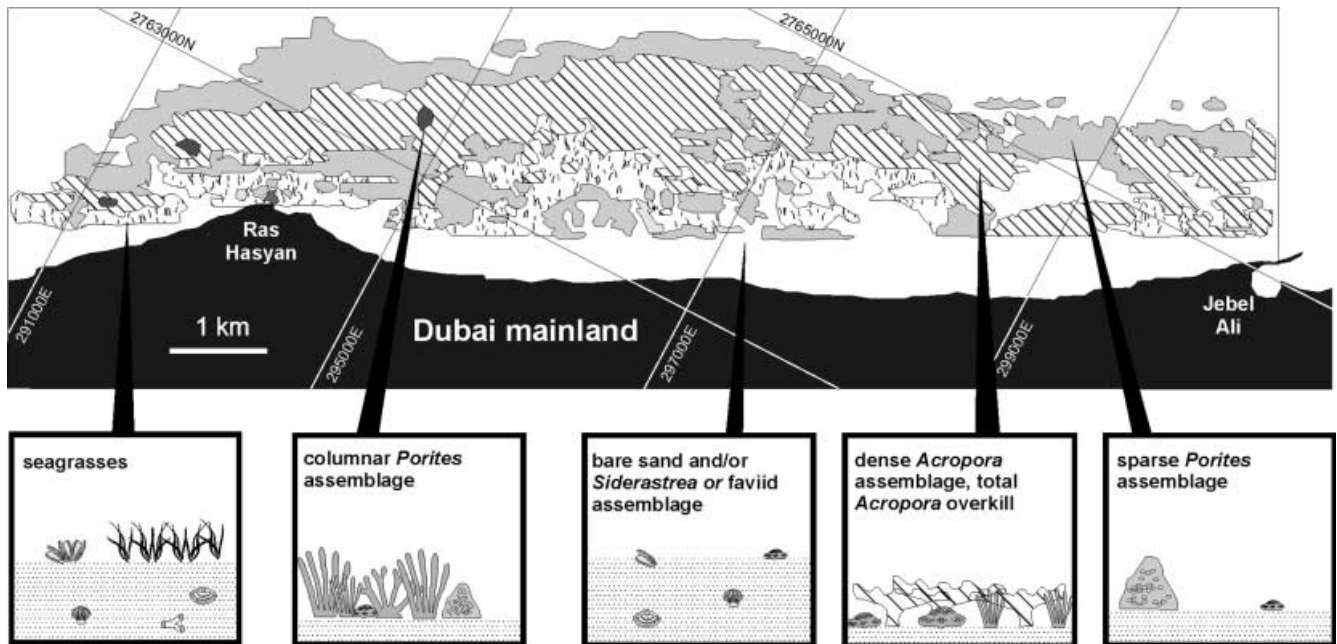
#### Framework breakdown

In April 1998 most *Acropora* skeletons were still standing and branches were covered by fine algal turf, but heavy overgrowth was absent. Strong erosion of surficial structures due to grazing echinoids (particularly *Echinometra mathei*) was apparent (Fig. 6b). Coral skeletons were still rigid and not easily broken. In November 1999, branches were heavily encrusted by layers of oysters (*Chama* sp., *Spondylus* sp.), and coralline algae and many were brittle and easy to break because they were bored into by clionid sponges. In 1999, many *Acropora* tables had started to degenerate into stumps surrounded by branch fragments. In a coral area west of Ras Ghantoot that had been killed 15 years previously, virtually no intact *Acropora* tables remained (Fig. 6c). Recruits near Ras Ghantoot ranged in size from 10–70 cm in maximum diameter (average 34 ± 15 cm), which would suggest a growth rate between 5 and 10 cm year<sup>-1</sup>. All grew on the caprock (original rocky attachment substratum), since the previous framework, which could have served as a base for settlement, had already

**Table 3** Changes in coral assemblage and framework characteristics in the Arabian Gulf study area between Jebel Ali and Ras Ghantoot after the 1996 coral mortality event. Coral cover refers to the percentage of transect samples that were covered by live

	1996	1998	1999	Significance	Post hoc difference
% Total coral cover of substratum (live and standing dead)	90 ± 12	83 ± 11	81 ± 6	$F=2.05, P>0.05$	n.a.
% Live coral cover of substratum (no standing dead included)	90 ± 12	26 ± 6	22 ± 10	$F=144.3, P<0.01$	1996–1998, 1996–1999
% Contribution of live <i>Acropora</i> to total cover	80 ± 22	0	0	n.a.	n.a.

