REPORT

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Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa)

Abstract The findings in this paper show that Arabian Gulf (Abu Dhabi, Dubai, Sharjah) corals have already been measurably affected by climate change and further negative impacts are expected. Corals in South Africa have been only weakly impacted and are expected to persist in this likely refuge. The Arabian Gulf has recently experienced high-frequency recurrences of temperature-related bleaching (1996, 1998, 2002). First evidence may suggest that bleaching patterns in corals changed due to phenotypic adaptation after two strong bleaching events in rapid succession, because *Acropora*, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair and recovered at Jebel Ali and Ras Hasyan. In South Africa, reef corals largely escaped the mass mortalities observed across the tropics in the late 1990s, although bleaching has also increased since 1999. These reefs are protected by local small-scale upwelling events in summer that, if they occur at the right time, keep temperatures below bleaching levels. Both areas, the Arabian Gulf and South Africa, have rich coral faunas but little to no recent reef-framework production. It is possible that many reefs worldwide may have similar dynamics in the future, if the changed climate (recurrence of temperature anomalies, changes in aragonite saturation state, etc.) suppresses sustained reef building at least temporarily. Global climate models predict the possibility of significant environmental changes, including increases in atmospheric temperature, sea-surface temperature (SST), and sea level. Monsoon and El Niño Southeastern Oscillation (ENSO) patterns might change, but climate models are not conclusive. Sea-level rise by up to 0.88 m is expected to be a problem in some low-lying areas, like the southern Arabian Gulf. Ocean aragonite saturation state is predicted to fall throughout the ocean but may not change reef dynamics in the two study areas.

Introduction

Recent reports on global climatic change suggest significant global warming trends over the past 30 years associated with continuously increasing greenhouse gas concentrations (Houghton et al. 2001). Coincident with global warming, the last few decades have seen large-scale disturbances in reef systems (Lough 2000; Wilkinson 2000; Buddemeier 2001). The largest ever recorded coral bleaching and mortality event was linked to the unusually strong 1997/98 El Niño Southern Oscillation (ENSO) event and affected many coral reefs across the globe (Goreau et al. 2000; Wilkinson 2000; Glynn and Colley 2001). Although high-latitude reefs suffered as well, damage patterns were different than on tropical reefs (George and John 1999; Jordan and Samways 2001; Celliers and Schleyer 2002; Floros 2002; Riegl 2002). Is this observation significant?

Throughout earth history, many biotic crises have occurred in the marine realm and affected reef systems (Copper 1994; Stanley 2001). Extinctions and faunal change commonly occur gradually, when certain genotypes are forced into disappearance and others (different genotypes within the same species or different species altogether) take their place. Such processes might be observable on today's reefs, stressed by a rate of warming unprecedented in the last 1,000 years (Houghton et al. 2001). Thus the adaptive and evolutionary relevance of the observed large-scale and repeated bleaching of corals has undergone close scrutiny (Buddemeier and Fautin 1993; Baker 2001; Baker et al. 2002). In general, high-latitude corals persist in more

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stressful environments than their tropical counterparts. Arabian Gulf corals, for example, survive the highest annual temperature variability encountered by any reef corals (Kinsman 1964; Sheppard et al. 2000). Therefore, these areas already now show stress levels that may eventually be commonplace on a broad range of coral reefs. Therefore, study of their dynamics might well reveal important lessons about mechanisms of reef survival (Glynn 1996).

This paper investigates two high-latitude areas in the Indian Ocean (southeastern Arabian Gulf, South Africa)

Fig. 1 Study area in the Arabian Gulf, United Arab Emirates (*UAE*). Sites are situated in three regions of distinct coastal geomorphology. Study sites Muqaraq and Ruweis comprise the western study area; they are situated along a convoluted coastline characterized by sheltered oceanographic conditions (*shaded area*) in the lee of both the Qatar peninsula and Great Pearl Bank. The Saddiyat site was situated in a sheltered location in a tidal canal between Abu Dhabi and Saddiyat islands on a coast characterized by barrier islands and lagoons. The Saddiyat site was protected from the open ocean and its conditions were more comparable to Muqaraq and Ruweis than the closer eastern study area. The generally leeward condition of the western study area is also inferred from weaker wind-driven surface flow (Lardner et al. 1993). The eastern study area (east of Al Taweela) is characterized by a straight shoreline perpendicular to the direction of wind-driven surface flow, exposed to higher wave energies with a longer fetch (Lardner et al. 1993)—sites between Al Taweela and Deira. Sir Abu Nuair is the only offshore site in deeper (−37 m) water, and was part of the eastern study area

during the last decade. One (Arabian Gulf) is among the most stressed reef environments on earth (Kinsman 1964; Sheppard et al. 1992; George and John 2000a, 2000b), while the other (South Africa) has had one of the lowest documented rates of major disturbances in the last decade (Schleyer 1999; Jordan and Samways 2001; Celliers and Schleyer 2002; Floros 2002).

Material and methods

Study areas

Arabian Gulf

Study areas investigated about one-fifth of the Arabian Gulf's southern continental coastline and were evenly spread along the coastlines of the Emirates of Abu Dhabi and Dubai, including the offshore island Sir Abu Nuair (Sharjah, United Arab Emirates). The most closely studied area is situated in Dubai Emirate between Jebel Ali port and Ras Hasyan (Fig. 1). Sites were studied annually between 1995 and 2002; however, not every site was visited repeatedly. Sites were investigated either by diver grid-surveys or transect studies. Repeated quantitative sampling only took place in the Jebel Ali/Ras Hasyan study area (1995, 1996, 1998, 1999, 2002) using 10-m, continuous-intercept line transects. Coral assemblage structure, skeleton breakdown, and recruitment were documented. Water depths in all near-shore sites were between 3 and 7 m. Dense coral assemblages spanning depths between 2 and 20 m were only encountered on Sir Abu Nuair.

