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Research Report 'Evolution of Reefs'

Factors Controlling Holocene Reef Growth: An Interdisciplinary Approach

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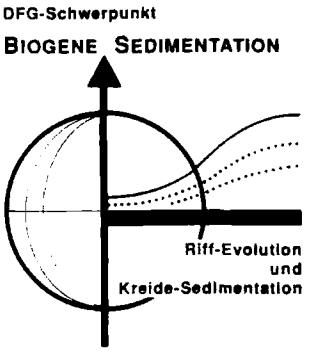

CONTENTS

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SUMMARY

This interim report deals with investigations on key factors controlling reef growth by zoophysiologists, ecologists, paleontologists and geologists. The different levels of emphasis are the coral animal and the reef community. The main study area is the Red Sea which reaches over 20° latitude up to the northernmost margin of the global coral reef belt. Supplementary results on microborer ecology are provided from the Bahamas.

The desert enclosed Red Sea, not influenced by land runoff and only minimally by anthropogenic (urban and touristic) nutrient inputs, is predestined for a study on the principal influence of light on calcification within bathymetrical and latitudinal gradients. Hence, on the level of the zooxanthellate scleractinian animal phototrophic and heterotrophic energy supply and its bearing on calcification are being measured in different coral species - in particular in *Porites* sp., one of the most important reef builders.

The growth of 15 zooxanthellate scleractinians in the Gulf of Aqaba correlates with the annual light cycle. This correlation is observable down to 40 m depth. Other growth promoting factors seem to have less influence on coral extension. The availability of organically enriched sediments in shallow water probably yields nutritional value, in particular for filter feeding species, thus restricting their distribution to those areas. Zooxanthellae, when isolated from *Mycedium elephantotus,* are different in their dependence on depth in maximum rates of photosynthesis and photosynthetic efficiency (-slope). Increasing concentrations of pigments as a function of depth could be determined. Maximum rates of photosynthesis of zooxanthellae in vivo, collected at corresponding depth, have been 4 times higher. Structural and physiological adaptations improving heterotrophic and phototrophic energy intake are highlighted.

Porites sp. was the subject of annual growth studies at locations extending from Aqaba in the North over the northern and southern Egyptian coast and islands, Sanganeb Atoll and Wingate reef offshore Sudan to the Gulf of Tadjoura in the Gulf of Aden (Djibouti). Mean growth rates in the shallow water zone increase with decreasing latitude and are highest at the southernmost studied reefs in the Gulf of Tadjoura. However, the observed latitudinal growth reduction is restricted to the upper ca. 15 m of the water column. The upper limit of growth potential decreases with depth parallel to the decrease of light availability. Highest growth rates are recorded in shallow depth (10-12.9 mm yr^{-1}). This zone reaches at Aqaba (29°30' N) to a depth of ca. 10 m. At the southern Egyptian reefs (24°30' N) this zone extends to ca. 15 m water depth. This effect is probably a result of the stronger reduction of winter light levels and water temperature in the northern regions. Compared to other oceans the decrease of growth with increasing latitude of Red Sea *Porites* corals is far less, and growth rates at Aqaba are the highest observed at these latitudes.

On the level of the community of reef inhabitants four principal topics are addressed:

The first one is the dynamics of the proportions of hermatypic and ahermatypic organisms and open space. The occurrence of stony and soft corals and the sharing of empty space in different reef sections at Aqaba and on Sanganeb Atoll were quantified. Soft corals, mainly *Sinularia*- and xeniid species, occupy decreasing shares with depth. Among the *Xenia* species a bathymetrical zonation pattern was detected.

The next issue is the growth impeding role of soft corals and gastropod parasites and predators on scleractinians. Experimental and field observations showed xeniid soft corals to be opportunistic i.e. occupying rapidly open space rather than to attacking and outcompeting stony corals. An increasingly specialized behaviour was detected among corallivorous gastropods of the family Coralliophilidae to exploit their coral hosts. Whereas these snails are more or less sessile and depend for a long time on the surrounding host polyps the mobile *Drupella cornus* (Thaididae) forms feeding aggregations which denude mainly branching corals on shallow reef parts.

Furthermore, the role counteracting reef growth of macro- and microbioeroders is investigated. *Diadema setosum* is a major destructive agent on reefs at Aqaba (not in the central Red Sea). The grazing sea urchins do not only keep potential colonization area free but also erode carbonate material (e. g. 1468 g/m^2/year, 10 m depth). Demographic and bathymetric patterns in the sea urchin population are analyzed including their bearing on bioerosion of the reef. Investigations on microboring organisms in carbonate material have started in the Red Sea; initial results, however, are only available from similar studies near Lee Stocking Island, Bahamas.

Three major environments have been identified based on the distribution of the different microborers. These are
1) the intertidal environment dominated by boring cyanobacteria,
2) reef sites from 2 to 30 m water depth dominated by a diverse assemblage of boring cyanobacteria and chlorophytes, and
3) the deep reef slope from 100 to 300 m dominated by boring green algae and heterotrophs.

The boring chlorophyte genus *Phaeophila* appears rapidly and dominates at sites from 2 to 30 m, but it leaves vacated borings and is replaced by *Ostreobium quekettii* after 1 year. Different substrate types show very different rates of colonization by microborers. The greatest excavation rates (100 g /m^2/3 months) occur in fine-grained limestone, while the slowest rates (0.5 g/m^2/3 months) occur in calcite crystals. Molluscan shell material shows intermediate rates of excavation. Light conditions appear very important in determining the growth rate and distribution of different microborers between the sites, however, the interaction of light with other factors, such as substrate, time period of exposure, and water quality conditions may be involved.

1 GENERAL INTRODUCTION

Terms such as keep-up reefs and give-up reefs (NEUMANN & MACINTYRE 1985) emphasize the crucial role of carbonate accumulation rates during rising Holocene sea level for the growth and distribution of modern coral reefs (CHAVE et al. 1972, SMITH & KINSEY 1974, GRIGG 1982). Reef growth results from a complex combination of factors that promote or hinder the proliferation of carbonate producing and destructive organisms (STEARN & SCOFFIN 1977, SCOFFIN et al. 1980, DAVIES 1983, HUBBARD 1988). These factors vary over broad scales of space and time. Unravelling this complex web of biological, ecological, and geological factors is a challenging task that requires an interdisciplinary understanding of reef organisms and processes.

The record of these interwoven factors preserved in the fossil reef record only rarely provides information about the intensity and duration of changes to individual controls on reef growth (eg. storm deposits, skeletal growth records). As a result, many of the influences on growth remain unidentified in reconstructions of the rates and type of carbonate deposition through the Holocene and reef geological history. There is an enormous range of net rates of reef growth that can occur in the transition of an environment from a dense community of fast growing coral species to a limestone bottom, bioeroded by an abundant population of *Diadema* sea urchins. Within this range are rates of growth produced by extremely diverse assemblages of bioconstructers and bioeroders that result from a wide range of environmental conditions. Even if a particular biological or environmental factor can be detected in fossil deposits, its spatial extent and temporal duration are difficult to reconstruct. Its impact however, may prove the difference between a keep-up or a give-up reef. Through the interdisciplinary study of Recent reefs, knowledge is sought of the key factors that should be considered in assessing the past and future development of reef environments.

The study of the factors influencing reef growth may best be studied over an environmental gradient. An ideal region for such a study exists in the Red Sea where continuous reef development extends from the northern marginal limit of reef development southward through 17° of latitude. GRIGG (1982) described how latitudinal variation in reef organisms and carbonate accumulation is fundamental in Holocene reef growth. Integration of organism and community level investigation over a latitudinal gradient of reef development would provide detailed insight into the factors that control the reef growth process. Therefore, an interdisciplinary group of geologists, ecologists, paleontologists, and zoophysiologists have collaborated in a major program of reef research to evaluate the factors that control reef growth in the Red Sea. Drawing upon data collected on Red Sea reefs and reef environments in the Bahamas, this team of scientists has endeavored to combine their different views of reef biological and geological processes to model the key factors influencing reef carbonate accumulation. This paper represents an initial integration of the diverse efforts by the individual groups.

As presented in studies by CHAVE et al (1972) and STEARN & SCOFFIN (1977), the carbonate budget of a reef is composed of:

- the calcification potential of its main constituents
- the relative coverage by hermatypic and ahermatypic organisms
- the distribution and intensity of coral predators and bioeroders of skeletal material.
- the import and export of sediments over time.

Within the following sections of this paper the individual research groups report on their particular studies that fit within these main budget categories. These reports begin with a study of the energy flow through the coral organism that is driven by the coral-zoozanthellae symbiosis. This is followed by results of investigations into the environmental responses of coral growth and its record within coral skeletons. Community level studies are then presented that influence the distribution of particular reef organisms and modify the growth potential of reef constructors. Finally, studies of the distribution of certain reef bioeroders document the potential fate of dead carbonate skeletons. These contributions come from ongoing research in the Red Sea and, for bioerosion, from the Red Sea and Bahamas. Further bioerosion studies and the abiotic control of sediment import and export within the carbonate budget are presently under investigation in the Red Sea but are not addressed in this paper.

It is not the purpose of this paper to construct the budget model for the Red Sea reefs. The studies are presented here to show how this model is being approached and how the integration of the different perspectives is contributing to the understanding of the complex reef environment. Physiologists differentiate the metabolic controls of calcification within the organism through the seasons of the year; ecologists focus on the dynamics of selected reef communities over years and decades; and paleontologists compare these organisms and communi-

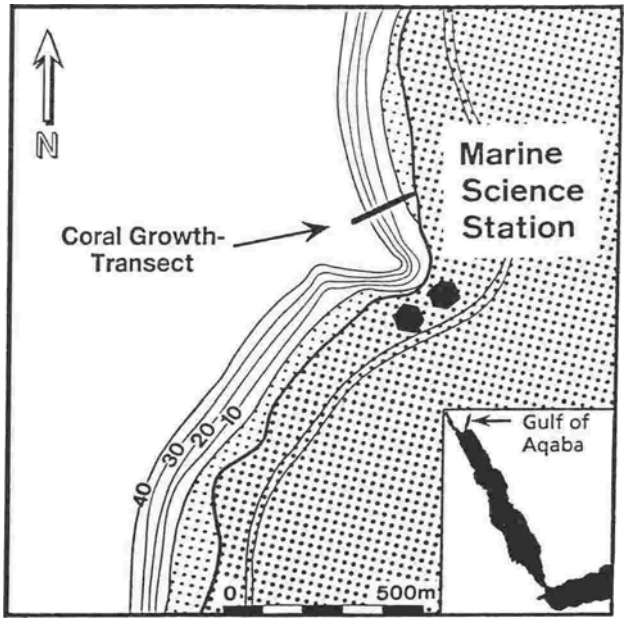


Fig. 1. Study site near the Marine Science Station, 10 km south of Aqaba.

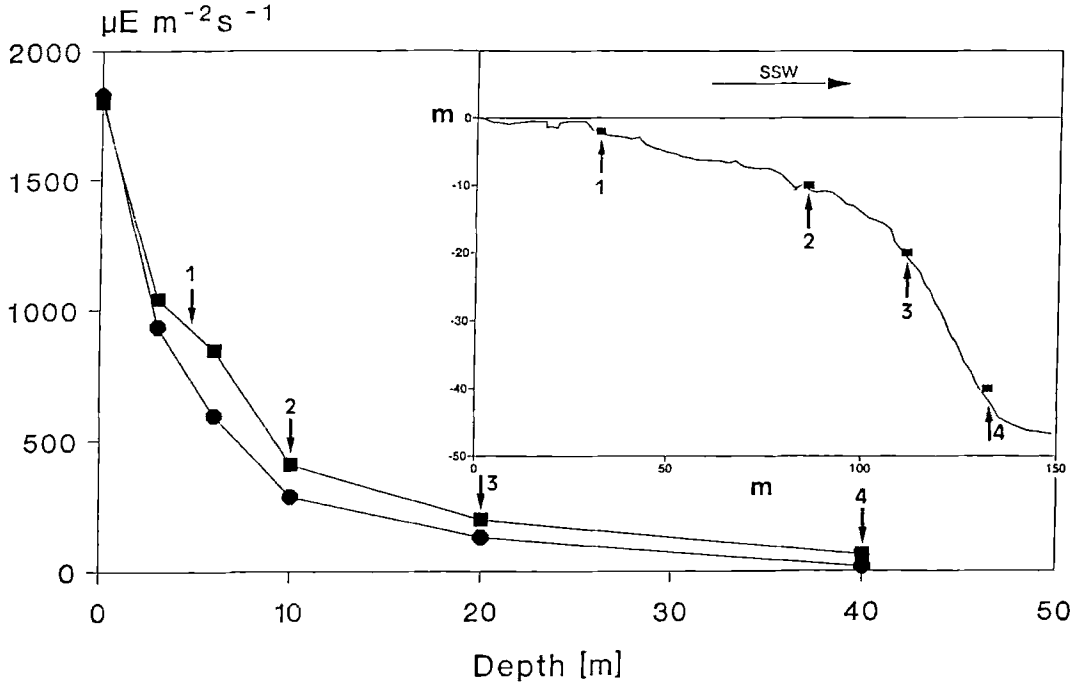


Fig. 2. Underwater light profile off the Marine Science Station Aqaba (29° 27' N). Measurements were taken in April/June 1992 (•) and June/September 1993 (■) between 9 am and 11 am local time at a steep reef slope (orientation S-SW, slope angle 60°) along a line connecting the experimental sites (including sediment traps) at 3-5, 10, 20 and 40 m depth, identified by arrows and numbers (see inset).

ties through the geologic ages. With these different degrees of resolution, factors which promote the deposition and removal of carbonate are reviewed and analyzed.

