

Is damage susceptibility linked to coral community structure? A case study from South Africa

Hängt die Verletzbarkeit von Korallengesellschaften von ihrer Struktur ab? Eine Studie aus Südafrika

by

Bernhard RIEGL* & Peter A. COOK**

RIEGL, B. & COOK, P.A., 1995. Is damage susceptibility linked to coral community structure? A case study from South Africa. — Beitr. Paläont., 20:65–73, 9 Figures, 2 Tables, Wien.

Abstract

Africa's southernmost coral communities are situated in northern Natal, South Africa (27°50' S), within the Maputaland and St. Lucia Marine Reserves. Growing concern about the possible impact of recreational activities on the health of the coral ecosystem prompted the present study on the structure and health of the reefs. Coral community studies by means of line transects identified three basic coral community types, which correlated with the geomorphology of the sandstone outcrops on which corals grew. 1) Fossil dunes were dominated by alcyonacea in depths between 8 and 24 m. 2) Flat outcrops between 18 and 24 m depth were dominated by scleractinia (mainly *Acropora*). Within these community types, a further small-scale differentiation into sub-communities inside and outside of gullies occurred. 3) Deep hard substrata between 25 and 34 m depth were dominated by sponges, ascidians and sea-fans. Quantitative damage assessment was used to correlate community structure to damage susceptibility. The flat-outcrop *Acropora* community was considered most fragile, while the other community types (dominated by leathery alcyonaceans or by sponges) were considered more robust. Such quantitative assessments can be of value to the development of zoning schemes for marine reserves.

Zusammenfassung

Die südlichsten Riffkorallengesellschaften Afrikas liegen im nördlichen Natal, Südafrika (27°50' Süd), innerhalb des Maputaland und des St. Lucia Meeresreservates. Sorge um mögliche Schädigung des Korallenökosystems durch touristische Nutzung führte zu dieser Studie über die Gesellschaftsstruktur und Gesundheit der Riffe.

Korallenvergesellschaftungen wurden mittels der Schnurtransekt Methode untersucht. Drei Gesellschaftstypen, welche an bestimmte geomorphologische Eigenschaften ihres Sandsteinsubstrats gebunden waren, wurden gefunden. 1) Fossile Dünen wurden zwischen 8 und 24 m Tiefe von Alcyonacea dominiert. 2) Flache Sandsteinriffe zwischen 18 und 24 m wurden von Scleractinien (vor allem *Acropora*) dominiert. Innerhalb dieser Gesellschaftstypen wurde eine weitere Differenzierung in verschiedene Untergesellschaften innerhalb und außerhalb sandiger Gräben beobachtet. 3) Tiefe Hartböden zwischen 25 und 34 m wurden von Schwämmen, Aszidien und Seefächern dominiert. Korallen-Gesellschaftsstruktur wurde mit quantitativen Daten über Schadenshäufigkeiten korreliert. Die *Acropora*-Gesellschaft der flachen Riffe zwischen 18 und 24 m zeigte die höchsten Schadenswerte und wurde als die empfindlichste Gesellschaft angesehen. Die anderen Gesellschaftstypen, welche von ledrigen Weichkorallen oder von Schwämmen dominiert waren, wurden als robuster eingeschätzt. Solche Analysen sind für die Entwicklung von Zonierungsplänen in Meeresreservaten wertvoll.

1. Introduction

Africa's southernmost coral reefs (27°50') are situated in northern Natal, South Africa, within the boundaries of two marine reserves, the St. Lucia and Maputaland Marine Reserves, which are administered by the Natal Parks Board, a provincial nature conservation authority. Coral reefs have been identified as systems of particularly high value to conservation (KENCHINGTON, 1988). This is partly due to their biological richness but also because of their enormous appeal to tourism (ROGERS et al., 1988; SYBESMA, 1988). South Africa's coral reefs are witnessing ever increasing popularity with game fishing, spear-

* Zoology Department, University of Cape Town, Rondebosch 7700, South Africa

present address: Institut für Paläontologie der Universität Wien, Geozentrum Althanstr. 14, 1090 Wien, Austria

**Zoology Department, University of Cape Town, Rondebosch 7700, South Africa

fishing, snorkelling, and particularly SCUBA-diving as the most commonly practiced recreational activities. Tourism in areas administered by conservation bodies provides welcome revenue which can be reinvested in the continued preservation of the money-producing resource or other systems in need of conservation.

The original zoning scheme of Maputaland reefs was primarily based on fisheries issues. Therefore, the question arose whether corals needed further management. It was therefore attempted to provide management options for the coral reefs within the St. Lucia and the Maputaland Marine Reserves, with a view to allow a maximum number of visitors to enjoy the reefs while doing the least damage to the coral communities. The aim of the study was to develop a concept based on coral community structure, which would provide the framework to classify reefs according to their damage-susceptibility.

2. Material and methods

2.1. The study area was situated in the Maputaland reef system in northern Natal, South Africa (Fig. 1). The geomorphology of these reefs differs from that of typical coral reefs (RAMSEY & MASON, 1991; RIEGL et al., 1995). They do not reach the surface (minimum depth 6–8 m) and lack a typical reef crest and a lagoon and have no pronounced reef slope (mostly sloping at less than 10°). Major topographical features are gullies and associated drop-offs of up to 5 m, dissecting the reefs in irregular intervals and orientation.

Two types of reef, which developed on two different types of underlying topography, occur: deep, flat outcrops between 18 and 24 m depth (4-Mile Reef, Kosi Bay Reef) and fossil dunes or shallow sandstone outcrops, reaching from 8 to about 34 m depth (2-Mile Reef, 9-Mile Reef, Red Sands Reef).