Analyses of transect data used the software PRIMER 5 (Clarke and Gorley 2001). Of all available transects ($n = 160$), a subset of 40
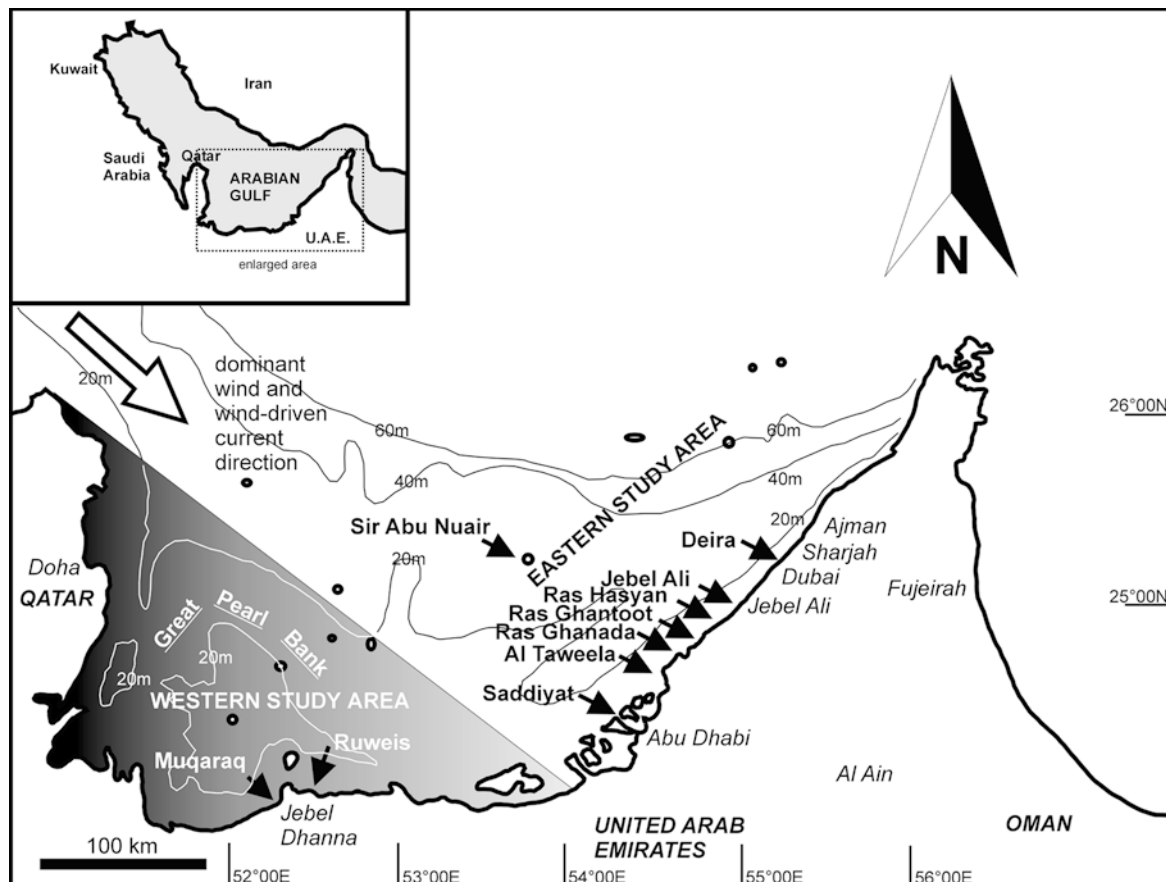
Fig. 2 Study area in South Africa. Corals grow on submerged Pleistocene dune and beachrock sequences (Ramsey 1994) and have little active frame-building (only in depths greater than 18 m; Riegl 2001). They are situated in the headwaters of the Agulhas current and not influenced by direct land runoff. All local rivers drain into extensive wetlands (swamps and floodplains in *striped area*) with only relatively small outlets (Kosi Lakes, Lake Mgobeseleni) or no outlets at all (Lakes Bhangazi, Sibaya) to the sea. Part **B** is based on Wright et al. (2000)
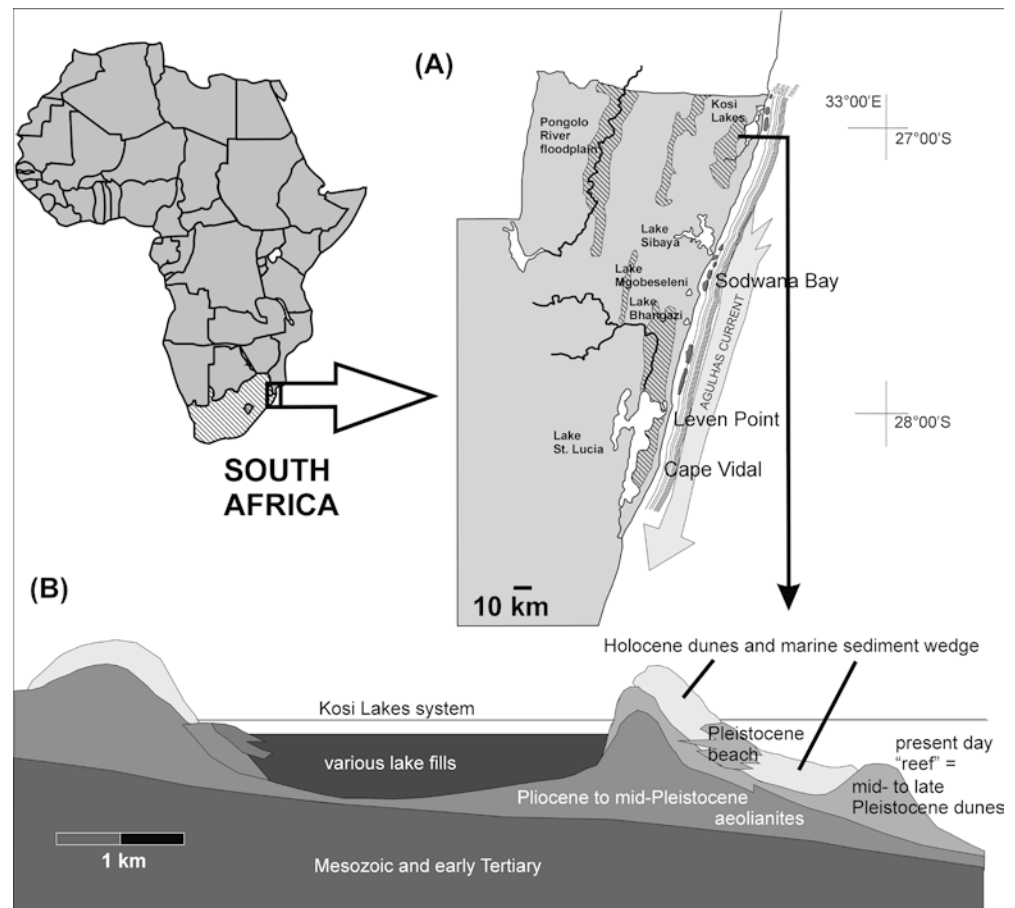
transects (10 each for the years 1995, 1998, 1999, and 2002) was used. Data processing for classification and ordination used a square matrix of coral cover. Data were square-root transformed and then subjected to first-stage MDS (non-metric multi-dimensional scaling) (Kruskal 1964; Clarke and Warwick 2001) to evaluate the spread of data-points (Clarke and Gorley 2001). The matrices, based on the Bray-Curtis similarity index for each sampling year, were Spearman rank-correlated, with the correlation coefficient defining proximity. This final matrix was subjected to second-level MDS, with the output showing the distance between the annually measured assemblages, which illustrates their ecological trajectory. The further a sample is from the disturbance, the closer it should come to the position of the original assemblage (Clarke and Warwick 2001).

Sea-surface temperature (SST) was obtained by in situ measurements provided by the Dubai municipality (data at 3-monthly intervals for the period 1993–97). Monthly and weekly averages of SST were obtained from the website http://ferret.wrc.noaa.gov/las1/climate_server from the COADS [Comprehensive Ocean Atmosphere Data Set, 2×2° grid compiled monthly data from ship reports) and NCEP (National Center for Environmental Prediction, 1×1° grid combining in situ and satellite data, referred to as Reynolds SST; Reynolds and Smith (1994)] data sets.

South Africa

The study sites were located at Sodwana Bay in the central reef complex of Maputaland (KwaZulu/Natal Province, South Africa), which encompasses some of the highest latitude reefs in the southwestern Indian Ocean. Coral communities (96 scleractinian species) occur on Pleistocene dune and beachrock to near Leven Point, at

latitude 28°S (Ramsey 1994; Riegl 1996; Schleyer 1999; Fig. 2). Further south, coral cover on hard substrata reduces sharply and species richness falls to 15 scleractinian species at Aliwal shoal, which is about 300 km south of Leven Point (Schleyer 1999, 2001) from where it attenuates further. Near the reefs, three canyons (Jesser Canyon, Wright Canyon, White Sands Canyon; Ramsay 1994; Ramsey and Miller 2002) dissect the shelf-slope. The area contains extensive coral assemblages in relatively shallow waters, but also at intermediate depths (8–34 m). Data were collected in 1991/92/93 and April/May 2000 using the same 10-m, line-transect method as in the Arabian Gulf. Weekly Reynolds SST data were obtained from the NCEP data set.

Results

Arabian Gulf—observations

The Arabian Gulf is subject to both extreme negative and positive temperature excursions (Fig. 3). Negative anomalies occur in winter, the most extreme caused by the Shamal, a cold north wind which blows from the Iranian highlands into the area of low atmospheric pressure over the Arabian peninsula (Murty and El Sabh 1984). Shinn (1976) attributed massive coral die-back in the southern Gulf (Qatar) to a severe Shamal, which caused surface cooling to 4 and to 14.1 °C at 18-m depth. Shamals may generate storm seas of up to 6-m wave height [caused by strong winds; 65 kph recorded

by Shinn (1976); see also Murty and El Sabh (1984) and Sheppard et al. (1992)], causing vertical mixing of the water column. Cooling by Shamals, sometimes coupled with extremely low tides amplified by negative storm surge (Murty and El Sabh 1984; Fadlallah et al. 1995), is a recognized factor causing repeated coral mortality (Shinn 1976; Coles and Fadlallah 1991; Fadlallah et al. 1995).