2 CONTROL OF CARBONATE PRODUCTION IN CORALS BY HETEROTROPHIC AND PHOTOTROPHIC ENERGY SUPPLY

H. Kampmann, M.L. Kuhrau and D. Schlichter

2.1 Introduction

The Gulf of Aqaba, extending to the northern boundary of the existence of photic tropical/subtropical reefs, was chosen to analyze the influence of abiotic and biotic factors in particular responsible for a respectable reef expansion under 'suboptimal' conditions. The growth of zooxanthellate scleractinians in dependence upon the annual supply of actual available phototrophic and heterotrophic energy is under observation.

The growth of corals, comprising the increase of living biomass and not only the deposition of calcium carbonate, depends on three nutritional pathways: 1. the utilization of particulate organic material = POM (plankton, organic detritus); 2. the epidermal absorption of dissolved organic material = DOM; and 3. the utilization of photoassimilates produced by the intracellular symbiotic algae. Alternatives 1 and 2 are heterotrophic pathways (the coral host lives as a secondary consumer) and the knowledge about heterotrophic fueling of the coral's metabolism is still fragmentary (e.g. Johannes et al. 1970, Lewis 1976, Porter 1978, Sorokin 1990). The third alternative, which is the fueling of the host's metabolism with photoassimilates, has been well studied since decades (e.g. McCloskey et al. 1978, Muscatine 1990). Phototrophic fueling means that the coral host is not a primary consumer in the common sense, for he does not use the algal biomass, but utilizes photoassimilates which are released 'voluntarily' into the cytoplasm of the host (Fogg 1983, Schlichter & Liebezeit 1991).

Besides the actual coral growth, we are interested in structural and physiological adaptations (of both partners of the symbiosis) improving the supply with energy of phototrophic (photoadaptations) or heterotrophic origin (adaptations enhancing the supply with POM, DOM).

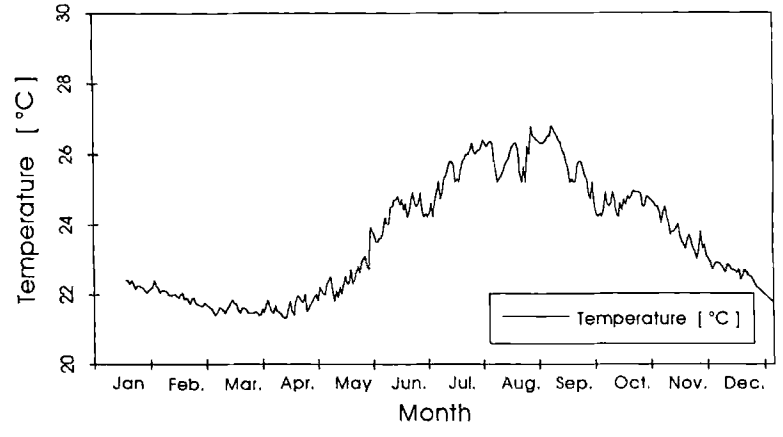


Fig. 3. Annual cycle of sea water temperature at Aqaba. Temperature was registered daily at 10 m depth. Temperature data for different seasons were measured between 1992 and 1994.

Species	Growth depth			
	2-5 m	10 m	20 m	40 m
Acropora variabilis	2	4	2	2
Acropora squarrosa	2	2	2	3
Stylophora pistillata	4	3	3	2
Porites sp. (lutea?)	2	3	2	2
Mycedium elephantotus	-	4	3	3
Favites peresi	-	2	2	2
Favites sp.	1	-	-	-
Favia stelligera	-	1	1	-
Platygyra lamellina	1	1	2	-
Goniastrea retiformis	-	1	1	1
Pavona cactus	-	1	-	-
Pavona decussata	-	1	-	-
Montipora (meandrina?)	-	-	-	1
Echinopora lamellosa	-	-	-	1
Leptoseris mycetoseroides	-	-	-	1

Tab. 1. Zooxanthellate scleractinians whose mass increment was measured by the buoyant weight method. The colonies grew permanently at the listed depths.

Trophic interactions between coral tissues and endolithic algae, which may putatively exist, are also under observation.

The intention of our project is to give an estimate of annual growth rates of hermatypic corals on the baseline of the increment in mass in time. Our data, together with those of the group of Dullo (Kiel) measuring linear coral growth on the basis of sclerochronology, may allow us ultimately, to give an idea about the development of reefs situated at the northern boundary of the existence of photic tropical/subtropical reefs. Bioerosion is studied by the groups of Schuhmacher (Essen) and Vogel (Frankfurt). The data taken from the Gulf of Aqaba might be also of relevance in latitudinal comparison to high productive photic tropical reefs located e.g. in Indopacific or Caribbean waters, which are already well studied. Our present investigations indicate, however, that calcification in the Gulf is, contrary to all expectations when starting the experiments, not at all low.

2.2 Experimental area

Off the Marine Science Station at Aqaba (see Fig. 1) we mounted four sampling platforms for stationary sediment traps (arrows in Fig. 2), along a steeply inclined (60) S-SW orientated reef slope in 3-5, 10, 20 and 40 m depth. In the neighbourhood of the sediment traps water samples were taken and the corals were chosen for the experiments or were transplanted from inverse depths into one of those areas. The light regime at the four stations is shown in Fig. 2. On a separate platform we continuously registered abiotic factors (light, temperature, oxygen). The annual temperature cycle of sea surface water is shown in Fig. 3. Long term measurements of salinity were taken by the Marine Science Station; it was fairly constant at 41 ‰, with an annual fluctuation of 0.5 ‰ only. In vivo photosynthesis of complete colonies was also measured within plexi-glass metabolic chambers on this platform.

2.3 Annual growth of zooxanthellate scleractinians

The growth (increment of buoyant weight - according to JOKIEL et al. 1978) of 15 coral species (71 specimens) differing in size, habitus and bathymetric distribution was determined (Table 1). The field studies have not been terminated until now; therefore, at this time, we can only give mass increments on a relative baseline. In addition, the linear growth was measured with staining methods (Alizarin, according to LAMBERTS 1978; and ^{14}C-labelling). The systematic specifications of the corals were based on SCHEER & PILLAI (1983) and SHEPPARD & SHEPPARD (1991).

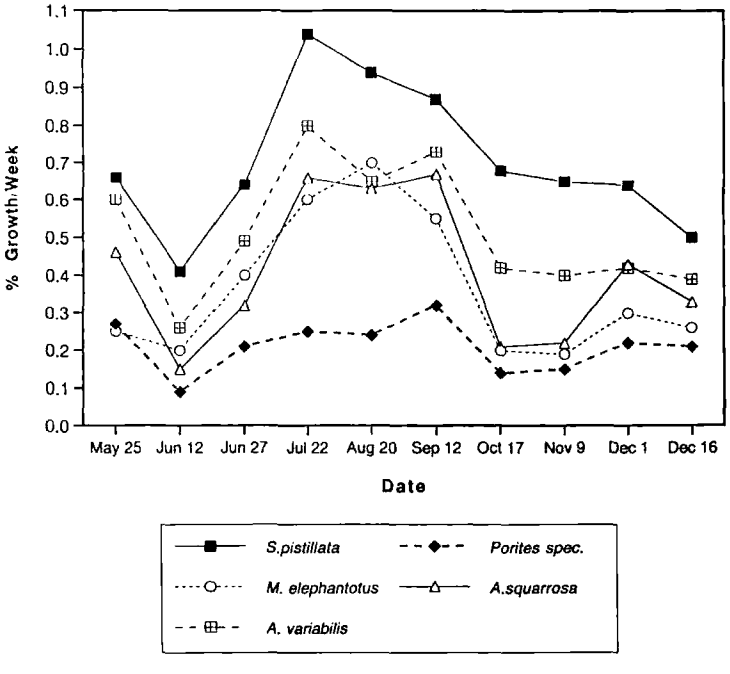


Fig. 4. Species specific growth rates of zooxanthellate scleractinians in the Gulf of Aqaba (increase in % initial buoyant weight). The mass increase of all species shows a clear annual cycle with highest growth rates during the summer months. Average values (n=10) of integrated growth rates were measured at 3-5, 10, 20 and 40 m depth for each species. The branched colonies of *Stylophora pistillata* are superior over the globular *Porites* sp..

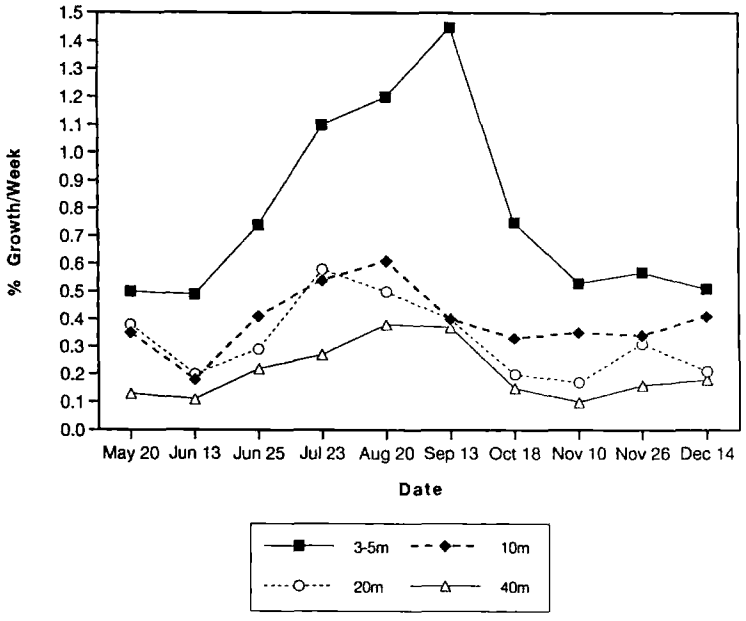


Fig. 5. Depth dependent growth rates of different zooxanthellate scleractinian species in the Gulf of Aqaba. Growth rates of all species (n=15) studied at each particular depth zone were combined. The mass increment decreases with depth, but the annual cycle in growth remains.

In Fig. 4 and 5 the annual growth data of 5 selected species are summarized. Fig. 4 shows the species' specific growth independent of depths (the data are 'pooled' average values of each particular species growing in the four experimental depth zones studied). The species' specific differences in growth exist through the whole year. *Stylophora pistillata* showed the highest and *Porites* sp. the lowest annual increase in mass, exhibiting maxima during the summer months. For linear growth of *Porites* sp. which shows a corresponding pattern, see Fig. 14. The differences in the species' specific growth rates are most probably due to the much larger external surface of the branched growing *S. pistillata* - i.e. the calicoblastic tissue (= aboral epidermis = aboral ectoderm) of this species is enlarged and thus enables the secretion of higher amounts of calcium carbonate compared to the globular (hemispheric, massive) growing *Porites* sp. (with less calicoblastic tissue involved in carbonate secretion). The three intermediate species show tendencies, which can be accounted for by the same argument.

In Fig. 5 the growth data of different species (n = 15) living in the same depth zones were combined and average values were calculated. As a function of depth (light, POM-, DOM-supply, see below) the increment of carbonate decreases. At all depths the seasonality mentioned above remains visible; even at 40 m depth, where the maximal growth rates are about 25 % of the shallow water rates. The linear extension determined for *Porites* sp. shows similar correlations of growth and depth; see Fig. 18.

The correlation between growth and depth is due to abiotic and biotic factors, which mutually interact. In this context, connections between growth and the supply of POM and the influence of light on growth is under observation.

Temperature effects seem to be not as important as the impact of light. The Red Sea is isothermal, the sea surface temperature varies between 20 °C and 28 °C during the year (Fig. 3). It is possible that the temperature drops below 20 °C above extended reef flats in the Gulf of Aqaba during the winter months.

