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Tissue damage in scleractinian and alcyonacean corals due to experimental exposure to sedimentation

Gewebeschäden an Hart- und Weichkorallen durch experimentelle Sedimentation

by

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Abstract

Four South African scleractinian corals (*Favia favus, Favites pentagona, Platygyra daedalea* and *Gyrosmilia interrupta*) and four alcyonacean corals (*Lobophytum depressum, Lobophytum venustum, Sinularia dura* and *Sinularia leptoclados*) were experimentally exposed to high sedimentation conditions in the laboratory during a period of six weeks. Experimental sedimentation corresponded to the highest measured sedimentation levels on South African coral reefs, being 200 mg $cm^{-2}h^{-1}$. Corals were monitored for tissue necroses and bleaching during the course of the experiment and histological sections were prepared after the termination of the experiment. During the experiment, tissue necroses appeared earlier and more frequently in alcyonacea than in scleractinia. Histological sections showed degeneration and necroses of epithelia and mucus-producing cells with accumulation of free mucous material in the epithelia as well as loss of zooxanthellae in all alcyonacea. Local bleaching, due to loss of zooxanthellae, was observed in three alcyonacea (*Lobophytum depressum, Sinularia dura, Sinularia leptoclados*). Not all parts of the alcyonacean colonies were equally affected by tissue damage and bleaching. In particular, elevated lobes and finger-like projections, which were never covered by sediment for long periods, did not exhibit the same severe damage or bleaching as flat parts of the colonies. Scleractinia did not suffer the same amount of tissue damage as alcyonacea, no bleaching was observed. Partial necroses and degeneration of epithelia as well as changes in mucus producing cells were also observed in scleractinia.

Zusammenfassung

Vier südafrikanische Hartkorallen-Arten (*Favia favus, Favites pentagona, Platygyra daedalea und Gyrosmilia interrupta*) sowie vier Weichkorallen-Arten (*Lobophytum depressum, Lobophytum venustum, Sinularia dura* und *Sinularia leptoclados*) wurden über einen Zeitraum von sechs Wochen in Laborexperimenten hohen Sedimentationsraten ausgesetzt. Die experimentellen Sedimentationsraten entsprachen Maximalwerten, welche direkt auf südafrikanischen Riffen gemessen wurden (200 mg $cm^{-2}h^{-1}$). Während des Experiments wurde das Auftreten von Nekrosen, sowie Bleichen ("bleaching") überwacht. Nach Beendigung des Experiments wurden histologische Schnitte angefertigt. Nekrosen traten während des Experiments früher und häufiger in Weichkorallen auf als in Hartkorallen. Histologische Schnitte zeigten Absterben von Epithelien und Mukus-produzierenden Zellen, welches gleichzeitig mit einer Akkumulation freien mukösen Materials in den Epithelien auftrat. Auch die Zahl der Zooxanthellen nahm ab. Lokales Bleichen ("bleaching") trat in drei Weichkorallen-Arten auf (*Lobophytum depressum, Sinularia dura, Sinularia leptoclados*). Nicht alle Teile der Korallen waren von diesem "bleaching" gleichermaßen betroffen. Vor allem Loben, welche nie ganz von Sediment bedeckt werden konnten, zeigten geringere Schädigung als flache Teile der Kolonien, welche ständig von Sediment bedeckt waren. In Hartkorallen trat kein Bleichen auf, auch die Gewebeschäden waren geringer als in Weichkorallen. Lokale Gewebenekrosen sowie Veränderungen in den Mukus-produzierenden Zellen traten auch in Hartkorallen auf.

1. Introduction

Sedimentation can be a major factor influencing corals and coral communities (DONE, 1982; ROGERS, 1990; DAI, 1991; RIEGL et al., 1995). It has been speculated that varying levels of sedimentation influence coral community structure, areas of low sedimentation being preferred by alcyonacean corals (DINESEN, 1983; DAI, 1991; RIEGL et al., 1995; RIEGL, 1995). While numerous studies exist on the reaction of scleractinia to sedimenta-

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tion (PETERS & PILSON, 1985; STAFFORD-SMITH & ORMOND; 1992, STAFFORD-SMITH, 1993), alcyonacea have received very little attention. Recently, differences in the behavioural responses and the survival rates of scleractinia and alcyonacea under experimentally induced high sedimentation conditions have been demonstrated (RIEGL, 1995; RIEGL & BRANCH, 1995). The physiological reaction and cost of sedimentation is, however, roughly the same between these two groups (RIEGL, 1993; RIEGL & BRANCH, 1995).

