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Possible refugia for reefs in times of environmental stress

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Abstract This paper investigates the refuge potential of (1) upwelling areas, (2) coral areas at medium depth, and (3) offshore bank and island reefs in a scenario of increased global warming, and thus increased sea surface temperature (SST) and increased solar UV radiation. (1) Observations on coral health and water temperature in the subtropical Atlantic (Eleuthera and Cat Island, Bahamas) and Indian Ocean (Sodwana Bay, South Africa) suggest a link between cool water delivered by upwelling and coral health. After the 1998 bleaching event, caused by strong SST anomalies, coral health and recovery from the previous year's bleaching was significantly better on the narrow southern Cat Island shelf (70% of corals healthy) where the presence of cold water was observed, which was attributed to small-scale upwelling, than on the wide northern Eleuthera shelf (44% of corals healthy), where downwelling of hot bank waters was believed to have damaged corals. In South Africa, regular, short-term upwelling events in five summers reduced SST to well below bleaching level. (2) In the northern Red Sea (Safaga Bay) and in South Africa (Sodwana Bay), wide areas with either coral frameworks or non-framework communities exist. Calculations show that if the top 10 m (20 m) of the ocean became inhospitable to corals, still 50.4% (17.5%) of the coral area would remain intact in the Red Sea and 99% (40%) in South Africa. (3) Offshore bank and island reefs investigated in the Turks, Caicos, and Mouchoir Banks and Grand and Little Cayman showed high rates of mortality and coral diseases. The most remote sites (Mouchoir Bank) were not the healthiest. Refuge areas appear to exist in (1) and (2), but in (3) only if vigorous water-circulation is encountered.

Keywords Coral reef · Upwelling · Reef health · Sea surface temperature · Bahamas · South Africa · Red Sea · Cayman Islands · Refuge

Introduction

Catastrophic mass mortality of corals on reefs generally occurs in the Recent ocean in times of temperature anomalies and/or under increased solar (ultraviolet, UV) radiation which exceed the physiological tolerance-limits of the subjected corals. A marked increase of catastrophic disturbances on coral reefs has been observed over the past few decades (Glynn 1996, 2000; Wilkinson 2000; Lough 2000). Anticipated global climatic change (Lough 2000; Buddemeier 2001), with concomitant changes in ocean surface water chemistry (increased greenhouse gas concentrations would change ocean pH and would thus likely lead to declines in coral calcification, Marubini and Atkinson 1999), appears to be in a direction that may disadvantage corals in the changed ocean. Since corals are the main framebuilders in the Cenozoic, this has led many scientists to critically evaluate the future of coral reefs (Chadwick-Furman 1996; Hoegh-Guldberg 1999; Aronson et al. 1998; Wellington et al. 2001; Buddemeier 2001). As a relatively sensitive system that reflects disturbances or environmental changes both in calcification as well as biotic composition, the chances for survival of coral reefs may at first sight appear slim and pessimistic scenarios were developed (Kleypas et al. 1999; Hoegh-Guldberg 1999). While some predict an almost wholesale loss of the system, others developed a more differentiated view. Glynn (1996) formulated a hypothesis that some environmental settings "...at moderate depth, in upwelling centers, on oceanic banks or island shores exposed to vigorous circulation, and at some high latitude sites..." have high refuge potential and corals there are more likely to survive in a scenario of raised global temperatures (Glynn 1996, p. 505).

Judging from earth history's climate record, much greater perturbances than those observed in the last few

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decades, and even those predicted to occur due to man-made climate change, existed. Yet, coral reefs, or at least coral-dominated sedimentary systems, have persisted through time (Veron 1995; Stanley 2001). Consequently, refuges must exist. Presently, although the exact causes leading to large-scale bleaching and coral death are still under discussion (Dunne and Brown 2001), one of the greatest threats to reefs is without doubt an increase in sea surface temperature (SST), which in itself adversely affects reefs but also triggers a whole cascade of related impacts (e.g., papers in Glynn and Colley 2001). A taste of what could happen to coral reefs was delivered during the 1997–1998 worldwide bleaching event (Wilkinson 2000). But also changes in global biogeochemical cycles, such as changes in atmospheric CO₂ content, could have significant impact on coral reefs, since their calcification potential is expected to decrease (Kleypas et al. 1999).

While many coral reefs may indeed be doomed, we find Glynn's (1996) logic compelling that reefs in a somewhat less traditional setting than in typical shallow, clear, tropical water may actually end up having an advantage and may be future (at least temporary) refuges. Having ourselves experience in several such areas, we decided to review some of our data for evidence supporting or refuting Glynn's (1996) hypothesis. Other authors (Reyes Bonilla 2001; Jimenez et al. 2001) have already demonstrated the validity of Glynn's (1996) thoughts.

We examined three hypotheses: (1) upwelling areas provide a certain refuge potential due to the presence of relatively cooler water (illustrated by examples from the Bahamas and South Africa); (2) big enough coral areas exist at medium depth, so that even if most near-surface reefs were lost, enough reproductive potential would be maintained in deeper water (illustrated by examples from South Africa and the Red Sea); and (3) that bank and island reefs could provide a possible refuge (illustrated by examples from the Turks and Caicos and Cayman Islands).

Material and methods

We quantitatively evaluated 10 sites in the Bahamas (5 on Eleuthera, 5 on Cat Island), 4 sites in South Africa (Maputaland in northern KwaZulu/Natal province), 28 sites in the Turks and Caicos, and 32 sites in the Cayman Islands (Fig. 1). Additionally we mapped the distribution of coral-dominated areas (reefs, coral carpets and coral-dominated hardgrounds) in the northern Red Sea (Safaga Bay) and in South Africa (Sodwana Bay) (Fig. 1).

The Bahamas, Turks and Caicos, and Cayman were sampled in summer 1999, South Africa in spring 2000. The Red Sea was mapped during repeated campaigns from 1984 to 1997. In the Bahamas, remnant bleaching from the 1998 bleaching event was still detectable at the time of sampling in summer 1999 and photo series from 15×1.5 m photo-transects oriented along-strike of the reef structure were taken and later scanned and imported into a

ZEISS KS 400 3.0 image analysis system to calculate coral cover. The outlines of each individual coral were digitized and the area in pixels calculated. Corals were assigned to health categories, which were “healthy” (normal color, no recent tissue loss as indicated by white parts of the skeleton), “bleached” (i.e., paler than usual, which is an indication of zooxanthellae loss), “sick” (bleached, exhibiting lesions or tissue loss), “diseased” (clearly exhibiting one of the well-described coral diseases, such as black-band-, white-band-disease, white plague, etc.), and “bleached and diseased” (pale corals with a disease). Bleaching was defined as deviation of “normal” coral color and used the categories proposed by Gleason (1993; see also Table 1). Black-band disease could be easily identified (Antonius 1995) and all white syndromes were lumped.