corals or unbroken skeletons (= standing dead) without any living tissues. Values are means and standard deviation of percentages. Employed tests were one-way ANOVA, with Student–Neuman–Keuls post hoc tests, or *t*-test (*n.a.* not applicable)



**Fig. 5** Map of coral assemblages in Dubai, Arabian Gulf. The striped area was covered by dense *Acropora* growth in 1995 and only by standing dead skeletons in 1998/1999. The small dark gray areas were covered by the columnar *Porites harrisoni* assemblage, the light gray areas by the massive *Porites lutea*-dominated community. The white areas were mainly sand, but included patches of *Siderastrea* and faviid-dominated sparse coral associations. Seagrasses are indicated with a leaf pattern

broken down for the most part (Fig. 6d). This was verified since the caprock delaminated easily, particularly where the bases of *Acropora* were attached, and was sampled repeatedly. This finding suggests that about 15 years after a mass mortality event most of the *Acropora* framework has disappeared in Dubai, but coral regeneration will still take place.

#### Coral diseases

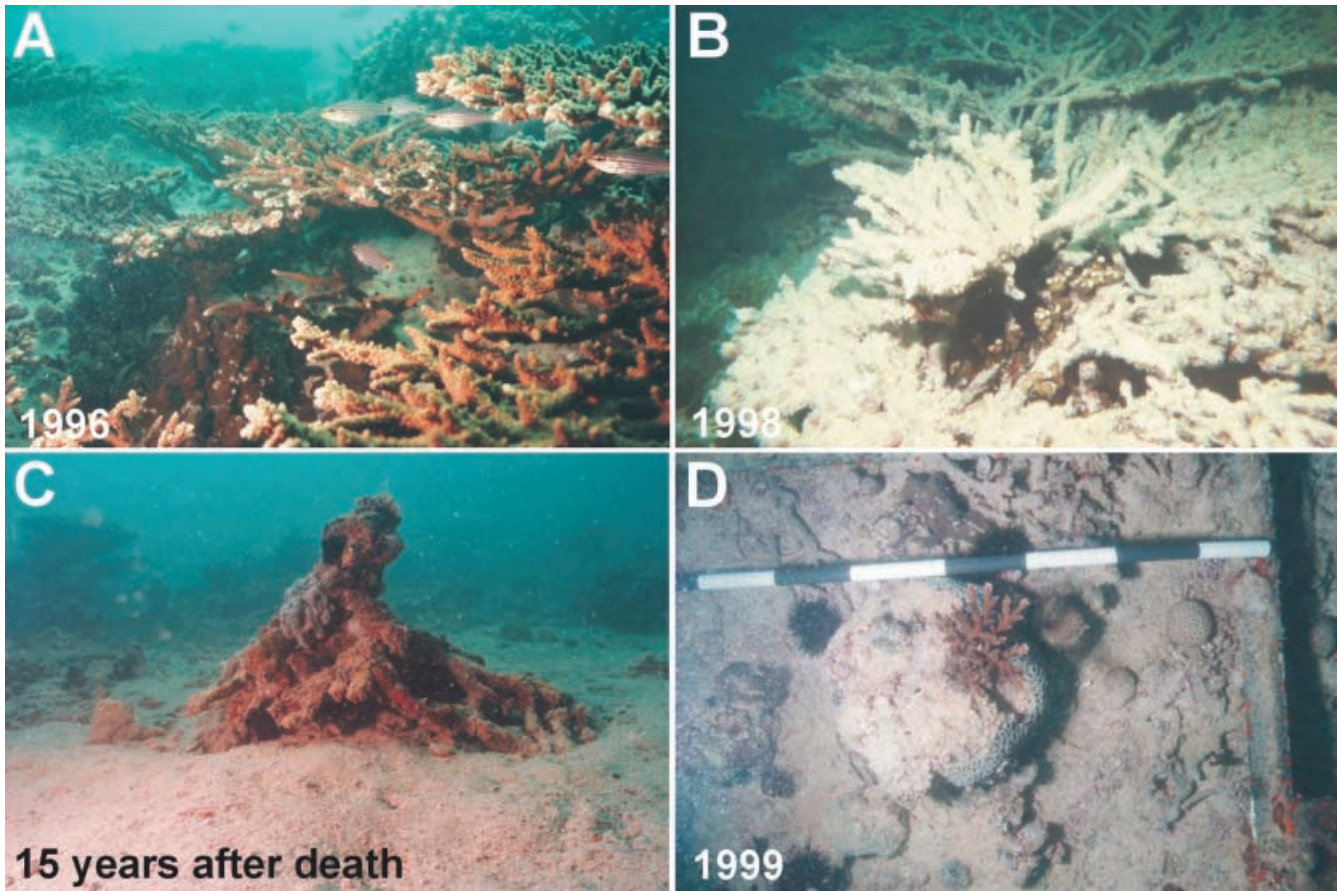
Coral diseases were identified visually only. More detailed microbiological investigations would have better revealed the diseases' true identities; however, most disease manifestations were clear enough to allow visual identification, which satisfied the purpose of this study. Black band disease (BBD) was the most common disease on branching corals during the summer of 1995 but disappeared in the winter of 1995/1996 and after the mass mortality in 1996. BBD was observed on four species of corals (Table 4). Prior to the coral mass mortality, some areas had 25% infection rates on *A. clathrata* and *A. downingi*. White band disease (WBD) was rare both prior to and after the mass mortality. It was not infectious, even in physical contact situations. In 1995/1996 it was found on ten species of corals (Table 4). In 1998/1999 on the same species except all *Acropora*, which were still absent from the study area. Yellow band disease (YBD) was widespread

