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Effects of sand deposition on scleractinian and alcyonacean corals

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Abstract The ability of corals to withstand experimental sand deposition was investigated for two experimental periods (17 h and 6 wk) in eight scleractinia (*Favia fava*, *Favites pentagona*, *Platygyra daedalea*, *Gyrosmlia interrupta*, *Galaxea fascicularis*, *Cyphastrea chalcidicum*, *Favites abdita*, *Goniopora djiboutensis*) and five alcyonacea (*Lobophytum depressum*, *L. venustum*, *Sinularia dura*, *S. leptoclados*, *Sarcophyton glaucum*) collected in 1992 from Natal, South Africa. Scleractinia were active sediment shedders, alcyonacea passive, relying on water motion and gravity. Short-term sand clearing efficiency was primarily dependent on corallum shape. Sand application led to hydrostatic inflation of polyps in scleractinia and the entire colony in alcyonacea as well as to increased tentacular action in the scleractinian *Gyrosmlia interrupta*. Under continuous sand application, inflation remained while other activities, such as tentacular motion, ceased completely. In scleractinia and alcyonacea, tissue necroses appeared after the first week of continuous sand application. Death of entire colonies and partial bleaching of continually sand-covered areas were observed in alcyonacea only. Different grain sizes of sand had no influence on clearing reaction or efficiencies.

Introduction

It is known that sedimentation is an important factor controlling coral growth and thus reef development (Hubbard

1986; Rogers 1990). Sedimentation can interfere with corals directly by influencing growth rates (Hubbard and Scaturro 1985), metabolism (Dallmeyer et al. 1982; Abdel-Salam and Porter 1988; Edmunds and Davies 1989) and fecundity (Tomascik and Sander 1987), as well as by causing histopathological damage (Peters and Pilson 1985); it can also interfere indirectly, at the population level, by either reducing or facilitating larval settlement (Rogers et al. 1984; Te 1992; Wittenberg and Hunte 1992).

Corals have developed various defence mechanisms to sedimentation. Scleractinia can reject sediment to a certain degree by means of morphological adaptations and by directed behaviour (Hubbard and Pocock 1972; Bak and Elgershuizen 1976; Lasker 1980; Stafford-Smith and Ormond 1992; Stafford-Smith 1993). Alcyonacea have, however, been neglected in experimental studies, and only circumstantial evidence exists of their ability to withstand sedimentation (Schuhmacher 1975; Dinesen 1983; Dai 1991), which has nevertheless been used to claim their better ability to survive sedimented conditions (Schuhmacher 1975; van Katwijk et al. 1993).

In the light of other studies (Dai 1991; Riegl et al. 1995) this appears unlikely. It has been postulated that resuspended and transported sand disadvantages alcyonacea rather than scleractinia (Dai 1991, 1993; Riegl et al. 1995). Therefore, it is important to gain experimental insight as to whether scleractinia and alcyonacea react differently to sedimentation.

It was decided to subject corals to artificial conditions for testing their reactions to sand deposition without the interference of natural factors such as inclination of the substratum and water motion. These can lead to "passive" cleaning of the corals and can mask possible taxon-specific reactions (Hodgson 1990).

The aims of the present study were: (1) to establish if there are differences in the mechanisms employed by scleractinia and alcyonacea in removing artificially deposited sand; (2) to evaluate differences in the corals' reaction to short-term and continuous sand application; (3) to gain more insight into the effects of sedimentation on coral communities.

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Methods

All experiments were conducted in the laboratory, as strictly regulated conditions were desired. The experimental corals were split into two groups. Nine species were used for the entire experimental period, as enough replicate colonies ($n=8$) were available for each of these species (the scleractinia *Favia fava*, *Favites pentagona*, *Platygyra daedalea*, *Gyrosmlia interrupta* and the alcyonacea *Lobophytum depressum*, *Lobophytum venustum*, *Sinularia dura*, *Sinularia leptocladus*, *Sarcophyton glaucum*). A second group of scleractinia (*Galaxea fascicularis*, *Cyphastrea chalcidicum*, *Favites abdita*, *Goniopora djiboutensis*) was also used in parts of the experiment. However, only single specimens of each species were available. While this severe limitation precluded any statements on species-specific responses, the data could be used as additional data-points for certain growth-form types.

All corals were collected in 1992 in northern Natal, South Africa (Fig. 1) and transported by truck in a 500-litre container with seawater slightly supersaturated with medical oxygen to Durban (transit time ca. 5 h). Corals were allowed to acclimate for 4 wk prior to the beginning of the experiment.

They were kept in flow-through tanks with well-point seawater at light levels roughly comparable to their natural habitat (50% of surface irradiation, measured with a LI-COR 185 quantum radiometer/photometer fitted alternately with an above-water and underwater probe. Maximum irradiance in the laboratory was 250 W m^{-2}).

All species were common, and previous community analysis (Riegl et al. 1995) had identified them as indicators in South Africa for either high sedimentation (*Favia fava*, *Favites pentagona*, *Lobophytum depressum*, *Sinularia dura*) or low sedimentation envi-

ronments (*L. venustum*, *S. leptocladus*), with three species (*Gyrosmlia interrupta*, *Platygyra daedalea*, *Sarcophyton glaucum*) not showing any habitat preferences.

Corals were fed twice a week with rotifers and brine-shrimp nauplii (Peters and Pilson 1985) to avoid starvation. Under the experimental light conditions all corals were autotrophic as shown by respirometry measurements (unpublished data).