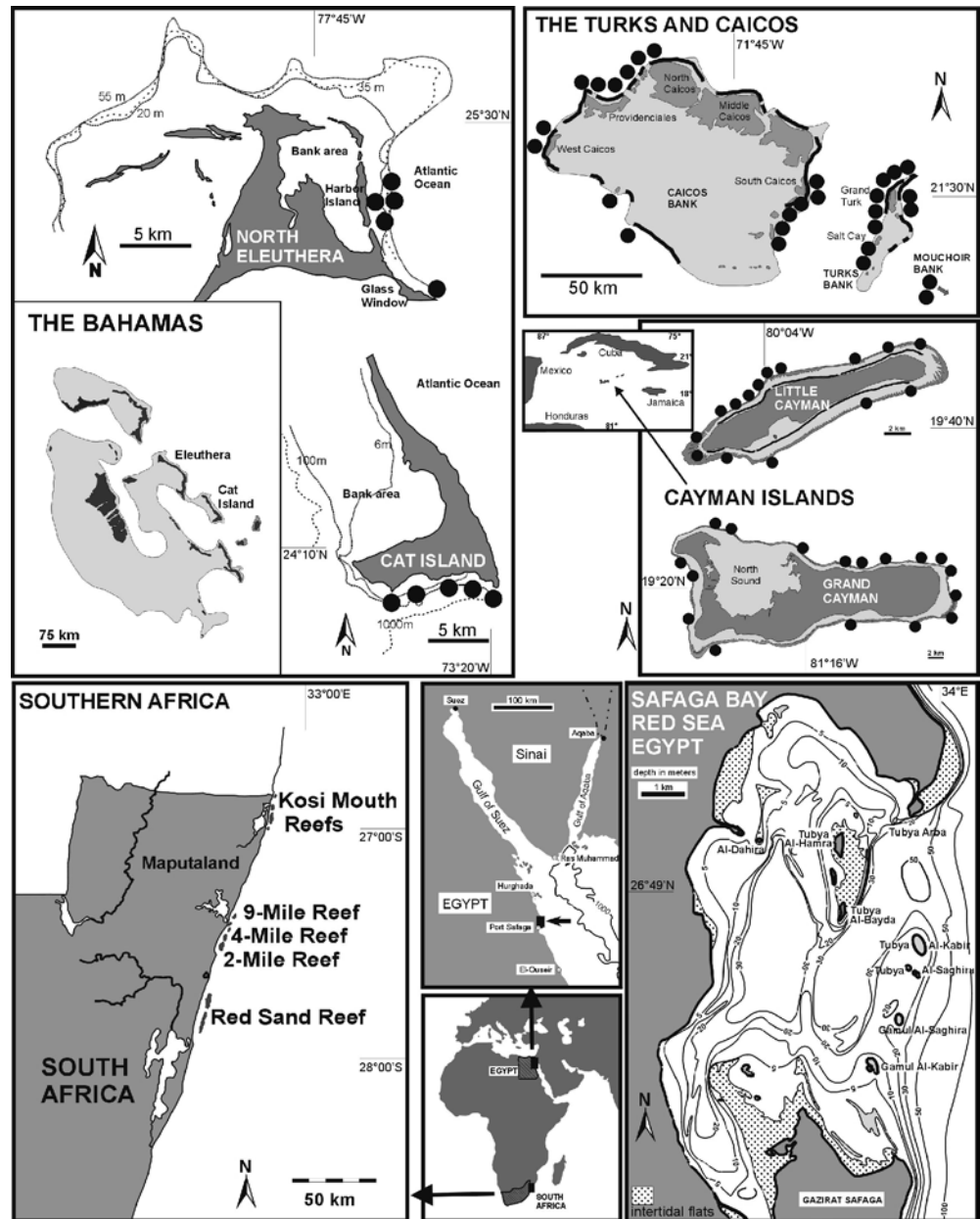
Sea surface temperature and the presence of upwelling in the Bahamas and South Africa was checked on AVHRR images from NOAA satellites (provided to us by the Rosenstiel School of Marine and Atmospheric Science). Images from the Bahamas were obtained from June 1999 to September 2000, images from the Agulhas current in South Africa from May to September 2000. Due to repeated high cloud cover over both areas during the sampling period, adequate images could only be obtained intermittently. Sea temperatures in South Africa were taken from Schleyer (1999), who had deployed an in situ temperature probe at 18 m depth on 9-Mile Reef in the Central Reef Complex, KwaZulu/Natal, South Africa. Additional SST records were obtained from satellite-derived data (weekly averages) from the website http://www.ferret.wrc.noaa.gov/las1/climate_server using the NCEP (National Center for Environmental Prediction) dataset. The NCEP dataset is an optimum interpolation of SST produced weekly on a 1×1 degree grid combining in situ and satellite data (Reynolds and Smith 1994), referred to as Reynolds SST. The average temperature for the entire dataset was calculated and the weekly positive and negative deviations graphed.

Maps of coral assemblage distribution with regards to depth in South Africa is based primarily on work by Ramsay and Mason (1990), Ramsay (1994), and Riegl and Riegl (1996). Coral health evaluation uses data provided by Jordan and Samways (2001). In the Red Sea, the spatial distribution of coral-dominated areas at different depths was mapped in northern Safaga Bay in order to gain information about the spatial distribution of coral resources away from shallow water. Original maps are based on the work of Piller and Pervesler (1989) and Riegl and Piller (1999). The various maps were imported into SigmaScan Pro 5.0, where the pixel areas occupied by dense coral assemblages at various depths were calculated.

Study sites

Study sites are situated in the subtropical Atlantic/Caribbean, the Red Sea, and the southwestern Indian

Fig. 1 Sample sites for the present study in the tropical Atlantic/Caribbean (Bahamas, Cayman Islands, Turks and Caicos Islands), the Indian Ocean (South Africa) and the Red Sea (Safaga Bay, Egypt). Dots indicate sample sites. Sampled reefs in South Africa are named. In the Red Sea, transects and point observations covered the entire illustrated area within northern Safaga Bay



Ocean.

Bahamas, Eleuthera (Harbor Island). Most scleractinian growth was encountered between 18 and 25–28 m. Groove-and-spur structures were developed between 28 and 16 m. Spurs were narrow at their apices and almost totally covered by scleractinian corals. A second groove-and-spur system was developed between 11 and 5 m depth. Another groove-and-spur system, made up largely by *Acropora palmata*, followed in shallower water.
Bahamas, Eleuthera (glass window). A combination of deep ridge-and-gully systems were oriented at right angles to each other. Gullies were steep, up to 10 m deep and up to 5 m wide, and covered in coral. Ridges

Table 1 Categories of bleaching and recovery level from Gleason (1993) adopted in this study

	Score description
Bleaching level (% of colony affected)	1 = none, colony healthy 2 = <10% or slight paling 3 = 10–50% affected 4 = >50% affected 5 = 100%, whole colony 6 = dead from bleaching
Recovery level	1 = recovered completely 2 = recovered zooxanthellae, but partial mortality 3 = still bleached but no partial mortality 4 = still bleached with partial mortality 5 = dead due to bleaching

were wide (5–10 m) and flat-topped and also covered with dense coral.