from 1995 through 1999, both in summer and winter. Within-colony spread of the disease was  $19.7 \pm 4.9$  mm week<sup>-1</sup> in summer and  $9.4 \pm 3.9$  mm week<sup>-1</sup> in winter (*U*-test,  $z = 2.67$ ,  $P < 0.001$ ). It was contagious and observed to naturally spread from one colony to the next. In transplantation experiments, broken and diseased pieces of *A. clathrata* and *A. downingi* strapped onto healthy colonies by means of cable ties ( $N = 10$  colonies) led to infection in seven colonies after 10 days. Only transplants of fresh disease (taken from the advancing front) were successful; older parts from behind the active yellow band failed to transmit the disease. nine species of corals (Table 4).

In 1995/1996, coral diseases were most frequent in areas of high coral coverage, particularly in *Acropora*-dominated areas, where frequent physical contact favored the spread of contagious diseases (Table 5). Space cover and percentage of diseased colonies showed a significantly positive correlation (Kendall's Tau = 0.73,  $P = 0.029$ ). The only outlier data in Table 5 are from square 28 (outside the area illustrated in Fig. 1), a regenerating coral area with high cover by living, small and well-spaced corals with little physical contact. This, and the good coral health in the area, hindered the spread of diseases. After the 1996 SST anomaly and *Acropora* mass mortality, areas of comparable coral density no longer existed (Figs. 4, 5), which led to the disappearance of any density effects in coral diseases.

Coral diseases were seasonal (Table 6; Fig. 7) prior to the mass mortality event. In areas where BBD dominated in summer (1995), there was a shift towards a higher frequency of YBD in winter (1995/1996, Table 6). However, differences in overall disease frequency were not significant between summer and winter (Wilcoxon matched-pairs signed-ranks test,  $z = -1.82$ ,  $P = 0.067$  for the seasons 1995–1996). After





**Fig. 6a–d** Ecological and framework consequences of Arabian Gulf SST anomalies. **a** Healthy areas of *Acropora clathrata* and *A. downingi* in 1996. Average size of colonies is between 1 and 1.5 m, indicating an age of about 10 years. **b** The same *A. clathrata* and *A. downingi* in April 1998, almost 2 years after the summer 1996 mass mortality event. The colonies are still intact, a few branches have broken off, but sea urchins are causing notable bioerosion from the outside. **c** An area near Ras Ghantoot that had been killed 15 years previously by a dredging spoil plume; it experienced no recruitment and had lost virtually its entire coral-built framework. After 15 years, most *Acropora* had disintegrated into piles of branch rubble and only individual stumps were left standing. **d** An *A. downingi* recruit near Ras Hasyan in 1999

the mortality event, seasonality ( $14 \pm 5\%$  of corals, mainly *Acropora*, were affected in summer;  $7 \pm 6\%$ , in winter, mainly massives) was lost and infection remained at winter levels ( $6 \pm 5\%$ , only massives infected; Fig. 7).