Sedimentation

Information about meaningful sediment sizes for the experiments was obtained by comparing the grain-size distribution in sediment collected from the reef and the sediment collected in sediment traps in moderate surge (water speed varying from 0.07 to 0.4 m s^{-1}). Sediment traps were open topped tubes of 11-cm bore, each of which projected by 15 cm from a rectangular vinyl container ($20 \times 10 \text{ cm}$) which served to accumulate sediments settling in the tube. Grain size analysis was performed using a mechanical shaker and nested sieves at 1 Phi interval (Dyer 1986).

The short-term sand deposition experiment

Sediment used was locally collected biogenic carbonate sand. Grain sizes were very fine sand ($< 0.125 \text{ mm}$), fine sand (0.125 to 0.25 mm) and coarse sand ($> 0.5 \text{ mm}$). Sand was applied to the corals through a funnel (to minimize undesired runoff) at 200 mg cm^{-2} , corresponding to maximum anticipated naturally occurring sedimentation levels on South African reefs. In order to estimate clearing rate (expressed in g min^{-1}) and clearance efficiency (expressed as proportion of sediment removed), rejected sand was collected in trays after 10, 100 and 1000 min, filtered through a sieve of 0.04-mm mesh, air-dried and weighed. After 1000 min all sediment remaining on the corals was removed and weighed.

A 8-h interval between experimental runs was kept. When trays were collected, the condition of the corals was noted, e.g. whether polyps were inflated, tentacles extended, mucous sheets apparent, or mesenterial filaments extruded. The behaviour of control individuals was observed simultaneously.

The continuous sand deposition experiment

Three to five specimens of each species were placed in adjacent tanks, one tank being used for control conditions and one for sedimented conditions. Care was taken to avoid physical contact among the corals to prevent tissue damage due to aggressive reactions, which could have distorted results. A constant flow of sand (fine carbonate sand, $< 0.25 \text{ mm}$) onto the experimental corals was maintained for 6 wk by means of a recirculatory system as illustrated in Fig. 2. Sand cover on the corals was maintained at roughly 200 mg cm^{-2} .

Description of colony morphology

As all scleractinia had a massive, more or less rounded growth form, it was necessary to describe their morphology in standardized terms. Degree of sphericity, i.e., how close to a hemisphere, was expressed by a height/diameter ratio, similar to that formulated by Lasker (1980):

$$I_s = \text{maximal height/maximal diameter}, \quad (1)$$

which is 0.5 for a hemisphere.

A meandriation index, as formulated by Veron et al. (1977) was used to describe the degree of fusion of individual corallites into longer series (also referred to as "valleys") in the "brain corals" *Platygyra daedalea* and *Gyrosmlia interrupta*.

$$I_m = \text{number of centres/numbers of valleys}. \quad (2)$$

The higher the value, the longer the valleys. Monocentric species have an I_m of 1.

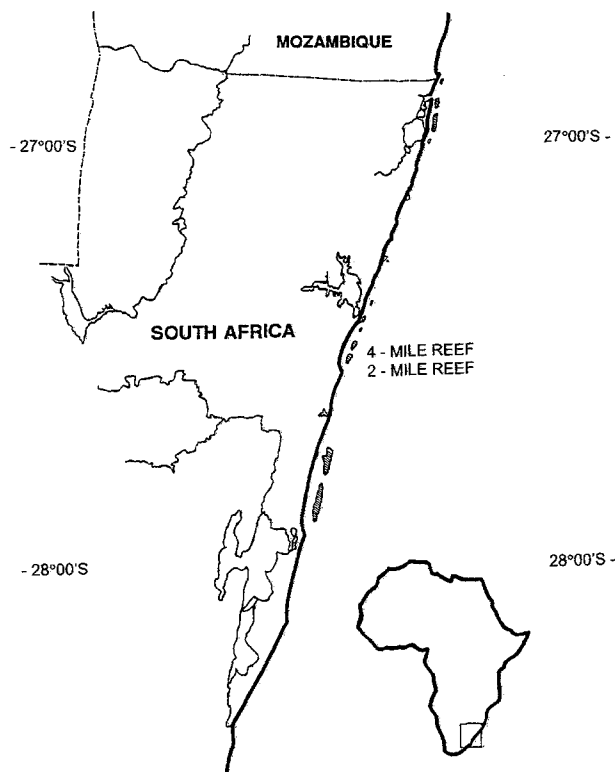


Fig. 1 Reef system off the Maputaland coast in northern Natal, South Africa. Coral communities grow on fossilized dunes parallel to the coast. Reefs from which corals were collected indicated by name

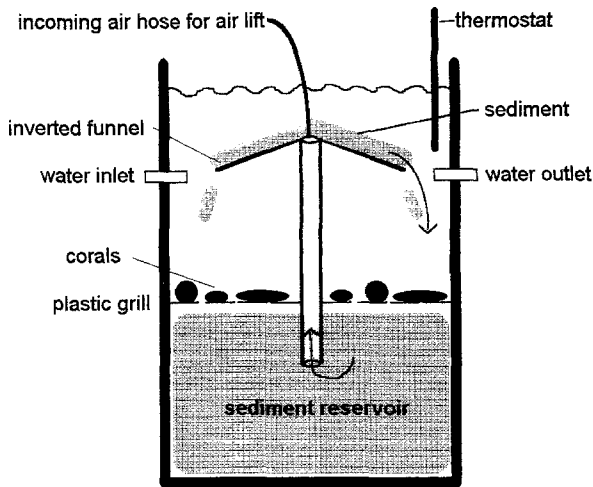


Fig. 2 Apparatus used to create a permanent high sedimentation environment. Corals were placed on a plastic grid which did not allow accumulation of sand other than on the corals themselves. Sediment was sucked up inside the central column by means of an air lift and distributed evenly using an inverted funnel, perforated at regular intervals, and by a circular current in the basin. Water supply was flow-through, total water replacement in the aquarium once every hour