Bahamas, Cat Island. Sites differed from Eleuthera with regards to shelf-width (narrower in Cat Island) and the position of reefs relative to the shelf-edge (in Eleuthera far from the shelf-edge, on Cat Island directly on the shelf-edge). In all study sites shelf-edge coral build-ups and a near-vertical drop-off at 20–30 m were found.

Cayman Islands, Grand Cayman Island. This island is situated on a horst structure that forms a small carbonate platform which is mostly emergent. Thus the shelf around Grand Cayman Island is very narrow. The island is surrounded by a biodetrital fringing reef (Blanchon et al. 1997; Riegl 2001), a mid-shelf reef, and a shelf-edge reef which does not reach the surface due to accretion-limitation by recurrent hurricanes (Blanchon and Jones 1997).

Cayman Islands, Little Cayman Island. This is also a horst structure, northeast of Grand Cayman. It is structurally similar but smaller than Grand Cayman. It is also surrounded by a biodetrital fringing reef that is better developed on the southern than the northern side. Also the mid-shelf and the shelf-edge reefs are better developed on the southern side, because the northern shelf forms a steep drop-off from shallow depth very close to shore (the famous Little Cayman wall).

Turks and Caicos Islands. The Turks and Caicos Islands (TCI) are situated on the southern banks in the Bahamian archipelago and consist of eight islands (seven of which are inhabited) and approximately 40 low-lying cays on the two banks (Turks Bank, Caicos Bank), plus part of the entirely submerged Mouchoir Bank. The reefs are patch reefs, mid-shelf reefs, and shelf-edge reefs comparable to those in the Bahamian and Caymanian study sites. Along the western parts of the Caicos and Turks Banks, shallow fringing reefs were developed (unknown whether biodetrital or in situ framework). Shallow patch reefs surrounded many of the islands and cays.

South Africa: Sodwana Bay (KwaZulu/Natal). Sites were located in the central reef complex of Maputaland, the northernmost coastal area of KwaZulu/Natal Province in South Africa. Coral communities were situated on Pleistocene dune and beachrock to a latitude of 27°50'S (Ramsey 1994; Riegl 2001; Fig. 1). Near the reefs, three canyons (Jesser Canyon, Wright Canyon, White Sands Canyon; Ramsay 1994) dissect the shelf-slope and provide a likely pathway for upwelled water. Furthermore, the area contained extensive coral assemblages at relatively shallow, but also at intermediate depths (8–34 m).

Egypt: Safaga Bay (northern Red Sea). All sites were located within northern Safaga Bay, a wide embayment originally mapped by Piller and Pervesler (1989). The

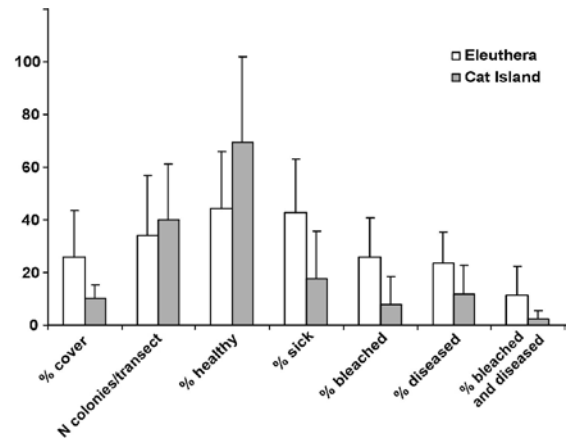


Fig. 2 Coral health in northern Eleuthera and Cat Island in July 1999, in the aftermath of strong bleaching teleconnected to the 1997/1998 ENSO event. Since values are averages and standard deviation of values over all transects, the cumulative values of all columns describing coral health do not add up to 100%

area contains a high diversity of bioconstructions and sedimentary settings dominated by corals such as true coral reefs (fringing reefs, patch reefs, and platform reefs), coral carpets, and non-framebuilding communities (see Riegl and Piller 1999, 2000 for definitions of terms). Coral assemblages were found in different exposure and at different depths. Safaga Bay has well-developed medium-depth coral carpets (biostromal coral frameworks) that, although totally different in structure, provided a good comparison to South African deeper coral assemblages due to their position relative to shallow assemblages.

Results

Upwelling areas as refuges?

Coral health in the Bahamas

The investigation took place after a well-developed positive SST anomaly over much of the Bahamas in summer 1998 which triggered coral bleaching. In July 1999, cover by living corals was significantly lower at southern Cat Island than at northern Eleuthera, while at the same time there were no significant differences in number of colonies among the transects (Fig. 2). This suggested smaller corals at Cat Islands. The percentage of healthy corals was significantly higher at Cat Island and the percentages of sick and bleached (on all levels of the Gleason (1993) scale) corals were significantly higher at Eleuthera (Fig. 2), which suggested a stronger impact of high temperatures in 1998 at Eleuthera. Corals at Eleuthera ranged on the Gleason (1993) scale (Table 1) between 3 and 6 in bleaching level, and between 3 and 5 in recovery level. At Cat Island, however, most corals ranged between 1 and 3 in bleaching level and 1 and 3 in recovery level. Therefore, the Eleuthera reefs were

Fig. 3 *Top* The sample sites in Eleuthera (Bahamas) and conceptual model of water dynamics, resulting in decreased coral health during SST anomalies. Reefs are subject to density cascades of warm (or cold), hyperpycnal waters from the bank area behind Harbor Island. *Bottom* Conceptual model of water dynamics in Cat Islands (Bahamas). Upwelled water is believed to be delivered by internal waves and/or tides, indicated by the wave. Wave length is compressed and amplitude exaggerated for reasons of graphical clarity

