

Biodiversity on the marginal coral reefs of South Africa: What does the future hold?

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Southern African coral communities form a continuum from the more typical, accretive reefs in the tropics of Mozambique to the marginal, southernmost African distribution of this fauna in KwaZulu-Natal. While the latter are limited in size, they are gaining increasing attention as they provide a model for the study of many of the stresses to which these valuable systems are globally being subjected. Soft coral cover, comprising relatively few species, exceeds that of scleractinians over much of the southern reefs, and the coral communities attain a high biodiversity at this latitude on the East African coast. A long-term monitoring programme has revealed small yet significant changes in community structure on the reefs in recent years, concurrent with consistent increases in mean and maximum temperature. Insignificant bleaching was encountered during the 1998 ENSO event, unlike elsewhere in East Africa, but quantifiable bleaching occurred during an extended period of warming in 2000. Outbreaks of crown-of-thorns starfish (COTS) have caused longer-term changes in isolated areas. A study of coral larval dispersal and recruitment has been initiated to establish the capacity of the reefs to recover from the latter form of disturbance. The marginal nature of the reefs is further manifested by corals that generate aseasonal and atypical natural products and have a reproductive pattern that conforms with the pattern found on marginal reefs in western Australia. Calcium deposition on the reefs is also low due to physico-chemical factors that are related to latitude. Published projections on the long-term effects of climate change indicate that more reefs will become marginal as a result of global warming. Current monitoring on the South African reefs is being expanded to investigate the extent to which they will elucidate the future of more typical reefs.

Introduction

Marginal coral reefs are those that are found near or beyond the “normal” limits of reef distribution (Kleypas, McManus & Menez, 1999), mainly at high latitudes. High-latitude, marginal coral communities appear small and unimportant compared to massive reef structures such as those found in Australia and in the central Indo-Pacific. However, Buddemeier & Kinzie (1998) suggested that the massive biogenic carbonate accumulation of oceanic reefs in oligotrophic waters, i.e. coral reef formation (Goreau, 1969, Stoddart, 1969), might be the result of ecological stagnation under favourable conditions. They concluded that reefs closely associated with the continental margin (such as those in South Africa) are not “second rate” and that the best place to study the survival and dynamics of coral reefs was on “not-yet-reefs, sort-of-reefs and used-to-be-reefs”. Coral communities in these categories form non-accretive communities, rather than large carbonate reef structures (Goreau, 1969).

Coral communities in South Africa constitute the southernmost distribution of this

fauna on the African coast and fall almost entirely within Marine Protected Areas (MPAs) in northern KwaZulu-Natal (Schleyer, 1999, 2000, fig. 1). The reefs on which they are found are not true, accretive reefs since corals merely grow as a thin veneer on the limited Pleistocene sandstone substrata in the region (Ramsay & Mason, 1990, Ramsay, 1996). Compared to true coral reefs they appear to satisfy the requirements for classification as marginal coral communities. Since their discovery in 1970 (Heydorn, 1972, 1982, Bowmaker, 1983), they have been the focus of a number of studies over the last three decades (table 1).