In this light it was important to see whether there were any apparent differences in histological effects of sedimentation in scleractinia and alcyonacea. Also, while reports of histological damage in scleractinia due to sedimentation exist (PETERS & PILSON, 1985), no such reports could be found for alcyonacea.

The aims of the present study were 1) to quantify tissue damage inflicted by a known concentration of sediment and rate of sedimentation and 2) to describe the histological damage patterns observed in scleractinia and alcyonacea.

2. Material and methods

The experimental corals were collected in the Maputaland Reef System in Northern Natal, South Africa (Fig. 1), from where they were transported by road in a 500 litre container with sea water slightly hypersaturated with medical oxygen to the laboratory in Durban. There they were kept in flow-through sea-water tanks with a one hour total replacement time. Light levels were roughly comparable to their natural habitat (RIEGL & BRANCH, 1995). Prior to the experiment, the animals were allowed a four week acclimatisation period. Series of six specimens in each species were used in the experiments for experimental and control conditions. The animals were fed twice a week with rotifers and brine-shrimp nauplii (PETERS & PILSON, 1985) to avoid starvation, in case heterotrophic energy uptake was necessary. Under the experimental conditions, however, control animals were autotrophic (RIEGL & BRANCH, 1995). Light levels were held at 50% PARs, which is equivalent to natural light conditions at the sampling site.

The specimens were placed in adjacent tanks, one for control conditions and one for sedimented conditions. Care was taken to avoid putting the animals into physical contact, as this could have resulted in aggressive reactions and tissue damage due to tentacular action, which could have distorted results. A constant flow of sediment onto the experimental corals was maintained for six weeks by means of a recirculatory system as illustrated in Fig. 2. The sediment cover on the corals was maintained at roughly 200 mg cm^{-2}, this being a level of sedimentation corresponding to that observed on the reefs (RIEGL, 1995).

Chlorophyll measurements were made in order to quantify any possible loss of zooxanthellae or pigment. Chlorophyll was extracted using hot methanol (NUSCH, 1980)

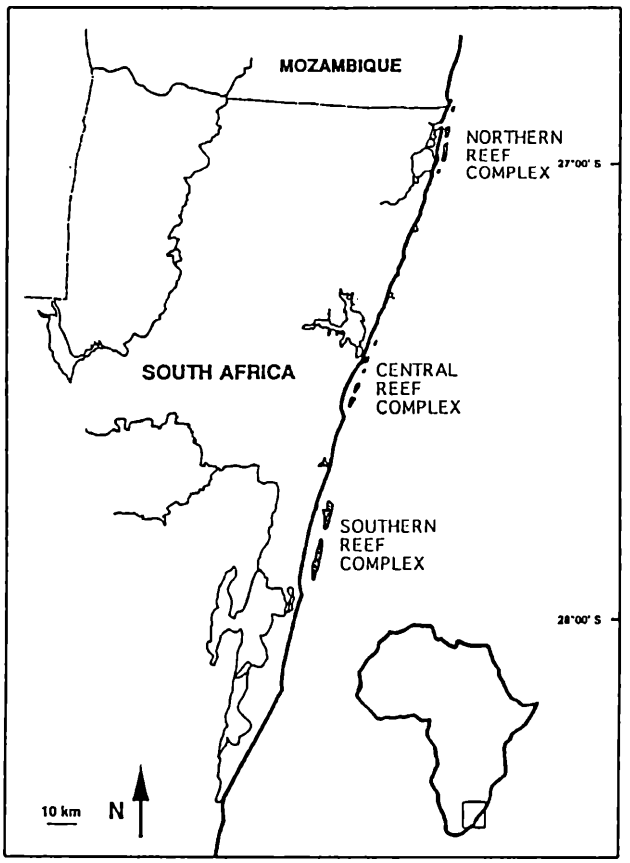

Figure 1: The location of coral reefs in South Africa. All specimens for the present study were collected in the Central Reef Complex.