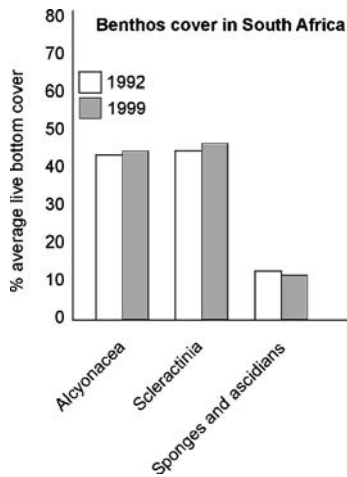
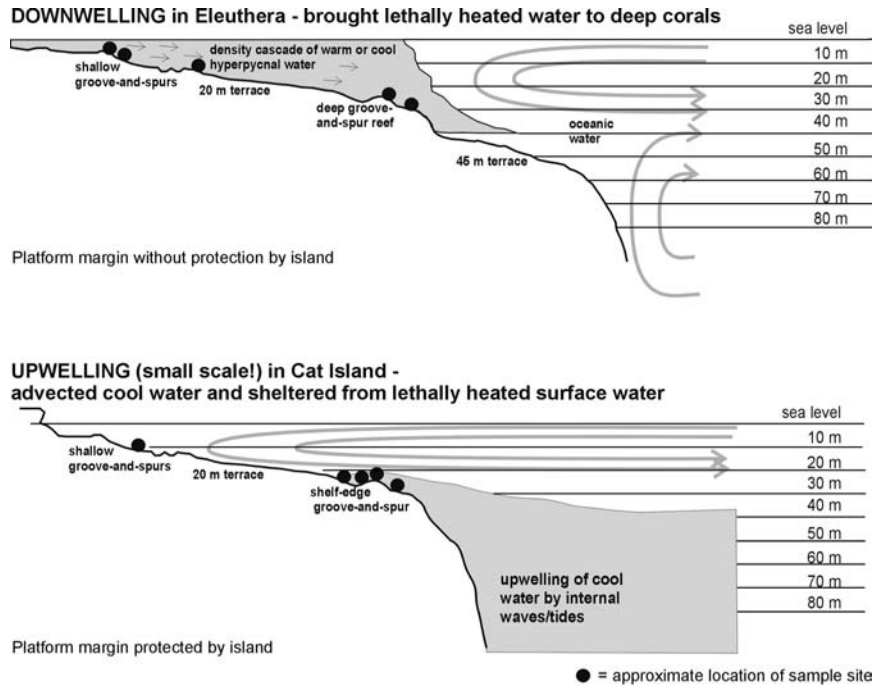


Fig. 4 Changes in live benthos cover on some Maputaland (northern KwaZulu/Natal province, South Africa) reefs (modified from Jordan and Samways 2001) showing the absence of a major mortality event in 1998 which is evidenced by the increase of coral cover from 1992 to 1999

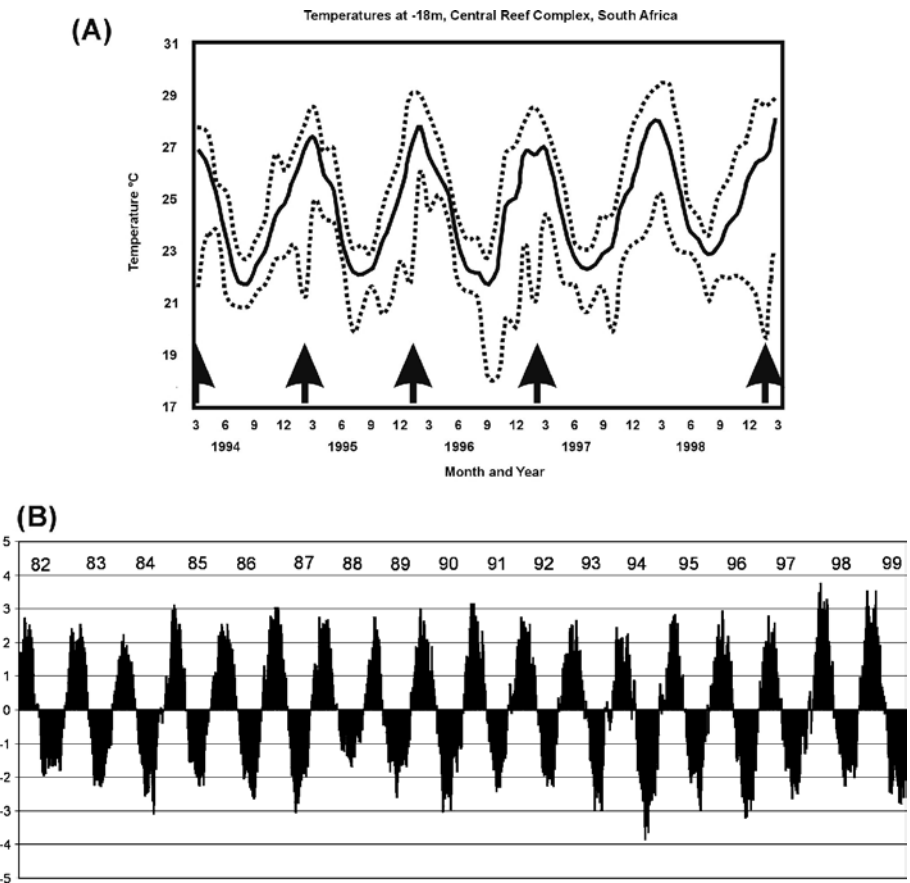
considered to be in a relatively worse state of health, while the Cat Island reefs were considered relatively healthy. The levels of diseases and bleaching observed in the Bahamas in 1999 were elevated in comparison with data obtained during the same season for the Cayman Islands and the Turks and Caicos Islands. In June 1999, average bleaching levels on shallow reefs in the Cayman Islands were 0.1% and disease levels 4.2%. In the Turks and Caicos Islands, no bleaching was observed and disease levels ranged from 2 to 10.6% (lowest on Turks Bank, highest on Mouchoir Bank, Fig. 9).

Water temperature in the Bahamas

During El Niño years, the northeasterly trade winds weaken (Curtis and Hastenrath 1995; Elliott et al. 2001) and doldrum conditions persist. In this time, corals are subjected to increased bleaching likelihood both due to increased SST as well as increased UV radiation through the calm water (Gleason and Wellington 1993; Glynn 2000). AVHRR satellite images of the study sites in the Bahamas show that the bank area behind Harbor Island on Eleuthera, which drains over some of the study sites (all Harbor Island sites) heats and cools more than the surrounding open ocean in summer and winter, respectively. It is known from the Bahamas that bank waters can become hyperpycnal either by heating or strong cooling and drain over the shelf-edge (Hickey et al. 2000; Smith 2001), where they can cause bleaching of corals (Lang et al. 1988). We assume that such a process happened in Eleuthera in Summer 1998 where heated, hyperpycnal shelf-water would have drained from the Bank area behind Harbor Island and probably propagated along the shelf-edge which caused the strong bleaching of corals not only at shallow but also at intermediate depths (1–30 m, Fig. 3). Since deeper growing corals are adapted to cooler temperatures (Cook et al. 1990), exposure to warm water may not only be the cause for bleaching, but also for lower tolerance to diseases. Heated bank water from the shelf, compounded with the already latent heat-stress of the 1998 SST anomaly of oceanic water may well have caused the strong bleaching of reef corals at Eleuthera, which was still visible in 1999.