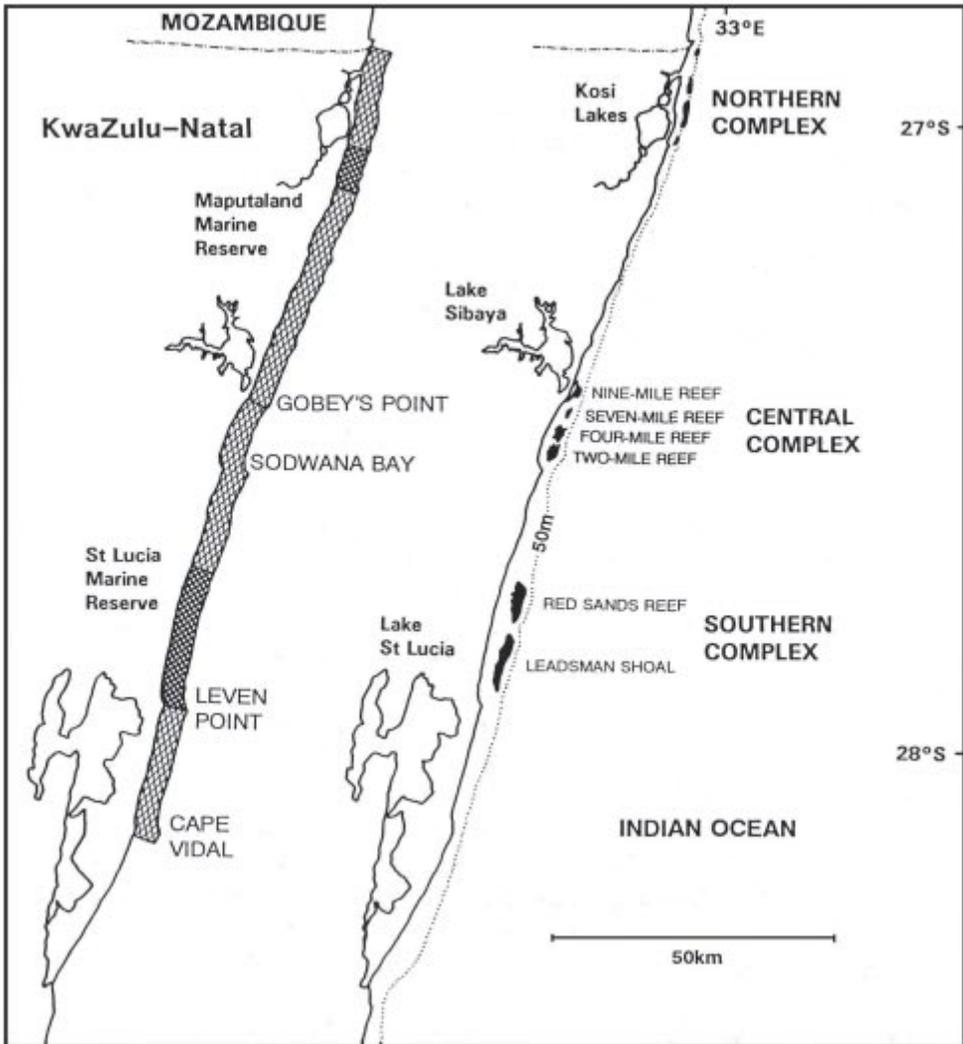


Figure 1. The major coral-inhabited reefs in KwaZulu-Natal fall within MPAs in reserve areas (light shading) and sanctuary areas (dark shading) in the Maputaland Marine Reserve (north of Gobey's Point) and the St Lucia Marine Reserve (to the south).

Table 1. Highlights and key events in South African coral research.

Year	Research/Publication	References
1950-1981	Boshoff collected and described the corals of the western Indian Ocean with an emphasis on Mozambique. He published an annotated <i>Checklist of Southern African Scleractinia</i> , the first comprehensive taxonomic study on the hard corals of the region.	Boshoff (1981)
1972	A report on the discovery of coral reefs of Tongaland was published in <i>African Wild Life</i> , with the first record of crown-of-thorns starfish (COTS) on the local reefs.	Heydorn (1972)
1979	Proclamation of the St. Lucia Marine Reserve.	
1980	<i>Studies on the Ecology of Maputaland</i> included a section on coral reefs.	Bruton & Cooper (1980)
1986	Publication of several papers on the soft corals of Southern Africa by Williams. Proclamation of the Maputaland Marine Reserve.	Williams (1986a, b) Williams (1988a, b) Williams (1989)
1987	Ezemvelo KZN Wildlife, then Natal Parks Board, records 20 070 recreational SCUBA dives at Sodwana Bay in one year.	
1991-1996	Comprehensive revision published on the region's hard coral taxonomy. Some aspects of the ecology of South African reef corals also addressed. A number of publications on sedimentation effects, coral community structure and biogeography follow. Work on the taxonomy and reproductive biology of Alcyonacean corals published. COTS outbreak reported on Two-mile Reef in the central reef complex at Sodwana Bay. The Oceanographic Research Institute commenced monitoring of COTS. Reef monitoring on Nine-mile Reef in the central reef complex at Sodwana Bay initiated in 1993 and an underwater temperature recorder installed in 1994. Publication of the marine geology of the Sodwana Bay continental shelf with physiographic and biological zoning of the coral reefs.	Riegl (1993), Riegl et al. (1995), Riegl (1995a, b, c), Riegl & Branch (1995), Riegl (1996a, b), Williams (1992), Benayahu (1993), Schleyer et al. (1997); Benayahu & Schleyer (1998a, b), Kruger et al. (1998); Kruger & Schleyer (1998); Ramsay & Mason (1990); Ramsay (1996)
1993-1999	Observations published on the COTS outbreak on the fore-reef of Two-mile Reef at Sodwana Bay and other reefs in Mozambique. COTS research programme launched 1998.	Schleyer (1998)
1996	Ezemvelo KZN Wildlife records 118 389 recreational SCUBA dives at Sodwana Bay in one year.	
1998	First record of coral bleaching in South Africa. Damage to corals negligible.	
1999	Synthesis of KwaZulu-Natal coral research published Larval settlement and recruitment study initiated by the Oceanographic Research Institute.	Schleyer (1999)
2000	Diver damage at Sodwana Bay quantified. Quantifiable coral bleaching recorded at Sodwana Bay.	Schleyer & Celliers (2000) Celliers & Schleyer (2002) Schleyer & Tomalin (2000)
2001	Installation of two more underwater temperature recorders, a wave height recorder and an acoustic Doppler current profiler at Sodwana Bay.	