2.2. Quantitative community analysis used the line-transect method with continuous recording of the intercepts of all organisms and geological features underlying the transect rope (LOYA, 1978). Ideal transect length was previously established to be at 10 m. On each reef, series of about 10 transects which followed the depth contour with one meter spacing between them were repeatedly recorded at randomly chosen sites. This approach was necessary due to the low topographical differentiation of the reefs. Depth of transects varied between 8 and 34 m, and 5–7 sample sites were surveyed per reef.

The intercepts of corals, all other major invertebrate groups such as sponges and ascidians, as well as sand and unoccupied rock were recorded. Unoccupied rock was defined as lacking macroalgae or invertebrates. All reef complexes were surveyed, although emphasis was laid on the Central Reef Complex which receives most visitor pressure.

A total of 171 transects were recorded on five reefs (Fig. 1). The transect-data were subjected to correspondence

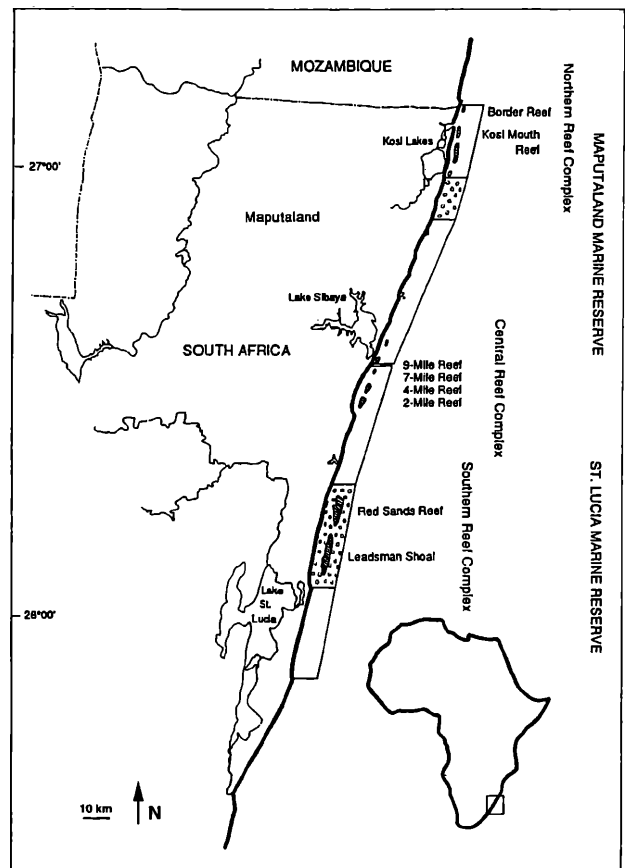


Figure 1: The Maputaland coral reefs in northern Natal, South Africa. Borders of the marine reserves are indicated. Sanctuary areas are dotted.

analysis and hierarchical, agglomerative cluster analysis (DIGBY & KEMPTON, 1984) in order to detect patterns. In a second step, the transects of each locality were pooled and localities were compared. Squared Euclidian distance or the Correlation Similarity Coefficient was used as distance measure with Ward's or centroid method of linkage (DIGBY & KEMPTON, 1984). The Shannon-Wiener Index (PIELOU, 1975) was used as diversity measure.

Coral communities were described by combining species identification with the concept of structural typology as described by BRADBURY et al. (1986) and BAK & POVEL (1988).

2.3. Quantitative damage assessment was performed using the modified line transect method described by RIEGL & VELIMIROV (1991): the status of each colony underlying the transect rope, whether broken or not, was recorded. Additional information was derived from literature, where details of damage susceptibility of individual species or growth form types were provided (RIEGL & VELIMIROV, 1991; LIDDLE, 1991; HAWKINS & ROBERTS, 1992). As coral growth form is generally related to damage susceptibility (RIEGL & VELIMIROV, 1991), this approach allowed us to assess the likelihood with which damage may occur within any given com-

munity type. Thus, coral communities were classified into “damage-susceptibility-categories”

3. Results

3.1. Coral community analysis

The correspondence analysis grouped the transects along two axes (Fig. 2), which were determined by the ratio of scleractinia/alcyonacea in the community (dominance by alcyonacea increasing along the positive x-axis) and corals versus sponges (dominance of sponges increasing along the positive y-axis). Three clusters could be defined, even though a wide area of overlap existed. One cluster, stretched along the negative x-axis, comprised only transects from 4-Mile Reef and Kosi Mouth Reef which were dominated by scleractinia (mainly *Acropora*). The second group of transects differentiated into two sub-clusters along the positive x- and y-axis. The central cluster, spread around the 0-point, included transects from almost all sampled reefs, but mainly from 2-Mile and 9-Mile Reefs, and was dominated by alcyonacea (*Sinularia* and *Lobophytum*); a third cluster, with the greatest distance to all other clusters was made up by transects from >25 m depth from 2-Mile Reef and Red Sands Reef and was dominated by sponges (Fig. 2). This indicated a partitioning of coral communities among reefs.

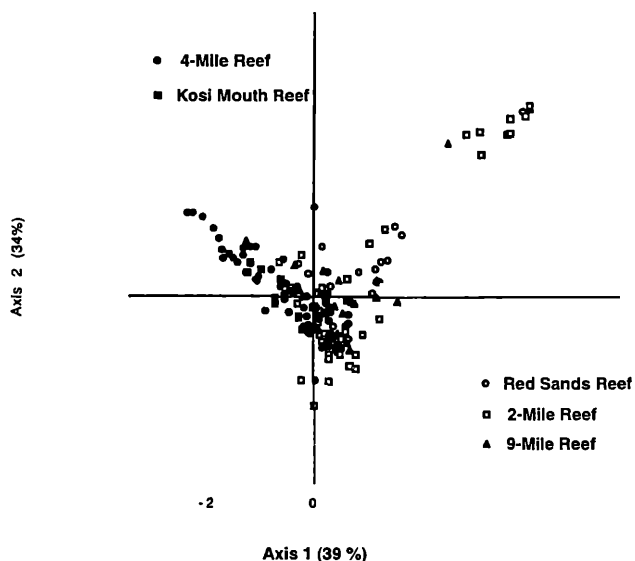


Figure 2: Correspondence analysis of all transects obtained from 5 reefs in northern Natal.