These indices were impractical for alcyonacea, which had either a completely flat surface (*Lobophytum depressum*, *Sinularia dura*) or a very complicated surface, with numerous ridges or finger like projections (*L. venustum*, *S. leptocladus*).

Chlorophyll analysis

This was only performed on alcyonacea. Chlorophyll was extracted from tissue blocks of 5 mm³ taken from different parts of the experimental colonies using hot (75 °C) methanol (Nusch 1980) in near dark conditions. No correction for phaeopigments was performed as: (1) most zooxanthellae were expected to be in a non-degraded state with little phaeopigment present; (2) negligible degradation of extracted chlorophylls was anticipated due to extraction in near darkness and spectrophotometric analysis within 20 min of extraction; and (3) acidification of methanol can be problematic (Nusch 1980). Optical densities were read at 664, 647 and 630 nm with correction for turbidity and coloured materials at 750 nm (Wetzel and Likens 1991) and converted to concentration of total chlorophylls using the formula derived by Branch and Branch (1980).

Results

Natural sedimentation level and grain sizes

Maximum measured sedimentation levels in high surge (water speed >0.7 m s⁻¹) were 107 mg cm⁻²h⁻¹ in sandy gullies and 43 mg cm⁻²h⁻¹ on elevated parts of the reefs. This was due to resuspended resident sediment, which was deposited again in the immediate vicinity. Levels of suspended sediment 40 cm above ground were 389 mg l⁻¹ in sandy gullies and 112 mg l⁻¹ on elevated reef parts.

The grain size distribution of sediment on gully floors and of the sediment collected in sediment traps in moderate surge conditions (0.07 to 0.41 m s⁻¹) are given in

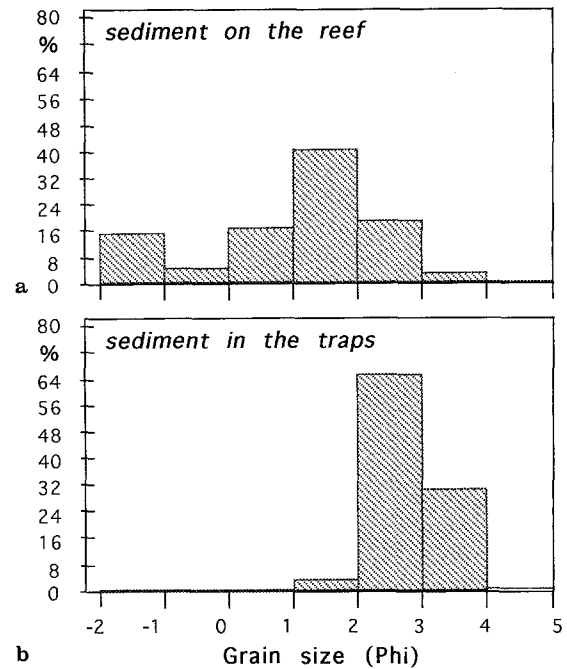


Fig. 3 Grain size distribution of **a** sediment collected on the reef and **b** sediment collected in sediment traps. Phi = $-\log_2$ (mm). -2 to -1: granules; -1 to 0: very coarse sand; 0 to 1: coarse sand; 1 to 2: medium sand; 2 to 3: fine sand; 3 to 4: very fine sand; 4 to 5: coarse silt (Dyer 1986)

Fig. 3. The most important fractions were very fine sand (diameter <0.125 mm, Phi between 3 and 4) and fine sand (diameter <0.25 mm, Phi between 2 and 3; Dyer 1986).

Reactions to experimental sand application

For the experiments, locally collected carbonate sand of the two most important grain sizes obtained in the sediment measurements were used. Very fine sand (<0.125 mm) and fine sand (0.125 to 0.25 mm) and, for comparative reasons, also coarse sand (>0.5 mm).

Clearing rate, efficiency and the influence of colony morphology

Major differences existed in the clearing rates and efficiencies of scleractinia and alcyonacea (Table 1, Figs. 4 and 5). This was supported by observations in the field. With the exception of *Sarcophyton glaucum*, alcyonacea were less efficient than scleractinia (Figs. 4, 5).