The southern coast of Cat Island, where all study sites were situated, repeatedly showed in AVHRR imagery cool water (1–2° below ambient) at the surface. During

Fig. 5 **A** Temperature recorded on 18 m depth off 9-Mile Reef in Sodwana Bay, South Africa by Schleyer (1999). Data are monthly means (*solid line*), minima and maxima (*broken lines*, modified from Schleyer 1999). *Arrows* indicate the position of the annual cold-water event in marine summer, attributed to upwelling. **B** Satellite-derived NCEP SST dataset for a 1×1 geographic degree tile centered on the coordinates 33°E and 27.5°S. The vertical bars are the deviation of weekly temperature from dataset mean. "Cool events" are easily visible wherever summer temperatures do not remain uniformly high



the study in summer 1999, water temperature on the reefs was 1–2° colder than on the surface and a marked thermocline was developed. The cold water layer was observed to either flood the shelf-edge reefal build-ups or to remain just below the shelf-edge (Fig. 3). No such thermocline of cooler water was experienced at Eleuthera. At Cat Island, the corals in the study sites were protected from unusually warm surface water by the presence of cool water, most likely provided by upwelling. This could have been caused by internal waves or bores created by offshore highs interfering with oncoming swells or it could be wind-driven (Smith 2001). Upwelling of cooler water (~24 °C) is also known from the western margin of Exuma Sound (Dill et al. 1989).

Coral health in South Africa

The Indian Ocean was strongly affected by widespread coral bleaching in 1998 and therefore its southwestern-most reefs were investigated in South Africa. However, between 1992 and 1999, coral cover on South African reefs increased slightly (Fig. 4), which clearly indicated that over 1997 and 1998 no significant bleaching and/or coral mortality occurred. Only 0.93% of corals bleached in 1998 and coral diseases affected 0.54% of colonies (data of Jordan and Samways 2001). These values were much lower than data obtained in winter 1999, a year

without bleaching events in either summer or winter in the tropical Indo-Pacific, when a genus-specific bleaching event affected *Montipora* only on some areas of 2-Mile Reef. Bleaching levels locally reached 10% of all corals [bleaching levels 3–5 on the Gleason (1993) scale]. This pattern was localized and not observed on all reefs and showed no clear depth or habitat dependence. Not all shallow reefs were affected the same way. The event is reported here to put the virtual absence of bleaching over 1997/1998, when many of the world's coral reefs suffered severely, into perspective.

Water temperature in South Africa

Over a five-year period, water temperature variability ranged between minima of 18 to maxima of 29 °C (Fig. 5A; Schleyer 1999). Each year, a cold-spike occurred shortly before the height of marine summer, decreasing average maximum temperatures. In summer 1997/1998, the usual cold-spike did not occur (Fig. 5A). This is when 0.93% bleaching was observed. These "cool events" were also repeatedly detected by the NCEP dataset on a 1×1 geographic degree grid, which suggests them indeed being regular, larger-scale phenomena (Fig. 5B). In 1998/1999, when bleaching occurred on nearby Indian Ocean reefs (Madagascar, Tanzania, Kenya, Comores, Reunion; Wilkinson 1998), the usual

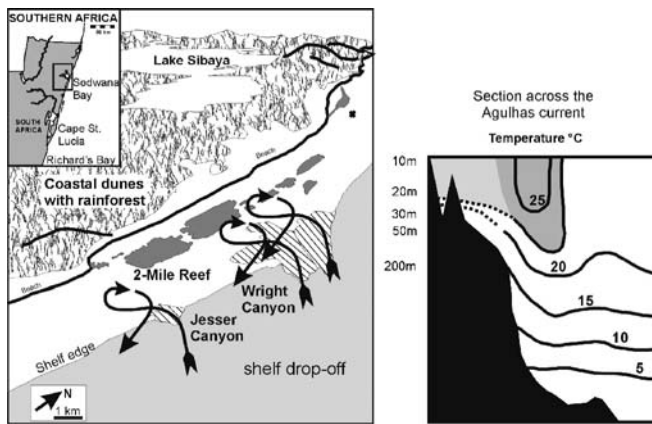


Fig. 6 Conceptual model of water dynamics on the Sodwana Bay shelf, South Africa (map modified from Ramsay 1994). Idealized cross section of the Agulhas current (shaded in gray) to show cool water creeping up on the inshore edge due to bottom Ekman veering (based on measurements near Richard's Bay from Angel et al. 1994). Since this is south of the immediate study area, temperature contour lines were not extended over the nearshore section of the continental shelf. The dotted lines show the likely extent of the isotherms, which were experienced by the authors, but not measured together with the illustrated profile. Therefore, also the inshore warm water is presented in a different shade of gray than the core of the Agulhas current as measured by Angel et al. (1994). Note that the vertical depth scale is logarithmic, the ridges with coral growth therefore appear exaggerated in profile. The shelf-edge is situated at about -40 m. Cold water is believed to be upwelling within the deep canyons from where it is then transported over the reefs and entrained into the generally southern flow direction. A cross indicates the position of the temperature logger of Schleyer (1999)

cold-spike occurred. In this year, no bleaching was observed. No temperature data for winter 1999/2000 are available. The annual cool water incursion sharply decreases temperatures in the South African marine summer. As a result, negligible mortality was observed during the same years when bleaching caused large-scale coral mortality on nearby Indian Ocean reefs (Wilkinson 1998).

The combination of in situ measured temperatures and AVHRR satellite imagery leads us to believe that the cold events in marine summer are likely caused by upwelling, which is also suggested by highly increased primary productivity and loss of water clarity due to phytoplankton blooms (unpublished, personal observation), suggesting increased nutrient levels. This upwelling seems to be site-specific and is also known elsewhere along the same coastline from two specific cells (Lutjeharms et al. 2000a, 2000b), the closest of which to the Maputaland reef system is at Cape St Lucia. It is known that strong boundary currents, like the Agulhas current, generate considerable Ekman veering at the bottom (Hsueh and O'Brien 1971, Angel et al. 1994) and this is also the case for the Agulhas current (Schumann 1986; Fig. 6). Therefore, cool deeper water creeps up on the inshore edge of the current and may find its way onto the shelf via the deep canyons that intersect the shelf-edge in the vicinity of Sodwana Bay. This leads to colder water (~ 17 °C)

being present over the shelf than at the same depth offshore. Also, northeasterly winds would help in removing some of the upper, warmer layer offshore, allowing colder bottom water to get nearer to the sea surface. Although no accurate measurements are available to test this hypothesis, it has been observed in other parts of the Agulhas system (Lutjeharms et al. 2000a, 2000b).

Areas at moderate depth as a refuge?