Soft coral cover, comprising relatively few species, exceeds that of the more diverse scleractinian cover over much of the reef area, yet the coral communities attain a high biodiversity (table 2) at this latitude on the East African coast (Riegl, Schleyer, Cook & Branch, 1995, Schleyer, 1999, 2000). The purpose of this review will be to assess how marginal the reefs are, the extent to which they may be affected by climate change and whether they will provide a model on the global future of corals by virtue of their unique attributes.

Table 2. Biodiversity on the South African coral reefs in terms of Milleporina and Scleractinia (Riegl, 1995b, c, 1996a, b, Riegl et al., 1995, Celliers & Schleyer, unpublished data), Alcyonacea (Benayahu, 1993, Benayahu & Schleyer, 1995, 1996), Ascidiacea (Monniot, Monniot, Griffiths & Schleyer, 2001, Schleyer, unpublished data) and Porifera (Schleyer, unpublished data). Information on the last-mentioned is only included in the summary, covering material identified thus far in current, incomplete work. Most Scleractinia are hermatypic; some that are listed here are ahermatypic (a). Of the non-scleractinian corals, a few are hermatypic (h). New records (nr) and new (n), endemic (e) and species of unresolved status (?) are also marked.

Summary	Genera	Species
Milleporina	1	1
Scleractinia	43	93
Alcyonacea	11	39
Ascidiacea	17	30
Porifera	20	?
Milleporina	<i>C. monnile</i>	<i>Goniopora djiboutensis</i>
<i>Millepora platyphylla</i>	<i>Cycloseris costulata</i>	<i>G. somaliensis</i>
	<i>C. cyclolites</i>	<i>Gyrosmlia interrupta</i>
Scleractinia	<i>C. cf. marginata</i>	<i>Herpolitha limax</i>
<i>Acanthastrea echinata</i>	<i>Cyphastrea chalcidicum</i>	<i>Horastrea indica</i>
<i>A. simplex</i>	<i>Dendrophyllia cf. robusta</i> (a)	<i>Hydnophora exesa</i>
<i>Acropora aculeus</i>	<i>Diaseris distorta</i>	<i>H. microconos</i>
<i>A. anthocercis</i>	<i>Echinophyllia aspera</i>	<i>Leptastrea purpurea</i>
<i>A. austera</i>	<i>Echinopora gemmacea</i>	<i>Leptoria phrygia</i> (nr)
<i>A. clathratha</i>	<i>E. hirsutissima</i>	<i>Leptoseria explanata</i>
<i>A. danai</i>	<i>Favia favus</i>	<i>Montastrea annuligera</i>
<i>A. florida</i>	<i>F. laxa</i>	<i>Montipora aequituberculata</i>
<i>A. horrida</i>	<i>F. matthaii</i>	<i>M. danae</i>
<i>A. humilis</i>	<i>F. pallida</i>	<i>M. monasteriata</i>
<i>A. hyacinthus</i>	<i>F. rotumana</i>	<i>M. spongodes</i>
<i>A. latistella</i>	<i>F. speciosa</i>	<i>M. tuberculosa</i>
<i>A. millepora</i>	<i>F. stelligera</i>	<i>M. turgescens</i>
<i>A. nasuta</i>	<i>Favites abdita</i>	<i>M. venosa</i>
<i>A. natalensis</i> (?)	<i>F. complanata</i>	<i>M. verrucosa</i>
<i>A. palifera</i>	<i>F. flexuosa</i>	<i>Oulophyllia crispa</i>
<i>A. sordiensis</i> (?)	<i>F. halicora</i>	<i>Pachyseris speciosa</i>
<i>A. tenuis</i>	<i>F. pentagona</i>	<i>Pavona clavus</i>
<i>Alveopora allingi</i>	<i>F. peresi</i>	<i>P. minuta</i>
<i>A. spongiosa</i>	<i>Fungia (Pleuractis) scutaria</i>	<i>Platygyra daedalea</i>
<i>Anomastrea irregularis</i>	<i>Galaxea fascicularis</i>	<i>Plesiastrea versipora</i>
<i>Astreopora myriophthalma</i>	<i>Gardineroseris planulata</i>	<i>Pocillopora damicornis</i>
<i>Blastomussa merleti</i>	<i>Goniastrea edwardsi</i>	<i>P. eydouxi</i>
<i>Coeloseris mayeri</i>	<i>G. pectinata</i>	<i>P. verrucosa</i>
<i>Coscinaraea cf. columna</i>	<i>G. retiformis</i>	<i>Podabacia crustacea</i>