Colony shape was important. In hemispherical scleractinia (sphericity index 0.4 to 0.5) significant differences existed in clearing rates after 10, 100 and 1000 min (ANOVA, $F=4.28$, $p<0.001$), being highest in the first 10 min. In flat scleractinia (sphericity <0.4) no differences were found (ANOVA, $F=0.92$, $p>0.05$). Significantly more sand was rejected by hemispherical scleractinia in

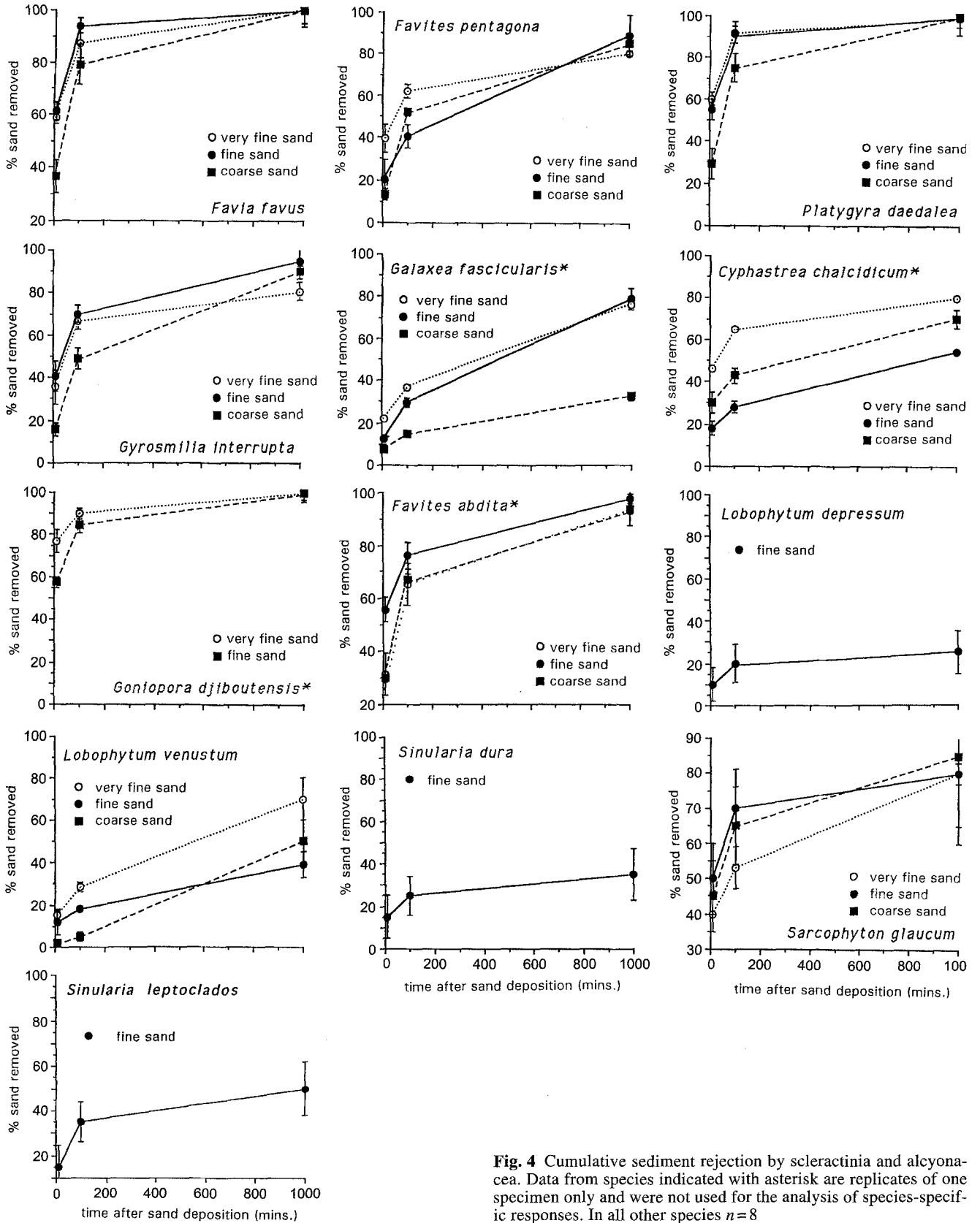


Fig. 4 Cumulative sediment rejection by scleractinia and alcyonacea. Data from species indicated with asterisk are replicates of one specimen only and were not used for the analysis of species-specific responses. In all other species $n=8$

Fig. 5 Sand shedding efficiency of the experimental species within a 1000-min period. Values are proportion of applied sand cleared by the corals. *Lobophytum depressum*, *Sinularia dura*, and *S. leptoclados* were only tested with one single grain size sand. Data from species indicated with asterisk are from one specimen only

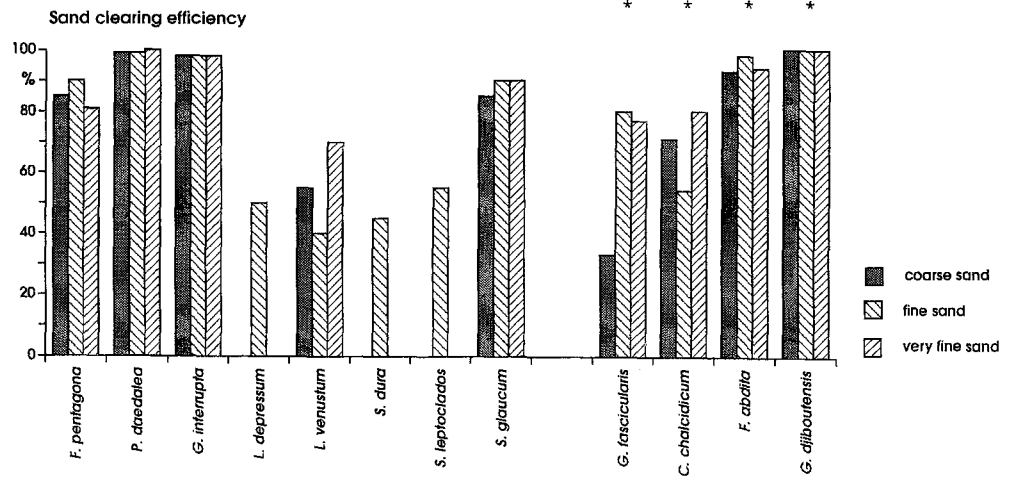


Table 1 Characterization of corals tested in experiments. Data from species indicated with asterisk are from one specimen only, in all other species $n=8$. (na not applicable; L large, >8 mm; M medium, 4 to 8 mm; S small, <4 mm)