from tissue blocks of 5 mm^3 taken from different parts of the experimental colonies. Optical densities were read at 664, 647 and 630 nm with correction for turbidity and coloured materials at 750 nm (WETZEL & LIKENS, 1991) and converted to concentration of total chlorophylls using the formula derived by BRANCH & BRANCH (1980). These measurements were only performed on alcyonacea. The scleractinia used in this study were too small to allow sacrificing tissue for chlorophyll analysis as it was needed for histology.

After experimental animals were killed, they were fixed for 24 hours in 5% formalin and later transferred to 70 % alcohol. A solution of 15 % sodium citrate and 50 % formic acid was used for decalcification. Specimens were embedded in wax, cut at 7 mm thickness and stained with Ehrlich's hematoxylin and eosin using standard procedures. Staining for mucus used Mayer's mucicarmine technique (LUNA, 1968; PETERS & PILSON, 1985).

3. Results

3.1. Macroscopically visible effects

Effects of sedimentation were most easily visible in tissue necroses in both scleractinia and alcyonacea and localized bleaching in alcyonacea only. Alcyonacea showed damage sooner than scleractinia. While alcyonacea already started

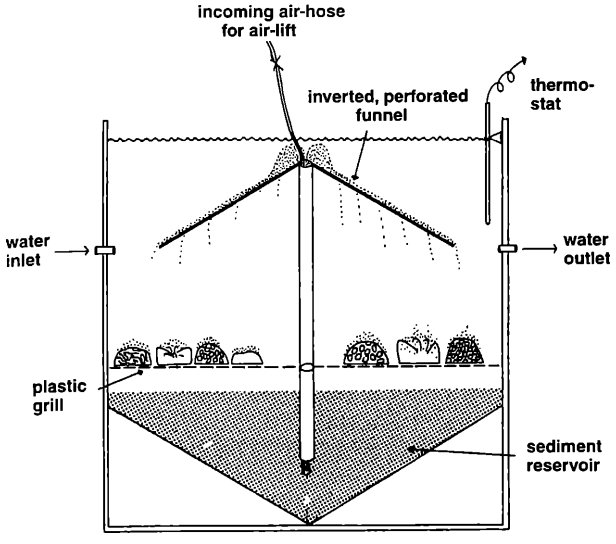

Figure 2: The apparatus used to create a permanent high sedimentation environment in the laboratory. Experimental corals were placed on a plastic grid, which did not allow any accumulation of sediment except on the animals themselves. Sediment was sucked up inside the central column by means of an air-lift and distributed evenly over the experimental area with the help of an inverted funnel, which was perforated at regular intervals. A circular current in the basin evenly distributed the sediment. Water supply was flow-through, the total volume of water was replaced once every hour.

to exhibit tissue necroses within the first experimental week (after three days, small, pitted necroses appeared in all species, which continued to enlarge during the experiment) the scleractinia only exhibited tissue necroses after 15 days. In alcyonacea, these necroses appeared randomly on the surface in flat specimens, or, in hillocky species (*L. venustum*, *S. dura*, *S. leptoclados*), on the flat parts of the colony between the hillocks. Necroses in scleractinia formed predominantly on the peripheries of the colonies (in *Favites pentagona*), where shed sediment accumulated. Other areas of necroses were in the centre of the colony, mostly on the thin tissue covering the thecae and coenosteum between individual corallites (in *Favia favus*).

Localized bleaching was observed in three alcyonacea (*Lobophytum venustum*, *Sinularia dura* and *Sinularia leptoclados*). The bleaching occurred in the same area as the necroses, on flat areas between hillocks. There was a significant difference between chlorophyll content in bleached and unbleached areas (Tab. 1). One species, *Lobophytum depressum*, did not bleach but suffered extensive necroses over most of the area that could have bleached.