#### Coral recruits

*Acropora* recruits were measured and counted (Fig. 6d). While in early 1998, no recruits were encountered, in November 1999 signs of active recruitment were observed between Ras Hasyan and Ras Ghantoot; 53 re-

**Table 4** Coral species affected by diseases in Dubai prior to the 1996 mass mortality (*BBD* black band disease; *YBD* yellow band disease; *WBD* white band disease)

	BBD	YBD	WBD
<i>Acropora clathrata</i>	X	X	X
<i>Acropora downingi</i>	X	X	X
<i>Acropora tenuis</i>		X	
<i>Acropora valida</i>		X	X
<i>Acropora pharaonis</i>	X		X
<i>Acropora florida</i>	X	X	X
<i>Porites lutea</i>		X	
<i>Porites harrisoni</i>		X	
<i>Porites nodifera</i>		X	
<i>Coscinarea monile</i>			X
<i>Platygyra lamellina</i>			X
<i>Platygyra daedalea</i>			X
<i>Favia fava</i>			X
<i>Turbinaria reniformis</i>		X	X

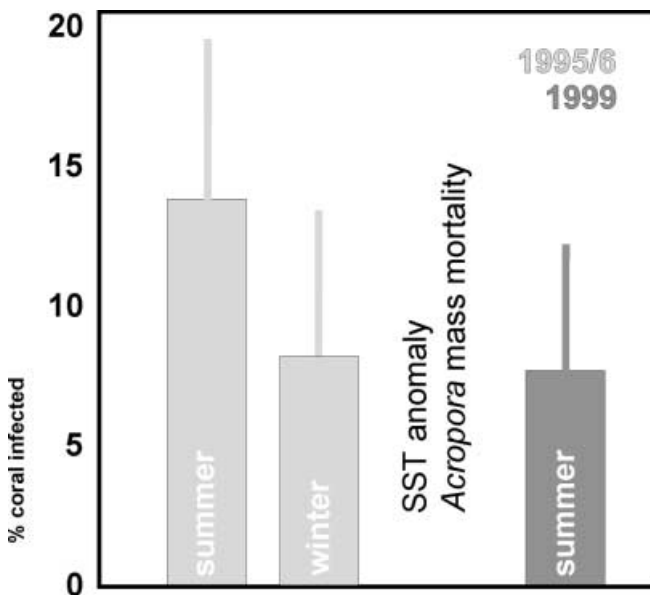


**Table 5** Disease frequency in relation to coral cover and species dominance in 1995 (pre-mortality in 1996). Means and standard deviation. Where diseases are present the correlation with cover is significant (Kendall's Tau = 0.73,  $P = 0.029$ ) (BBD black band disease; YBD yellow band disease; WBD white band disease)

Area	Total coral cover (%)	% Cover of diseased colonies per transect	Dominant disease	Dominant species
Square 6	16 ± 4	0	–	Faviids
Square 7	58 ± 14	9 ± 6	BBD, YBD	<i>A. clathrata</i> / <i>A. downingi</i>
Square 8	40 ± 5	19 ± 27	BBD, WBD	<i>A. clathrata</i> / <i>A. downingi</i>
Square 9	66 ± 17	10 ± 1	WBD, BBD	<i>A. clathrata</i> / <i>A. downingi</i>
Square 11	38 ± 15	4 ± 6	YBD, BBD	<i>Acropora</i> spp.
Square 13	66 ± 31	17 ± 16	BBD, YBD	<i>Acropora</i> spp.
Square 15	25 ± 7	0	–	<i>A. clathrata</i> / <i>A. downingi</i>
Square 28	41 ± 16	0	–	<i>A. clathrata</i> / <i>A. downingi</i>
Square 29	26 ± 6	0	–	<i>Porites</i>
Square 30	3	0	–	Dead corals

**Table 6** Seasonality of disease frequency (pre-mortality in 1996). Values are a proportion of the number of diseased colonies versus the total number of encountered colonies at the sample site

Area	% Corals diseased in summer	% Corals diseased in winter
Square 2	5	2
Square 7	16	4
Square 8	17	17
Square 9	15	12
Square 13	20	2



**Fig. 7** Changes in the frequency of coral diseases in Dubai, Arabian Gulf, in response to SST-anomaly-triggered *Acropora* mass mortality in 1996

recruits (average diameter  $7.6 \pm 3.5$  cm) were found. In the area between Ras Hasyan and Jebel Ali, only six recruits were encountered. The recruitment trend followed the dominant easterly current direction, which suggests that seeding populations were situated in Abu Dhabi, west of Ras Ghantoot. The size of the recruits and an assumed

growth rate of about  $10 \text{ cm year}^{-1}$  (see above and Coles and Fadlallah 1991) suggest that most recruits settled in the summer of 1998, while a few large recruits (diameter 25 cm,  $N = 3$ ) had probably already settled in 1997, but were overlooked in the previous years.