Species	Calyx arrangement	Meandriation index	Sphericity index	Polyp size	No. of polyps per 3 cm ²	Clearance rates (g min ⁻¹) ± SD		
						Very fine sand	Fine sand	Coarse sand
<i>Favia fava</i>	Plocoid	1	0.3–0.5	L	6– 8	0.04 ± 0.02	0.05 ± 0.01	0.07 ± 0.03
<i>Favites pentagona</i>	Plocoid	1	0.2–0.5	M	22– 24	0.04 ± 0.01	0.03 ± 0.01	0.07 ± 0.01
<i>Platygyra daedalea</i>	Plocoid	3.3–6.2	0.3–0.5	M	29– 35	0.05 ± 0.02	0.05 ± 0.01	0.08 ± 0.02
<i>Gyrosmlia interrupta</i>	Plocoid	3.8–5.1	0.3–0.6	M	7– 10	0.06 ± 0.02	0.05 ± 0.01	0.06 ± 0.02
<i>Lobophytum venustum</i>	na	1	na	S	110–120	0.02 ± 0.01	0.02 ± 0.01	0.03 ± 0.01
<i>Sarcophyton glaucum</i>	na	1	na	S	60– 70	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.01
<i>Galaxea fascicularis</i> *	Phaceloid	1	0.39	M	17	0.02 ± 0.01	0.03 ± 0.01	0.02 ± 0.01
<i>Cyphastrea chalcidicum</i> *	Plocoid	1	0.39	S	170	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.01
<i>Goniopora djiboutensis</i> *	Plocoid	1	0.33	S	83	0.02 ± 0.01	–	0.05 ± 0.02
<i>Favites abdita</i> *	Plocoid	1	0.42	L	4	0.05 ± 0.03	0.03 ± 0.02	0.06 ± 0.02

the first 10 min than in flatter ones (sphericity index less than 0.4, t -test, $t=-4.01$, $p<0.01$). This was mostly due to runoff. However, over the entire 1000-min period no differences were found in overall clearing success between the two shape groups ($t=-0.56$, $p>0.05$ with very fine sand; $t=-1.15$, $p>0.05$ with fine sand; $t=-0.03$, $p>0.05$ with coarse sand) and no correlation existed between sphericity and either clearing rate or efficiency ($r=0.53$, $p>0.05$ with very fine sand; $r=0.30$, $p>0.05$ with fine sand; $r=0.37$, $p>0.05$ with coarse sand; Table 1) indicating the importance of other morphological and behavioural factors.

All scleractinia cleared away over 50% of the sand within 1000 min.

Alcyonacea showed much less activity and success in rejecting sand than the scleractinia. Passive runoff rates were low due to flat growth forms, except in small specimens of *Sarcophyton glaucum* (around 5 cm in length), which were distorted under the weight of the sand. This was not the case in large specimens (around 20 cm length) on which sand remained.

Runoff and concentration of sand in certain areas was enhanced by the radially arranged ridges in *Lobophytum venustum* and *Sinularia dura* and the finger-like projec-

tions in *S. leptoclados*. None of the alcyonacea showed any polyp-activity, but inflation of the colonies by as much as 30% of their resting volume was observed.

The importance of calyx size and the degree of meandriation in scleractinia was unclear. A linear relationship between calyx size and clearing rate was obtained in plocoid corals (*Galaxea fascicularis*, *Cyphastrea chalcidicum*, *Favia fava*, *Favites pentagona*, *Goniopora djiboutensis*, *Hydnophora microconos*) only with very fine sand or when the reactions to all sand sizes were averaged (Fig. 6). The situation was similar with degree of meandriation, which only correlated with clearing rate when fine sand was used or the clearing rates were averaged between the sand size classes (Fig. 7).

No correlation was found between number of calices per surface area unit and clearing rate ($r=-0.44$, $p>0.05$ with very fine sand, $r=-0.54$, $p>0.05$ with fine sand; $r=-0.49$, $p>0.05$ with coarse sand).

There were no differences in clearing rates between plocoid and meandroid species (*Favia fava*, *Favites pentagona*, *Favites abdita*, *Cyphastrea chalcidicum* versus *Platygyra daedalea*, *Gyrosmlia interrupta*: $t=-2.2$, $p>0.05$ with very fine sand; $t=-1.91$, $p>0.05$ with fine sand; $t=-1.89$, $p>0.05$ with coarse sand).