Table 1: Space occupation of major benthic invertebrate groups on northern Natal reefs. Percentage values for organism groups are proportions of total cover. Percentage values for total cover are proportions of total transect length.

	Kosi Mouth Reef	4-Mile Reef	9-Mile Reef	2-Mile Reef	Red Sands Reef
Alcyonacea	35±20 %	35±16 %	54±28 %	43±23 %	42±18 %
Scleractinia	62±19 %	63±17 %	39±24 %	45±21 %	43±17 %
Porifera	1±1 %	2±3 %	6±11 %	10±18 %	11±14 %
Ascidiacea	2±2 %	1±1 %	2±7 %	2±4 %	4±6 %
Total cover	76±8 %	68±21 %	54±20 %	50±23 %	39±13 %

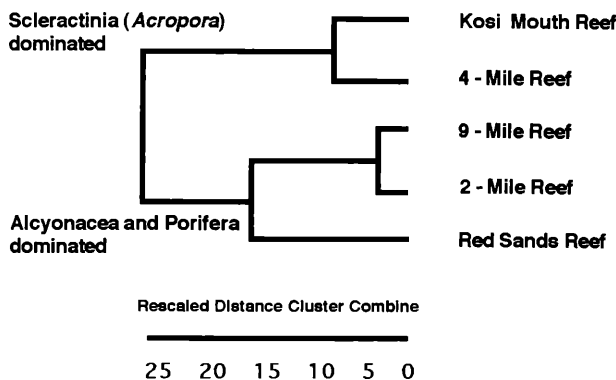


Figure 3: Classification of pooled data in each surveyed locality using centroid method of linkage and the correlation similarity coefficient.

This pattern was also observed by cluster analysis of data pooled in each locality (Fig. 3): deep, flat outcrops (18 to 24 m depth, 4-Mile Reef and Kosi Mouth Reef) were characterized by *Acropora* dominated communities, with a high frequency of branching and tabular species. The other reefs, which had a higher relief (stretching from 8 to 34 m depth; 2-Mile Reef, 9-Mile Reef, Red Sands Reef) were characterized by a more equable frequency of scleractinia, alcyonacea and other taxa (Tab. 1).

Within reef community analyses revealed that communities differentiated primarily into sub-communities in gullies and outside of gullies. This situation was the same in the scleractinia dominated community as well as in the alcyonacea dominated community. The deep, flat reefs (4-Mile and Kosi Mouth Reefs) were dominated over wide areas by branching or tabular *Acropora*. Other dominant corals included the alcyonacean genus *Sarcophyton*. Its dominance was however restricted. The dominant species in this community had branching and tabular growth forms (Fig. 4).

The fossil dunes showed a more accentuated community differentiation (Figs. 5, 6). Principal division was along a sedimentation gradient into gully and reef-top communities, and along a depth gradient. The shallow and medium deep parts (8–24 m) were dominated by alcyonacea. A zone between 18 and 25 m showed alternating dominance by alcyonacea or by *Acropora* species (*A. austera*, *A. clathrata*). This zone was, however, not well defined and in the cluster analysis (Fig. 5) the transects from this zone grouped with the other reef-top transects, which were alcyonacea dominated. The deep parts (25–24 m) were