#### Fish

Over the entire study period, a total of 103 fish species was encountered (95 species in 1995, 64 species in 1999). Fish inventories counted 28 species in 1995 versus 25 in 1999. The three species not counted in 1999 (*Lutjanus quinquelineatus*, *Lethrinus microdon*, *Amphiprion clarkii*) were still present in the survey area, but not counted. Both prior to and after the coral mass mortality event, snappers (Lutjanidae) were the most abundant fish family (24% in 1995, 39% of all counts in 1999). Damselfish (Pomacentridae), grunts (Haemulidae), two-bar seabream (*Acanthopagrus bifasciatus*; Sparidae) and yellowbar angelfish (*Pomacanthus maculosus*; Pomacanthidae) accounted for another 36% in 1995 and 33% in 1999 of the fish counts (Fig. 8). Except for dark dotyback (*Pseudochromis persicus*; Pseudochromidae), which increased significantly in abundance ( $P = 0.019$ ), no significant differences in frequency were observed in any fish family. The frequency of fish arranged into trophic guilds (herbivores, invertivores, planktivores, piscivores) showed a clear trend of change, but without statistical differences between 1995 and 1999 (Fig. 9). Herbivores and planktivores increased, while invertivores decreased. Piscivores remained unchanged.

#### Discussion

The results of this study show clearly that, at least in Dubai, the main coral mortality was triggered by a positive SST anomaly in 1996, with negligible mortality in 1998. Since the 1996 SST anomaly affected the entire Gulf, it is not unlikely that some of the mortality at-

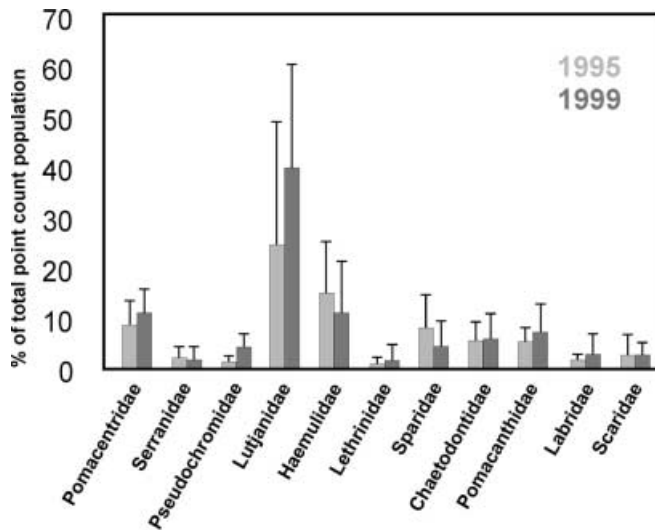


Fig. 8 Frequency of reef fish on live (1995) and dead (1999) *Acropora* frameworks in Dubai, Arabian Gulf

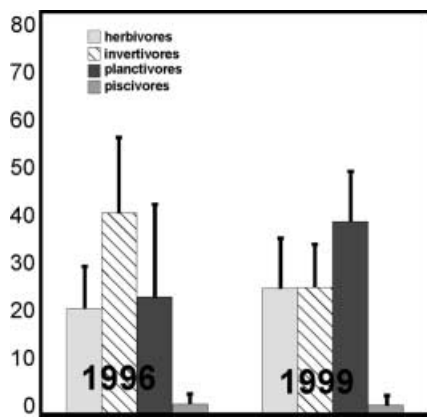


Fig. 9 Guild structure of reef fishes on live (1995) and dead (1999) *Acropora* frameworks in Dubai, Arabian Gulf

tributed in the literature to the 1998 SST anomaly (e.g. Goreau et al. 2000) could have already happened in 1996. The 1996 mortality event is the first documented large-scale coral kill by a positive SST anomaly in the Arabian Gulf, while kills by negative SST anomalies have been reported several times previously (Shinn 1972; Coles and Fadlallah 1991; Fadlallah et al. 1995).