2.4 Heterotrophy: The annual availability of POM

The quantification of the potential trophic contribution of sediments to the nutrition of scleractinians was in focus when sediment traps were mounted at the sample sites marked in Fig. 2. Each trap consists of 9 subtraps with a

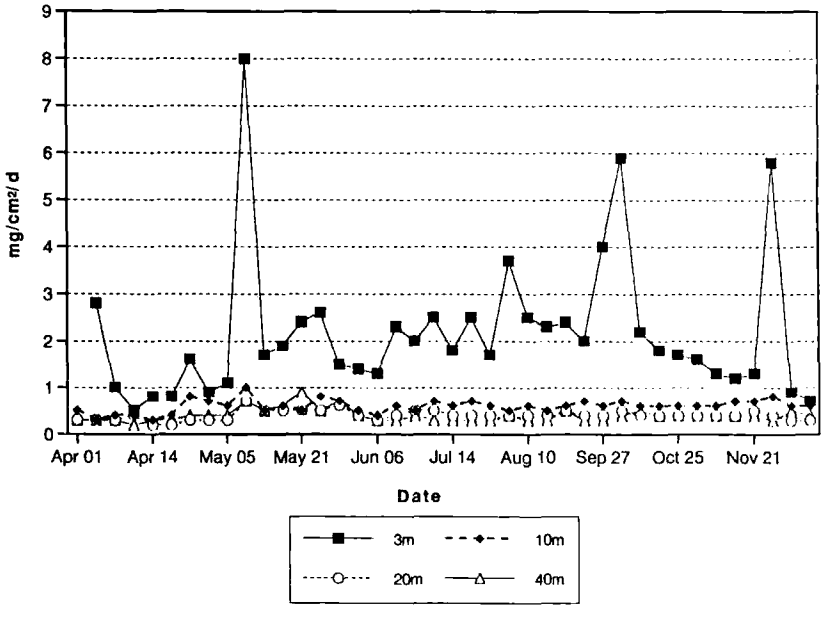


Fig. 6. Total rates of sedimentation (organic plus inorganic components) as function of depth at the sampling sites shown in Fig. 2. At the three deeper stations, the amount is fairly constant all year-round. The total sedimentation at the 3-5 m station is higher compared to the deep stations, the peaks were wheather-induced.

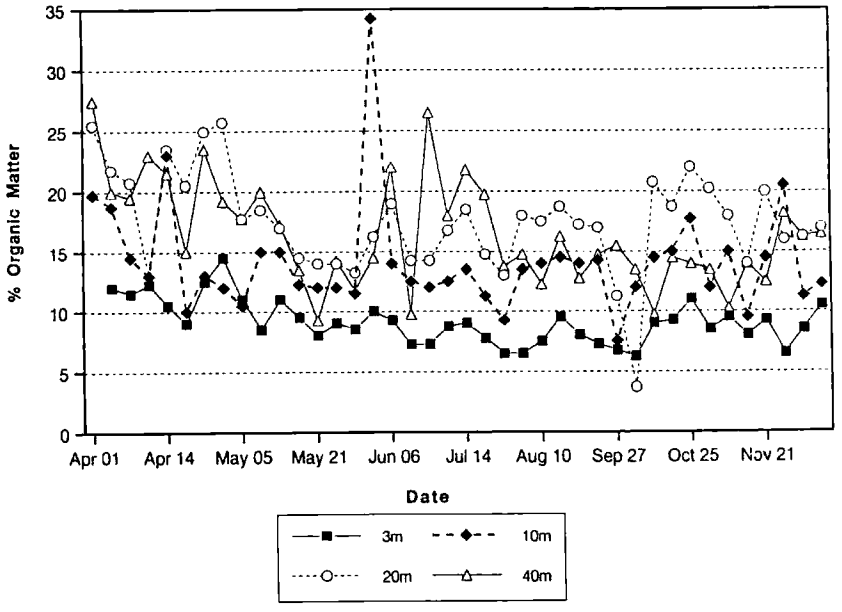


Fig. 7. Content of organic carbon in the sediment samples shown in Fig. 6 (% organic carbon of total weight). The relative amount of organic carbon at the three deep stations appears to be higher compared to 3-5 m samples; but the absolute amounts of organic carbon in 3-5 m samples is 4-5 times higher and may have higher nutritive power.

surface of 49.1 cm^2 and a volume of 2.4 l each. The content of the subtraps (after 7 days of exposure) was sucked through preweighed glassfibrefilters (MACHERY & NAGEL MN 85/90 BF, porewidth 0.4 µm). The filters were either chemically fixed or stored in a deep freeze for further analyses, e.g. determination of POM and extraction of pigments. The weight and the content of organic carbon of subsamples was determined according to standard methods (e.g. MARSHALL 1978).

The total amount of POM (sum of living and dead particulate organic material) and of inorganic components in the water column was also determined with the glassfibrefilter methods in analogy. At the stations 1-4, water samples were taken with a 10 l water sampler (Nansen-Pettersson type).

The annual availability of particulate material on the reef is shown in the Figs. 6-8. The rate of total sedimentation (Fig. 6: [mg/cm^2/d]) shows no periodicity, except in 3-5 m depth, but these fluctuations are due to bad weather. The content of organic carbon of the sediments, however, displays an annual pattern with lowest values at the end of May. The data in Fig. 7 show also that the quantity of organic carbon in 3-5 m sediment samples is low compared to those sediments collected in greater depths, i.e. the potential nutritive value of 3-5 m sediments seems to be low. But on an absolute baseline the content in organic carbon of 3-5 m samples is 4-5 times higher when compared to the other sediment samples.

The content of living plus dead organic and inorganic material in the water column shows an annual cycle with fairly constant concentrations from June till November and minima at the end of April and May with an intermediate maximum in May.

In the Figs. 4-8 three months are missing, and it is actually that period, which is under study.

If one compares the annual growth data with the annual availability of POM, an obvious correlation does not seem to exist, except when looking at the higher

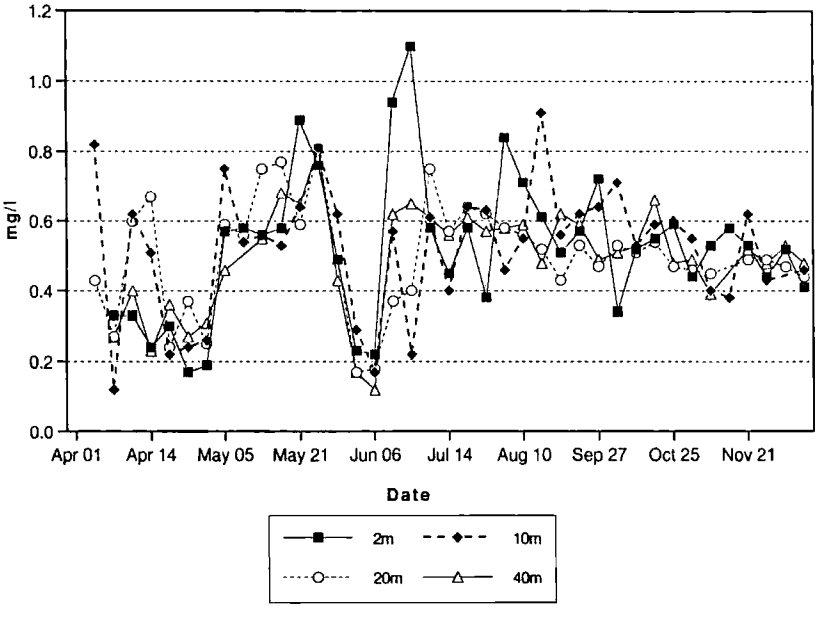


Fig. 8. Amount of seston (living plus dead organic and inorganic particulate matter) in the water column. Water samples were taken between 10 am and 12 am local time. A clear annual cycle is discernible.

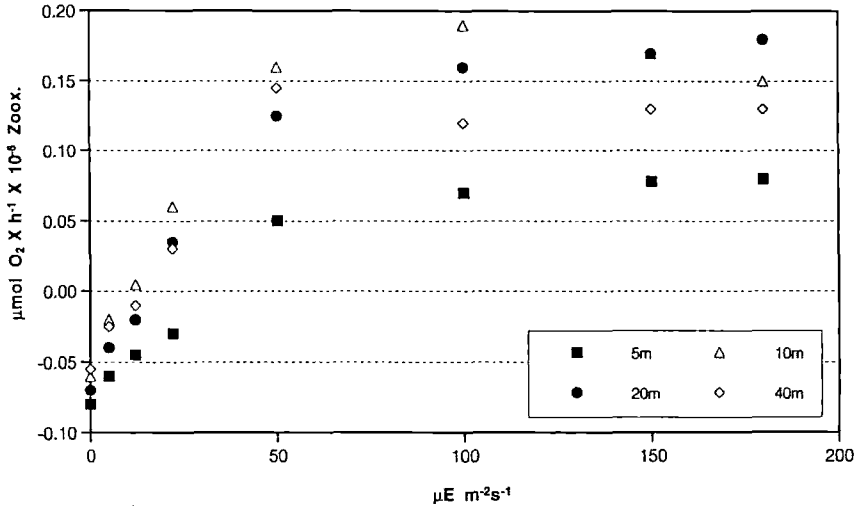


Fig. 9. Respiration and photosynthetic oxygen production of isolated zooxanthellae as a function of light intensity (P/I response). Zooxanthellae were isolated from specimens of *Mycedium elephantotus* collected at different depths:
■ 5 m (n = 5)
Δ 10 m (n = 10)
● 20 m (n = 5)
◇ 40 m (n = 3).
Symbiotic algae prepared from shallow water colonies show lower rates of maximal photosynthesis (Pmax) compared to zooxanthellae isolated from corals growing at greater depth.

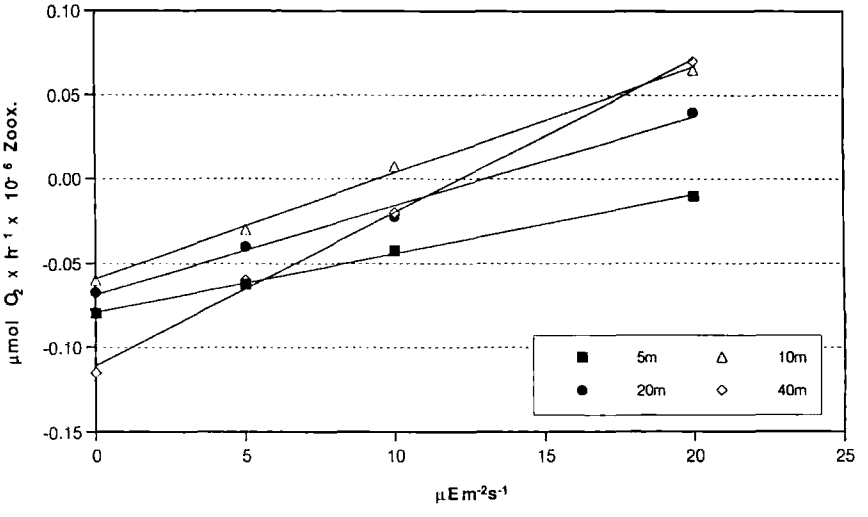


Fig. 10. Photosynthetic efficiency of zooxanthellae isolated from specimens collected at different depth. Symbols as in Fig. 9. The slope for the 40 m zooxanthellae is steepest and for the 5 m-algae slightest. The deep water algae are obviously photoadapted to low irradiance levels which is documented by the highest photosynthetic efficiency.

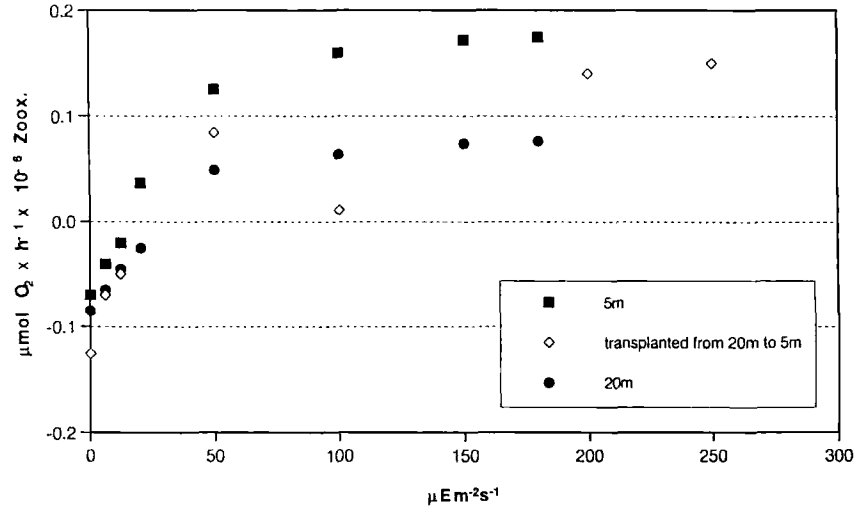


Fig. 11. The effect of transplantation of colonies of *Mycedium elephantotus* from 20 to 5 m depth upon photobiological parameters of isolated symbiotic algae.
● response of zooxanthellae prepared from 20 m specimens.
■ response of zooxanthellae isolated from 5 m specimens.
◇ response of zooxanthellae from 20 m specimens transplanted to 5 m.
After three month under higher light intensities the original 20 m algae lose their former photosynthetic efficiency and the Pmax decreased.

content of organic carbon in sediments at shallow depth. This phenomenon should be taken into account for any evaluation in future. At least in shallow waters the POM supply could be partly responsible for the actual distribution of those species which are predominantly dependent on POM-nutrition by suspension/filter feeding or mucous sheet feeding.

It is well documented that calcification of zooxanthellate scleractinians depends on light (caused via photosynthesis of the zooxanthellae) and temperature (e.g. Rosen 1971, Barnes & Chalker 1990, Falkowski et al. 1990). In the Gulf of Aqaba both factors are cyclic and the annual light cycle itself is superimposed by a diurnal light cycle of varying intensity and duration. Effects of temperature are restricted to shallow water species during the winter months (Fig. 3).