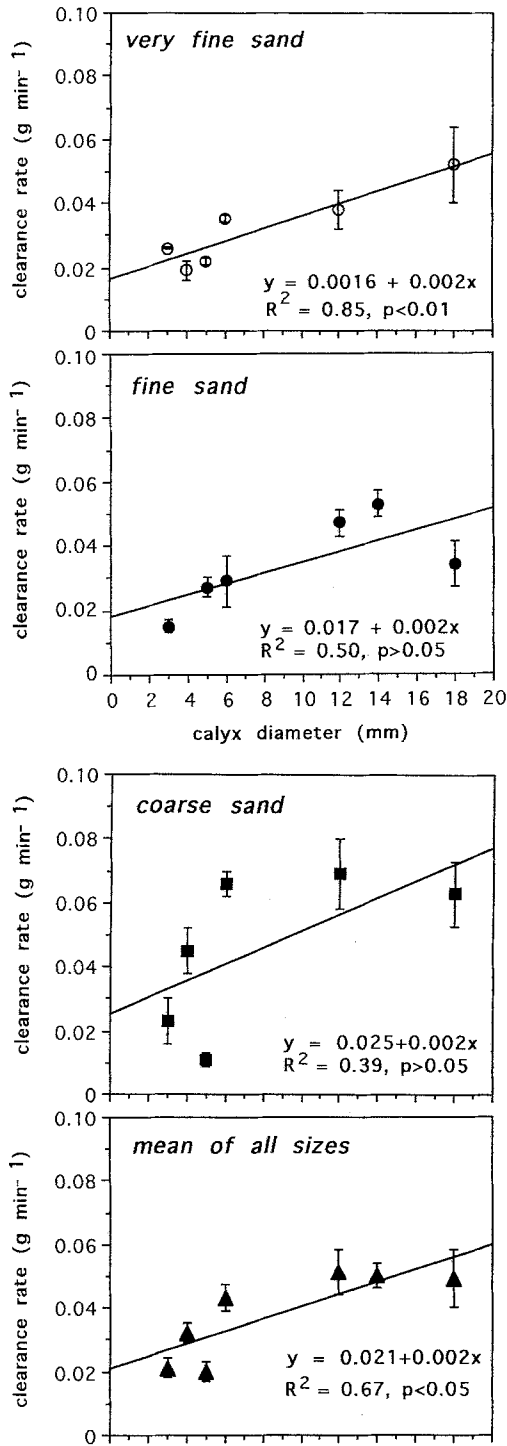


Fig. 6 Relationship between calyx diameter and clearing rate in the plocoid species (see Table 1)

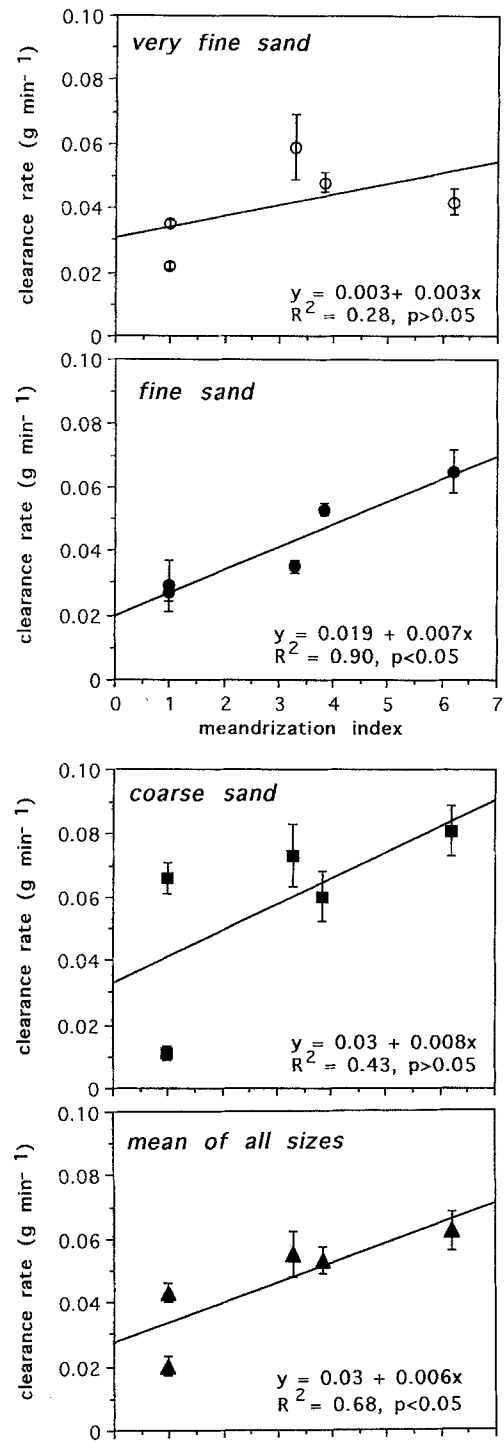


Fig. 7 Relationship between meandrization index and clearing rate in the meandroid species (see Table 1)

Sand application led to hydrostatic inflation of polyps in scleractinia, or of the entire corallum in alcyonacea. This enhanced runoff, especially from hemispherical scleractinia and from the sloping edges of alcyonacea. *Favia fava* and *Favites pentagona* used mainly inflated polyps to reject sand. On flat coralla of *Favia fava*, *Favites pentagona*, *Hydnophora microconos* and *Platygyra daedalea*,

differential inflation of polyps in specific areas was used to shift sand. Removal of sand led to eventual polyp-deflation within 30 min. Tentacular action was observed in *Gyrosmlia interrupta*. *Platygyra daedalea* used inflated polyps and ciliar activity was inferred, but could not be proven, by the way sand moved along the valleys of fused corallites.