Positive temperature excursions occurred in all studied areas but were more pronounced in the western study area (see also George and John 2000a, 2000b). They increased in frequency in both study areas in the late 1990s (Fig. 3). In 1996, 1998, and 2002, SST anomalies of $+2$–2.5 °C above average in situ measured summer maximum temperatures (33 °C in July 1994 and 1995,

Dubai Municipality) persisted from April to September. Local maxima of in situ measured temperatures were 35.5 °C in 1996 and 37 °C in 2002. These strong local excursions are not apparent in the 1×1° averaged NCEP SST data set presented in Fig. 3, but the overall positive excursion is clearly visible. The climatic factors associated with these positive anomalies are not well understood, but it is possible that at least the 1998 and 2002 events were connected to Pacific ENSO that might have affected the Indian monsoon and thus the climate in the Arabian Gulf region (possibly via 200-mb circulation anomalies; Rasmusson 1991; Bottomley 1996). The 1996 anomaly was likely an extreme expression of the Indian Ocean zonal mode (Loschnigg et al. 2003)

For the examination of past temperature anomalies that may have caused mass mortality of corals or at least their bleaching, a combined COADS/NCEP data set was used for the period 1955–1999. This data set shows more negative than positive SST anomalies. In the eastern study area, no hot events comparable to 1996 and 1998 had been recorded previously. The apparent novelty of these events is consistent with global warming trends observed by Lough (2000) and Houghton (2001).

UAE corals were affected by bleaching events and *Acropora* coral mortality events several times. According to Shinn (1976) a mortality event in 1964 was

Fig. 3 Combined SST data sets for (*above*) western study region (center point for grid calculation: 25°N, 53°E) and (*below*) eastern study region (center point for grid calculation: 25.5°N, 54°E). Between 1955 and 15 Dec 1993, data are 2×2° gridded monthly data from the COADS data set. From 21 Dec 1993, data are weekly, 1×1° gridded Reynolds SST data from the NCEP data set. It is clearly visible that the western study area is subject to stronger temperature variability, due to more restricted oceanographic conditions than the eastern study area. In both study areas the 1996 and 1998 positive anomalies that caused bleaching and coral mortality are clearly visible. Data format is M/DD/YY

Western study region, ARABIAN GULF

Eastern study region, ARABIAN GULF
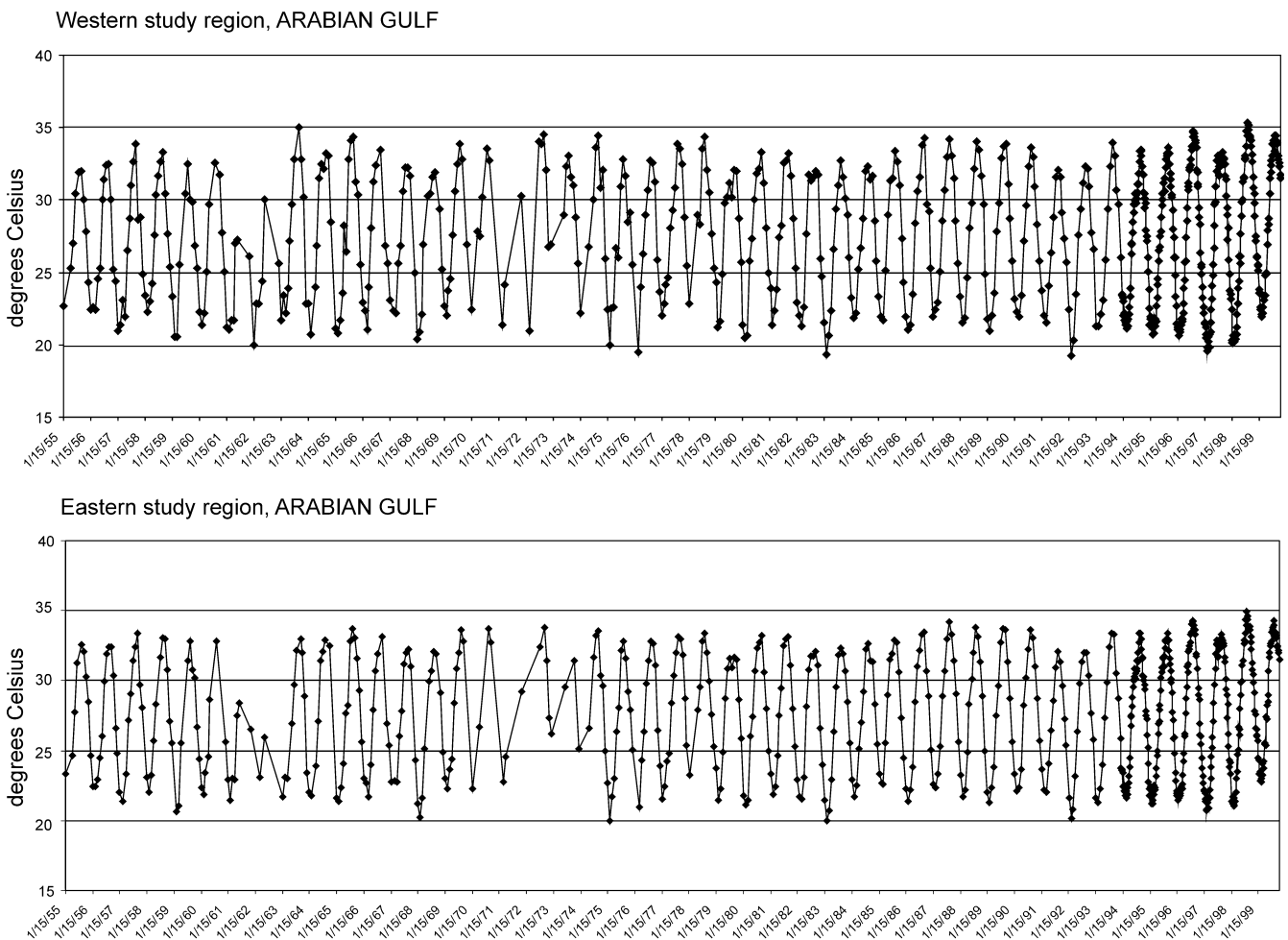
caused by a cold event. However, the COADS data set shows a hot event comparable to 1996 and 1998 in summer 1964; this suggests that in 1964 corals were subjected to unusually low winter temperatures as well as unusually high summer temperatures. According to Holt Titgen (1982), an *Acropora* mass mortality occurred in the Jebel Ali/Ras Hasyan area between 1975 and 1980; indeed, the COADS data set for the eastern study region (Fig. 3) records low temperatures in 1975, the monthly average over 2×2° possibly masking an extreme, short duration cold event that could have triggered the mortality. Other already mentioned mortality events occurred in 1996, 1998 (the hot events clearly reflected in the NCEP data set), and 2002 (not yet in the data set).

Coral assemblage structure was quantitatively investigated at Jebel Ali, Ras Hasyan, and Ras Ghantoot, and was qualitatively assessed at Muqaraq, Ruweis, Saddiyat, Al Taweelah, Ras Ghanada, Deira, and Sir Abu Nuair. Based on detailed studies between Jebel Ali and Ras Hasyan (Riegl 2001, 2002) and qualitative observations in the other areas, five typical coral assemblages of variable live cover were found:

A. Large, widely spaced *Porites lutea* and other *Porites* occur with several other, mainly massive, species interspersed. This assemblage was widely distributed on hardgrounds with sparse sand cover, and suffered only moderately in 1996 and 1998 in the eastern study area. In the western study area, many dead knolls and *Porites* colonies were encountered. In summer 2002, most *P. lutea*, *P. solida*, and *P. lobata* were bleached white (Fig. 4F) but had recovered by November 2002.

B. Mainly tabular colonies of *Acropora clathrata* and *A. downingi* were present with high (40–90%) live cover and frequent overtopping of competitively inferior massive corals, like *Porites* spp., *Cyphastrea* spp., and *Platygyra* spp. Heavy mortality occurred in 1996 (Fig. 4A), less in 1998 (most *Acropora* were already dead). Small stands of *Acropora* survived at Ras Ghantoot, Deira, and Sir Abu Nuair. *Acropora* recruited strongly into the entire area east of Al Taweela (Fig. 4C). In summer 2002, *Acropora* bleached at Jebel Ali and Ras Hasyan, but not at Sir Abu Nuair (Fig. 4D, E). Most bleached corals, including *Acropora*, regained color by November 2002.

C. Groups of faviids (most notably *Platygyra lamellina*, *P. daedalea*, *Cyphastrea serailia*, and *Favia* spp.) were either widely spaced or densely packed. The densest faviid assemblages were found on Sir Abu Nuair Island, at between 7 and 20 m depth, below the *Acropora* assemblage (Fig. 4D). Faviid colonies bleached but suffered little mortality in 1996, 1998, and 2002.