3.2. Microscopically visible damage

The most obvious changes in tissues occurred in all species in their outer body wall epidermis. Tissue changes in scleractinia were less obvious than in alcyonacea. In all four scleractinian species, the body wall epithelia showed only limited atrophy and overall few necrotic areas. In *F. favus* and *G. interrupta* a thinning of the body wall epithelium was observed (Pl. 2).

No decrease in number or density of zooxanthellae was observed in either species. It appeared in all species that the number of fully functioning mucus cells in the ectoderm had decreased. This was deduced from less mucoid material inside the cells, a thinner appearance and overall less mucoid material within and around the epithelia (Pl. 1, Figs. B, D; Pl. 2, Figs. B, D).

In alcyonacea, a uniform picture emerged. Tissue damage varied between hillocky and flat parts of the coralla. The body-wall epithelia showed a clear tendency for necrosis, which progressed from thinning but remaining intact, through partial loss of coherence to total loss of all epithelia. The number and size of mucus cells increased in moderately damaged parts of the corals but decreased again in badly damaged parts. Also the consistency of the mucus had changed. It stained green in damaged animals (using Mayer's mucicarmine method) while red to yellow in healthy animals. Patches of extracellular, apparently congealed mucous material were found, particularly in damaged and necrotic areas. While the frequency of these mucus patches increased in moderately damaged areas it decreased again in badly damaged areas (Pl. 3, Figs. B, D; Pl. 4, Figs. B, D).

Also the number of zooxanthellae in the endoderm showed a tendency to decrease, which is in accordance with the observed local bleaching (Pl. 3, Pl. 4; Tab. 1).

In alcyonacea, two grades of tissue damage were observed: moderate and severe damage, which were well seperable. This was not the case in scleractinia (Tab. 2).

4. Discussion

Sedimentation had serious histopathological effects on reef-building scleractinia and alcyonacea. The effects were more profound in alcyonacea than in scleractinia. This may at least partly be attributed to the behavioural reactions of the corals (RIEGL, 1995). The appearance of tissue necroses was linked to the capability of the corals to shed accumulated sediment. Necroses always formed in areas where sediment accumulated and remained for several

	bleached area	unbleached area	t-value	level of significance
Lobophytum depressum	–	3.13±1.03	–	–
Lobophytum venustum	1.41±0.81	3.21±0.63	–4.64	0.0001
Sinularia dura	0.44±0.22	1.06±0.17	–5.36	0.001
Sinularia leptoclados	0.79±0.35	1.71±1.01	–1.71	0.13

Table 1: Chlorophyll content in bleached and unbleached areas of alcyonacean corals after six weeks of experimentally induced sedimentation.

Scleractinia		*Alcyonacea*
Thick epithelia, numerous mucus producing cells filled with mucus, no extracellular mucoid material, numerous zooxanthellae in endoderm.	**undamaged**	Thick epithelia, numerous mucus producing cells filled with mucus in outer body wall and gastrodermis, no extracellular mucoid material, numerous zooxanthellae.
	moderate damage	Epithelia thinning, mucus producing cells decreasing, beginning accumulation of extracellular mucoid material, no loss of zooxanthellae.
Thin epithelia, mucus producing cells still numerous but mostly empty, local accumulation of extracellular mucoid material, partial loss of zooxanthellae.	**severe damage**	Epithelia necrotic, few mucus producing cells in either epithelia or gastrodermis, extracellular accumulation of mucoid material, loss of zooxanthellae.

Table 2: Observed tissue damage in scleractinia and alcyonacea after six weeks of experimentally induced long-term sedimentation.

days. Only in scleractinia did areas where sediment almost never accumulated, such as the tissues over the corallite walls, also show a tendency to become thin and develop local necroses.

Local bleaching in alcyonacea followed the same pattern. Only areas in which sediment could accumulate bleached, while the hillocks which were never covered by sediment did not bleach and showed no tissue damage. The body-wall epithelia in alcyonacea are thinner than in scleractinia and may therefore be more susceptible to damage caused by sediment accumulation.