Depth distribution of coral-covered areas in the Red Sea and South Africa

Over much of the tropical oceans, the most vigorous coral growth takes place in less than 10 m. This is generally where the highest coral, and thus reef-growth rates are encountered and where living coral cover tends to be highest. Also, this is the depth in which coral mortality due to temperature or UV anomalies is most frequently recorded. We analyzed a reefal area in the northern Red Sea where the distribution of reefs, coral carpets, and reef-associated biota is well known. We utilized maps of coral assemblage distribution in northern Safaga Bay, Egypt, to examine the distribution and spatial extent of coral assemblages. In the Red Sea, coral growth and coral frameworks occupy all depth zones from 0 to 40 m. Framebuilding assemblages can be grouped into reefs (i.e., biohermal structures reaching the surface) and coral carpets (i.e., biostromal structures that largely follow the bedrock contour and frequently do not catch-up to the surface). Coral carpets occupy mainly the areas of flat, medium-deep seafloor (5–30 m) while reefs are primarily tied to topographic highs, such as the steep mainland coastline at Ras Abu Soma and the Tubya islands (Fig. 7). Patch reefs are found on the Tubya-Gamul ridge, there surrounded by medium-deep coral carpet framework and sand with coral patches. From the map (Fig. 7) we conservatively calculated reef frameworks to occupy approximately 1.1 km² within northern Safaga Bay (their reef-flat area plus the reef slope), while coral carpets occupied about 11.6 km² and scleractinian non-frameworks (patches and non-framework coral communities) occupied 9 km². The *Acropora* dominated coral patches were included in this calculation with the non-frameworks, since they do not form a continuous framework. In terms of total surface area, carpet frameworks cover approximately ten times more space than reef frameworks in northern Safaga Bay. Carpet frameworks and non-frameworks in medium-deep areas together cover almost 20 times as much space as reefs. Of the total coral covered area (21.7 km²), 49.6% were situated above 10 m, 82.5% above 20 m. Consequently, wide areas at "intermediate depth" exist.

In South Africa, no reefs break the surface and areas with framework potential are limited to depths greater than 18 m. Shallow areas, which are subject to high wave-energies are home to a less diverse coral assemblage than deeper (>18 m) areas. The densest scleractinian (reef-

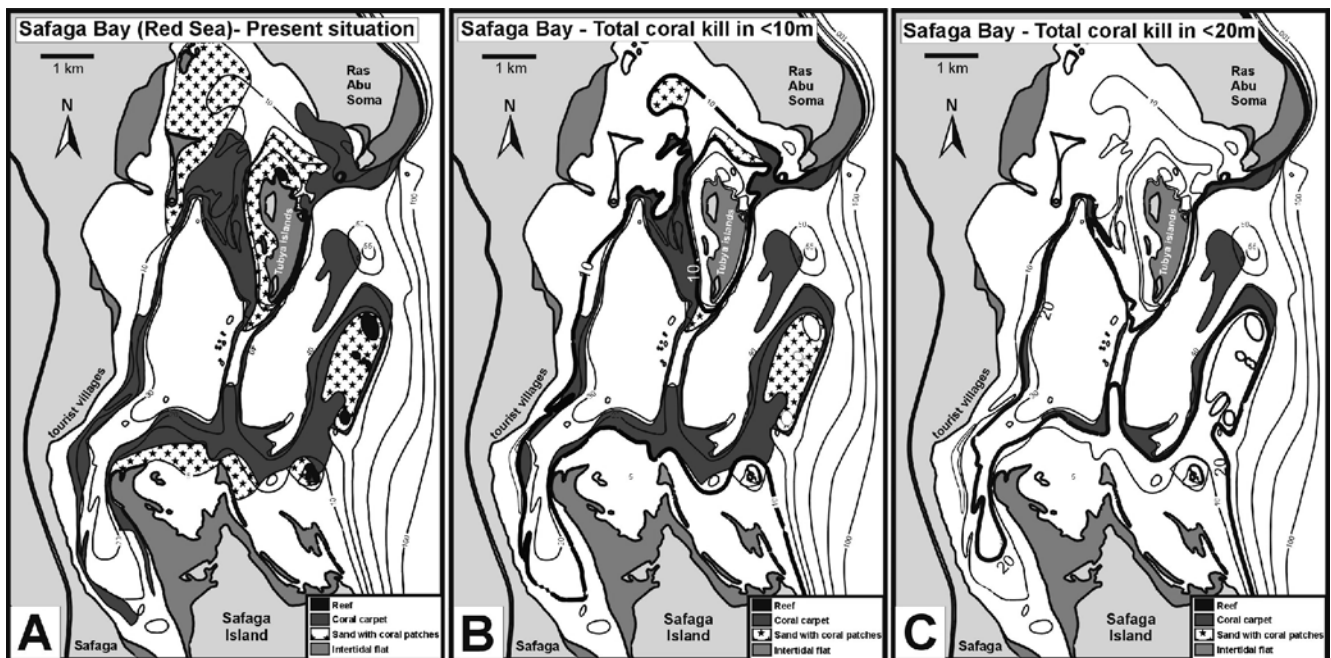


Fig. 7 A Map of the present distribution of coral framework types in the Red Sea, northern Safaga Bay. B Remaining coral area if all coral areas in <10 m are removed. The 10 m contour line is drawn

fatter than all other contour lines. C Remaining coral area if all coral areas <20 m depth are removed. The 20 m contour line is drawn fatter than all other contour lines

building hard coral) growth is also found in areas >18 m depth. Of the total coral covered area on 2-Mile Reef in Sodwana Bay (1.18 km²), only 1.1% were situated above 10 m, 60.1% above 20 m. Consequently, also here, wide areas at “intermediate depth” exist. In South Africa, it is especially these areas that presently have the densest and most diverse coral cover.

While no unambiguous models regarding the depth-distribution of possible future death of coral reefs exist, we examined two very simple scenarios. Based on literature reports from the so far most extensive bleaching and coral mass mortality event recorded (Wilkinson 2000; Glynn and Colley 2001), we assumed two models: (1) the top 10 m of the water column would become hostile to sustained coral growth and (2) that the top 20 m of the water column would become inhospitable to corals. We then calculated the surviving coral areas by simply eliminating all coral areas above the respective (10 m, 20 m) depth contours (Table 2; Fig. 7B, C).

Both scenarios suggest that in northern Safaga Bay the about 1.1 km² of reef in the present state would be totally lost. This is largely because the typical reef-associated coral assemblages only stretch to a depth of about 12 m. At this depth, most steep reef slopes meet a sandy fore-reef area, where the continuous coral growth of the reef breaks up into a series of knolls. The coral associations on the reef (windward *Acropora* community, leeward *Porites* community, semi-exposed *Millepora* community, reef flat *Stylophoralfaviid* community, from Riegl and Piller 1999) would be lost.