D. Widely spaced *Siderastrea savignyana* colonies occurred which were not affected either in 1996, 1998, or 2002.

E. Densely spaced (80% coral cover) columnar *Porites harrisoni* colonies were present, intermingled with massive colonies (mainly faviids, *Favia* sp., and *Platygyra* sp.), with patchy distribution found mainly in the eastern study area and on Sir Abu Nuair. Intermediate bleaching took place in 1996, with low mortality, and some mortality occurred in 1998 and 2002.

The analysis of coral transect time-series between Jebel Ali and Ras Hasyan showed the biggest difference in assemblage composition between data taken before and after the 1996 *Acropora* mass mortality (Fig. 5). While the 1998 SST anomaly caused only a few additional percent mortality (decrease of space cover from $26 \pm 6\%$ SD to $22 \pm 10\%$ SD), it continued to move the assemblage further from the pre-1996 state. Mortality in 1998 affected mostly *Porites harrisoni*, *Platygyra lamellina*, and *Cyphastrea microphthalma*, with subsequent rapid recovery (Fig. 6). Until 1999, variability in space cover of the survivors, especially poritids and faviids, and absence of *Acropora*, further moved the assemblage away from the 1995/96 condition. In 2002, the assemblage had moved onto a trajectory towards the pre-1996 condition (Fig. 5) due to strong recruitment and slowly increasing space cover by *Acropora* (Fig. 6).

This pattern of disturbance and regeneration was not found everywhere. The impacts of the 1990s bleaching were worst in the western study area. At Muqaraq in November 1999, the coral area was small and consisted mainly of assemblages C and D, with assemblage B broken down to rubble. At Ruweis in November 1997, all five assemblages were present and covered a large area but had suffered significant mortality in 1996. Much of assemblage A had suffered significant mortality, and assemblage B had lost all live *Acropora*. At Saddiyat in July 2000, only *Porites*-dominated patch reefs were investigated, the corals of which had suffered about 50% mortality. All *Acropora* were dead. Near Al Taweelah, in October 2001, healthy A, C, and D with small and isolated patches of B, which showed *Acropora* recruitment but no old colonies, were found. The densest coral areas consisting of several square kilometers of B existed at Ras Ghanada and Ras Hasyan, but all live *Acropora* had been lost in 1996. Recruitment had started noticeably in 1998. Smaller B existed near Ras Ghantoot and Deira. In both areas, A and C were also encountered. Assemblage B near Ras Ghantoot and Deira suffered only partial *Acropora* mortality in 1996 and 1998. Sir Abu Nuair island had dense B, C, and E, in particular the densest stands of large, tabular *Acropora*, which suggested that neither in 1996 nor in 1998 had a total *Acropora* mortality occurred. During summer 2002, all corals except *Acropora downingi* and *A. clathrata* and some *Porites harrisoni* bleached, which was a total reversal of the bleaching situation observed in the other sites in 1996.
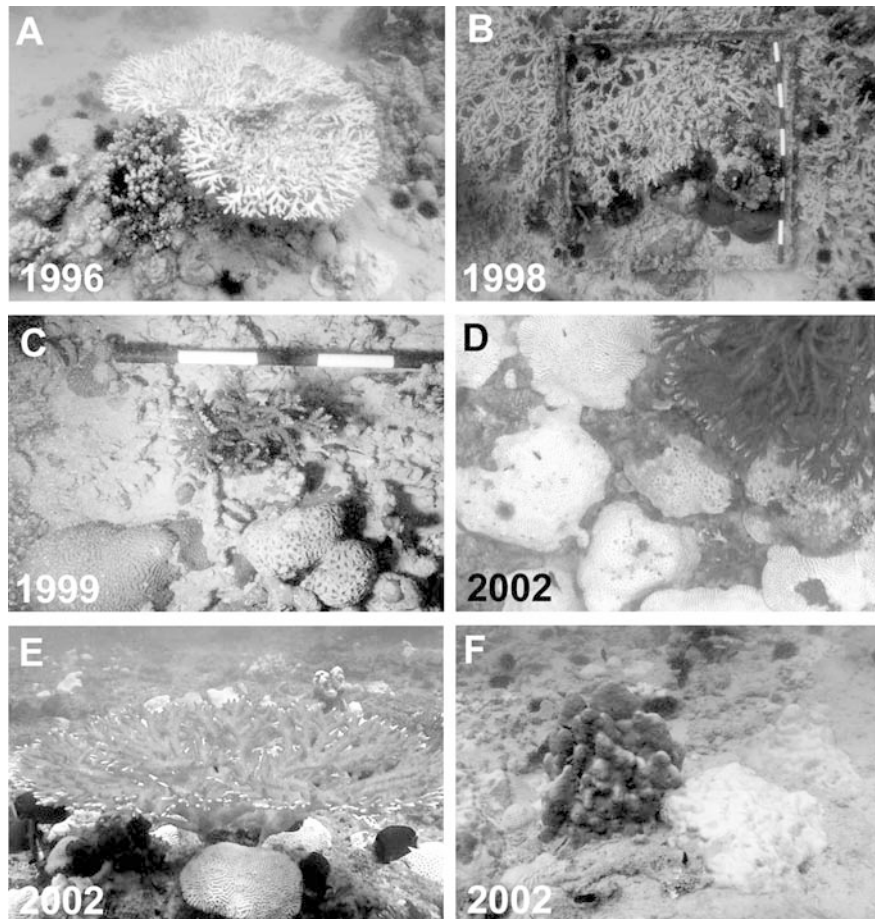
Fig. 4 Sequence of temperature-driven mortality and regeneration in Arabian Gulf coral assemblages near Ras Hasyan, Dubai, and Sir Abu Nuair, Sharjah. **A** Summer 1996 near Ras Hasyan. SST exceeded 35 °C for over 2 months, resulting in widespread bleaching and mortality, preferentially in the genus *Acropora*. **B** In early 1998, all *Acropora* near Ras Hasyan were dead, but there was little mortality in all other coral genera. In summer 1998, another hot event led to further mortality among survivors of the 1996 hot event. **C** Not all *Acropora* in the southern Arabian Gulf died, and active regeneration took place immediately after the mortality events. In 1999, strong *Acropora* recruitment into the area near Ras Hasyan was evident. **D** and **E** During the 2002 hot event, most reef corals on Sir Abu Nuair bleached except *Acropora*, many of which had regenerated after the 1996 hot event [evident by their size range between 10 and 40 cm radius; annual growth rates are about 10 cm (Coles and Fadlallah 1991) and suggest that they settled after 1996]. This could be the result of phenotypic adaptation to heat events (Baker 2001; Baker et al. 2002). **F** Also near Ras Hasyan, not all corals bleached in the 2002 hot event. A normally colored *Cyphastrea microphthalma* stands next to a bleached *Porites lutea*

Arabian Gulf—interpretations

The mortality patterns can in part be explained by oceanographic conditions. The dominant wind direction is from the northwest (Purser and Evans 1973), making the eastern study area (Ras Hanjurah to Ras al Khaimah—study sites Al Taweela to Deira) more exposed to wind and waves (Purser and Evans 1973; Lardner et al.

1993; George and John 2002). This results in deeper mixing of the water column than in the western study area, which is in the lee of the Qatar peninsula. The coastal sites are additionally in the lee of the Great Pearl Bank (Khor al Bazm)—this quasi-lagoonal situation likely increasing the potential for raised SST and heat stress. Sir Abu Nuair, which has the largest *Acropora* population, is the only offshore site and depths greater than 30 m are encountered near the island. Therefore, the water column may heat less readily than in the coastal areas, where water depth over the corals is never greater than 10 m (usually around 5–7 m).