In Dubai, effects of the 1996 SST anomaly were detectable on several levels. On a coral assemblage level, a total shift of dominance away from branching *Acropora* species, which all died, to the surviving massive taxa (of which *Porites* was the most common) occurred (Riegl 1999). This corresponds well with data from other areas in the Indo-Pacific (Fisk and Done 1985; Brown and Suharsono 1990; Gleason 1993; Marshall and Baird 2000), where Acroporidae were found to be among the most sensitive taxa to bleaching stress, while Poritidae were less and *Cyphastrea* were the least susceptible. The data presented here show that the 1996 anomaly

destroyed all *Acropora* and greatly reduced overall coral cover, while the 1998 anomaly took a much smaller toll among the survivors, mainly *Porites* and faviids (*Cyphastrea* among the most common). It is not surprising that the 1998 SST anomaly had very little effect on corals – the surviving taxa were those with low bleaching susceptibility.

It is interesting to note that not all *Acropora* in the area died. Surviving pockets of healthy *Acropora* existed in 1999 at a distance of about 30 km to either side of the area affected by mass mortality. This also corresponds well to data from the literature (Marshall and Baird 2000). It was found that bleaching severity could differ between sites and that acclimatization due to a more severe bleaching history could help corals survive. In the study area, the surviving *Acropora* areas were close to major channels (Al Jazira population close to Al Jazira channel, a major channel leading to enclosed basins inland. Water with increased temperature and salinity drains as density flows (i.e. distinct water masses which generally mix little with the surrounding water, Lang et al. 1988; Hickey et al. 2000) along the bottom of the channel and is likely to repeatedly impact the nearby coral population) and ports (Deira population adjacent to Port Rashid, a major industrial port). These populations are more likely to have repeatedly experienced severe environmental stresses than the corals between Jebel Ali and Ras Hasyan.

Corresponding with the loss of *Acropora*, coral diseases which preferentially occurred on *Acropora* (like BBD) disappeared from the area. Prior to the 1996 coral mass mortality, high permanent levels of coral diseases with preferential distribution in dense coral areas were encountered, a situation also reported from the northern Arabian Sea (Coles 1994, 1997; Coles and Seapy 1998). In the Caribbean and tropical Atlantic, coral diseases are becoming increasingly prevalent; WBD has been made responsible for the disappearance of *A. cervicornis* over wide areas (Bak and Crieens 1981; Rogers 1985; Bythell et al. 1989; Shinn et al. 1989; Williams and Bunkley-Williams 1990; Aronson and Precht 1997) and BBD appears to slowly eliminate massive corals in Jamaica (Bruckner and Bruckner 1997a,b). The 1996 mass mortality event in the Arabian Gulf provides evidence that the frequency of diseases could, in some cases, be regulated by the availability of preferred “target species”. Coral diseases acted in a density-dependent manner and appeared in the present study to have evolved to target the most common species. When all *Acropora* died in 1996, at least one disease (BBD) had virtually disappeared, and, since fewer corals were left overall, the other coral diseases decreased in frequency. In the Caribbean, no such situation is observed, since after the virtual disappearance of *A. cervicornis*, WBD now primarily affects the small-polyp *Montastrea*.

The fish assemblage did not suffer the abrupt changes witnessed in the coral assemblage, but subtle changes had started to take place (Fig. 8). Besides a drop in the

number of species observed, guild composition of fishes changed (Fig. 9), although most differences were not yet significant. The increase in herbivores and the decrease in invertivores reflects the change in substratum, from a live coral framework with abundant invertebrate fauna to a dead framework overgrown by algae. The studies of Sano et al. (1984, 1987) in the Ryukyu Islands indicated no difference in mean fish diversity between living and dead reefs. This is supported by the present study in which mean diversity also remained the same. However, Bell and Galzin (1984) compared reefs with similar structural complexity but with different portions of living corals and found a positive relationship between live coral cover and fish assemblage parameters. This is also supported by the current study, since the guild structure, i.e. the fish assemblage, was starting to change. It is possible that in the Dubai study area structural complexity was still high enough 3 years after the coral mass mortality event to maintain similar numbers of fish as before. Severe shifts in fish abundance and assemblage structure can likely be expected only after the breakdown of the standing dead skeletons, as suggested by data from Riegl and Luke (1998).