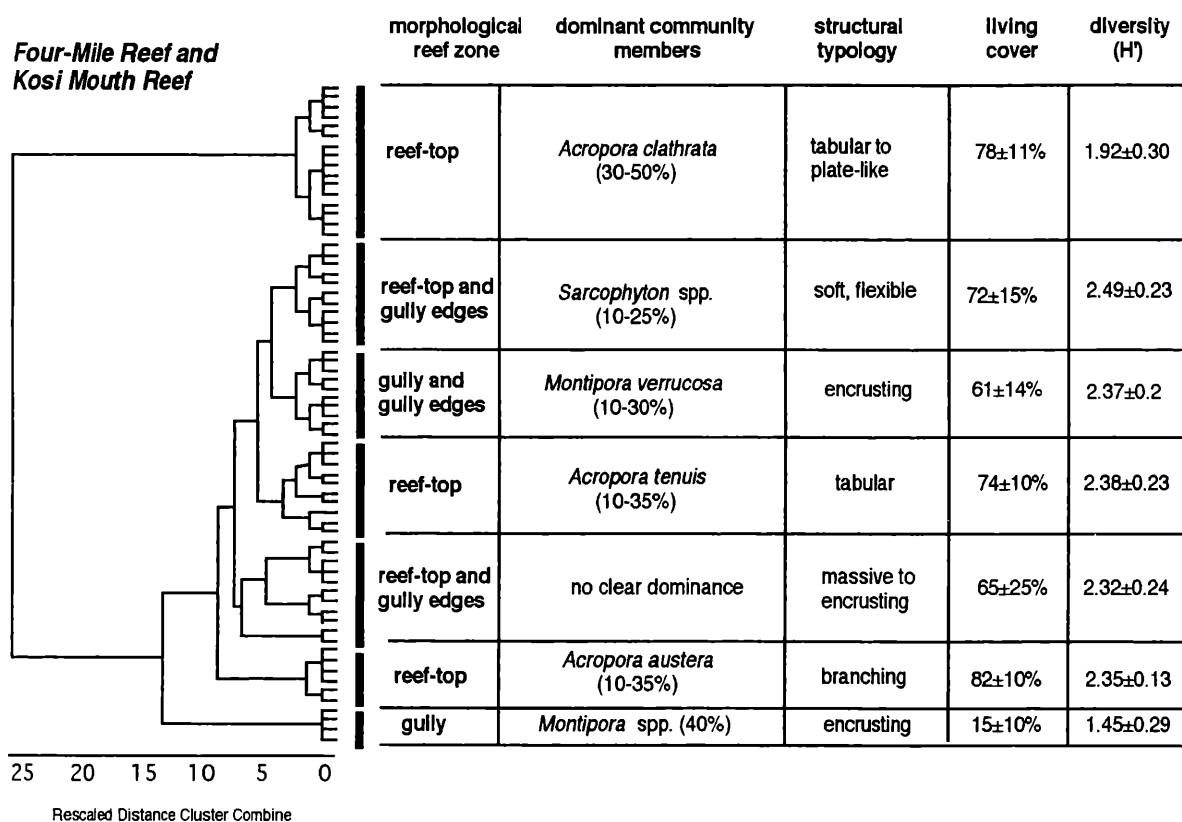


Figure 4: Community differentiation on 4-Mile Reef and Kosi Mouth Reef. Due to the small number of transects taken on Kosi Mouth Reef (N = 6) and the geomorphological similarity of the two reefs, data were pooled. Agglomerative, hierarchical cluster analysis using Ward's method of linkage and Squared Euclidian Distance. The space occupation of dominant community members within the community is given as proportional coverage. Living cover gives proportional substratum cover of the entire community. Diversity is measured by the Shannon-Wiener (H') diversity-index.

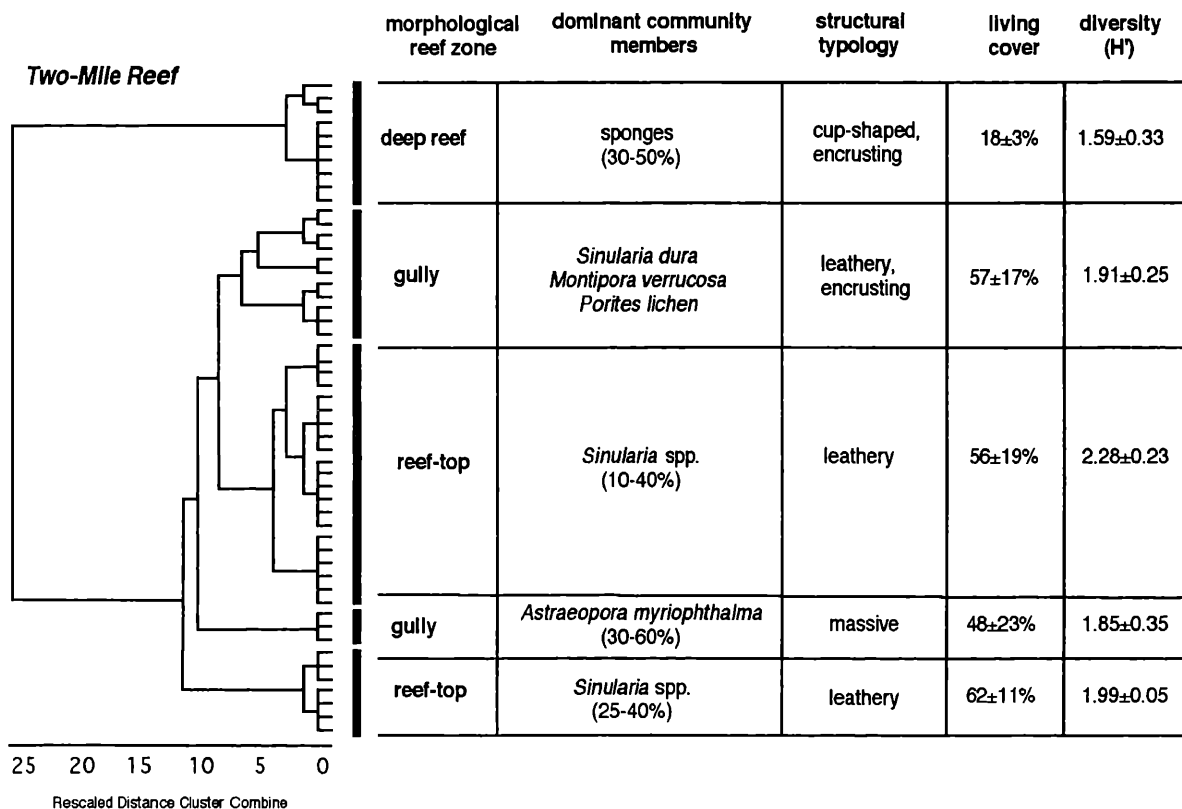


Figure 5: Community differentiation on 2-Mile Reef.