<i>Porites lichen</i>	<i>S. flexuosum</i>	<i>A. mernoensis</i>
<i>P. lutea</i>	<i>S. glaucum</i>	<i>A. monile</i> (n, e)
<i>P. solida</i>	<i>S. infundibuliforme</i>	<i>Atrium marsupialis</i>
<i>Psammocora haimeana</i>	<i>S. trocheliophorum</i>	<i>Botryllus gregalis</i>
<i>Seriatopora caliendrum</i>	<i>Simularia abrupta</i>	<i>Cystodytes dellechiaiei</i>
<i>Scolymia cf. vitiensis</i>	<i>S. brassica</i>	<i>Didemnum leopardi</i> (n, e)
<i>Stylophora pistillata</i>	<i>S. erecta</i>	<i>D. molle</i>
<i>Stylocoeniella guentheri</i> (nr)	<i>S. firma</i>	<i>D. ?obscurum</i>
<i>Symphyllia valenciennesi</i>	<i>S. gardineri</i>	<i>D. rodriguezii</i>
<i>S. ehrenbergi</i>	<i>S. gyrosa</i>	<i>Diplosoma virens</i>
<i>Turbinaria mesenterina</i>	<i>S. heterospiculata</i>	<i>Eudistoma bituminis</i> (n)
<i>Tubastrea micranthus</i> (a)	<i>S. hirta</i>	<i>E. caeruleum</i>
	<i>S. leptoclados</i>	<i>E. hospitale</i>
Alcyonacea	<i>S. muralis</i>	<i>E. modestum</i>
<i>Anthelia flava</i>	<i>S. notanda</i>	<i>Lissoclinum bistratum</i>
<i>A. glauca</i>	<i>S. querciformis</i>	<i>Polycarpa insulsa</i>
<i>Cladiella australis</i>	<i>S. schleyeri</i> (e, n)	<i>P. mytiligera</i>
<i>C. kashmani</i> (e, n)	<i>S. triangula</i>	<i>P. seychellensis</i>
<i>C. kremppii</i>	<i>S. variabilis</i>	<i>P. rubida</i>
<i>Efflatounaria sodwanae</i> (e, n)	<i>Sympodium caeruleum</i>	<i>Polycitor africanus</i>
<i>Eleutherobia aurea</i> (e, n)	<i>Tubipora musica</i> (h)	<i>Polysyncraton ?aspiculatum</i>
<i>Heteroxenia fuscescens</i>	<i>Xenia crassa</i>	<i>P. millepore</i>
<i>Lobophytum crassum</i>	<i>X. garciae</i>	<i>Pseudodistoma africanum</i> (e)
<i>L. depressum</i>	<i>X. kükenthali</i>	<i>P. delicatum</i> (n, e)
<i>L. latilobatum</i>		<i>Pyura herdmani/stolonifera</i>
<i>L. patulum</i>	Ascidacea	<i>Sigillina</i> sp
<i>L. venustum</i>	<i>Aplidiosis tubiferus</i> (n)	<i>Symplegma ?bahraini</i>
<i>Sarcophyton crassum</i>	<i>Aplidium flavolineatum</i> (e)	<i>Trididemnum cerebriforme</i>

Background

Kleypas et al. (1999) assessed the limitations on coral growth of a number of physico-chemical determinants at different latitudes using modelling techniques. They concluded that, in terms of the parameters they considered (salinity, the nutrients NO_3 and PO_4 , light penetration, temperature and aragonite saturation state), the South African reefs fall within the marginal limits of the last three for coral growth (table 3). They anticipate that marginal reef development at high latitudes will become increasingly subject to the divergent forces of increasing temperature, resulting in reef expansion, and declining levels of aragonite saturation, resulting in diminished reef accretion. They do not expect the incidence of light or light penetration to change or affect coral growth beyond the present level.

As we hope to demonstrate, we believe that the South African reefs are presently experiencing increased coral growth in the short-term due to the warming, greenhouse effect of increasing global atmospheric CO_2 (table 4). However, in the long-term, Kleypas et al. (1999) expect that the CO_2 build-up will globally and radically retard coral accretion through a reduction in the marine aragonite saturation state. The present thin accretion on our reefs is already a manifestation of the marginal degree of aragonite saturation in South African waters and, with a further decrease, accretion will again diminish.

Table 3. Statistically derived global means and extremes in physico-chemical parameters on coral reefs (from Kleypas et al., 1999), compared with values measured on South African reefs. The projections of Kleypas et al. (1999) are included if no data were available for the South African reefs.