At the bases of the reef slopes and in areas of flat topography, a biostromal framework type known as coral

carpets is found. They can grow adjacent to reefs or in lieu of reefs into depths as shallow as 5 m. Of the presently found coral carpets, about 25% would disappear (Table 2). Virtually the entire mortality would take place within the *Porites* carpet community that is generally only encountered in depths down to 15 m. The deeper faviid carpet community would suffer almost no mortality, while the shallow depauperate faviid carpets would mostly disappear. Adjacent to reefs and coral carpets are non-frameworks with nevertheless relatively dense coral growth. The non-frameworks cover 9 km² and would suffer a die-back of about 6.8 km² (Table 2).

This quick analysis shows that while reefs would suffer badly in a scenario of total coral die-back in less than 10 m, enough coral resources exist in medium-deep water. Only about 50% of the total area occupied by reef-building corals (frameworks and non-frameworks) would disappear. If, however, the top 20 m became inhospitable to corals, the situation would change dramatically, with >80% of the area occupied by corals being lost (Fig. 7).

In South Africa, a more peripheral reef system, the survival and mortality pattern is quite different (Fig. 8). Since very few coral areas occur at less than 10 m, only 1.1% of the coral-covered area would be lost if the top 10 m of the water column was a dead zone. If, however, the top 20 m became hostile to coral growth, 60.1% of the coral area would be lost, which also includes a large portion of the framebuilding assemblage (Table 2).

Fig. 8 A Map of the present distribution of coral areas on 2-Mile Reef in South Africa, Sodwana Bay (map modified after Ramsay and Mason 1990). **B** Remaining coral area if all coral areas in <10 m are removed. **C** Remaining coral area if all coral areas <20 m depth are removed. This is one of the shallowest reefs in South Africa

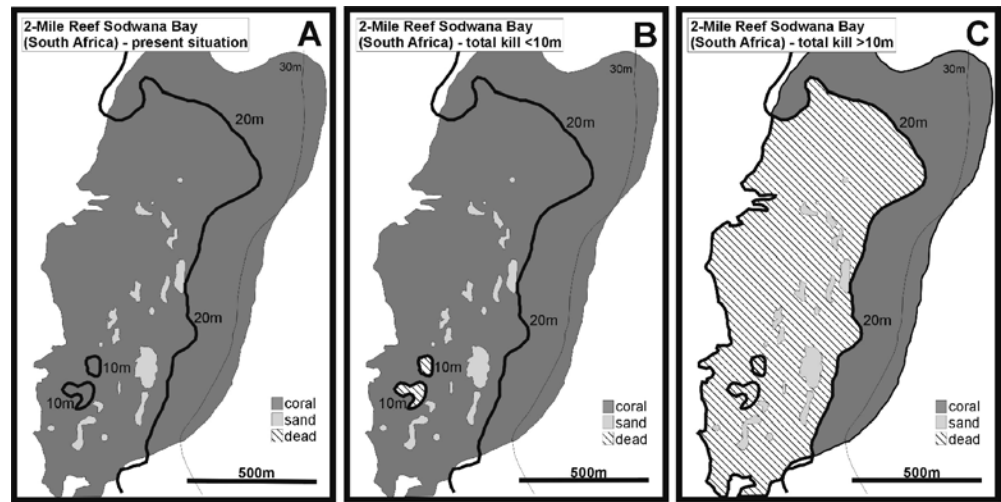


Table 2 Areas of coral frameworks as calculated in plane view. Since this includes only reef flats and backreefs and not reef slopes, the entire reef area is therefore somewhat underestimated. Coral framework types are named in accordance with Riegl and Piller (1999, 2000)

	Framework type	Area in km ²	% of original area remaining
Red Sea			
Situation now	Coral patches	9.0	100
	Coral carpets	11.6	100
	Coral reefs	1.1	100
	Total	21.7	100
Overkill in <10 m	Coral patches	2.2	24.7
	Coral carpets	8.6	75.6
	Coral reefs	0.1	8.5
	Total	10.9	50.4
Overkill in <20 m	Coral patches	0	0
	Coral carpets	3.8	32.5
	Coral reefs	0	0
	Total	3.8	17.5
South Africa (2-Mile Reef)			
Situation now	Coral community	1.18	100
Overkill in <10 m	Coral community	1.16	98.9
Overkill in <20 m	Coral community	0.47	39.9

Oceanic banks or island shores exposed to vigorous circulation as refuge?

Although Glynn’s (1996) original hypothesis expressly states “vigorous circulation” as a prerequisite for the refuge, we looked only at the first part of the theory, namely whether by virtue of being removed from land (and therefore human population, pollution, and run-off centers) offshore reefs would be so healthy as to appear as good refuges. We compared the health status of five reef areas in an oceanic setting: 28 sites around the Turks and Caicos Islands and 32 sites on Grand and Little Cayman were assessed. While this study does not provide direct comparison with sites nearer to the mainland coast, it nevertheless shows the overall health status of reefs in oceanic settings at the time of sampling (1999).

In all sites, significant coral mortality (the category mortality counted the percentage of a coral that was not covered by live tissue, Fig. 9) was encountered. In June 1999, in the Cayman Islands average bleaching levels on

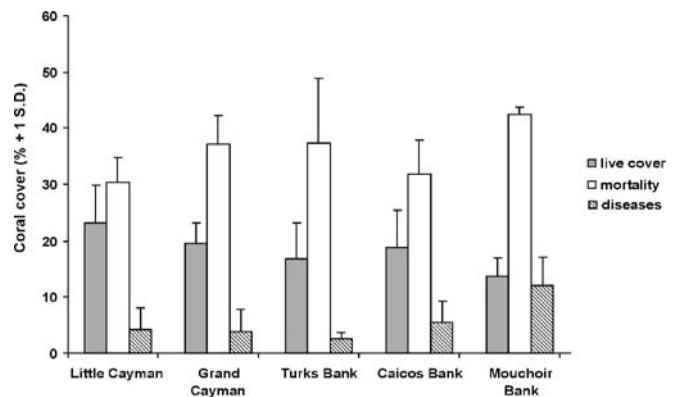


Fig. 9 Parameters of coral health in five Caribbean offshore locations. “Diseases” refers to the percentage of diseased corals (any syndrome) within the sampled assemblage. Live cover and mortality columns cannot be added to make up 100% because “mortality” measures parts of colonies that are dead while “live cover” measures the total area covered by coral skeletons with undefined amounts of living tissue on them. Thus, the “mortality” is in reality a percentage of the “live cover” value

shallow reefs were 0.1% and disease levels 4.2%. In August 1999 in the Turks and Caicos Islands, no bleaching was observed and disease levels ranged from 2 to 10.6% (lowest on Turks Bank, highest on Mouchoir Bank). It is interesting to note that the apparently most isolated bank of all, the Mouchoir Bank which has no emergent land and therefore no human settlement, had the lowest living coral cover, the highest rates of coral mortality, and the highest disease level.