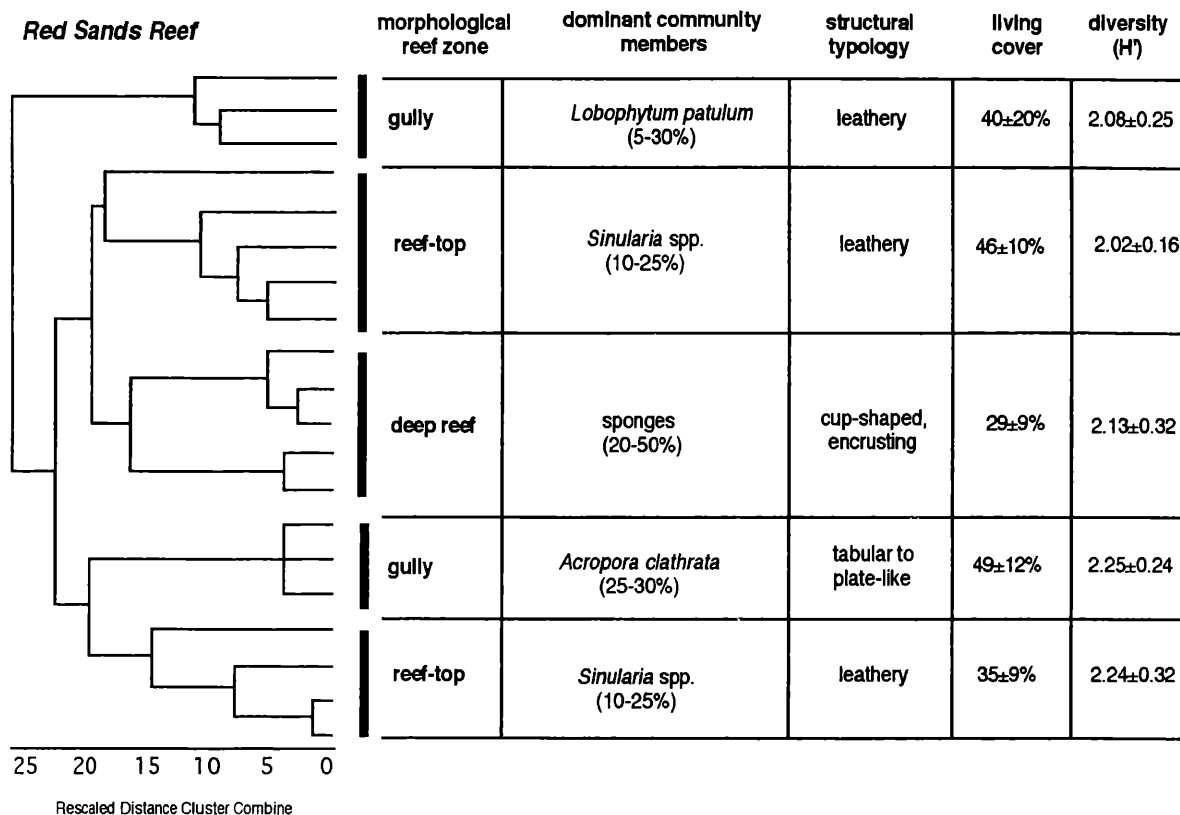


Figure 6: Community differentiation on Red Sands Reef.

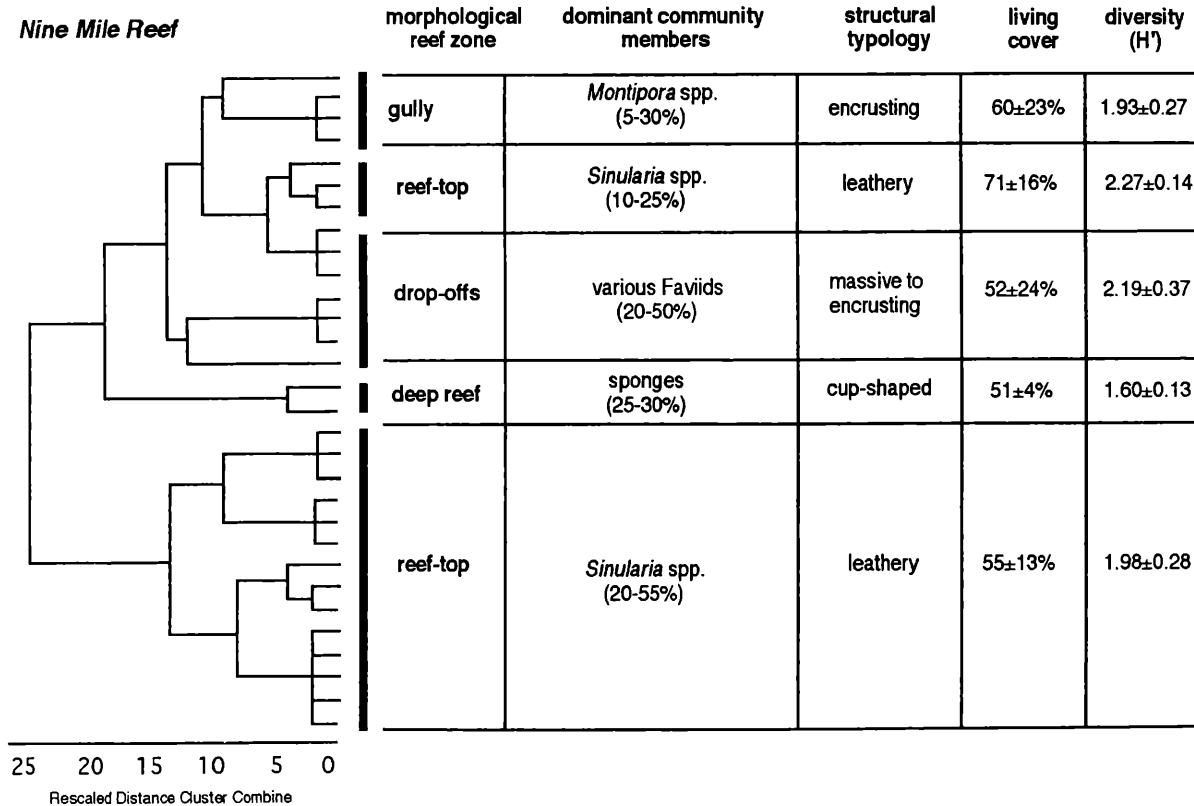


Figure 7: Community differentiation on 9-Mile Reef.