South Africa—observations

Africa's southernmost reef-coral assemblages occur in South Africa in the Maputaland reef complexes off KwaZulu/Natal Province. Individual corals occur also in the Eastern Cape Province with the southernmost coral colonies reported near Port Elizabeth; however, the bulk of hermatypic corals ranges only to Cape Vidal (28°15′S). Coral assemblages are dominated in shallow areas by large alcyonacea and small scleractinia (Fig. 7A, B) without any appreciable frame building (corals grow directly on Pleistocene aeolianites, Fig 2). The only areas where some frame building is observed
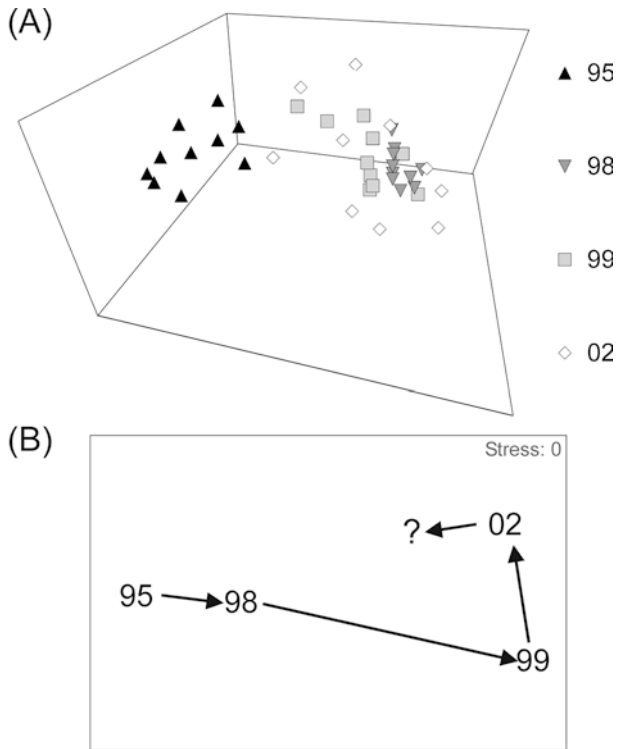
Fig. 5 Similarity of coral assemblages sampled before and after the hot events. **A** Ordination of 40 transects by non-metric MDS. Regeneration of *Acropora* growth is clearly indicated by proximity of 1995 and 2002 samples. **B** Ecological trajectory of the assemblages as illustrated by a second-stage MDS based on Spearman rank-correlation of the four underlying similarity matrices (one for each sampling year). The 1996 *Acropora* mass mortality caused assemblage structure of the 1995 and 1998 samples to diverge strongly (loss of *Acropora*, the dominant genus). Although the 1998 hot event did not cause a significant loss in coral cover, it nevertheless had strong effects on assemblage structure. Between 1999 and 2002, the assemblage did not change much, but beginning *Acropora* regeneration had set the assemblage onto a trajectory oriented towards the original assemblage structure

are deeper areas (> 18 m), where branching and tabular *Acropora* form dense stands (Fig. 7C).

While the 1997/98 ENSO led to significant bleaching and coral death in East Africa, Madagascar, and Bassas da India (Wilkinson 2000), South African corals did not experience significant bleaching and/or coral mortality, with only 0.93% of corals bleached in 1998. The absence of major perturbations was indicated by a slight increase in coral cover between 1992 and 1999 measured by Jordan and Samways (2001). Also, no temperature-related outbreaks of disease epizootics were observed, only 0.5% of corals suffering from coral diseases (Jordan and Samways 2001). Bleaching, however, started to occur in 2000 and increased in severity in 2001. In 2000, bleaching began on shallow reefs in South Africa and by May, in the austral autumn, white bleaching levels locally reached 10% of all corals, mainly affecting the scleractinian genus *Montipora* (Fig. 7D) (see also Celliers and Schleyer 2002). In 2002, Floros (2002) reported 5–10% bleaching, citing the alcyonacean coral genus

Sarcophyton and again the scleractinian coral genus *Montipora* as the most affected.

South Africa—interpretations

Maputaland coral reefs are protected from extreme heating by the very active water dynamics on the shelf, caused largely by the Agulhas current and a swell-generated inshore counterflow (Ramsey 1989). In situ water temperatures measured by Schleyer (1999) on the Maputaland reefs ranged between 18 and 29 °C from 1994 to 1999, and 1×1° gridded SST reached a maximum of 28.4 °C in austral summer 1998 (Fig. 8). In summer, SST did not remain uniformly high but marked "cool-events" were observed, most likely caused by upwelling (Riegl and Piller 2003). Such events are also visible in remotely sensed SST records from the same area in Floros (2002) and the NCEP Reynolds SST data (Fig. 8). In summer 1997/98, SST was higher than in the previous 15 years and 0.93% bleaching was observed (Jordan and Samways 2001). In 1998, bleaching occurred on nearby Indian Ocean reefs (Madagascar, Tanzania, Kenya, Comores, Reunion; Wilkinson 2000), and temperatures were higher than in previous years, but cool-events were also clearly visible. No bleaching was recorded in South Africa.

The cool-events are believed to be linked to small-scale, localized shoaling of the thermocline at the base of the Agulhas Current's core, allowing colder water to well up at its inshore edge. The Agulhas current is a western boundary current that hugs the steep South African shelf. Bottom Ekman veering deflects the bottom layers of this warm current away from the coast and thus allows cooler, deeper water to rise to shallower depth on the current's inshore edge (Lutjeharms et al. 2000). This cooler water flows onto the shallow shelf via deep gullies dissecting the shelf-edge immediately offshore the reef system, which results in a net cooling of the upper surface waters within which the coral assemblages are situated (Fig. 9). This mechanism decreased water temperature enough in 1998 to avoid bleaching, and helped to avoid catastrophic bleaching in 2002 (Floros 2002).

Discussion

The high-latitude reefs investigated in this study showed different disturbance dynamics from those in tropical areas over the latter part of the last decade. The Arabian Gulf experienced disturbances at a higher frequency than both the tropics and South Africa. Can these observations be interpreted in terms of global climate change? According to Houghton et al. (2001), the globally averaged surface temperature of the Earth is likely to increase by a range of 1.4–5.8 °C over the period 1990 to 2100, which is a higher rate of temperature increase than during the 20th century and without

Fig. 6 Variability in species-specific space-cover in the area between Jebel Ali and Ras Hasyan between 1995 and 2002. Values are percent space cover on ten arbitrarily chosen transects per year taken from the entire data set. *Acropora clathrata/downingi* are lumped together, since the taxonomic situation is unresolved and the name *A. downingi* was introduced only in 1999 (Wallace 1999). Values for *Acropora* cover in 1995 are lower than reported elsewhere (Riegl 2001, 2002) for dense *Acropora*-dominated areas. This is because the present data set contains also transects from areas without dense *Acropora* cover and is therefore an average of all assemblage types
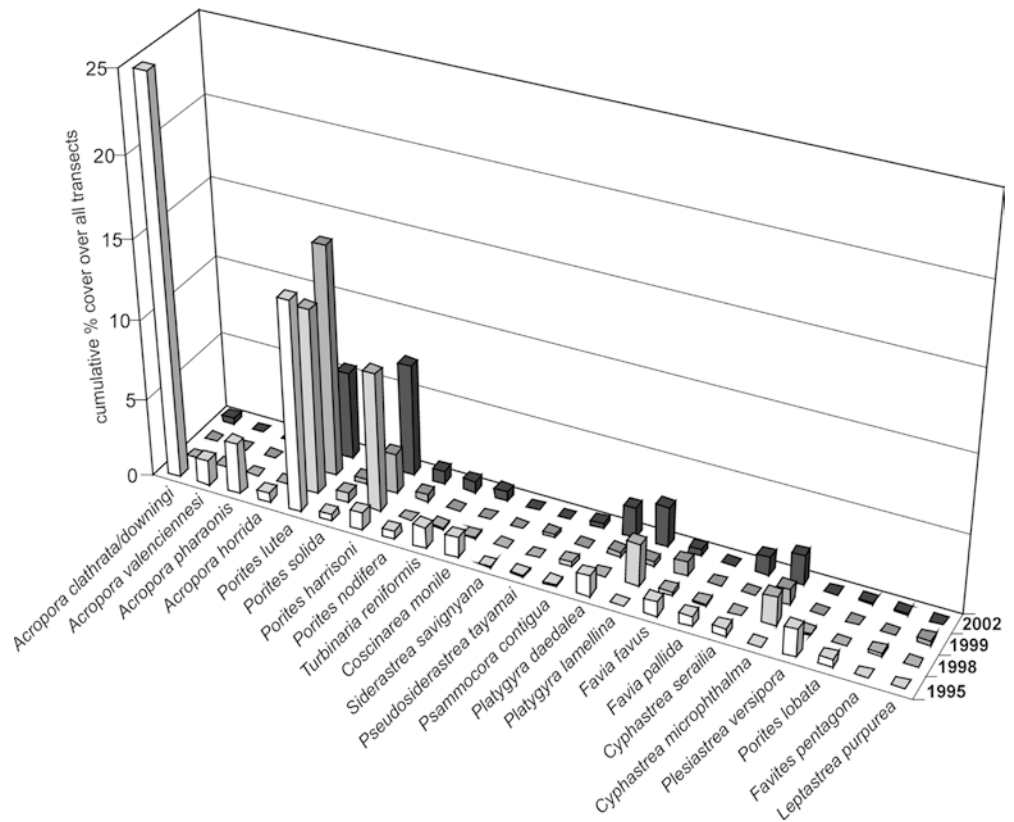