These histological findings correspond well to the physiological reactions of the same animals in parallel experiments (RIEGL, 1995; RIEGL & BRANCH, 1995). Under sedimented conditions all animals exhibited reduced productivity but increased respiration and increased mucus output. This is reflected in the denser mucus producing cells and the accumulation of mucus in moderately damaged animals (Pl. 3, Fig. D; Pl. 4, Fig. D). The production of mucous sheets as a countermeasure to sedimentation (COFFROTH, 1988) was found to be energetically extremely expensive (RIEGL & BRANCH, 1995). In the course of the experiment, behavioural responses which had been apparent at the beginning of the experiment, such as increased mucus production (RIEGL, 1995; RIEGL & BRANCH, 1995), stopped. This situation was particularly dramatic in alcyonacea. The degeneration of tissues and the apparent loss of healthy mucus producing cells, as observed in the present and other studies (PETERS & PILSON, 1985), explain why no continued stepping up of mucus production is possible. The corals appear to "burn out" after about one week of continuous sedimentation. Shortly thereafter tissue necroses appeared. Also numerous empty mucus producing cells in the epithelia of the sediment stressed scleractinia indicate that only a limited amount of mucus production is possible.

As sedimentation also severely interferes with feeding and photosynthetic productivity (RIEGL, 1995; RIEGL & BRANCH, 1995), the thinning of tissues and the loss of mucus-producing cells is probably a result of energetic exhaustion.

The present results also indicate the importance of colony shape, particularly in alcyonacea. As alcyonacea do not actively shed sediment (RIEGL, 1995), it is important for them to keep some areas of the corallum permanently free of sediment and therefore undamaged. This is achieved by the hillocky growth form.

In South Africa and elsewhere, coral community structure diversifies, among others, along a sedimentation gradient (DINESEN, 1983; DAI, 1991; RIEGL, 1993; RIEGL et al., 1995). The areas of high sedimentation are dominated by scleractinia, while those of low sedimentation are alcyonacean dominated (DAI, 1991; RIEGL, 1993; RIEGL et al., 1995). The present results clearly indicate that alcyonacea have a lower tolerance to high sediment loads than scleractinia which possibly excludes them from high-sedimentation areas on the reefs.

5. Conclusion

Scleractinia exhibited less tissue damage due to sedimentation than alcyonacea. In scleractinia, no thinning of epithelia was observed and only in one species (*Gyrosmilia interrupta*) zooxanthellae appeared to have decreased in numbers. In all species, the frequency of mucus cells in the epithelia decreased. In alcyonacea, epithelia showed a clear tendency for necrosis. Mucus cells decreased in size and frequency. Zooxanthellae in the endodermis decreased in number, leading to local bleaching. Damage was not uniform over the colonies. In scleractinia, the damage was concentrated on the colony edges as well as over the thecae, while in alcyonacea damage was concentrated on flat parts. Hillocks, which had not been covered by sediment, remained unaffected.

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PLATE 1

Photomicrographs of *Favites pentagona* (A, B) and *Platygyra daedalea* (C, D) tissues, stained with Mayer's mucicarmine technique to demonstrate changes in mucus producing cells. The endodermal layer (gastrodermis) is characterized by the presence of zooxanthellae (z). The body wall epithelium shows numerous filled mucus cells (mc) in control animals (A, C) but numerous empty mucus cells (emc) in sediment stressed animals (B, D). Sections are horizontal through the polyp. Scale bar = 10 micrometers.