Theoretical global estimates				South African reefs	
	Min	Max	Mean	Mean	Notes
Temperature (°C)					
Average	21.0	29.5	27.6	24.7	(UTR data)
Minimum	16.0	28.2	24.8	22.3	Minimum = 16.1°C
Maximum	24.7	34.4	30.2	26.1	Maximum = 30.1°C
Salinity (‰)					
Minimum	23.3	40.0	34.3	34.3	(Pearce, 1973)
Maximum	31.2	41.8	35.5	35.5	
Nutrients (mmol.L⁻¹)					
NO ₃	0.00	3.34	0.25	0.22	(Pearce, 1973)
PO ₄ 0.00	0.54	0.13	0.23		
Aragonite saturation (Ω-arag)					
Mean values	3.28	4.06	3.83	<3.5	(Kleypas et al., 1999)
Light penetration (m)					
Average	-9	-81	-53	-	Only horizontal visibility
Minimum	-7	-72	-40	-	estimates available
Maximum	-10	-91	-65	-	(mean approximately 11 m)

Table 4. The anticipated effects of climate change on coral growth in South Africa resulting from increasing atmospheric CO₂ (derived from Kleypas et al., 1999).

	Effects on physico-chemical parameter	Effects on coral growth and reef formation
CO ₂ Increase	Temperature ↑	Could increase in the short-term
	Aragonite saturation state ↓	Will decrease in the long-term
	Light (unchanged)	Unchanged

The status of the South African reefs

These changes were, to a degree, anticipated in the Coral Programme of the Oceanographic Research Institute (ORI) some years ago. A long-term monitoring site was established on one of the reefs at Sodwana Bay in 1993 and fixed quadrats have subsequently been photographed annually and stored for image analysis. An underwater temperature recorder (UTR) was also installed at the site in 1994 and this has yielded temperature records manifesting a steady temperature increase of 0.27°C p.a. (Celliers & Schleyer, 2002, fig. 2a). Long-term regional data (Celliers & Schleyer, 2002, fig. 2b) confirm that there has been a protracted increase in sea surface temperatures but at a lower rate. A comparison of the Sodwana Bay region with other coral reef localities revealed an increase in sea temperature of similar magnitude, viz. 0.1°C.decade⁻¹ (table 5). The recent, more dramatic increase is thus probably a macro-cyclical phenomenon and is unlikely to be maintained. The area is nevertheless undoubtedly undergoing the general temperature increase associated with global warming.