Fig. 7 South African coral assemblages were characterized by **A** large, alcyonacean corals that suggest long periods without serious mortality. *Measuring stick* is 1 m long with 10-cm increments. **B** In shallow water (<18 m), scleractinian corals are small and adapted to high wave energies (created by tropical cyclones in the Mozambique Channel and Southern Ocean swells). **C** Construction of thin frameworks by branching *Acropora* is restricted to deeper (>18 m) areas. **D** Bleaching in 2000 affected mainly the scleractinian genus *Montipora* (*extreme right*), and affected less than 10% of total coral cover
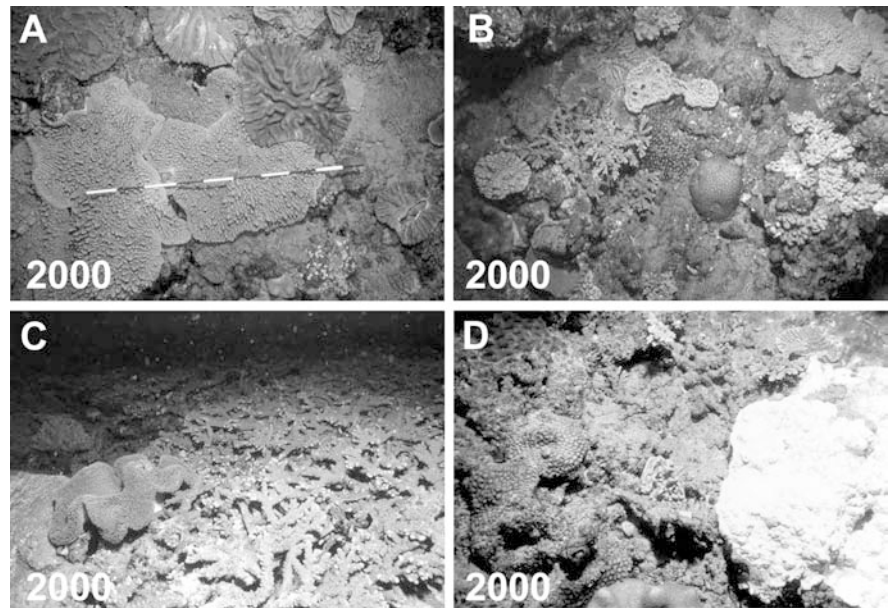
precedent in paleoclimatic data of the last 1,000 years. Warming of the oceans would be relatively slower than that of Earth's land surface. Tropical ocean surface waters will be warmer and the 30 °C isotherm is likely to extend further into higher latitudes (Guinotte et al., 10.1007/s00338-003-0330-331-4). The Arabian Gulf region is likely to experience greater than average atmospheric warming (Houghton et al. 2001). Predictive models for the southern African region are less clear, indicating either an inconsistent magnitude of warming or greater than average warming (Houghton et al. 2001). Modeling studies have indicated that worldwide bleaching temperatures will be reached much more frequently in the future and regeneration times for coral assemblages could be dramatically shortened (Johnson et al. 2002; Sheppard 2002, 2003) unless rapid adaptation
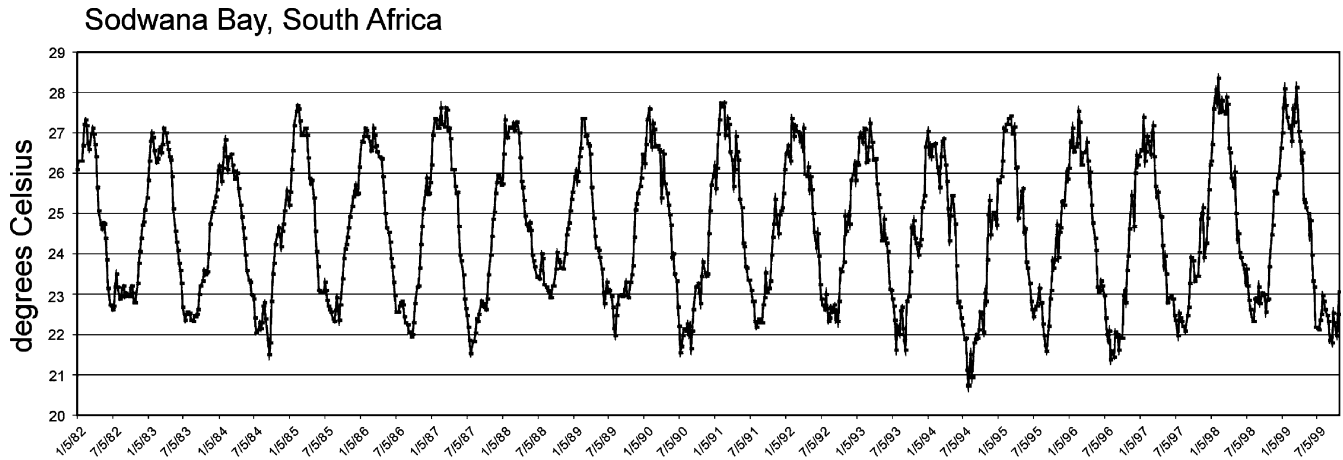
Sodwana Bay, South Africa

Fig. 8 Maputaland reefs 1×1° gridded Reynolds SST from the NCEP data set based on the center point 33°S, 27.5°E. Especially in summer, small-scale upwelling events decreasing temperature are clearly visible. Years 1998 and 1999 are the warmest in the data set, which resulted in small-scale, but not catastrophic, bleaching

of corals to these changed conditions takes place (Buddemeier and Fautin 1993; Baker 2001).

The situation in the Arabian Gulf, rapidly recurring positive SST anomalies in 1996, 1998, and 2002, could thus be interpreted as providing a "glimpse into the future" with the anticipated high bleaching frequency (Sheppard 2002, 2003). It is interesting to note that Arabian Gulf corals appear to exhibit some resilience to this kind of environmental change. The density of *Acropora* populations on Sir Abu Nuair in 2002, and their resistance to bleaching, may support the hypothesis of Glynn (1996) that offshore reefs with vigorous circulation may be refuges, which is supported by Nakamura et al. (2003). Sir Abu Nuair is situated on the distal part of the Arabian

carbonate ramp where depths exceed 30 m, which means that there is greater water circulation over these reefs than over reefs in the proximal (near-shore) shallow (< 10 m) part of the ramp, which heats more rapidly and consistently. The unexpected resistance of Sir Abu Nuair *Acropora* to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker et al. (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching—an hypothesis that is contested by Savage et al. (2002). Due to the higher frequency of disturbances than in the tropics, the high-latitude coral reefs of the Arabian Gulf might therefore provide an ideal natural laboratory to study such questions.

While corals in the Arabian Gulf may have started to adapt to a warmer climate, the process of reef-framework production may be compromised. Riegl (2001) suggested that no extensive reefal coral frameworks exist in the nearshore southeastern Arabian Gulf in response