Locality	Total break in %	Reef zone with most breakage in %	Dominant species in that community	Most frequently broken species
2-Mile Reef	2	medium depth (18–25 m): 75	<i>Lobophyton</i> spp.	<i>Acropora</i> spp.
9-Mile Reef	0.3	reef tops (8–10 m): 90	<i>Sinularia gyrosa</i>	<i>Pocillopora verrucosa</i>
Red Sands Reef	0	–	–	–
Kosi Mouth Reef	3	medium depth (18–14 m): 100	<i>Acropora tenuis</i>	<i>Acropora tenuis</i>
4 Mile Reef	10	medium depth (18–24 m): 100	<i>Acropora austera</i>	<i>Acropora austera</i>

Table 2: Characterization of breakage in different coral communities.

dominated by porifera (Fig. 5, 6). The dominant growth forms on these reefs was leathery in alcyonacea (*Lobophyton*, *Sinularia*) massive in scleractinia (Faviidae, Poritidae) with only few branching or tabular scleractinia, the majority of which occurred between 18 and 24 m depth. On shallow reefs, such as 9-Mile Reef (6–18 m), a differentiation into gully, reef-top and drop-off sub-communities was found (Fig. 7). On hard substrata in front of this reef, which extended beyond the reef structure into deeper water, a deep reef community was found, which was comparable to that observed on 2-Mile Reef and Red Sands Reef.

3.2. Quantitative damage assessment

Although quantitative damage assessment was undertaken to determine the amount of coral breakage and tissue damage inflicted by divers and boats, it did not yield good results. Due to the high wave action on all investigated reefs, broken parts of corals, which are the most common and easily visible signs of diver damage (ROGERS et al., 1988; RIEGL & VELIMIROV, 1991), were quickly washed away. They accumulated in a wide fringe of calcareous fragments around the reefs (RAMSEY & MASON, 1990). Due to the short period of time in which the fragments stayed in the area where they were broken, it was difficult to keep track of breakage quantitatively. A general count of all encountered broken fragments was not useful, as it would not have been possible to allocate the fragments to the coral community from which they were derived. The only possibility of quantitatively estimating breakage was by searching for signs of breakage on the corals remaining in situ. Frequency of breakage on branching and tabular *Acropora* could be easily assessed due to shape anomalies (missing branches, different mode of attachment to the substrate than in sexually produced fragments). This approach, however, did not allow to separate human from natural breakage. Breakage values in the *Acropora* dominated community on 4-Mile Reef were far higher than in the alcyonacea dominated communities on other reefs (2-Mile Reef, 9-Mile Reef, Fig. 8, Tab. 2).

Tissue damage was not important and always remained far below 5% of all colonies in a transect. Most tissue damage could be directly related to natural causes (preda-

tion, aggression, damage due to sedimentation). Also, no incidence of bleaching was observed. During the entire survey and subsequent 36-month research period, only one crown-of-thorns starfish (*Acanthaster planci*) was seen, which indicates a low density of this potentially harmful predator.

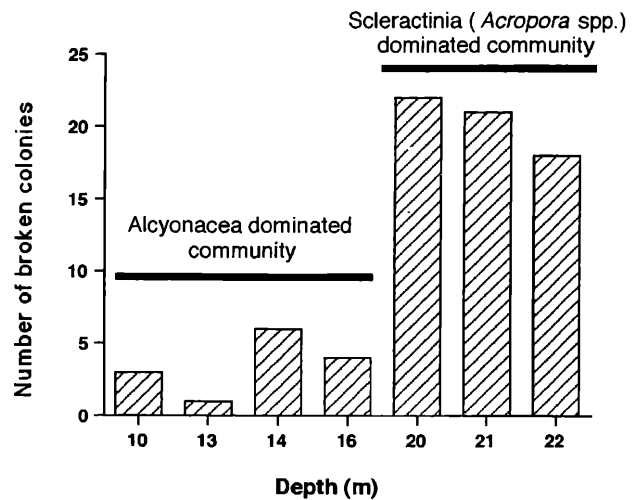


Figure 8: Frequency of broken colonies at different depths on 4-Mile Reef, 9-Mile Reef and 2-Mile Reef.

4. Discussion

While within-reef community analysis gave a clear picture about the ecological functioning of South African reefs (see also RIEGL et al., 1995; RIEGL, 1995; RIEGL & RIEGL, in press), small scale patterns were not particularly useful for management purposes. The areas covered by the sub-communities (gully and reef-top sub-communities), was too small to be used for zonation schemes, but the three major communities, which were largely substratum specific, formed big enough entities. In the following, we offer a model to characterize “type-communities”, which are believed to reflect the damage susceptibility, and therefore offer a tool for the introduction of coral-community specific zonation schemes. Additional to the direct counting approach, it was attempted to use the nature and species composition of the coral communities to predict their susceptibility to damage.

4.1. Type 1 Coral Community

This community was found on the flat, deep outcrops, such as 4-Mile Reef in the Central Reef Complex and Kosi Mouth Reef in the Northern Reef Complex (Fig. 3). It was dominated by either branching *Acropora austera* and *A. florida*, tabular *A. hyacinthus* and *A. latistella* or plate-like *A. clathrata*, which are susceptible to breakage due to their growth-form (LIDDLE, 1991; RIEGL & VELIMIROV, 1991; HAWKINS & ROBERTS, 1993). This is a very diverse, highly structured community (the most diverse encountered in South Africa). The maximum variety of growth-forms occur here, with a dominance of branching and tabular species. The highest breakage values on South African reefs were observed in this community type. While natural breakage may aid asexual reproduction (HIGHSMITH, 1982), breakage experiments (RIEGL & RIEGL, in press) indicated that most fragments caused by anthropogenic breakage did not survive.