PLATE 1

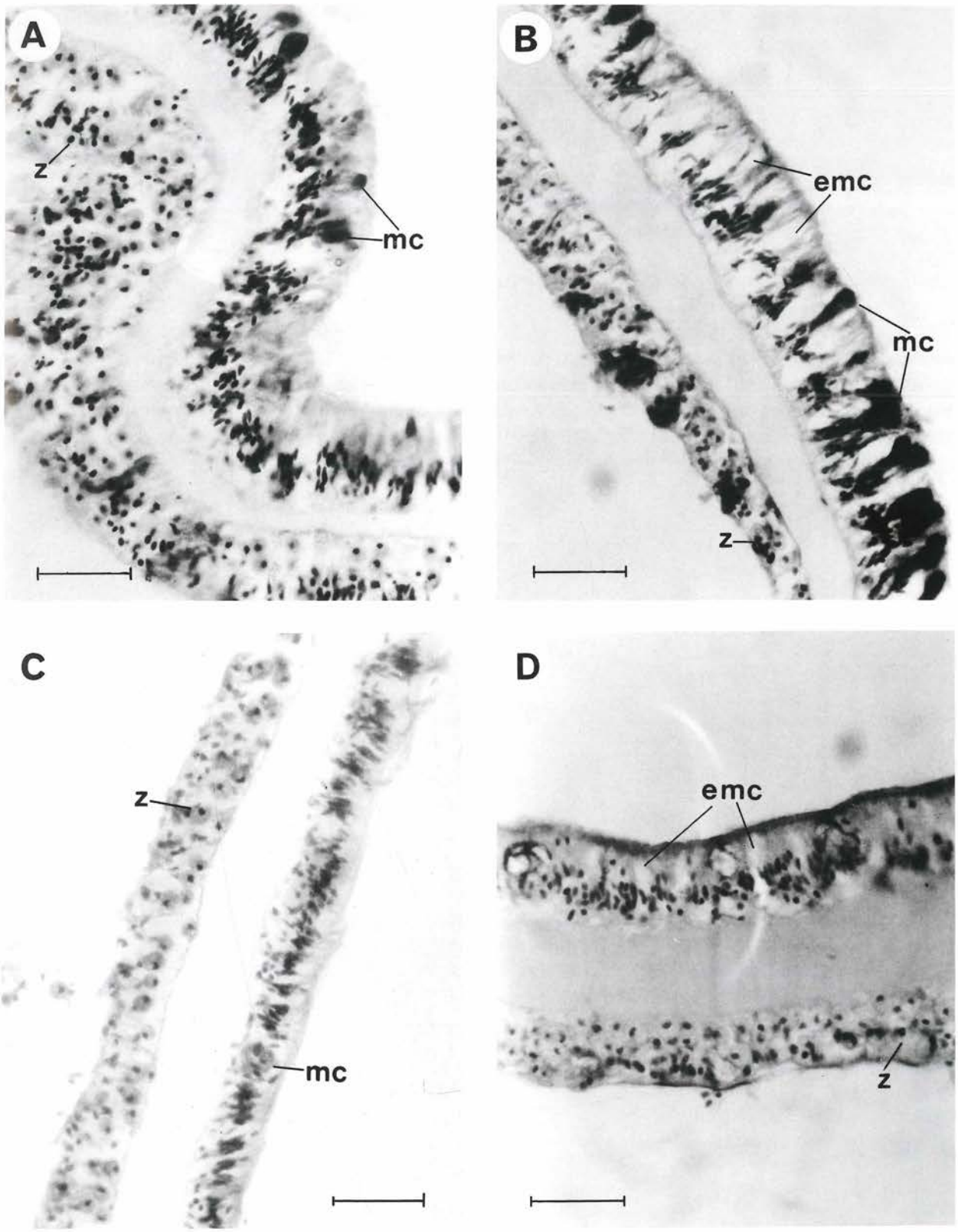

PLATE 2

Photomicrographs of *Favia favus* (A, B) and *Gyrosmilia interrupta* (C, D) tissues, stained with hematoxylin to demonstrate changes in tissue thickness. The gastrodermis is characterized by the presence of zooxanthellae (z). The body wall epithelium as well as the gastrodermis are thicker in control animals (A, C) and show numerous mucus producing cells (mc). In sediment stressed animals (B, D) epithelia are thinner and empty mucus cells (emc) can be seen. Sections are horizontal through the polyp. Scale bar=10 micrometers.