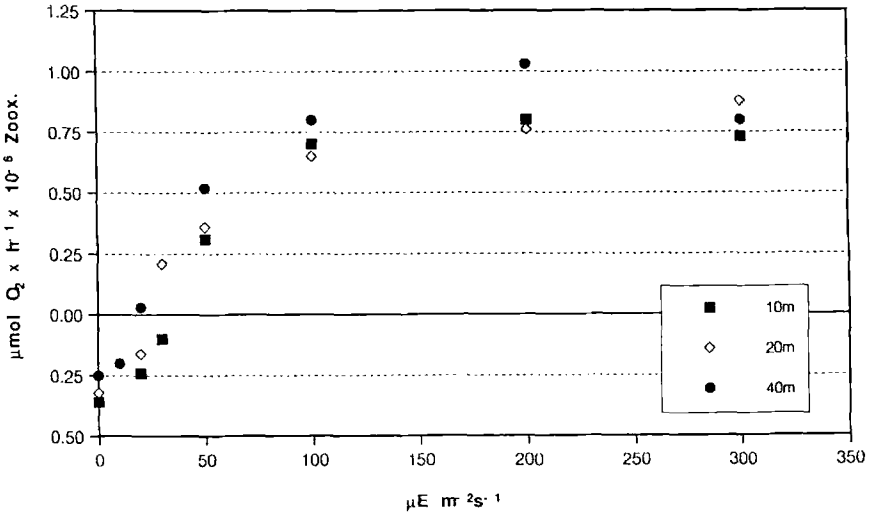


Fig. 12. Respiration and photosynthetic oxygen production by zooxanthellae within tissues of *Mycedium elephantotus* as function of light intensity. The maximum rate of zooxanthellate photosynthesis within the host specimens of all depth zones are 3-4 times higher compared to the photosynthetic capacity of isolated zooxanthellae prepared from colonies growing permanently at the corresponding depths (compare with Fig. 9).

The control of coral or reef growth is complex and almost innumerable growth-promoting or growth controlling factors interact mutually (e.g. FAGERSTROM 1987). The POM data (sediment, seston) may give an impression about the complexity: our POM measurements give only quantitative data, qualitative aspects were not taken into consideration till now. But the quality of POM (composition, nutritive power) and the acceptability by different coral species may differ, i.e. they may have different food preference and the supply may change annually, thus triggering the deposition of calciumcarbonate.

2.5 Phototrophy: Photobiological aspects

In the Gulf of Aqaba distinct seasons, with a pronounced annual cycle in light intensity with a maximum in summer, the period of max. coral growth, exist (Figs. 4, 5). The annual temperature cycle of surface water in the Gulf (18 - 31 °C) may also have an impact upon corals living in shallow depth, for photosynthesis of zooxanthellae is temperature sensitive.

The second energetic input essential for growth and skeleton secretion of corals has its origin in the zooxanthellae. In that context we are studying the availability of light on coral growth as numerous researchers have done before since decades. The hints from our experiments to light enhanced carbonate deposition are indirect; the annual cycle in increment of mass proposes this dependence, however. Primarily we are measuring photosynthesis as a function of light intensity and we conclude in analogy from results of former experiments of other authors (e g. BARNES & CHALKER 1990) that photosynthesis and calcification are positively correlated.

Indispensable in situ respiration and photosynthetic oxygen production measurements produce basic data for the calculation of energy budget of complete colonies. Besides that we are interested in the question whether the symbiotic unicellular algae of zooxanthellate corals are genetically different with respect to photosynthetic efficiency/capacity, or if different 'strains' of zooxanthellae possess high phenotypic plasticity.

To discriminate between photobiological differences, we are analyzing photobiological parameters of isolated zooxanthellae prepared from steno- and eurytope coral species. In subsequent experiments we try to discriminate different genotypes on the basis of allozyme electrophoretic analysis.

The zooxanthellae were prepared from individuals of eurybathic species growing well at different depths and from stenobathic species living predominantly either in shallow or deep waters. The selected specimens were transplanted to inverse depths i.e. light regimes. After an exposure time of at least three months under the new experimental light regimes the isolated zooxanthellae were tested for their photobiologic features. Relevant photoadaptive parameters (viz. pigment concentration, pigment ratio, maximal photosynthetic rate = Pmax, photosynthetic efficiency) were determined.

The preparation method in short: tissue was removed from the skeletons with an air brush system. After homogenization the zooxanthellae were isolated and enriched by density centrifugation (Percoll gradient, Pharmacia) according to TYTLER & SPENCER DAVIS (1983). Pigments were determined after HISCOX & ISRAELSTAM (1978) and quantified according to JEFFREY & HUMPHREY (1975); zooxanthellae were counted with a coulter counter (Casy 1, system Schaerfe); protein was quantified according to MARKWELL et al. 1978, with ovalbumin as a standard. Respiration and oxygen production (= P) as a function of light intensity (= I, P/I response) was measured in 2 ml micro metabolic chambers (Bachofer, FRG), illuminated with luminous tube lamps (Dulux L18W/21, Osram). From all types of experiments zooxanthellae samples were deep-frozen and stored at -80 °C for subsequent gel-electrophoretical investigations.

Photoadaptations towards dim light conditions of complete zooxanthellate corals include various strategies (e.g. JOKIEL 1988, FALKOWSKI et al. 1990). Provided that the host depends in fact on a vital amount of photoassimilates it may regulate the amount of algae within its body. As a function of light availability, the export to the host by the symbionts is reduced. This effect can be compensated by

the host increasing its number of zooxanthellae, but this works only down to a certain depth (light intensity) at which this strategy is ruled out by self-shading of the algae. Not only the total number of zooxanthellae differs from species to species (baseline cm⁻² surface), but the bathymetric regulation of the amount of zooxanthellae and of the pigment content respectively differ specifically for each species as well (REES 1991, KAISER et al. 1993). Reactions of the zooxanthellae themselves towards light limitation include structural and physiological adaptations (FALKOWSKI & LAROCHE, 1990, KAISER et al. 1993). Those photoadaptations include alterations in the content of pigments (chlorophyll *a*, light harvesting pigments) in quantity, quality and their ratio, an increased synthesis, and the formation of larger photosynthetic units, thus enhancing the photosynthetic efficiency/capacity. Enzymatical reactions can also be taken into consideration in the context of improved photosynthesis under reduced light regimes. CHANG et al. (1983) studied photoadaptations of zooxanthellae isolated from molluscs, sea anemones and scleractinians under constant culture conditions. The results of the mentioned authors indicate that the different types (strains) of zooxanthellae are provided with quite different strategies to compensate light deficiency.

The results shown in the Figs. 9 and 10, were obtained with symbionts isolated from colonies of *Mycedium elephantotus* growing permanently at the listed depths. The photokinetic parameters from 5 m algae differ significantly from the others, the max. rate of photosynthesis is less (Fig. 9). Fig. 10 shows clearly that 40 m algae possess the highest photosynthetic efficiency (steepest slope). These results are in accordance e.g. with data from PORTER et al. (1984) who investigated shade and light adapted specimens of *Stylophora pistillata*.

After transplantation of specimens to inverse light regimes (depths) the zooxanthellae react differently as they do under original conditions. One example is given in Fig. 11: the P/I response curves obtained with zooxanthellae from transplanted corals are intermediate, i.e. the photokinetic parameters had changed but have not yet reached the characteristics of zooxanthellae from corals living permanently at that particular depth.

In Fig. 12 photosynthesis as a function of light intensity (P/I response-curves) of zooxanthellae in vivo (polarographic measurements in plexi-glass metabolic chambers) i.e. living within coral tissue, is shown. The over all reaction pattern of the colonies from the three tested depth zones is similar. Striking differences exist, if one compares the in vivo with the in vitro results: in vivo, i.e. under natural conditions maximum rates of photosynthesis are quadrupled despite higher respiration rates. That effect was already described by e.g. SCOTT & JITTS (1977) and SCHLICHTER et al. (1983). Optimal growing conditions within the host vacuole, including fertilization through metabolic endproducts of the host, account for the higher productivity in vivo.

That result is striking in so far that, even under conditions of light limitations, the in vivo and in vitro photosynthetic productions differ, i.e. the photosynthetic efficiency/capacity in vivo is improved. In other words, the transformation of light energy into chemical energy (= the synthesis of assimilates) differs dramatically, and it is hard to explain the differences on the basis of the availability of light alone.

2.6 Impact of light on algal pigments

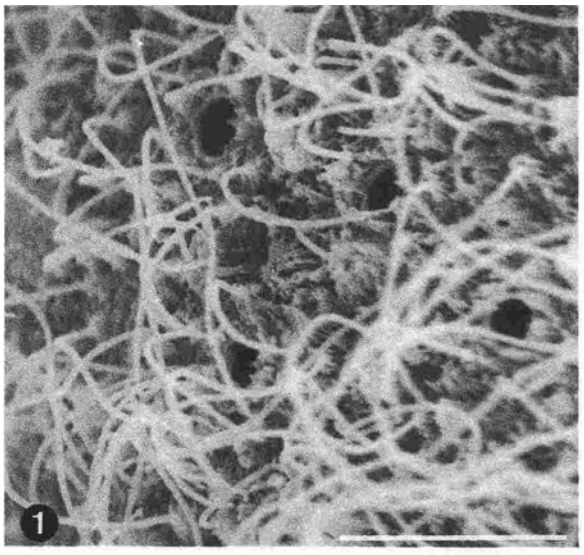
Chlorophyll *a* (chl*a*) and chlorophyll c_2 (chlc_2) content of zooxanthellae from specimens of *Mycedium elephantotus* living in original depths and from zooxanthellae of all P/I-experiments were determined and standardized on one baseline (amount of pigments per 1 Mio. zooxanthellae).

Plate 30 Special adaptations of low light corals to increase heterotrophic and phototrophic energy supply.

Figs. 1., 2. The external body wall (oral epidermis plus oral gastrodermis) of *Leptoseris fragilis* is perforated by pores with a diameter of 1-2 µm through which the gastrovascular cavity communicates with the surrounding water. The gastrovascular cavity does not terminate blindly according to the conventional concept. Water entering through the mouth leaves the body also through the pores. This flow-through system (analogous to those in poriferan or tunicates) improves the retention and accumulation of suspended food particles as well as other functions of the polyfunctional gastrovascular cavity. Scale bars: in Fig. 1 = 8.6 µm; in Fig. 2 = 3.0 µm.

Figs. 3.-5. Photomicrographs of tissue samples (pellicle preparations) of various zooxanthellate scleractinians excited with light of 390 nm. The zooxanthellae (reddish dots) are laying in the gastrodermis on a fluorescent screen or carpet which is formed by ramifications of multilobed chromatophores, densely packed with pigment granules. This arrangement is a common characteristic of all species belonging to the Agariciidae (Fig. 3-5). After excitation with short wavelengths the pigments of the host emit light of longer wavelengths which are photosynthetically more useful. Through light transformation by host pigments the total amount of photosynthetically more effective photons is increased and thus photosynthesis of the zooxanthellae is improved which raises the phototrophic energy supply. Scale for all micrographs: diameter of the zooxanthellae 7-9 µm. Fig. 3, 4: *Leptoseris fragilis*. Fig. 5: *Pachyseris speciosa*.