This type of coral community is considered sensitive to breakage by careless divers and by anchoring. Repeated anchor dropping could reduce even initially large branching or tabular colonies to numerous small fragments with little chances of survival (RIEGL & VELIMIROV, 1991; RIEGL & RIEGL, in press; HAWKINS & ROBERTS, 1992, 1993). Also in other parts of the world, *Acropora*-dominated communities proved to be very susceptible to environmental changes, as could be associated with increased tourism. Major losses in *Acropora*-dominated habitats have been reported (JAAP et al., 1988; PORTER & MEIER, 1992). Therefore, the Type 1 Community is considered the most fragile coral community occurring in South Africa. Measures for its protection should include strict prohibition of anchoring on or near these reefs and a limit to maximum allowable dives per day. As this community type was primarily found on the deep, flat outcrops (4-Mile Reef, Kosi Mouth Reef, 18–24 m), it can be protected by according these reefs a special protection status (Fig. 9a).

4.2. Type 2 Coral Community

This community was the most common on reefs in Maputaland and covered most of the hard substrata in less than 18 m depth. It was found in all shallow areas in the Southern Reef Complex (Leadsman Shoal, Red Sands Reef), the Central Reef Complex (2-Mile Reef, 9-Mile Reef) and the Northern Reef Complex (Fig. 9). Within this community type, further differentiations were caused by differential sedimentation levels (RIEGL et al., 1995; RIEGL, 1995). The sub-communities occurring within this community type could be grouped for the damage-risk analysis as the growth form of the dominant corals was the same. Typical of this community type were alcyonacea (*Lobophytum*, *Sinularia*, *Sarcophyton*) and massive, hemispherical scleractinia (Faviidae, Poritidae). The growth form of these corals did not make them susceptible to breakage.

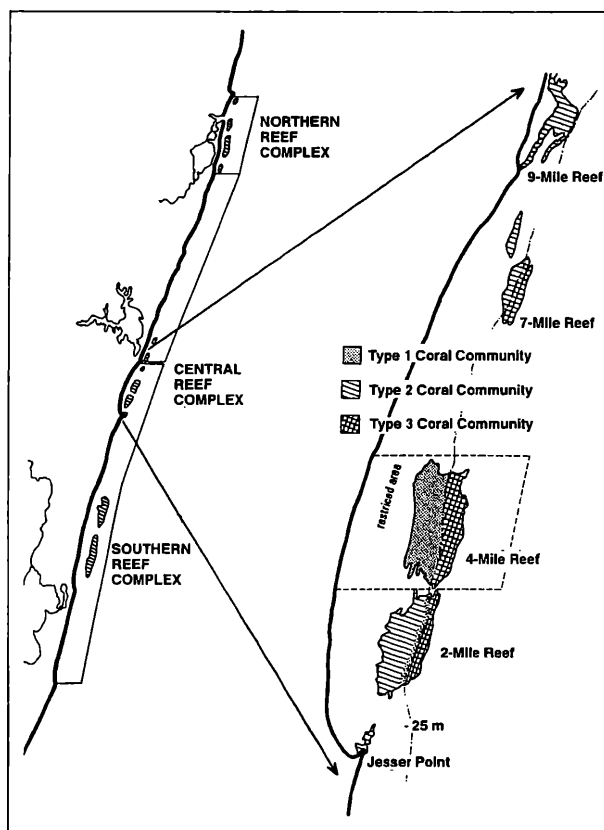


Figure 9: Distribution of “damage-susceptibility-type-communities” in the Central Reef Complex, South Africa. Zoning options based on this analysis are indicated.

The major dangers to the corals of these communities were tissue lesions caused by contact with divers, or boat anchors. In scleractinia, these can become infected by bacteria or algae and lead to dieback or outbreaks of black or white band disease (ANTONIUS, 1985) which can potentially damage wide area. The relatively low surface cover by corals, however, results in more free space between corals than in the “Type 1 Coral Community” One might therefore speculate that contagious diseases, such as “shut-down-reaction” (ANTONIUS, 1985), will spread slower and less efficiently in the “Type 2 Coral Community” This community appeared to be the least susceptible to damage and we therefore assume that no special conservation measures are necessary.

4.3. Type 3 Coral Community

In the cluster analyses this was the least clearly defined, as it appeared as a sub-community of the fossil-dune community. The low importance of corals and dominance of sponges, however, makes it a distinct community, rather than a sub-community of a coral-dominated system. It was only found on the deepest parts of the reefs in more than 25 m depth and was dominated by sponges (cup-sponges, *Ircinia* spp.) and sea-fans (*Acabaria* spp., *Homophyton* spp.). In this area, numerous unattached species of hard coral were found (*Cycloseris costulata*, *C. marginata*, *C. cyclolites*, *Diaseris distorta*), which are easy

to collect and could easily be decimated by poaching. Neither the sponges nor the gorgonians could be easily damaged by divers.

As this community grew under very low light conditions, at the lower edge of the depth-range of photosynthetic activity in most corals and sponges (WILKINSON, 1987; RIEGL & BRANCH, 1995), it can be assumed that growth and regeneration rates are slow and incurred damage persist for a long time.