PLATE 2

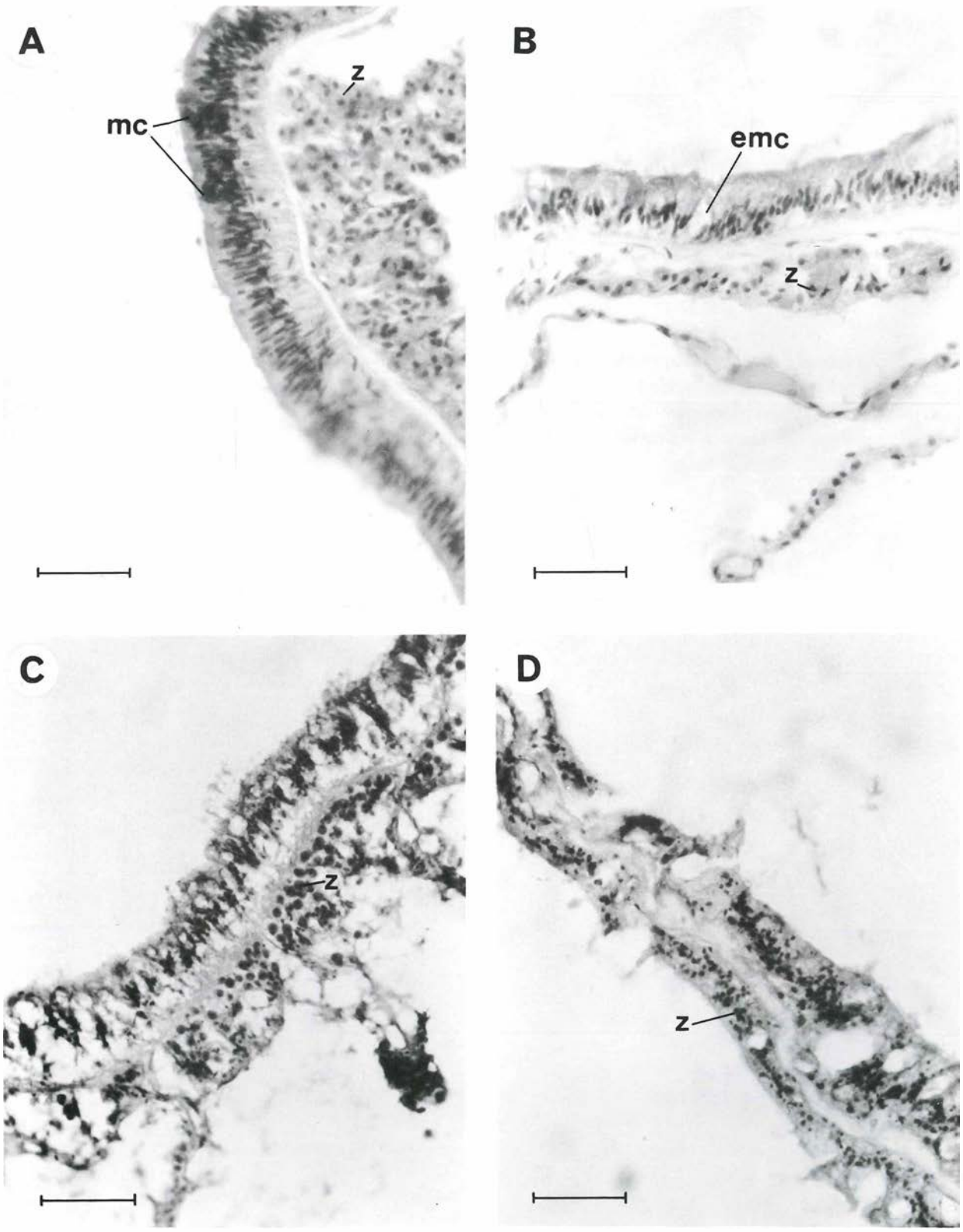

PLATE 3

Photomicrographs of *Lobophytum depressum* (A, B) and *Lobophytum venustum* (C, D) tissues, stained with hematoxylin to demonstrate changes in epithelia. Epithelia of control animals (A, C) are intact and show individual mucus producing cells (mc), while epithelia of sediment stressed animals are thin and partially necrotic (n) with accumulations of mucus (m). z = zooxanthellae. Sections are perpendicular to the colony's surface, scale bar = 10 micrometers.