Fig. 6. *Mycedium elephantotus* (Pectiniidae) is provided with autofluorescent chromatophores in the oral epidermis.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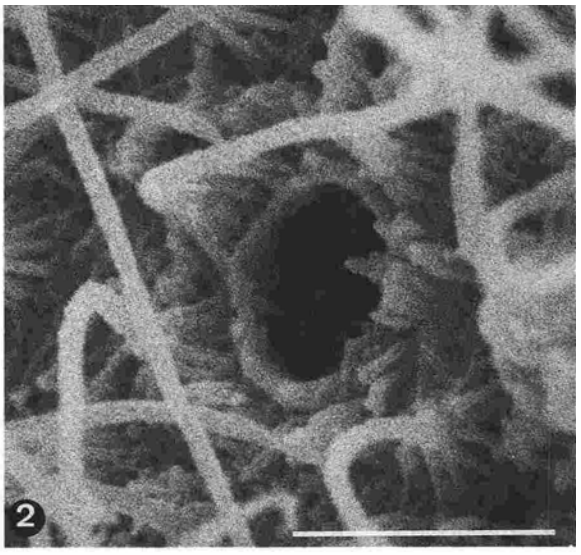
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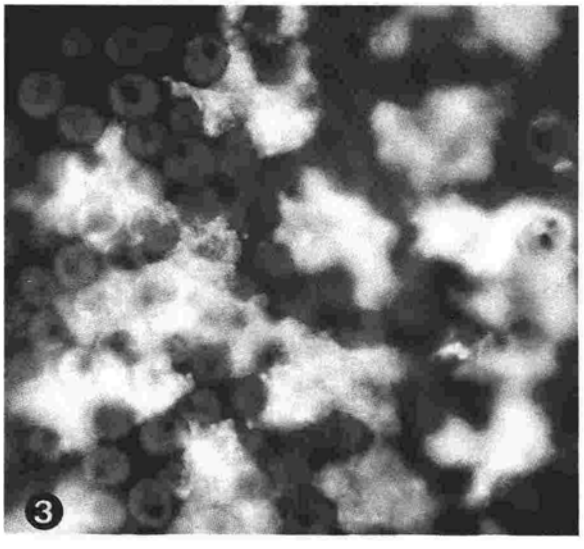
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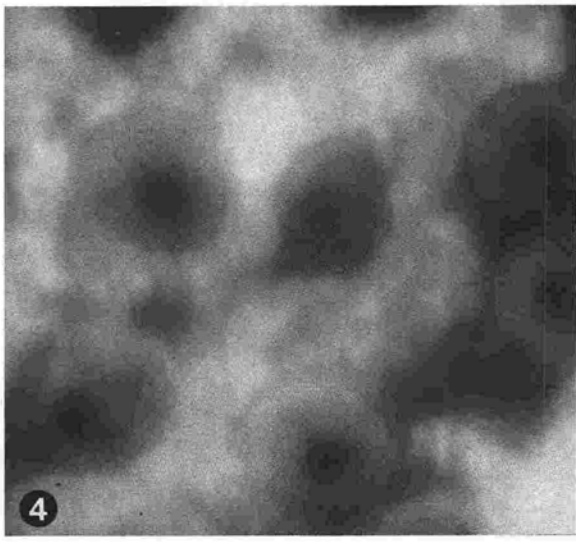
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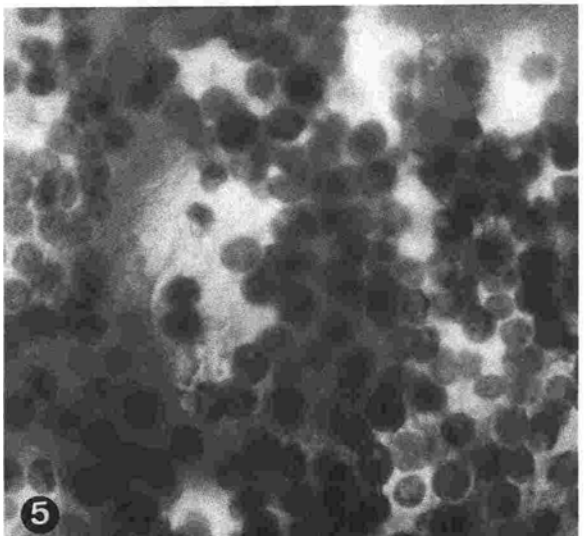
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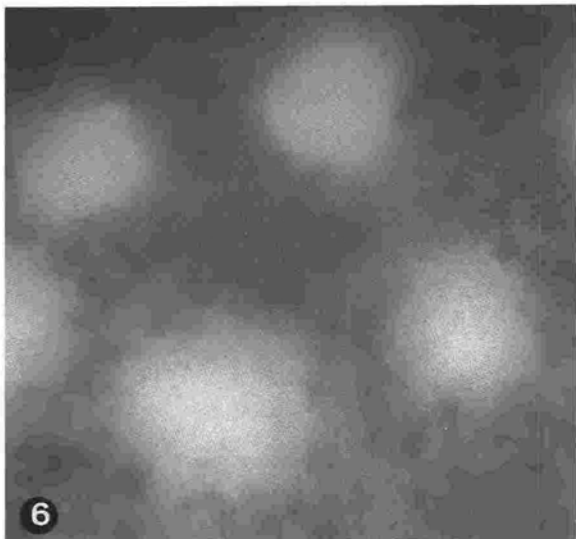
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Species	Depth [m]	n	µg Chla/ 10^6 Zoox. SD(±)	µg $Chlc_2$/ 10^6 Zoox. SD(±)	$Chlc_2$:Chla
M.elephantotus	5	10	2.42 (0.466)	2.16 (0.173)	0.893
M.elephantotus	40	16	4.35 (2.120)	2.11 (1.008)	0.490
A.squarrosa	5	15	4.10 (0.468)	2.81 (0.350)	0.685
A.squarrosa	40	5	5.99 (0.454)	4.78 (0.526)	0.797
S.pistillata	5	3	1.48 (0.245)	1.38 (0.249)	1.154
S.pistillata	40	10	2.23 (1.410)	2.41 (0.935)	1.265

Tab. 2. The content of pigments of zooxanthellae isolated from the listed scleractinian species growing permanently at the listed depths. In dependence on increasing depth the Chl*a* content increased in all species. The $chlc_2$ content remained constant in *M. elephantotus*, in contrast $chlc_2$ increased with depth in *A. squarrosa* and *S. pistillata*.

In addition, data from other eurybatic species are added. The data are summarized in table 2. In bathymetric dependence the chl*a* concentration increased; in contrast, the $chlc_2$ content remained fairly constant in zooxanthellae of *M. elephantotus*, thus the ratio of $chlc_2$: chl*a* declined. This means that $chlc_2$ seems to be less involved in light harvesting in that species and that this function seems to be done by peridinin, but depth dependent alterations of this pigment is not analyzed till now. For the two other species the $chlc_2$ content increased with depth, indicating improved light harvesting through this pigment (PREZELIN & ALBERTE 1978, KAISER et al. 1993). An increase in chl*a* is a common photoadaptation towards light limitation in unicellular algae, including zooxanthellae (FALKOWSKI & LAROCHE 1991, REES 1991). The different reactions of zooxanthellae isolated from the three species might indicate genetic heterogenity.

In summary, the growth of zooxanthellate scleractinians and the annual cycle in extension in the Gulf of Aqaba correlates best with the annual light cycle. Other factors seem to have less influence on growth. The availability of sediments, which are rich in organic carbon, in shallow areas might be of nutritional value for filter feeding species. The continuous availability of POM in free water (minima exist in spring), however, cannot be accounted for the maximal growth of corals during the summer months.

2.7 Improvement of energy intake

2.7.1 Heterotrophy

As mentioned in the introduction, a main goal of our investigations is to determine the growth of scleractinians in dependence of phototrophic and heterotrophic energy supply. Furthermore, we study adaptations, which may improve energy intake.

To exclude misunderstandings in discussing the results of our studies, we like to state that the energetic contribution of each of the three ways of nutrition (see section 2.1) may differ between species. Azooxanthellate corals exemplify, and this is trivial, that corals can live purely heterotrophically (on POM plus DOM). In any scleractinian species each possibility of nutrition depends on environmental conditions of the particular habitat. In other words, if adaptations exist which improve e.g. photosynthesis, we can conclude that those species are superior above species without particular photoadaptations. But those species less potent in phototrophy can compensate this disadvantage through adaptations enhancing heterotrophic energy supply, thus coexisting (living syntopically) in the same habitat on the basis of different strategies.

The zooxanthellate coral *Leptoseris fragilis* inhabits the Golf of Aqaba at depths down to 145 m. In situ respiration and photosynthetic oxygen production experiments have shown that during the months with low solar elevation the corals' metabolism needs vital heterotrophic fueling to compensate for phototrophic deficiency, though special photoadaptations exist to support photosynthesis (see below, SCHLICHTER et al. 1985, FRICKE et al. 1987). The supply with POM seems to be problematic at first glance: the discoidal-shaped coral lacks tentacles, prerequisites for capturing plankton, and the habitat is far away from the productive zones near the surface.

The architecture of the corallite and the histology of the polyparium were analysed for adaptations enabling efficient capture and retention of particles (organic detritus, bacteria, minute plankton) which would increase heterotrophic energy supply (SCHLICHTER 1991, 1992). The investigations indicate that the gastrovascular system of *L. fragilis* is not, according to the conventional concept of coral coelenterons, a blind ending but a flow-through system. Water pumped into the coelenteron through the mouth does not only leave the body exclusively through the same opening -as it was generally assumed- but also through microscopic pores (1-2 µm) located in groups near the crests of the sclerosepta in the external body wall (oral gastrodermis/oral epidermis, Pl. 30/1-2). The shape of the pores suggests that water flows in one direction. The diameter of the pores is small enough to keep back minute particles, including e.g. bacterioplankton. The water stream within the coelenteron is generated by flagellae. Irrigation could also be achieved by muscle action. The *unidirectional* water flow in the gastrovascular cavity leads to the accumulation of particles, including nutritive ones. The unidirectional water current also promotes other functions of the polyfunctional coelenteron. The flow-through system of *L. fragilis* operates putatively much more efficiently than gastrovascular systems with blind endings. The particular advantage of a perforated coelenteron could be the utilization of suspended microbial biomass and detritus. Both trophic resources are available in abundance

in reef areas although their nutritional importance is underestimated (ALONGI 1988, DUCKLOW 1990). It is most probable that other coral species are also provided with perforated coelenterons, thus exploiting specific resources of the habitat. The porosity of a coelenteron, which is a contradiction in terms, might have general consequences with respect to taxonomic and evolutionary aspects.

2.7.2 Phototrophy

KAWAGUTI (1970) presumed that greenish, epidermal pigments of corals might be involved in photosynthesis of the zooxanthellae. Kawaguti's hypothesis was supported for the zooxanthellate deep water coral *Leptoseris fragilis* by SCHLICHTER et al. (1985, 1986, 1988) and SCHLICHTER & FRICKE (1990, 1991).

Therefore it was of interest to study other scleractinian species for the provision with autofluorescent chromatophores of the type found in *L. fragilis*. Autofluorescent chromatophores were detected in 17 out of 71 zooxanthellate coral species studied. Autofluorescent chromatophores are localized either in the oral gastrodermis (endoderm) or oral epidermis (ectoderm). The pigment granules, within the multilobed chromatophores (0.5 - 1.0 µm in diameter) of the gastrodermis show brilliant light-blue/turquoise autofluorescence (see Pl. 30/3-5, emission between 430 and 500 nm) after excitation with light of 365-410 nm. All species, in which the autofluorescent gastrodermal chromatophores form a compact layer, embedding (wrapping) the zooxanthellae, belong to the family Agariciidae (Pl.30/3-5). This family includes predominantly deep water or cryptic living species, but also very successful pioneer species (e.g. *Pavona varians*). In contrast to that, some species of the Faviidae (2), Pectiniidae (1) and Mussidae (1) were found to have distinct, autofluorescent chromatophores in the oral epidermis (Pl. 30/6).

In analogy to *L. fragilis* photosynthesis might be improved in the Agariciidae by the following mechanisms: short wavelength irradiance (390-410 nm), less suitable for photosynthesis by the zooxanthellae themselves, is transformed by host pigments into longer wavelengths which are photosynthetically more effective. In addition, scattering and reflection of photons on the pigment granules of the chromatophores may contribute to an enhanced light supply of the zooxanthellae. For epidermal chromatophores the situation differs, but improvement of photosynthesis may work through comparable mechanisms.

A few species of hermatypic, zooxanthellate scleractinians appear to have evolved photoadaptations which allow the utilization of radiation in the short waveband. The supplementary utilization of short wavelengths by zooxanthellate scleractinian species provided with autofluorescent chromatophores leads to advantages concerning energy supply and carbonate deposition.

From an adaptive point of view the correlation between the presence of light transforming pigments in certain zooxanthellate scleractinian species and the availability of light in reefs seems to be of general ecological interest. The provision of autofluorescent chromatophores/pigments enables those species to settle in dim-light habitats in general. Those species may extend their bathymetric distribution. They can live in shady, cryptic habitats. Light supplying adaptations of the host could be advantageous in situations where colonies may potentially be overgrown by faster growing species. Autofluorescence may partially compensate within one colony for the reduction of photosynthesis due to self-shading by growth. The daily period of photosynthesis may be extended and intensified, leading to faster growth including carbonate deposition.

3 CARBONATE PRODUCTION RECORDED IN CORAL GROWTH RATES

G. A. HEISS and W.-C. DULLO

3.1 Introduction

Environmental factors which could influence coral growth are almost unlimited in number (BUDDEMEIER & KINZIE 1976). Water depth and geographical location are the factors most easy to determine. The relation of the growth of scleractinian corals to water depth has long been recognized (VAUGHAN 1919). Depth is a mixed environmental variable, including mainly the effects of light, water movement, and resuspension of sediment. A thorough review of the extensive studies on environmental relations to coral growth is given by BUDDEMEIER & KINZIE (1976).

Light is assumed to be the primary environmental factor controlling growth and carbonate production of hermatypic corals, and light-enhanced calcification is responsible for most of the skeletal growth and carbonate production of reef-building corals (GOREAU 1959, CHALKER et al. 1988, BOSSCHER 1992).

In laboratory experiments the dependency of coral growth on both temperature and insolation was observed for corals of the genera *Porites, Pocillopora, Montipora, Cyphastrea* and *Pavona* (HOUCK et al. 1977). Some species had sharp growth optima at characteristic temperatures (*Porites, Pocillopora*), while *Montipora* had a poorly defined maximum. Response to decreasing insolation is also different. *Porites* and *Pocillopora* growth decreased with decreasing light intensity, while *Montipora* growth was enhanced (HOUCK et al. 1977).