Fig. 9 Conceptual model of water dynamics on the Sodwana Bay shelf, South Africa (modified from Riegl and Piller 2003). Idealized cross section of the Agulhas current (*shaded in grey*, based on Angel et al. 1994) shows cool water creeping up on the inshore edge due to bottom Ekman veering (Lutjeharms et al. 2000) and flooding the reefs via shelf-edge canyons. These events can be seen in Fig. 8 when SST drops rapidly within a season (mostly in summer). The shelf-edge is situated at about −40 m
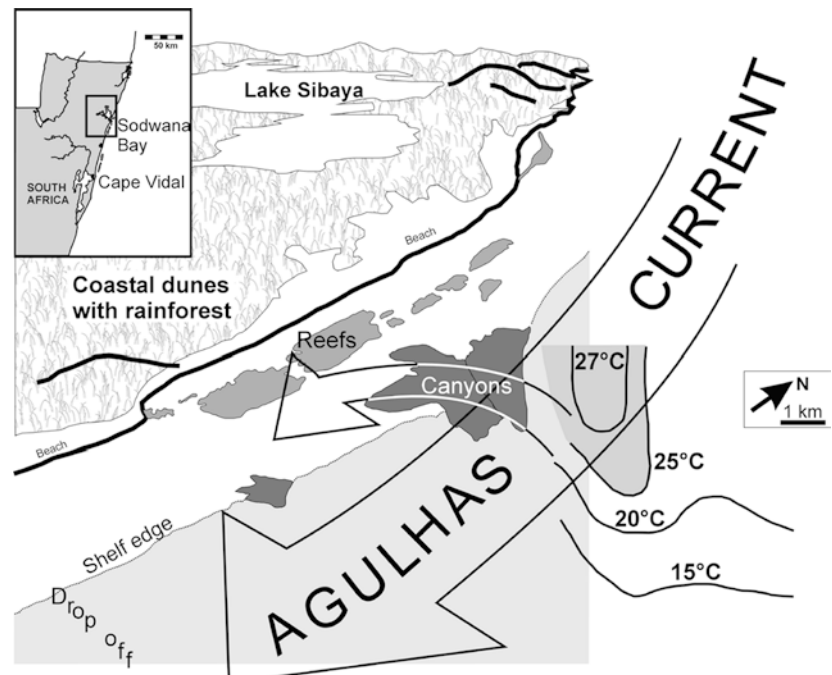
to repetitive coral mass mortality due to extreme temperatures. The temperature data presented here (Fig. 3) and reports from the literature (Downing 1985; Coles and Fadlallah 1991; Fadlallah et al. 1995) indicate that these were primarily cold events (like Shamals), but, recently, hot events appear to have become the dominant source of disturbance (George and John 1999; 2000a, 2000b). The frequency of disturbances was so high in the recent past that it may indeed be "curtains for coral reefs in the Arabian Gulf" (quote from George and John 2002), at least in the sense that corals will not be able to build sizeable carbonate frameworks, i.e. reefs. If the very recent pattern observed in the temperature record (Fig. 3) continued, then a switch from environmental "cold modulation" to "hot modulation" might have been in place since the late 1980s, which is consistent with global warming trends (Lough 2000; Houghton et al. 2001). Other factors also suggest that more hot anomalies can be expected. The weather of the Arabian Gulf is dependent on the Indian Monsoon (Sheppard et al. 2000), which is connected to the Pacific ENSO (Loschnigg et al. 2003). The coral mortality observed in the Arabian Gulf concurred with (1998, 2002) or preceded (1996) major ENSOs (1997/98). Although at first sight a primarily Pacific phenomenon, the ENSO has been recognized as one of the most important large-scale atmospheric events affecting weather worldwide via a series of intricate teleconnections (Philander 1990; Rasmusson 1991; Ruddiman 2001). Whether ENSO events will change in frequency or amplitude is not clear. Depending on the predictive model, either little change (Houghton et al. 2001) or an increase in frequency (Timmermann et al. 1999) is anticipated. Some archaeological evidence points to an increase in ENSO frequency over the last 50 years (Huckleberry 2002); however, it is unclear whether this is just a short-term effect or a local sampling phenomenon. Worldwide, atmospheric surface temperatures are projected to become more El Niño-like, with the eastern tropical Pacific warming more than the western tropical Pacific and a corresponding eastward shift of precipitation. Due to ENSO-teleconnections, global warming is also likely to cause greater variation in precipitation of the Asian summer monsoon (Houghton et al. 2001) and changes in the Indian monsoon (Pfeiffer et al. 2001). Changes in precipitation variability or the general strength of the monsoons may affect the high-latitude reefs of the Arabian Gulf along with neighboring reefal areas (e.g. the Red Sea and Arabian Sea).

Sea-level rise, projected to be 0.09–0.88 m between 1990 and 2100, is not expected to be problematic for most reef areas, but could have severe impacts on nearshore Arabian Gulf corals (less on those growing on offshore islands, like Sir Abu Nuair, and carbonate banks; Fig. 10). Much of the southern Arabian Gulf shoreline is low-lying sabkha (evaporitic intertidal flat consisting of fine-grained, largely wind-blown sediments), which is barely above sea level. The effects of flooding are presently unclear. Flooding could remobilize the fine sediments (Fig. 10), leading to highly turbid conditions (Larcombe et al. 1995) with the now flooded sabkha "shooting the reefs in the back", with resultant reef switch-off in a comparable situation to that described by Neumann and Macintyre (1985) from flooded lagoons and drowned barrier reefs in the US Virgin Islands. On the contrary, rapid hardground formation, as is presently observed throughout the Persian Gulf (Shinn 1969), coupled with an expected decrease in local winds (in analogy with the Holocene Climatic Optimum, which had a similar regional climate to what can be expected due to greenhouse changes; Sanlaville 1992; Glennie 1996), would suggest that any increased turbidity would not last long.

More damaging for corals would be the extensive areas of extremely shallow sea created by the flooding. These would be subject to strong heating/cooling in summer/winter with associated water density changes due to evaporation. The hyperpycnal, lethally heated/cooled waters flowing off such areas would have a tendency to sink and move along the seafloor, thus likely killing all nearby corals (Roberts et al. 1992). Aiding in the formation of hyperpycnal flows, at least during early flooding, could be the additional salinity provided by the dissolution of the extensive sabkha halite deposits. Much of the newly flooded areas would be an even more extreme environment than today's Gulf of Salwah (the marine cul-de-sac between Saudi Arabia, Qatar, and Bahrain), which does not support any mentionable dense coral growth (Sheppard et al. 1992).

While the Arabian Gulf perhaps provides us with some aspects which might be described as a "glimpse into the future," with a rapid succession of high-temperature disturbance events and hopes for at least some level of coral/zooxanthellae adaptation, South Africa provides us with a "glimpse of the past"—a relatively undisturbed coral system dominated by large, old corals, in this particular case primarily alcyonacean soft corals (Fig. 7B), which have similar growth and population dynamics to hard corals (Fabricius 1995). In South Africa, bleaching events have increased in frequency and bleaching increased in severity from 1% in 1999 to 10% in 2001 (Celliers and Schleyer 2002; Floros 2002), but by far less than in other areas of the central and southern Indian Ocean (Wilkinson 2000; Floros 2002). South African corals do not form true coral reefs but are a thin veneer on a submerged Pleistocene foredune system (Ramsey 1994) and are protected from extreme heat by periodic upwelling events in summer (Fig. 9). Based on recent reports by Reyes Bonilla (2001) from the Gulf of California, by Klaus and Turner (2002) from Socotra, and by Wilson (2002) from Oman, it appears that several such high-latitude "upwelling refuges" exist.