PLATE 3

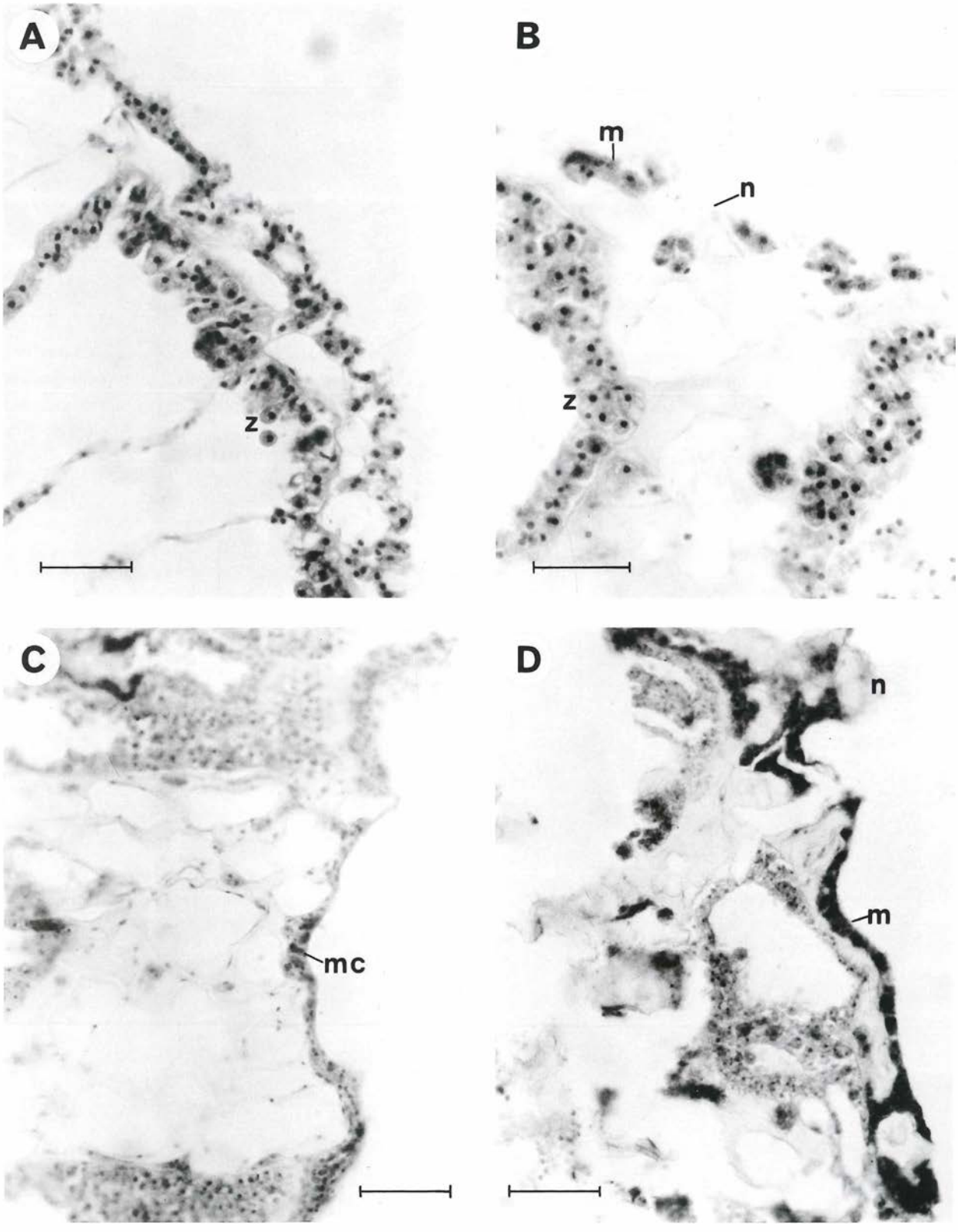

PLATE 4

Photomicrographs of *Sinularia dura* (A, B) and *Sinularia leptoclados* (C, D) tissues, stained with hematoxylin to demonstrate changes in epithelia. Epithelia in control animals (A, C) are intact and continuous, mucus cells (mc) are found in the gastrodermis and the body wall epithelium. In sediment stressed animals necroses (n) of the body wall epithelium are apparent, as are accumulations of mucus (m) and enlarged mucus cells (mc). z = zooxanthellae, sections are perpendicular to the colony's surface, scale bar = 10 micrometers.

PLATE 4