Discussion

The exact causes for large-scale coral mortality due to climatic factors are still under some debate as is the capability of corals to persist after large-scale disturbances of this type (Baker 2001; Dunne and Brown 2001; Hoegh-Guldberg et al. 2002). However, general consensus considers the physiological stress associated with unusually high water temperatures alone or combined with increased solar UV irradiation due to unusually low cloud cover as the deciding factors (Hoegh-Guldberg 1999; Dunne and Brown 2001). Since the survival scenarios proposed by Glynn (1996) and explored in this paper are based on above-mentioned assumptions, we believe that they bear some relevance to the real world.

While being aware of the limitations of our data, which we do not claim to be an exhaustive survey of all discussed environmental settings, we nevertheless believe that our study supports Glynn's (1996) hypotheses that (1) upwelling areas could indeed be refuges and (2) that enough coral resources may exist in medium-deep water. Provided mortality does not extend to these depths, the medium-deep corals may serve as "regeneration batteries" for denuded shallow areas. Alternatively, if life at more shallow depths becomes impossible for corals, the medium-deep areas may indeed be the refuges. Our results regarding hypothesis (3), that offshore banks and islands exposed to vigorous circulation could serve as refuges are not conclusive, largely because of the absence of non-island comparison sites, but certainly cannot be used to refute the hypothesis.

1. Upwelling areas as refuges. Our study provides evidence from two areas in two completely different environmental settings that small-scale, localized upwelling (not to be confounded with major oceanic upwelling such as found along the west coasts of South America and Africa) can be beneficial by counteracting lethal SST heating. A similar process was observed by Reyes Bonilla (2001) in the Gulf of California, by Jimenez et al. (2001) in Costa Rica (Murcielagos Islands), and by Podesta and Glynn (2001) in the Gulf of Panama. Also reports from Zanzibar (Muhando personal communication in Obura et al. 2000) suggest that upwelling may have played a part in protecting local reefs from bleaching in 1998. A model for coral populations by Fong and Glynn (2001) also seems to support this notion. However, what may be a blessing

in one instance, could be a curse in another since coral mortality due to excessive cooling by upwelling was reported by Glynn et al. (1983) and D'Croz et al. (2001) demonstrated that corals from upwelling environments bleach earlier in elevated temperatures.

Therefore, what can sometimes be a protective mechanism is likely to cause increased mortality when occurring excessively (cold water kill; Roberts et al. 1982) or when not strong enough or absent in times of warming. This underlines the importance of local oceanographic conditions with regards to temperature and UV-related coral death (several papers in Glynn and Colley 2001). It also puts into perspective the statement of Vermeij (1986) that upwelling areas may serve as refuges for many organisms but not corals, since these areas are generally believed to be trophically too rich for corals to persist. Since the upwellings discussed in our results (Bahamas and South Africa) are "shallow upwellings", i.e., only deeper surface waters or upper middle waters are brought to the surface (see Figs. 3, 6), the nutrient enrichment is far less severe than in classical upwelling areas where deep, nutrient-rich water is involved. This may be the process that allows corals and reefs to persist in these areas.

2. Areas at moderate depth acting as a refuge. Our results from the Red Sea and South Africa appear to support this hypothesis. While we do not have data regarding differences in mortality within the same system, the literature provides us with ample indications that coral mortality caused by increased SST temperature and UV radiation is indeed depth-dependent and that deeper coral areas may suffer less (Glynn et al. 2001; Feingold 2001). Our study shows clearly that wide areas of medium-deep coral frameworks exist, and that even wider areas are covered by non-framework assemblages. In the Red Sea study area, 20 times more area is covered by corals outside reefs than on reefs themselves (irrespective of depth). Such a pattern may be typical for many areas with wide, flat shelves, in particular in the Indo-Pacific. The Red Sea has several areas with seafloor morphology comparable to Safaga Bay and good coral carpet development (Egypt: area between Straits of Gubal and Hurghada, entire Safaga Bay, Foul Bay, islands off Marsa Alam, Hamata Islands, Wadi Gimal islands, etc.; see Riegl and Piller 1999, 2000). Other potential areas for good coral carpet and non-framework coral development outside the reefs proper exist in the Saudi Arabian Red Sea in the Al Wajh Banks, Farasan Banks, the Umm al-Qamari islands, the Jeddah barrier system, and the shelf areas south of Tiran Island. Also in the Eritrean Red Sea, the Dahlak archipelago is likely to have important areas of coral growth at middle depths. McManus (1997) reported from South East Asia wide areas with coral-fragments as predominant sediments and speculates on the possibility of thousands of square kilometers of coral growth outside reefs in medium depth. Also our results from the tropical

Atlantic/Caribbean indicate that, at least in some areas, wide coral areas at medium depth may exist. The Mouchoir Bank is one such example. These areas would only serve as refuge, however, if the shallowest (i.e., upper 10 or at best upper 20 m) areas of the ocean became inhospitable to corals.

3. Oceanic banks or island shores exposed to vigorous circulation as refuge: Our data do not provide clear evidence either for or against this hypothesis. This is partly due to the fact that the data were originally not designed to test this hypothesis. We lack a control site on the mainland and we also did not test for vigorous circulation. Our data show clear evidence that offshore or not, reefs in the Caribbean clearly suffered from mortality and diseases. The high values of mortality and disease found in the five offshore bank sites are reminiscent of those in sites closer to the mainland (i.e., Florida Keys, Porter and Porter 2002). Also, our data from the Mouchoir Bank show that distance to or total absence of human habitation do not seem to have an apparent effect on coral reef health. One of the reasons why the corals at the Mouchoir Bank may be in such relatively poor health could be an intense, sometimes illegal fishery, in this largely uncontrolled area close to the densely populated Dominican Republic. Glynn et al. (2001) found higher mortality on offshore than on onshore and nearshore sites in Panama and Ecuador during the 1997–1998 ENSO event. Also Ginsburg et al. (2001) provide clear evidence that, at least in Florida patch reefs, little evidence of human-induced degradation is visible, despite their proximity to major population centers. It appears that indeed vigorous circulation is required around banks and reefs to create a refuge. We believe that the Cat Island small-scale upwelling could be seen as such an instance.

The scenario proposed here mainly concentrates on disturbances caused by the direct influence of physical factors, such as SST heating and/or increases in solar UV irradiation. Other chemical factors, such as changes in ocean carbonate saturation state (Kleypas et al. 1999) were not included in our deliberations. Also, secondary factors may contribute to the disappearance of reefs, such as increased virulence of marine pathogens in warmer water (Kushmaro et al. 1997; Toren et al. 1998; Alker et al. 2001). This mechanism appears to cause at least part of the present crisis faced by Caribbean reefs. However, since this phenomenon has not yet been described on a worldwide scale, we have excluded it largely from our thought process.

The necessary shortcomings of our thought-experiment notwithstanding we are confident to state that while coral reefs undoubtedly appear to face threats and even a possible crisis, it appears that refuge areas may indeed exist. We agree with Glynn (1996) where to look for them.

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