Effect of different grain sizes

There were no significant differences in clearing efficiency after 10, 100 and 1000 min, total clearing efficiency, and clearing rates between the three types of sand used (ANOVAs, $F=2.554$, $p=0.09$ after 10 min; $F=0.773$, $p=0.47$ after 100 min; $F=0.125$, $p=0.88$ after 1000 min; $F=1.19$, $p=0.32$ for clearing rate, $F=0.373$, $p=0.69$ for clearing efficiency).

Reactions to continuous sand application

Levels of activity

In *Favia fавus*, *Favites pentagona* and *Platygyra daedalea*, contact with sand led to inflation of polyps. Continued cover resulted in the extrusion of mesenterial filaments. After 1 wk of continuous sand cover many of the polyps were fully extended with inflated peristome. This behaviour continued throughout the entire experimental period. *Gyrosmlia interrupta* retracted tentacles, which during short-term sand application were active in removing sand. Reactions of scleractinia are summarized in Table 2.

Alcyonacea, except *Lobophytum depressum*, retracted all polyps with the onset of sand application and most colonies inflated. Specimens which suffered tissue damage remained constantly inflated, while other specimens showed no consistent pattern. Maximum inflation led to about 30% volume increase compared to control conditions. Some *Sarcophyton glaucum* colonies became limp and deflated at times. This aided to clear off sand. In these specimens, inflation alternated with deflation. Behavioural reactions of alcyonacea are summarized in Table 2.

Tissue necroses

These were defined as macroscopically visible areas in which body wall tissue had retreated or was in the process of retreating, and the lighter subepidermal cell-layers were clearly visible.

In scleractinia, tissue necroses appeared after 15 d. In *Favia fавus*, *Favites pentagona* and *Platygyra daedalea* necroses formed predominantly on the colony periphery, in *Gyrosmlia interrupta* in the colony centre. Over the next 2 wk, necroses healed on one *Favia fавus*. On other specimens, tissue necroses approximately doubled their size. In all species, tissues appeared very thin and early necroses most frequently appeared on the tops of the thecae. After 4 wk, most tissue necroses were stable. Only one *Favites pentagona* lost two thirds of its tissue. In all other corals, only individual polyps or series of up to three polyps were lost. Reactions of scleractinia to continuous sand application are summarized in Table 2.

In alcyonacea, tissue necroses were present in *Lobophytum depressum* prior to the experiment and increased in size within 3 d. New tissue necroses formed on one *L. venustum* and *Sinularia leptoclados*. In *Sarcophyton glaucum*, tissue necroses appeared on the hood and the stem. After 14 d one *S. glaucum* and one *L. depressum* died. Necroses continued to form and enlarge in all alcyonacea. These were mostly round pits, which kept enlarging towards their periphery. Most necroses were located in flat parts. The most serious necroses were found on *S. glaucum* and *L. depressum*. However, while *S. glaucum* tended to die very quickly after the onset of necroses, *L. depressum* continued to live, despite serious tissue damage. Reactions of alcyonacea to continuous sand application are summarized in Table 2.

Bleaching

Serious bleaching was observed after 5 wk on the alcyonacea *Lobophytum venustum* and *Sinularia dura*. Only the central flat part of the colony was affected. The ridges, which at no stage were completely covered by sand, did not bleach.

Significant differences were found in the chlorophyll concentrations of bleached and non-bleached parts in two of the three species (Table 3). Of the scleractinia, only one specimen of *Favites pentagona* bleached shortly after the beginning of the experiment.

Table 2 Responses of scleractinia alcyonacea to long-term sedimentation during a 6-wk experimental period. Only responses observed for more than at least 1 wk at a time are noted

	Scleractinia				Alcyonacea				
	<i>Favia fавus</i>	<i>Favites pentagona</i>	<i>Platygyra daedalea</i>	<i>Gyrosmlia interrupta</i>	<i>Lobophytum depressum</i>	<i>L. venustum</i>	<i>Sinularia dura</i>	<i>S. leptoclados</i>	<i>Sarcophyton glaucum</i>
Hydrostatic inflation	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No
Tentacular activity	No	No	No	No	Partly	No	No	No	Partly
Increased mucus	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Congealed sediment	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No
Small necroses	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Large necroses	No	Yes	No	No	Yes	No	No	No	Yes
Death of colonies	No	No	No	No	Yes	No	No	No	Yes
Local bleaching	No	Yes	No	No	No	Yes	Yes	Yes	No

Table 3 Chlorophyll content in four partially bleached alcyonacea. Values in μg chlorophyll per 5 mm^2 surface tissue. *Lobophytum depressum* was included for comparative reasons. *Sarcophyton glaucum* did not bleach

	<i>Lobophytum depressum</i>	<i>L. venustum</i>	<i>Sinularia dura</i>	<i>S. leptoclados</i>
Bleached area	–	1.41 ± 0.081	0.44 ± 0.22	0.79 ± 0.35
Unbleached area	3.13 ± 1.03	3.21 ± 0.63	1.06 ± 0.17	1.71 ± 1.01
<i>t</i> -value	–	–4.64	–5.36	–1.711
Significance	–	0.0001	0.001	0.13

Mucous sheets

No mucous sheets comparable to those observed under natural conditions were observed during the entire experiment. However, in all alcyonacea of the genera *Lobophytum* and *Sinularia* sand particles stuck to the surface of the colonies on what appeared to be congealed mucus. In scleractinia, the presence of mucus was inferred by sand particles stuck together and hanging from the edge of the colonies. This was most frequently observed in flat specimens.