South African reefs are also well protected from tropical cyclones, which are frequent in the Mozambique Channel, 500 km to the north. The reefs are subject to periodic cyclone-generated swells from the north as well as Southern Ocean swells from the south, and coral growth-form is adapted to this high-energy
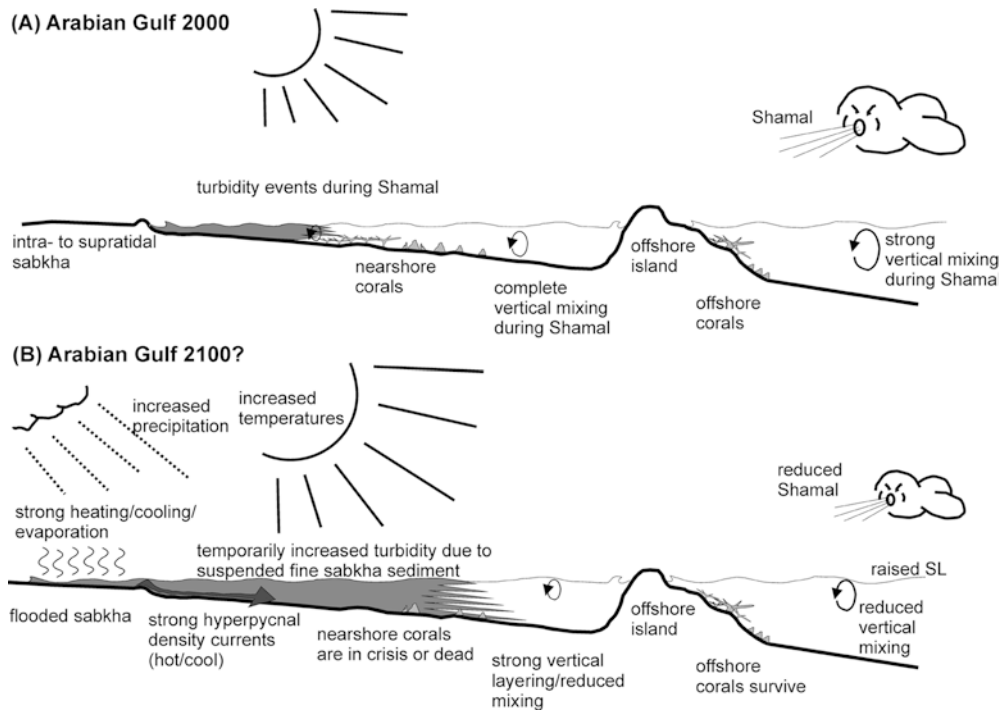
Fig. 10 Anticipated effects of global change on Arabian Gulf corals. Sabkhas are intra- to supratidal mudflats characterized by evaporite deposition. **A** is the present environmental setting. Major climatic determinants are temperature (symbolized by a *sun*) and winds, in particular the Shamal (symbolized by a *cloud*). Wind action causes strong, but often incomplete, vertical mixing of the water column in deep water, but causes complete mixing in shallow water (*elliptical arrows*). In the shallowest areas, wind-generated wave-action causes marked turbidity events. Corals avoid the shallower areas and occupy a zone just outside the average extent of the strongest turbidity events. Presently, dense coral growth is found along the mainland coastline and on offshore islands/shoals. **B** is the likely scenario in the projected 2100 greenhouse climate. Temperature has increased (*larger sun*) but winds have weakened (*smaller cloud*). This leads to reduced vertical mixing and increased layering of the water column (*smaller elliptical arrows*). Sea level (*SL*) has increased by just under 1 m and has flooded extensive areas of sabkha. Also precipitation has increased. Flooding of the sabkha remobilized the fine sediments which, together with increased runoff due to rain, creates a wide turbidity envelope, making coral growth in the previously coral-occupied zone difficult. Additionally, wide shallow areas over the flooded sabkha are subject to intense heating/cooling in summer/winter which, coupled with strong evaporation, generates hyperpycnal density flows influencing the nearshore subtidal. Since weaker winds reduced vertical mixing, the density currents also support vertical layering of the water column with dense cold/hot water at the level of previous coral growth. This further disadvantages corals. The situation is most typical of the western study area

environment. It is not anticipated that the predicted < 1-m increase in water depth would cause considerable changes in coral community patterns since keep-up is not an option for these largely non-frame-building communities (Riegl 2001). It would also most likely not cause a very strong shift of coastline with associated changes in sedimentation or turbidity regimes. Therefore, the overall environment can, within limits, be expected to remain comparable (Fig. 11).

Wider implications

Do these findings allow us to evaluate differences in impacts between high- and low-latitude reefs? From a global-warming perspective, the reefs situated in northern high latitudes (e.g. Arabian Gulf, Red Sea, Ryukyu Islands, Florida, parts of the eastern Pacific) are within an area of projected greater- or much-greater-than-average increase in atmospheric temperature (Houghton et al. 2001). The atmospheric temperature projections for areas in southern high latitudes (Australia, South Africa, Brazil) indicate slower temperature increase (Houghton et al. 2001). Therefore, the pattern observed in the present study could be expected to persist: stronger warming and impacts in the Arabian Gulf than in South Africa—in general stronger impacts in the northern high latitudes than in the southern. This might suggest that the high-latitude refuges suggested by Glynn (1996) might be mainly situated in the southern hemisphere and, maybe, parts of the eastern Pacific. However, it is not clear how uniformly ocean temperatures will react to increases in atmospheric temperature, and the above extrapolations from atmospheric temperature predictions remain problematic.

A factor that might help corals in high latitudes survive better than their tropical counterparts is the fact that they have persisted in stressful environments, such as the Arabian Gulf (Kinsman 1964; Sheppard et al. 1992; George and John 1999; Riegl 2001). Brown et al. (2002) have recently demonstrated that bleaching susceptibility of corals is correlated with their previous stress history—corals that are able to acclimatize to high irradiance may be able to obtain increased thermo-tolerance. Similar mechanisms might have been at work
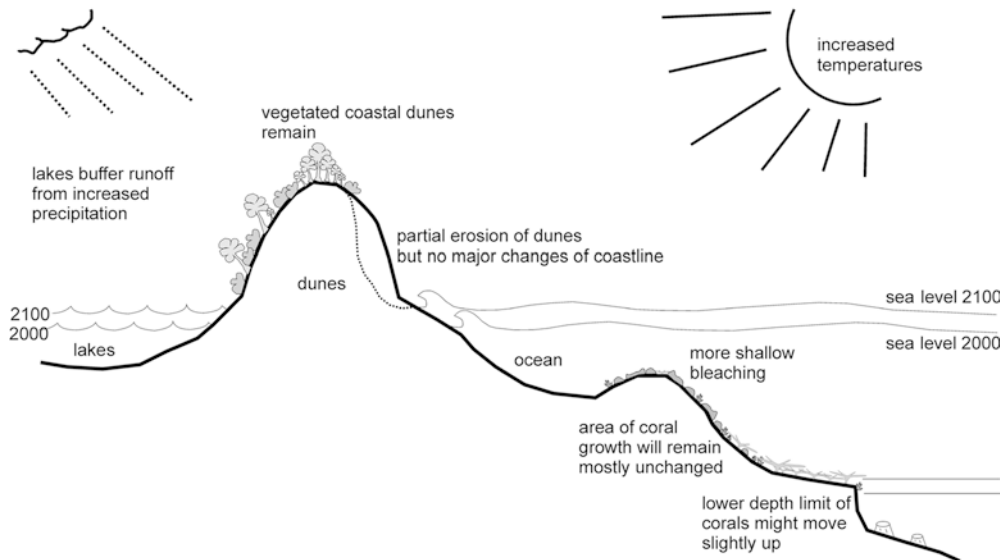
South Africa: 2000-2100?

Fig. 11 Anticipated effects of climate change on South African corals. Increases in precipitation due to tropical cyclone holding more moisture (Houghton et al. 2001) and possibly penetrating into higher latitudes is unlikely to cause strongly increased runoff since the lakes and wetlands behind the dune system would act as buffer. Sea level rise would lead to some erosion of the dunes and some adjustments in coastline, which are expected to be relatively minor. Corals grow on submerged Pleistocene dunes and beachrock and mostly do not build frameworks—this situation will not change. The lower depth limit for coral growth might track the increase in sea level. A warmer climate is likely to cause more bleaching, even if ameliorated by local upwelling (Fig. 9)

when *Acropora* did not bleach at Sir Abu Nuair and survived bleaching in Jebel Ali and Ras Hasyan during the 2002 bleaching event. Therefore, refuges for corals might even exist in the historically most stressed areas, like the Arabian Gulf. These areas might have bred resilient strains of corals that could recolonize areas where corals did not have a chance to acclimatize.

Therefore, from a conservation viewpoint, it appears justifiable to look towards the high latitudes for refugia. In the southern high latitudes and the eastern Pacific, they may exist because of the slower local climate change, whereas in the northern high latitudes, individual areas may survive simply because the corals might better acclimatize to the stresses.

The reasoning in this paper assumes that changes in ocean-surface water chemistry will remain sufficiently small so that the considerations discussed above remain valid. Kleypas et al. (1999) and Guinotte et al. (10.1007/s00338-003-331-4) argue that changes in the aragonite saturation state of the ocean would first disadvantage high-latitude areas and the tropics only later. If this is true, and no buffering mechanisms like dissolution of carbonate sediments or carbonate rocks emerge, building of coral reef frameworks might be compromised over much of the reef belt. However, even if reef growth came to a halt, it is likely that corals will survive, even if their

skeletons may be more fragile. Certain high-latitude areas with their cooler climate may indeed be the refuges envisaged by Glynn (1996), because corals could escape death by high temperatures. The two discussed areas in the southwestern Arabian Gulf and South Africa are already without formation of extensive reef frameworks, largely due to a severe environmental regime (Riegl 2001), yet they harbor rich coral faunas (South Africa: 96 species, southeastern Arabian Gulf: 34 species). The composition of the assemblages would likely remain unchanged even if their constituent corals calcified less. Will more reefs resemble these high-latitude sites in the future?

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