A decrease in growth rates with increasing water depth is generally caused by the decrease of illumination and was reported for the Caribbean corals *Montastrea annularis*, (BAKER & WEBER 1975, DUSTAN 1975, HUBBARD & SCATURO 1985, HUSTON 1985), *Porites astreoides* and *Diploria labyrinthiformis* (LOGAN & TOMASCIK 1991). A similar pattern is reported for Indopacific species like *Porites lutea*, *Favia pallida*, and *Goniastrea retiformis* (BUDDEMEIER et al. 1974, HIGHSMITH 1979). BOSSCHER (1992) could show that the growth rate of *Montastrea annularis* decreases exponentially with depth following a photosynthetic hyperbolic tangent function.

Growth rates of scleractinian corals decrease generally with increasing latitude in the Atlantic, Pacific and Indian

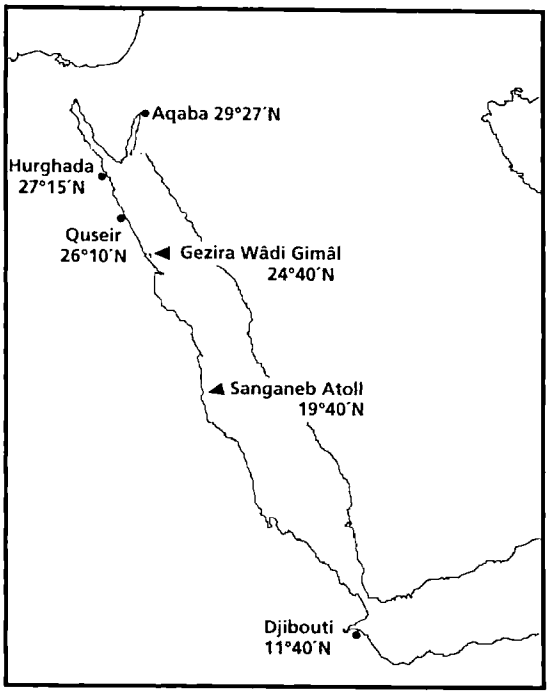


Fig. 13. Collection sites in the Red Sea and Gulf of Aden.

Oceans (GRIGG 1982, CROSSLAND et al. 1991, LOGAN & TOMASCIK 1991). Although the coral *Montastrea annularis* in the Caribbean is extensively studied, the relation between growth and latitude for this species is ambiguous (review by LOGAN & TOMASCIK 1991). Nevertheless the general trend remains a credible theory. The Red Sea with its extension over almost 20° of latitude and living coral reefs growing along the greatest part of its coastline presents a unique area for study of latitudinal effects on coral growth. The Red Sea is today a desert-enclosed sea. This fact is important if we consider that the growth patterns of corals are influenced by precipitation, cloud cover, and freshwater discharge with its effects on salinity and turbidity. In the Red Sea at least these environmental factors remain unchanged over its whole extension. However, in the Gulf of Aqaba clouds and episodical rainfalls as well as groundwater discharge occur occasionally during winter.

The main objective of this study was to compare coral growth patterns of the genus *Porites* in relation to latitude and water depth in the Red Sea-Gulf of Aden reef province. Our study area extends from Aqaba, at the northern end of the Gulf of Aqaba, through the reefs of the northern Red Sea off Hurghada and off the southern Egyptian coast to the reefs in the western Gulf of Aden (Fig. 13). *Porites* was chosen because corals of this genus are probably the most important reef builders due to their ubiquitism and their ability to secrete huge massive colonies. Furthermore, *Porites* skeletons display in most cases a clear defined density banding, which enables the measurement of annual linear extension rates. As *Porites* is a common scleractinian genus in all major reefs of the world, these data facilitate comparison of growth rates and carbonate production. Studies on coral growth are rare for the Red Sea, but a few data are published from the reefs at Eilat, Gulf of Aqaba (KLEIN & LOYA 1991, KLEIN et al. 1993).

Extensive studies on coral reefs exist from the Gulf of Aqaba (e.g. MERGNER & SCHUHMACHER 1974, 1981, MERGNER 1979, BOUCHON et al. 1981, SCHUHMACHER & MERGNER 1985, KLEIN & LOYA 1991, KLEIN et al. 1993). Even though not a part of the proper Red Sea, the reefs in the Gulf of Tadjoura belong biogeographically to the Red Sea coral reef province. The Gulf of Tadjoura is almost unknown in the coral literature. There has been no work on corals in this region published since GRAVIER (1911).

3.2 Materials

In total 100 complete coral colonies and 6 core samples of the genus *Porites* were sampled. Twenty samples from Aqaba (Fig. 13) were taken at the fringing reef off the Marine Science Station at water depths from 1 to 50 m. At a fore-reef slope close to the Jordan-Saudi Arabian border eighteen samples were collected from depths between 2 and 45 m, and one sample at a depth of 3 m halfway between the Marine Science Station and the Saudi border site.

In order to increase the sample size, growth rate data from six cores (HEISS 1994) from the Marine Science Station reef are included in the calculations. Growth rate data of nine samples from a *Porites* pinnacle in the fore-reef of the Marine Science Station are displayed for comparison in Fig. 14. However, these samples are not included in the calculations shown in Tables 3 and 4 because this pinnacle provides particular conditions different from the reef bottom (see HEISS 1994).

Samples from the northern part of the Egyptian coast (14 specimen) derive from the islands of Gûbal, Tawîla, Giftûn el Kabîr, Giftûn el Saghîr, and Abu Rimâthi, a fringing reef off Hurghada, and a fringing reef north of Quseir (Fig. 13). The colonies were sampled in depths between 1 and 15 m from lagoonal to fore-reef environments.

Twenty-two samples were collected in the reefs of the islands Gezira Showârît and Gezira Wadî Gîmal and the coastal fringing reef at Ras Abu Ghusum. Another ten specimen were sampled from 2.4 m to 42 m water depth at the slope of a fringing reef off the Southern Egyptian coast at Gezira Showârît (Fig. 13).

Five samples were collected at the reef crest of two fringing reefs (Arta Plage and Doralé, water depth 4 to 6 m) at the southern coast of the Gulf of Tadjoura, Djibouti (Fig. 13).

Five core samples were drilled from *Porites* colonies at the fore-reef at Sanganeb-Atoll and Wingate reef offshore Port Sudan at depths from 1 to 11.5 m (Fig. 13). The growth bands were measured at the top of all colonies. For detailed information about the methods used for the determination of growth rates refer to HEISS et al. (1993).

3.3 Results

At Aqaba growth rates of single *Porites* specimen ranged from 4 to approx. 10 mm yr^{-1} in shallow water and

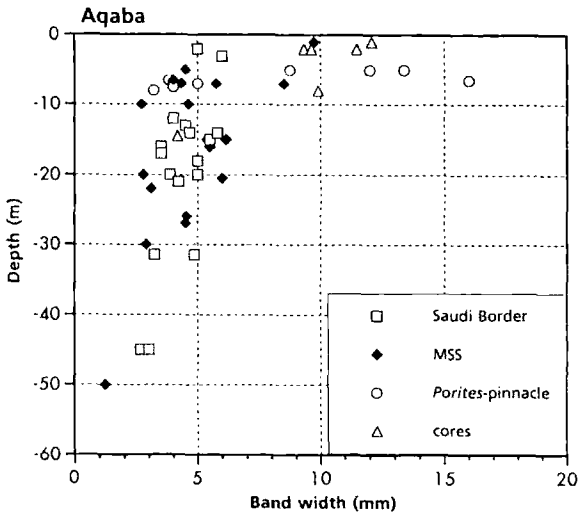


Fig. 14. Width of annual bands of *Porites* sp. in the fringing reefs at the Saudi Border and the reef at the Marine Science Station (MSS), both south of Aqaba. Samples from a *Porites* pinnacle and core samples derive also from the MSS reef. These samples display the highest growth rates observed. Pinnacle samples are not used for the calculations of table 3 and 4 (explanation see text).

decreased to 1.25 mm yr^{-1} in a depth of 50 m (Fig. 14). Values from the sampling sites at the Marine Science Station and at the Saudi Border are in the same range and thus can be regarded as parts of the same population (Table 3, Fig. 14). Growth rates higher than 8 mm yr^{-1} occur in colonies which derive from an isolated *Porites* pinnacle (Heiss 1994), and in core samples drilled from large colonies at the reef edge (Fig. 14) derived from the Marine Science Station reef.

Corals from the northern Egyptian coast, sampled in depths between 1 and 15 m, show a range of linear extension from 4 to 12.9 mm yr^{-1} (Fig. 15). Growth rate does not display a dependence on depth. Colonies with the lowest growth rates derive from reef flat environments at a reef off Hurghada.

The results from the southern Egyptian coast display a more detailed picture (Fig. 16). In greater water depths (16 m, to 38.6 m) the growth rate was less than 4 mm yr^{-1}. Extension slowly increases with decreasing depth from 40 m to about 15 m. In shallower water high growth rates with values greater than 7 mm yr^{-1} are frequent.

Extension rates measured from core samples offshore Sudan range from 8.9 mm yr^{-1} (11.5 m) to 14.7 mm yr^{-1} (2 m) and decrease with increasing depth (Fig. 17). Samples from Djibouti grew with a rate of 7.3 to 13.3 mm yr^{-1} (Fig. 16). From linear extension rates seen in X-ray images we calculated mean growth rates for different depth zones (Table 4). At all sites the growth rates in shallow depths are of a much wider range than in depths below ca. 10-15 m (Figs. 14-17, and Table 4).

The sample size allows a comparison between the data obtained from hand specimen at Aqaba and the southern Egyptian reefs. Mean growth rates in the different depth zones are remarkably similar (Table 4, Fig. 16). A decrease of growth with increasing depth is evident in both regions (Fig. 18). The greater part of this decrease occurs in shallow water above ca. 15 m depth (Figs. 14, 16, 18). The variation within each depth zone, shown by standard deviation, is highest in shallow depth. The samples display more consistency in deeper parts of the reefs (Table 4). At Aqaba growth rate distribution is relatively consistent from 10 m downwards, while at South Egypt the variation is still high and stabilizes below 20 m. The samples from Djibouti fall in the fast growing group of studied corals and display the highest mean value (10.81 mm yr^{-1}) for the upper 5 m (Table 4 and Fig. 17)

Comparing the core samples from Aqaba and Sudan we observe higher extension rates at Sudan over the entire depth range (Fig. 17).

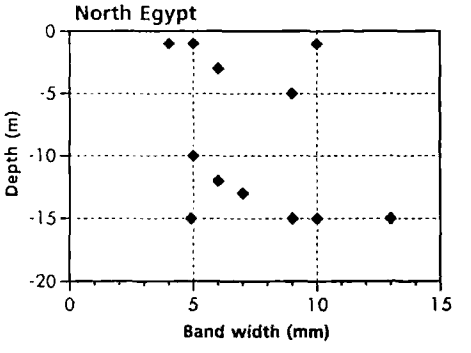


Fig. 15. Width of annual bands of *Porites* sp. in the reefs at the northern part of the Egyptian coast.

3.4 Discussion

3.4.1 Growth rate vs. depth

In the discussion on the growth rate-depth relationship we refer mainly to the results obtained at Aqaba, South Egypt and Sudan.

a

MSS	Mean	SD	Min	Max	n
0-5 m	10.46	1.24	9.33	12.08	5
5-10 m	6.16	2.47	4.00	9.90	6
10-20 m	4.76	1.23	2.70	6.17	6
20-30 m	4.19	1.29	2.78	6.00	5
30-50 m	2.07	1.17	1.25	2.90	2

b

Saudi Border	Mean	SD	Min	Max	n
0-5 m	5.50	0.71	5.00	6.00	2
5-10 m	-	-	-	-	-
10-20 m	4.43	1.01	3.00	5.80	8
20-30 m	4.35	0.59	3.86	5.00	3
30-50 m	3.44	0.98	2.66	4.86	4

Tab. 3a,b. Summary statistics for annual mean growth rates of *Porites* sp. (mm yr^{-1}), standard deviation (SD), minimum value (Min), Maximum value (Max), and number of colonies sampled (n) at each depth zone at the Marine Science Station reef (MSS) and the reef slope at the Saudi border. Core samples are included in the calculation.

Depth zone	Mean growth rate (±SD)			
	Aqaba	N-Egypt	S-Egypt	Djibouti
0-5 m	8.41 ±3.02 (6.19±2.51)	5.83 ±2.14	8.19 ±1.11	10.81 ±2.55
5-10 m	6.16 ±2.47	9.00	5.66 ±3.27	
10-20 m	4.57 ±1.08 (4.60 ±1.11)	7.84 ±2.98	5.81 ±2.99	
20-30 m	4.25 ±1.03		3.69 ±1.04	
30-50 m	2.98 ±1.16		2.32 ±0.87	

Tab. 4. Mean growth rates of *Porites* sp. from four localities in the Red Sea, grouped in depth zones (± standard deviation SD). Values in brackets are calculated without respecting core samples.