Discussion

Even though the experiments were conducted in the laboratory, the results allow conclusions to be made about field implications. Parallel observations in the field and local community structure data (Riegl et al. 1995) supported laboratory findings.

The laboratory environment simulated extreme conditions, such as high sedimentation and practically zero water motion in which the corals' attempts at sand clearing were completely unaided. In Natal, such conditions are likely to occur in winter months of May to July, where high, storm-created swells alternate with almost absolutely calm seas and where no water movement is detectable on the reefs. Surge stirs up sediment which settles again in calm seas and makes it necessary for corals to clean their surfaces. In other reef areas of the world, this situation would occur when strong sediment pulses are input by river discharge and not removed by currents and wave action (Cortes and Risk 1985; Hodgson 1994). However, sediment grain sizes would be finer in such a situation (Cortes and Risk 1985).

The continuous sand application experiment represented the worst possible case for the corals, an environment with high sedimentation but no water movement to help clearing. The results allow us to judge the differential abilities of corals to cope with continuous sand cover over a restricted period of time.

Both scleractinia and alcyonacea were well able to withstand short-term episodic sand application, while continuous sand application resulted in various stress responses or death of entire colonies. Overall, scleractinia coped better with continuous sand cover than alcyonacea.

At first glance, this result appears strange when compared to field situations and data from the literature. Some authors claim that alcyonacea are less susceptible to sedimentation than scleractinia (Schuhmacher 1975; Hong and

Sasekumar 1979; van Katwijk et al. 1993). In many reef areas of the Indo-Pacific, alcyonacea are commonly found on the most inshore parts of the reefs (Tursch and Tursch 1982; Sheppard et al. 1992), areas where one would anticipate sedimentation to be high. In South Africa as well, many alcyonacea are often found growing in sandy gullies with extremely high values of sand resuspension and re-sedimentation.

However, while in the experiment alcyonacea were not able to actively clear themselves from applied sand, in nature they can be passively cleaned by water movement. Therefore, they are more likely to be found in areas of high water motion, e.g. exposed and elevated parts of reefs. In South African sandy gullies, they were mostly limited to near vertical rock faces or areas of high water motion, which allowed passive sand clearance. They generally favoured elevated parts of the reefs which were exposed to lower sedimentation levels as well as high water motion (Riegl et al. 1995) which is likely to wash off settled sand. In these reef areas, alcyonacea have the advantage of being able to survive physical disturbances caused by floating debris and catastrophic low tides better than scleractinia (Schuhmacher 1975; Benayahu and Loya 1977; Tursch and Tursch 1982; Dai 1991). These factors may lead to their dominance.

The alleged sedimentation tolerance of alcyonacea (Schuhmacher 1975; van Katwijk et al. 1993) is mainly inferred by the position of the corals on the reefs, and experimental proof is inconclusive or lacking. There is, however, the possibility that regional differences exist.

Certain aspects of colony morphology proved crucial for the coral's ability to cope with sedimentation. Sphericity of colonies is important in the early phases of sand shedding, as it obviously enhances run-off and determines the ability of a colony to clear sand quickly.

The morphology of alcyonacea ensured that at least some parts of the colony were not covered by sediment. The numerous radial ridges in *Lobophytum venustum* and *Sinularia dura*, as well as the finger-like projections in *S. leptoclados*, always kept a large portion of the corals' surface sand-free. The covered parts suffered necroses and localized bleaching, especially under continuous sedimentation.

In scleractinia, calyx size and meander length were not of obvious importance. Although an influence of calyx size on the rate and efficiency of sand clearing is reported (Hubbard and Pocock 1972; Hubbard 1973; Stafford-Smith 1993), it is not clear why calyx size should have a strong influence on sand clearance. The general behavioural response of most scleractinia to sedimentation was polyp in-

flation (Stafford-Smith 1993; present study), the inflated polyps forming a smooth surface which encourages runoff. There would appear to be no intrinsic advantage for sediment shedding in having larger polyps. Therefore, it is also not surprising that no differences existed in the sand clearing efficiency of meandroid and plocoid corals.

In short, scleractinia are "active sediment shedders" and appear able to withstand applied sediment through their own strength, while alcyonacea are "passive sediment shedders" which rely on water motion or gravity (when growing on inclined substrata). Continuous sedimentation could, therefore, more rapidly disadvantage alcyonacea, particularly when the latter grow in areas of low water motion and/or horizontal areas, which do not allow passive clearing.

It appears that many more factors than just the coral's reaction to sediment actually determine their survival chances. On South African reefs, values of maximum sediment resuspension and sediment in the water were higher than in other areas described as sedimentation-stressed (Cortes and Risk 1985; van Katwijk et al. 1993; Cortes 1994). Nevertheless, in South Africa, reefs are functioning under these conditions, and corals appear to be in good condition.

We may draw the conclusion that corals, both scleractinia and alcyonacea, are, at least over several weeks, capable of coping with important amounts of sand deposition and possibly also siltation. If enough water motion is present to prevent smothering of the entire reef (Macintyre et al. 1994), physical contact of the sediment with the corals is probably rarely the decisive lethal factor. Therefore, declining reef health in sedimented areas may rather be due to altered environmental conditions than to the coral's reaction to contact with the sediment itself.

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