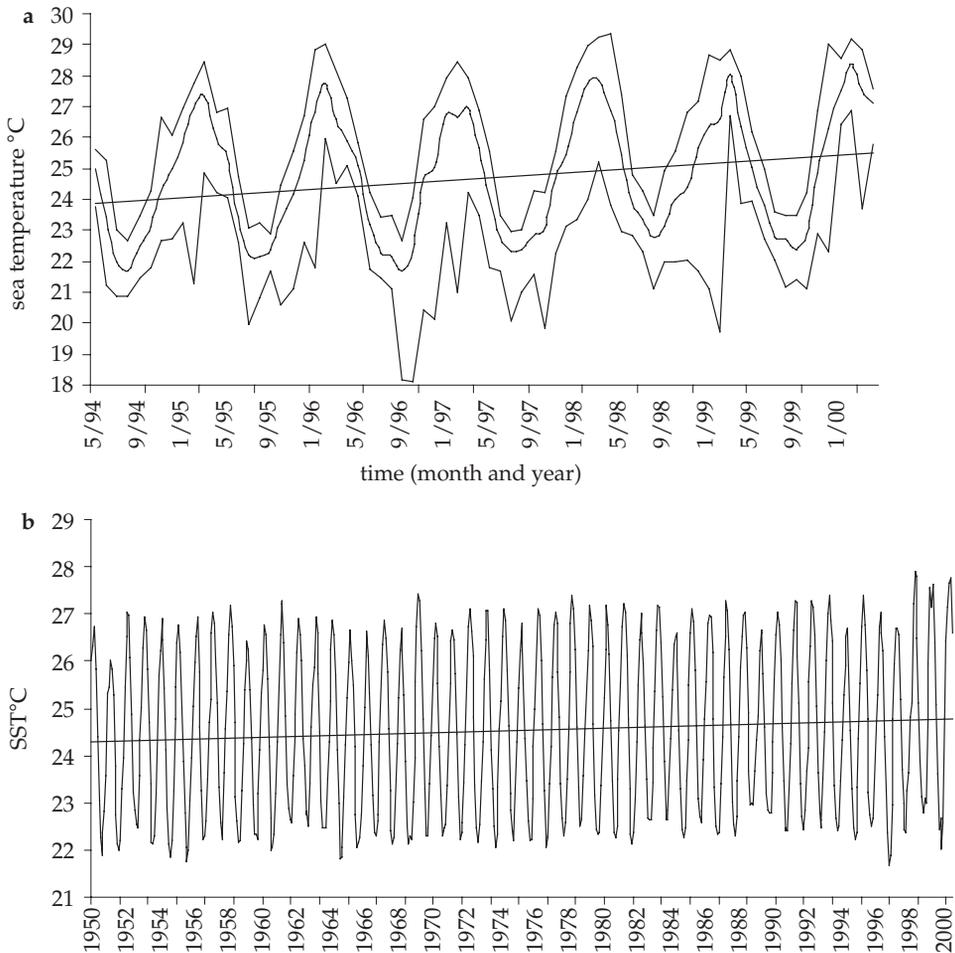


Figure 2. a) Monthly maximum, mean, and minimum sea temperatures recorded at a depth of 17 m (low tide) at a fixed monitoring station located at Sodwana Bay between May 1994 and April 2000. The regression line for the mean temperature data is included (temperature increase= $0.27^{\circ}\text{C}\cdot\text{y}^{-1}$). b) Monthly mean sea surface temperatures for the 2° latitude x longitude block incorporating Sodwana Bay. The regression line for all points is shown (reconstructed SST fields supplied by the South African Weather Service; temperature increase= $0.01^{\circ}\text{C}\cdot\text{y}^{-1}$).

A preliminary assessment of changes in community structure by image analysis of the first five years of quadrat photographs yielded small changes in community structure (Schleyer et al., 1998) and a ten-year data set is presently under investigation. The data is being analysed for changes in community structure and coral recruitment, growth and mortality. Examples of results for the first are presented in fig. 3 and show that, overall, the hard coral cover on the reef is increasing while that of the soft corals is decreasing (table 6; Schleyer & Celliers, in prep.) except in a distinct reef-sediment interface community where sediment-tolerant soft corals (Schleyer & Celliers, in press) remain dominant. It would thus appear that the $>2^{\circ}\text{C}$ increase measured on the

Sodwana reefs in the last decade has, up to now, encouraged scleractinian calcification and growth. If the projections modelled by Kleypas et al. (1999) prove correct, the scleractinian cover will later decrease as the aragonite saturation state diminishes and calcification becomes more inhibited. The monitoring is ongoing and is being expanded to include measurements of light and aragonite saturation state.