We observe some interesting patterns in the variation of growth rates within different depth zones. The greatest variation is measured in the samples from a depth zone shallower than 10 m at Aqaba and 15 m at South Egypt (Fig. 18). In studies on coral growth from the Caribbean a similar pattern is observed (HUBBARD & SCATURO 1985, BOSSCHER 1992). At Jamaica HUSTON (1985) studied the growth of several scleractinian species in relation to depth. Data for *Porites astreoides* display a similar trend like the samples from the Red Sea and the Gulf of Aqaba. At Aqaba two groups seem to be present. One group displays an almost linear increase of growth rate from 1-2 mm yr^{-1} at the outer fore-reef at 50 m depth to about 6 mm yr^{-1} in the shallow upper fore-reef. The second group is characterised by annual extension rates higher than 8 mm. All corals which were sampled by drilling fall in this group (Fig. 14). This is probably an effect of the selection of samples. When we collected entire specimens, we took relatively small colonies maximal as big as a fist. For drilling, colonies of at least 0.5 m diameter were chosen. Thus the cores represent growth patterns of quite large and old colonies. These are growing particularly at the reef crest. Colonies in the fore-reef rarely reach this size.

The colonies which derive from a *Porites* pinnacle in the fore-reef contribute the other part of the fast-growing group. These colonies grew at the top of a 5 m high pinnacle under favoured conditions with very low sediment stress (see HEISS 1994). Samples from Egypt were all entire specimen taken from the reef ground and thus do not represent particular environmental or size conditions.

Temperature effects are most probably not the reason for the decrease of growth rates with depth. Red Sea and Gulf of Aqaba are isothermal over the studied depth range. Only at the reef flat extreme temperatures in summer and winter may occur. Sedimentation and resuspension also can not induce a decrease of growth, as both are highest in the shallow parts of the reef. Thus, light seems to be the primary controlling factor of coral growth rates in the Red Sea, as it is in the other oceans. From the Caribbean a critical depth of 15 to 18 m for growth of large spherical and hemispherical colonies, which divides shallow from deep populations, is reported (DUSTAN 1975, HUBBARD & SCATURO 1985, BOSSCHER 1992). BOSSCHER (1992) suggests that this sharp decrease reflects the lower limit of light saturation. Our observations do not contradict this assumption. However, a relation to a photosynthetic hyperbolic tangent function, as described by Bosscher, is not evident. This might be the effect of the intenser light penetration in the Red Sea, which is also responsible for the extended depth limit of living scleractinians (FRICKE & SCHUHMACHER 1983, HALLOCK & SCHLAGER 1986).

The growth potential of *Porites* seems to be controlled mainly by light availability. If the light saturation limit is exceeded, the genetical potential can lead to high growth rates in shallow depths, unless no suppressing factors like sedimentation, salinity and temperature changes, etc. occur.

3.4.2 Growth rate vs. latitude

As colony size seems to have a distinct influence on extension rates we compare similar sized hand specimens and core samples separately. A sudden increase of size-independent growth rates occurs at Aqaba above 10 m depth, while values above 8 mmyr^{-1} are reached at Egypt already at 15 m depth (Figs. 14, 16, 18). Furthermore, most of the samples in shallow depths grew with relatively high rates compared to Aqaba. The mean growth rate at Aqaba

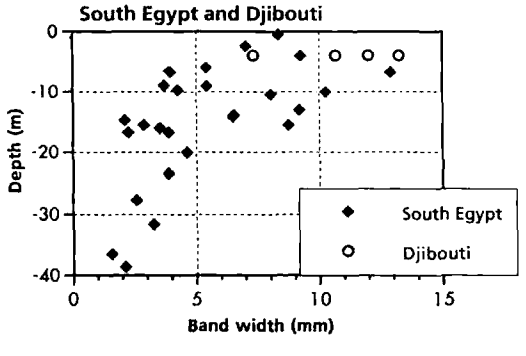


Fig. 16. Width of annual bands of *Porites* sp. in the reefs at the southern part of the Egyptian coast and the Gulf of Tadjoura (Djibouti).

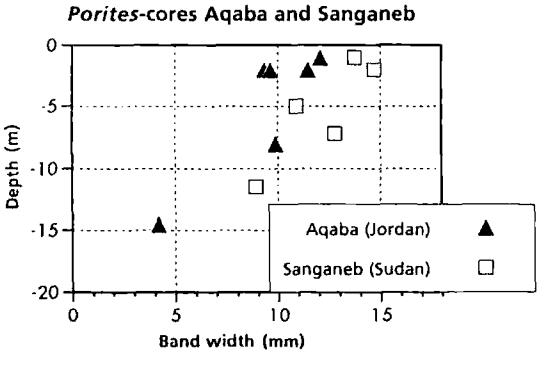


Fig. 17. Width of annual bands of *Porites*-cores drilled at Aqaba and Sanganeb. Growth rates of Sudan-corals are higher by 3 to 4 mm yr^{-1}. Calculated with a density of ca 1.7 g cm^{-3} potential production is higher by 5 to 7 kg m^{-2} yr^{-1} (0.5 to 0.7 g cm^{-2} yr^{-1}).

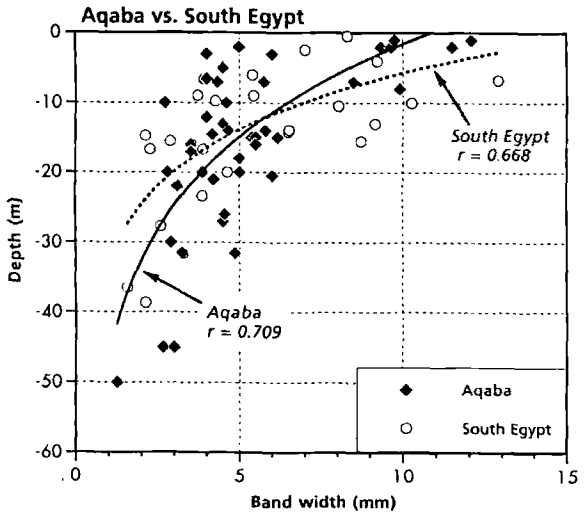


Fig. 18. Width of annual bands of *Porites* sp. at Aqaba (including MSS samples, cores, and Saudi border samples) and South Egypt. Curve fit is logarhythmic. The decrease of growth rate with depth is evident. In the southern Egyptian reefs the growth reaches high values down to a depth of about 16 m, while at the Gulf of Aqaba fast growth is restricted to the upper 10 m.

computed only for whole specimen samples for the 0-10 m depth zone is 6.17 mm yr^{-1}, thus similar to the results from northern Egypt and slightly lower than at southern Egypt with 6.42 mm yr^{-1}. If core samples are included (Table 4), corals from Aqaba show the highest values, which is also an effect of sample selection (see above). Differences between 10 m and 20 m depth with lowest values at Aqaba are prominent. The growth of shallow samples from Djibouti lies in the upper range of the values recorded from the Red Sea and suggests generally high growth rates in the Gulf of Tadjoura. However, due to the small sample size this remains to be proven.

At each depth extension rate measured from core samples is higher at Sudan than at Aqaba. Mean values for the upper 5 m are 10.63 (± 1.35) mm yr^{-1} at Aqaba and 13.2 (± 1.98) mm yr^{-1} at Sudan.

GRIGG (1982) found at the Hawaiian Archipelago an inverse relationship between latitude and coral growth. Growth rates declined from 13 mm yr^{-1} at the southeastern end of the chain to 3 mm yr^{-1} in the northwest, within ca. 9° of latitude. A comparison between growth rates for *Diploria labyrinthiformis* and *Porites astreoides* at the high-latitude reefs of Bermuda with those of low latitude West Indian localities revealed also an inverse relationship of growth rates with latitude (LOGAN & TOMASCIK 1991). These differences are controlled by reduction of winter water temperatures and light levels with increasing latitude (LOGAN & TOMASCIK 1991).

The growth rate of *Porites* in the Red Sea seems to decrease as well to higher latitudes. However, the dimension of this decrease over an even higher latitude range of 17° between Aqaba and Djibouti is far less than that observed in the Pacific by Grigg. The main cause for the low rate of decrease are the high growth rates in the Gulf of Aqaba up to 29° 30'N. The high species diversity suggests that the reefs at Aqaba do not mark the northernmost ecophysiological outpost of the Indian Ocean (SCHUHMACHER & MERGNER 1985). Reefs would occur at even higher latitudes, if the Gulf extended further north. This conclusion is supported by the results of growth rate investigations presented in this study.

What does enable the unexpected high growth rates in the northern part of the Red Sea and the Gulf of Aqaba? The Red Sea has very particular oceanic parameters. As a semi-enclosed basin with restricted water exchange with the Indian Ocean and no connection to the north, it provides generally better conditions for coral growth than most other areas at the same latitudes. Water is of exceptional transparency in the Red Sea and Gulf of Aqaba, which permits coral growth to extreme depth (Fricke & KNAUER 1986).

The inverse relationship between latitude and growth rates in the Atlantic and Caribbean was explained by LOGAN AND TOMASCIK (1991) to result from reduction of winter water temperatures and illumination. Probably the same effects can be attributed to the observed pattern in the Red Sea. The temperature difference between northern and southern Red Sea is ca. 5-6 °C in winter and summer. Difference from the Gulf of Aqaba to the northern Red Sea off southern Egypt is about 3 °C. We assume the higher yearly growth rates to the South to be enabled by higher temperatures and light levels in winter. The suppression of growth is probably not as strong as in the Gulf of Aqaba, where light availability is reduced by cloud cover and the shorter period of daylight. Water temperature occasionally falls below 20 °C, thus approaching the lower limit of coral growth (BUDDEMEIER & KINZIE 1976). In summer the environmental conditions enable high extension rates at the Gulf of Aqaba, while in the central and southern Red Sea temperature exceeds 30 °C, which is much higher than the field of growth optimum (27 °C, BUDDEMEIER & KINZIE 1976). Additionally the higher oceanic productivity levels in the southern Red Sea might have negative influences on coral growth. At the northern end coral growth is suppressed by low temperatures and light levels in winter (December and January), while in the southern areas high temperatures and productivity levels probably reduce growth rates in summer (July and August). Latitudinal differences in annual growth rates are therefore more ambiguous and sensitive to local influences as in other parts of the world. The detailed study of seasonal growth rate patterns of corals from the central and southern Red Sea will clarify these hypothesis.

An indication for higher growth rates towards the South of the Red Sea is detectable from our results. However, varying number and depth distribution of samples, and the differences of local environmental influences, which could not be investigated in detail make us cautious in conclusions on latitudinal control of coral growth. Mainly the selection of study areas should receive special attention. Islands in some distance from coastal sedimentary influx promise to provide the most illustrative results.

4 COMPOSITION OF REEF COMMUNITIES WITH REGARD TO HERMATYPIC PROPERTIES IN THE NORTHERN AND CENTRAL RED SEA

D. K. KROLL, G. B. REINICKE and H. SCHUHMACHER

4.1 Introduction

In the foregoing parts it has been shown that the calcification rate of scleractinian corals differs among species and varies with season, depth and geographical latitude. The rate of carbonate deposition of a coral reef community (deposition per area) depends on the proportions of hermatypic and ahermatypic reef inhabitants (mainly scleractinians and alcyonaceans) and on the sharing of empty space. The spatial and temporal variance in these proportions overlies that of the specific calcification rates and may be more significant for reef growth. The composition of characteristic communities on the fringing reef at Aqaba and on Sanganeb-Atoll was quantitatively analysed using the transect and quadrat method.

At Aqaba, 10 m transects were distributed on the reef between the reef flat and the deep fore reef down to 50 m, about 150 m off the Marine Science Station (Fig. 19) and near the border of Saudi Arabia (Fig. 20). Descriptions of this area have been given by MERGNER & SCHUHMACHER (1974, 1981). The study areas on Sanganeb-Atoll (refered to as test square TQ I - TQ IV, Fig. 21) were four 5 x 5 m squares at a depth of 10 m, two at the outer side, two at the lagoon side of the reef. Hereto detailed descriptions have been given by MERGNER & SCHUHMACHER (1985a). In addition, line transects at the outer SSW side of the atoll down to 30 m and in the lagoon were used.

Cover of living organisms, coral rock and sand were assessed by transect mappings and photographs. These data were supplemented by visual qualitative records in selected fore reef habitats.

Data obtained in detail from repeated mappings of test areas (U-7 at Aqaba, TQ I-IV on Sanganeb-Atoll, see MERGNER & SCHUHMACHER 1981, 1985a, 1985b, MERGNER et al. 1994, SCHUHMACHER & MERGNER 1985, SCHUHMACHER et al. in press) are not considered here, since investigations focussing on the long-term dynamics of a community will be reported separately.

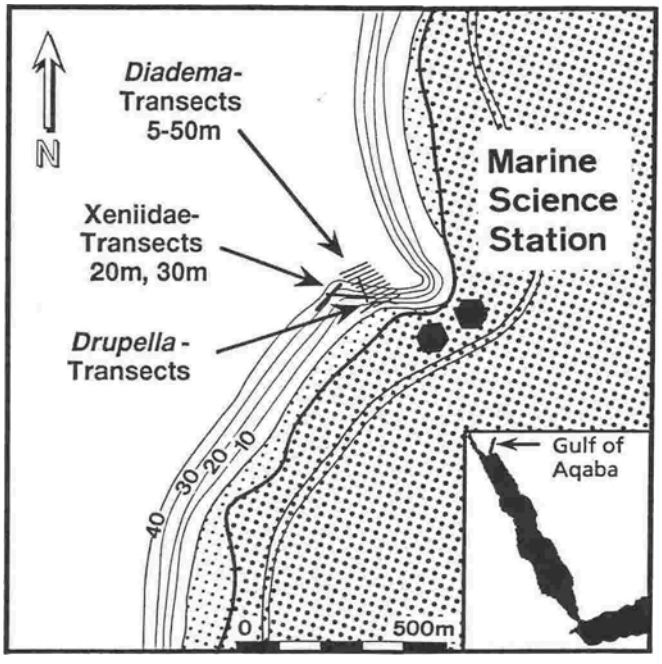


Fig. 19. Observation and collection sites south of the town of Aqaba at the Marine Science Station, Gulf of Aqaba.