5. Conclusion

Coral community analysis allowed to identify three community types on South African coral reefs, which could be ranked according to their susceptibility to damage. Damage-likelihood was estimated by quantitative observation and deduction from growth-form characteristics of dominant community members. The "Type 1 Coral Community", the most susceptible to damage, was dominated by branching and tabular corals (mainly *Acropora*). In this community the highest breakage-values were observed. The "Type 2 Coral Community", the least susceptible to damage, was dominated by leathery alcyonacea (mainly *Sinularia* and *Lobophytum*) and massive-growing scleractinia (Faviidae, Poritidae). The "Type 3 Coral Community" was dominated by sponges. Type 2 and Type 3 Coral Communities were considered robust, without the need for special protection. As these communities are largely typical of individual reef-types ("Type 1 Coral Community" on flat outcrops between 18 and 24 m. "Type 2" on fossil dunes between 8 and 24 m. "Type 3 Coral Community" on hard substrata between 24 and 34 m), this evaluation can be used to assign special protection to reefs with "fragile" communities.

Acknowledgements

This paper is a result of Natal Parks Board/University of Cape Town Research project SM 6/1/14. Financial assistance by the Foundation for Research Development, the Department of National Education, the South African Association for Marine Biological Research is acknowledged gratefully. Logistic support was provided by the Natal Parks Board, the Oceanographic Research Institute and W. and S. Prinsloo. Critical remarks by B. Hatcher and W.E. Piller greatly improved the quality of the manuscript.

6. References

- ANTONIUS, A., 1985. Coral diseases in the Indo-Pacific: a first record. — P.S.Z.N.I. Marine Ecology, **6**:197–218, Berlin.
- ANTONIUS, A., 1985. Coral mortality in reefs: a problem for science and management. — Proc. 3rd Int. Coral Reef Symp., Miami :617–623, Miami.
- BAK, R.P.M. & POVEL, G.D.E., 1988. Ecological structure in a range of Indonesian fore-reef slope coral communities. — Proc. 6th Int. Coral Reef Symp., Australia, **3**:191–196, Townsville.
- BRADBURY, R.H., LOYA, Y., REICHEL, R.E. & WILLIAMS, W.T., 1986. Patterns in the structural typology on two coral reefs of the central Great Barrier Reef. — Coral Reefs, **4**:161–167, Berlin.
- DIGBY, P.E. & KEMPTON, R.A., 1987. Multivariate analysis of ecological communities. — 206 pp., London (Chapman & Hall).
- HAWKINS, J.P. & ROBERTS, C.M., 1992. Effects of recreational SCUBA diving on fore-reef slope communities of coral reefs. — Biol. Conserv., **62**:171–178, Amsterdam.
- HAWKINS, J.P. & ROBERTS, C.M., 1993. Effects of recreational diving on coral reefs. Trampling of reef-flat communities. — J. Appl. Ecol., **30**:25–30, Oxford.
- HIGHSMITH, R.C., 1982. Reproduction by fragmentation in corals. — Mar. Ecol. Progr. Ser., **8**:37–52, Oxford.
- JAAP, W.C., HALAS, J.C. & MULLER, R.C., 1988. Community dynamics of stony corals (Milleporina and Scleractinia) at Key Largo National Marine Sanctuary, Florida, during 1981–1986. — Proc. 6th Int. Coral Reef Symp. Australia, **2**:237–243, Townsville.
- KENCHINGTON, R.A., 1988. Managing reefs and inter-reefal environments and resources for sustained exploitative, extractive and recreational uses. — Proc. 6th Int. Coral Reef Symp., Australia, **1**:81–87, Townsville.
- LIDDLE, M.J., 1991. Recreation ecology: effects of trampling on plants and corals. — Trends Ecol. Evol., **6**(1):13–17.
- LOYA, Y., 1978. Plotless and transect methods. — [in:] STODDART, D.R. & JOHANNES, R.E. (eds.). Coral reefs – research methods. — UNESCO Paris, 581–591, Paris.
- PIELOU, E.C., 1975. Ecological diversity. — 165 pp., New York (John Wiley & Sons).
- PORTER, J.W. & MEIER, O.W., 1992. Quantification of loss and change in Floridian reef coral populations. — Amer. Zool., **32**:625–640, New York.
- RAMSEY, P.J. & MASON, T.R., 1990. Development of a type zoning model for Zululand coral reefs, Sodwana Bay, South Africa. — J. Coastal Res., **6**(4):829–852, Ft. Lauderdale.
- RIEGL, B. & VELIMIROV, B., 1991. How many damaged corals in Red Sea reef systems? A quantitative survey. — Hydrobiologia, **216/217**:249–256, Dordrecht.
- RIEGL, B., 1995. Effects of sand deposition on scleractinian and alcyonacean corals. — Mar. Biol., **121**(3):517–526, Berlin.
- RIEGL, B., SCHLEYER, M.H., COOK, P.J. & BRANCH, G.M., 1995. Structure of Africa's southernmost coral communities. — Bull. Mar. Sci. **56**(2):676–691, Miami.
- RIEGL, B., & BRANCH, G.M., 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. — J. exp. Mar. Biol. Ecol., **186**(2):259–275, Amsterdam.

- RIEGL, B., & RIEGL, A., in press. How episodic coral breakage can determine community structure: a South African coral reef example. — Proc. 29th European Marine Biology Symp., Vienna 1994.
- ROGERS, C.S., McLAIN, L. & ZULLO, E., 1988. Damage to coral reefs in Virgin Island National Park and Biosphere Reserve from recreational activities. — Proc. 6th Int. Coral Reef Symposium, Australia, 2:405–410, Townsville.
- SYBESMA, J., 1988. Marine resource protection versus marine tourism in Curacao: a management problem?. — Proc. 6th Int. Coral Reef Symp., Australia, 2:411–414, Townsville.
- WILKINSON, C.R., 1987. Productivity and abundance of large sponge populations on Flinders Reef flats, Coral Sea. — Coral Reefs, 5:183–188, Berlin.