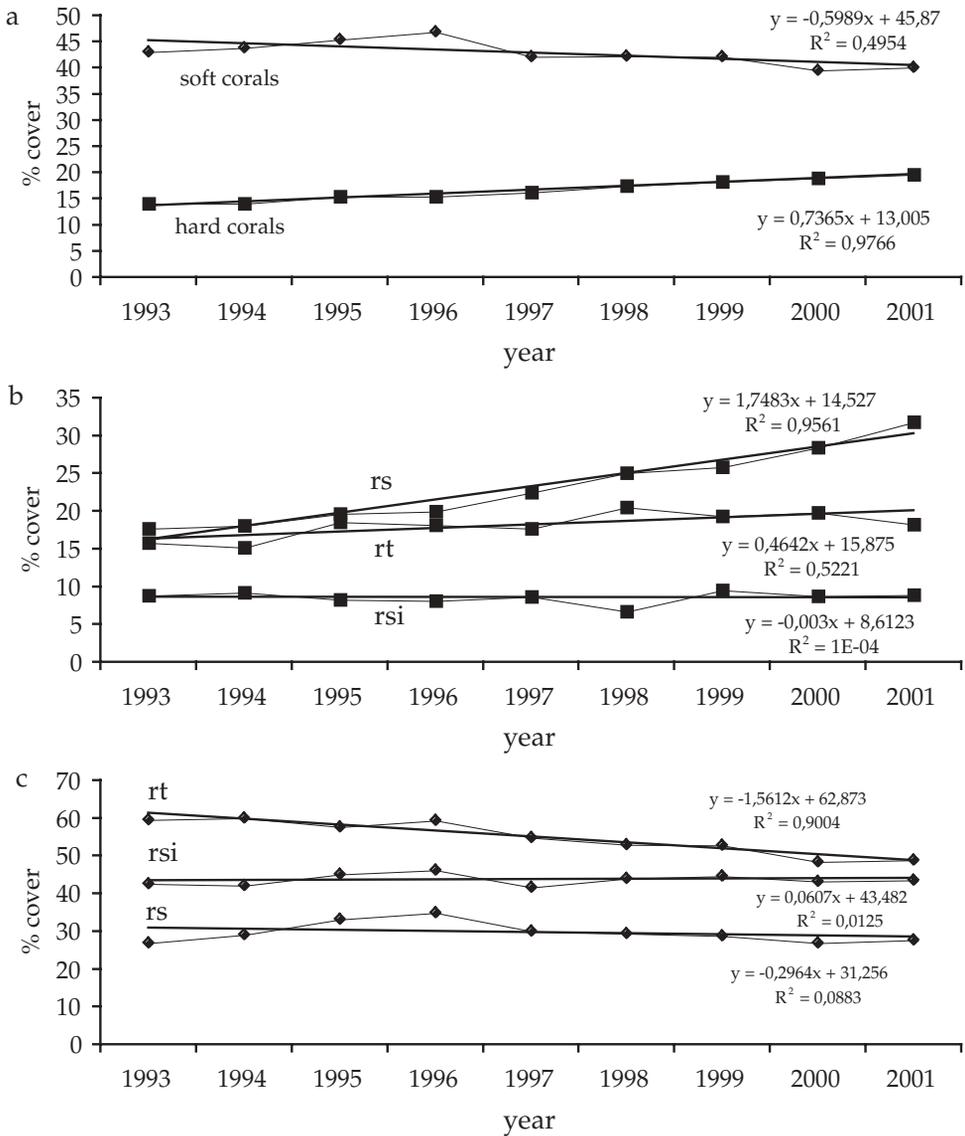


Figure 3. Percentage a) total, b) hard and c) soft coral cover recorded in fixed quadrats at a long-term monitoring site on Nine-mile Reef at Sodwana Bay between 1993-2001. Data are presented for the reef zones; rt=reef top, rs=reef slope and rsi=reef-sediment interface.

Table 5. Rates of sea temperature increase ($^{\circ}\text{C}.\text{decade}^{-1}$) for a selection of tropical reef locations (adapted from Fitt et al., 2001) compared with long-term data for Sodwana Bay.

Locality	Period	Rate of increase ($^{\circ}\text{C}.\text{decade}^{-1}$)	Source
Jamaica	1903-1999	0.125	Hoegh-Guldberg (1999)
Phuket, Thailand	1904-1999	0.154	Hoegh-Guldberg (1999)
Phuket, Thailand	1945-1995	0.126	Brown, Dunne & Chansang (1996)
Tahiti	1926-1999	0.069	Hoegh-Guldberg (1999)
Tahiti	1956-1995	0.08	Brown (1997)
GBR, Australia	1902-1999	0.125-0.168 ¹	Hoegh-Guldberg (1999)
Tropical oceans	1982-1996	0.001-0.053 ¹	Strong, Kearns & Gjovig (2000)
Sodwana Bay, SA	1950-2001	0.1	Celliers & Schleyer (2002)

¹latitude dependant

Table 6. Rate of change in % coral cover in the distinct reef zones on Nine-mile Reef at Sodwana Bay, South Africa, over nine years between 1993 and 2001.

	$\Delta\%$ Total coral cover per annum ⁻¹	$\Delta\%$ Hard coral cover per annum ⁻¹	$\Delta\%$ Soft coral cover per annum ⁻¹
Reef top	-1.1	+0.5	-1.6
Reef slope	+1.4	+1.7	-0.3
Reef-sediment interface	<+0.1	<+0.1	<+0.1

Interestingly, only slight bleaching was recorded on the South African reefs prior to and including the dramatic El Niño Southern Oscillation (ENSO) event in 1998 (Celliers & Schleyer, 2002) that so devastated coral reefs in East Africa (Schleyer, Obura, Motta & Rodrigues, 1999, Obura, Mohammed, Motta & Schleyer, 2000). Despite the temperature increase, the "marginal" temperatures in the South African latitudes did not attain hazardous levels for the corals. However, a protracted period of elevated temperatures (see fig. 2) with high levels of irradiance caused by exceptional water clarity elicited measurable bleaching in 2000 (Celliers & Schleyer, 2002). The critical temperature at which bleaching appeared to be engendered was $\sim 28.8^{\circ}\text{C}$.

A crown-of-thorns starfish (COTS; *Acanthaster planci*) outbreak was also encountered on the reefs during the last decade (Schleyer, 1998) and became the subject of a Ph.D. study (Celliers, 2001). The behaviour of the COTS was atypical as they aggregated in summer, apparently to breed rather than feed in a swarm, and they dispersed in winter (Schleyer, 1998). They thus grew faster than COTS swarming and competing for food on the Great Barrier Reef (Celliers, 2001), providing further evidence that the biota on the South African reefs live under marginal conditions. The outbreak caused a severe but patchy reduction in hard coral cover (fig. 4). The affected reef communities entered alternative stable states subsequent to the outbreak, dominated either by soft corals of low diversity or hard corals of high diversity (Celliers, 2001).