Despite the drop in species number, the Dubai reef fish fauna reported here is one of the richest in the Gulf (55–72 species reported from Bahrain: Smith and Saleh 1987; 85 species from Kuwait: Downing 1985; between 70 and 187 species from Saudi Arabia: Basson et al. 1977; McCain et al. 1984; Coles and Tarr 1990; Krupp and Mueller 1994).

From a framebuilding perspective, the rapid breakdown of coral skeletons (Fig. 6) demonstrates the importance of bioerosion and biocorrosion in framework breakdown (Glynn 1988, 1990, 1997; Hibino and van Woesik 2000). While on the outside of the skeletons some significant bioaccretion occurred (in particular settlement of bivalves and polychaetes), the mechanical stability of the whole structure was compromised by clionid sponges and mytilid mussels boring through the inside of the branches and the tables' stems. Similar observations have been reported from other areas (Tunncliffe 1979; Highsmith 1981; Scott and Risk 1988; Hassan 1998). Since virtually the entire framebuilding coral population died at the same time, skeleton breakdown could proceed at the same pace in the whole area, which likely led to destruction of the framework over the entire area and removal of the fragments by waves and currents. Had only individual colonies died and broken down, their fragments would have remained trapped between the living corals, which could have led to reef buildup. The resultant structure could have been a fringing reef (Fig. 5). One possible generalization from this study may be that catastrophic mortality of entire coral populations can have negative repercussions on framebuilding potential, while death of individual colonies need not.

Active sexual recruitment into the area was observed 2 years after the mass mortality event, with the first few recruits possibly having arrived already 1 year after the

mass mortality. It appears that seeding populations, although also undoubtedly stressed by the thermal anomaly, nevertheless completed their reproductive cycle. Fadlallah et al. (1992) and Fadlallah (1996) observed *Acropora* spp. to spawn even after a major negative temperature anomaly that caused widespread coral mortality in Saudi Arabia. Although disturbances and stress are known to reduce coral fecundity (Szmant and Gassman 1990; Hoegh-Guldberg 1999) it appears that surviving Arabian Gulf corals were sufficiently fecund to reproduce and supply viable larvae that could potentially provide progeny to replenish coral losses after such major stress events. This has important implications for the temporal persistence of the coral systems.

The difference in effects of the disturbance on competitively inferior species (poritids and faviids, Fig. 4) and the dominant competitor (*Acropora*) seems to support concepts for the maintenance of diversity in ecological communities like the intermediate disturbance hypothesis and the concept of compensatory mortality (Connell 1978; Sousa 1984). These hypotheses assume consistent asymmetrical outcomes in competitive encounters, with one of a pair of competitors always winning over the other (Sousa 1984). For the weaker party to persist in the system, the stronger needs to be regularly, or preferentially, stunted (see also Baird and Hughes 2000). Since the conditions required by these hypotheses are by and large met in Dubai coral assemblages (*Acropora* was winning over all other species and preempted most space; competitively inferior species start to rebound after disturbance), nature has provided us with an experiment that may support these findings. The observed disturbing factors were both coral diseases and the SST anomaly, which both effected compensatory mortality in the dominant competitor. Whether the mortality caused by the two SST anomalies can be counted as intermediate disturbance that will enhance the system's diversity (such as previous cold-events may have done) or rather a final disturbance to which the system is not adapted (Hoegh-Guldberg 1999; Aronson et al. 2000; Lough 2000) remains to be seen.

In conclusion, the following points should be emphasized:

- Of the two positive SST anomalies affecting the Dubai (Arabian Gulf) study area in 1996 and 1998, only the 1996 event had severe impacts.
- The 1996 SST anomaly caused a coral mass mortality event that removed all *Acropora* from the study area and reduced species richness from 34 to 27 species.
- Coral cover in areas with dense coral growth was decreased by 64% in 1996, but only by 4% in 1998.
- This decrease destroyed 98.7% of the area with framebuilding potential.
- Only subtle changes in fish frequency or guild structure were observed 3 years after coral death.
- Coral diseases decreased in frequency and lost seasonality. Diseases specific to *Acropora* disappeared.

- Recruitment of *Acropora* started strongly in 1998, with first recruits in 1997, suggesting that upstream survivors remained fecund.

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