Recreational SCUBA diving underwent an increase on the accessible reefs during the 1980s and 1990s (Schleyer, 1999) and nearly 120 000 recreational SCUBA dives were logged on the reefs at Sodwana Bay in 1996. Despite there being a decline in div-

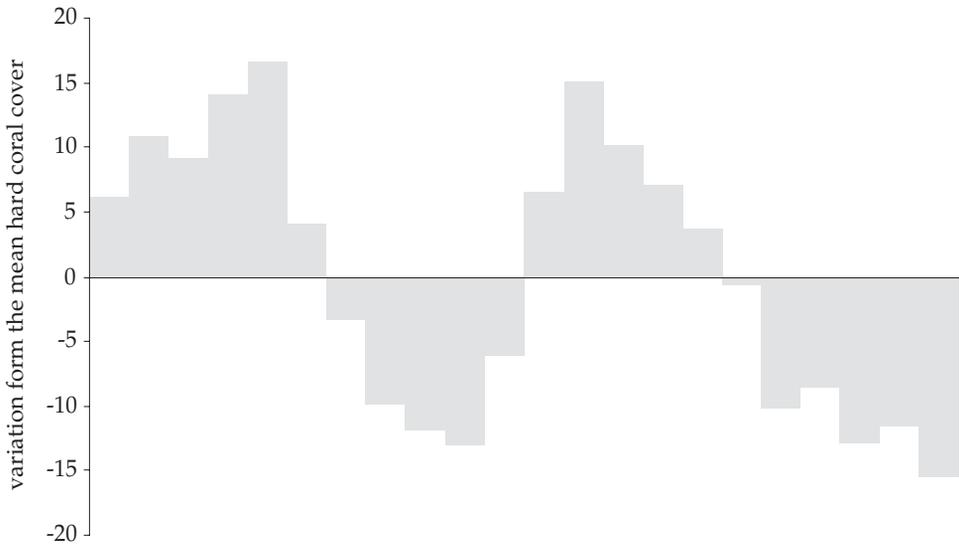


Figure 4. Variation around the mean of hard coral cover in transects along the fore-reef of Two-mile Reef at Sodwana Bay after a COTS outbreak that lasted from 1994-2000 (Celliers, 2001).

ing intensity in more recent years with a down-turn in the South African economy, recommendations were made for the management of this activity (Schleyer & Tomalin, 2000) in view of the marginal nature of the reefs.

Coral reproduction was studied in the light of the marginal nature of the reefs to establish whether the local communities are self-perpetuating or dependant on recruitment from reefs to the north. Seven coral species, manifesting the full range of reproductive strategies, were thus examined histologically and normal reproduction was encountered (table 7). It is of note that no evidence of the mass spawning in early summer typical of corals on tropical reefs was found. The alcyonacean broadcasting spawners studied did, however, appear to synchronise their spawning with the lunar cycle late in summer similar to hard corals found on marginal reefs off Western Australia (Schleyer et al., 1997).

Table 7. Reproductive strategies found in the corals studied on the Maputaland coral reefs (Schleyer et al., 1997, submitted, Kruger & Schleyer, 1998, Kruger et al., 1998).

Species	Mode of reproduction
<i>Anthelia glauca</i>	Gonochoric brooder, repetitive seasonal planulation
<i>Lobophytum crassum</i>	
<i>Lobophytum depressum</i>	
<i>Sarcophyton glaucum</i>	Gonochoric seasonal broadcast spawners
<i>Simularia dura</i>	
<i>Simularia gyrosa</i>	
<i>Pocillopora verrucosa</i>	Hermaphroditic seasonal broadcast spawner

Having established that the coral communities on the South African reefs are sexually active, it remains to be demonstrated that they are also self-seeding. A study of coral larval dispersal and recruitment has thus been initiated to establish the capacity of the reefs to recover from COTS and bleaching events. Monitoring of settlement is being accompanied by oceanographic measurements to assess dispersal using an acoustic Doppler current profiler (ADCP), wave height recorder, additional UTRs and CTD (conductivity, temperature and depth) determinations.

Finally, a correlation was anticipated between toxin production and gametogenesis during the reproductive cycle in the soft corals. These natural products are known to have a number of functions in soft coral reproduction, e.g. sperm attraction and larval defence, and are usually produced in an annual cycle (Ketzinal, 1997). However, Ketzinal (1997) found no such correlation in South Africa. She studied two soft coral species, *Lobophytum crassum* and *Eleutherobia aurea*, and they respectively produced five and eight different natural products randomly throughout the year, some of which were unique (Ketzinal et al., 1996). This may be construed as further atypical behaviour of the corals in a marginal environment.

In conclusion, it is apparent that the South African reefs are marginal in terms of temperature, light, aragonite saturation state and many aspects of their biology. The effects of climate change are causing warming of our coastal waters, resulting in a shift in the coral community structure from soft to hard corals. This is probably related to an increase in coral accretion attributable to the rise in sea temperature. The trend will probably be short-lived as temperatures are now approaching the local coral bleaching threshold. A further build-up of the atmospheric CO₂ that is causing climate change is expected to reduce the marine aragonite saturation state globally, leading to a commensurate decline in reef formation and the scleractinian composition in coral communities. Changes on South African reefs are likely to precede those on more typical, tropical reefs. Studies on the former will thus elucidate the relationship between these complex mechanisms and may provide an insight to the global future of coral reefs.

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