'Coral cover' multiplied by growth rate of a distinct scleractinian species (e.g. *Porites* sp.) is a conventional approach to estimate the amount of precipitated $CaCO_3$ on a reef. This chapter provides two caveats to this approach. 1. Zooxanthellate and hermatypic is not the same (see SCHUHMACHER & ZIBROWIUS 1985) and 2. in benthic communities stony corals should sharply be discriminated against soft corals. In contrast to scleractinians, alcyonacean reef dwellers are still rather unknown regarding their productivity and population ecology. This is mainly due to a lack of taxonomic familiarity with the group. The Xeniidae as most conspicuous elements of soft coral cover in the Red Sea benthic communities were given particular consideration in the investigations.

4.2 Characteristic associations

At Aqaba on the reef flat towards the reef crest colonies of *Sinularia polydactyla* and *S. leptoclados* form dense

Plate 31 Significance of alcyonacean corals in Red Sea reef communities.

Fig. 1. Edge of the reef flat with stands of the alcyonacean *Litophyton arboreum*; Aqaba near Marine Science Station, depth 1.5 m.

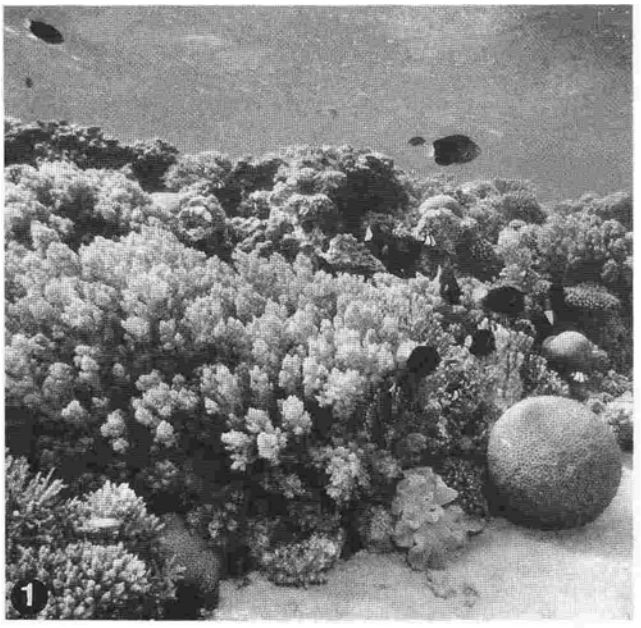
Fig. 2. Fore reef section dominated by *Anthelia glauca* (center) and *Sinularia* (on the left) species; Sanganeb-Atoll, southern outer reef slope below TQI, depth 20 m.

Fig. 3. Community of scleractinians and alcyonaceans. Colonies of *Acropora hemprichi*, *Porites* sp., *Xenia* spp., *Sarcophyton ehrenbergi* and *Sinularia* sp. can be distinguished; Sanganeb-Atoll, southern slope, depth 10 m. Scale: 20 cm.

Fig. 4. Extended stands of *Xenia macrospiculata*, *X. obscuronata* and *X. faraunensis* on the lower fore reef; Aqaba, near Marine Science Station, depth 18 m. Scale: 20 cm.

Fig. 5. Aspect of the turbid lagoon near TQII with dead *Acropora* and other coral skeletons covered mostly by xeniid colonies; Sanganeb-Atoll, depth 18 m. The *Acropora* table (top right) is 1 m in diameter.

Fig. 6. Dead *Acropora* table (1.2 m diameter) covered by xeniid species; Sanganeb-Atoll lagoon, depth 18 m.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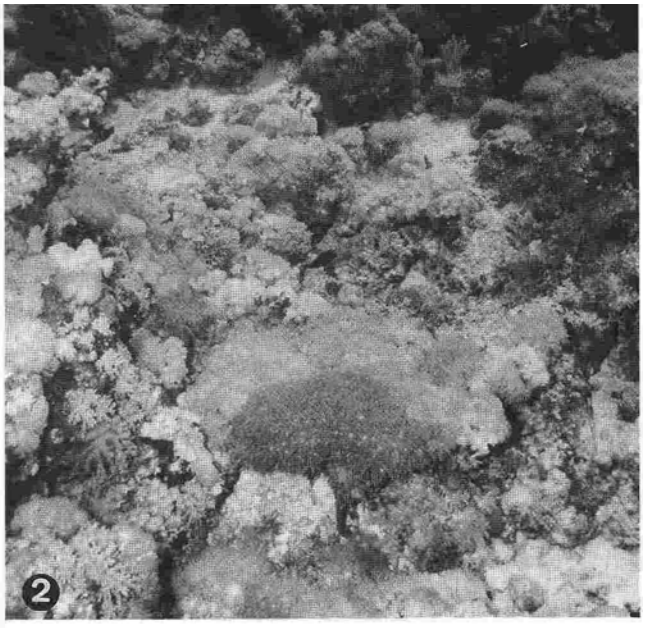
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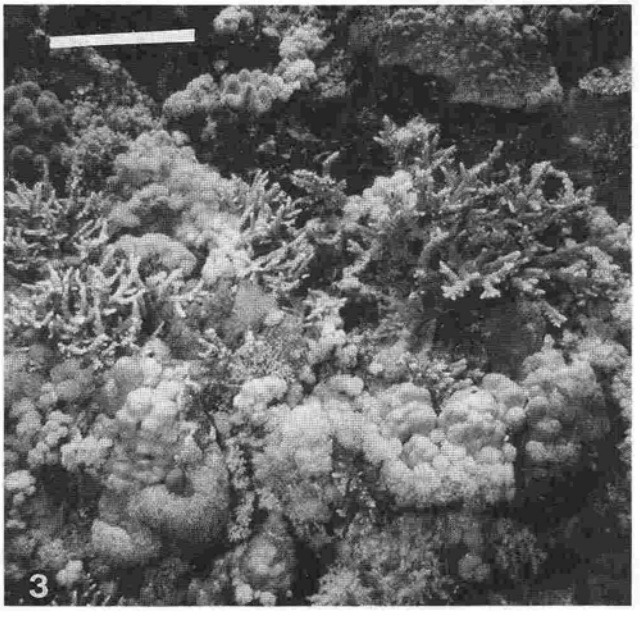
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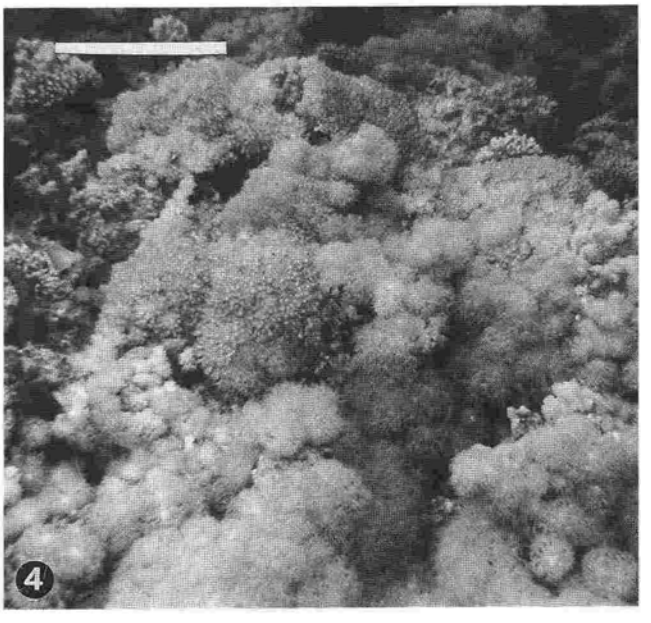
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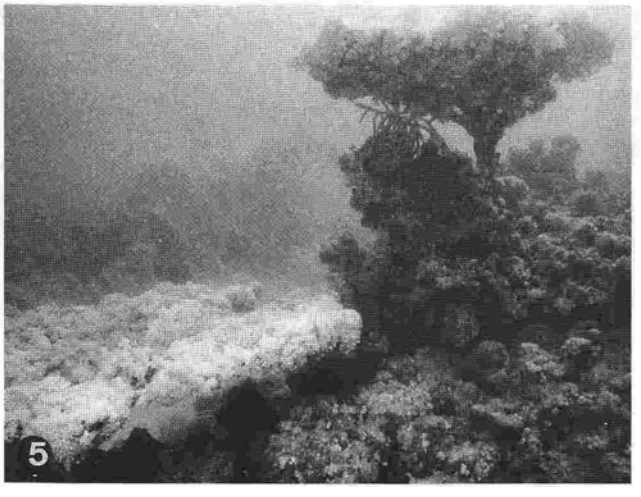
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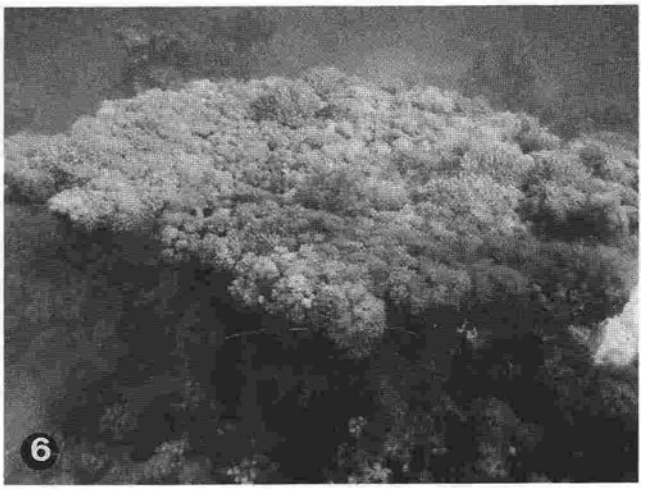
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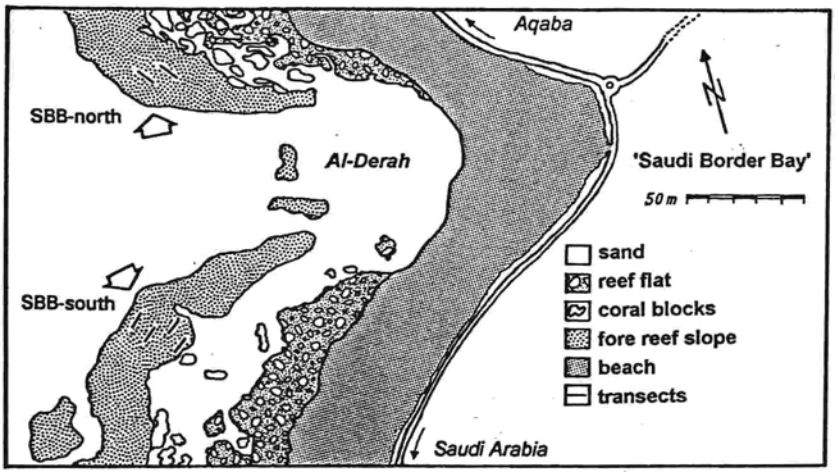


Fig. 20. Study sites in the 'Saudi Border Bay', north of the border Jordan/Saudi Arabia.

carpets covering the substrate. Along the reef edge and on the shallow fore reef colonies of *Litophyton arboreum* (Pl. 31/1) are the most conspicuous alcyonacean corals (*Sinularia-Litophyton arboreum*-assemblage, MERGNER & SCHUHMACHER 1974, BENAYAHU & LOYA 1977), among scleractinians *Acropora variabilis* is dominating, which was defined as 'Leitart' by MERGNER & SCHUHMACHER (1974).

The extended fore reef area falling at an angle of 10 - 20° down to a depth of 20 m is dominated by *Stylophora pistillata*, *Acropora variabilis* and *Acropora squarrosa* among scleractinian corals. Alcyonacean species, mainly of the genus *Xenia*, can form extended colony beds, thus providing 5-70 % of living coral cover (LC) at 10-30 m depth (Pl. 31/4, table 5).

Although varying considerably, the relative abundance of alcyonacean corals decreases with depth whereas scleractinian corals dominate the deeper reef slope sections. In the study area the composition of the scleractinian community changes from a *Stylophora pistillata-Acropora variabilis-Acropora squarrosa*-assemblage in the upper fore reef to a *Montipora-Porites-Pavona varians*-assemblage in the lower fore reef (20 m and deeper). Fig. 22 gives examples of the bathymetrical change in the shares of stony and soft corals.

depth [m] reef section	living cover [% LC]	Scleractinia [% LC]	dominant forms [% LC]		Alcyonacea [% LC]	number of species	dominant forms [% LC]	
10 m fore reef SBB-S	44.1	26.8	*Acropora* spp.	7.9	70.1	7	*X. umbellata*	45.1
			Montipora spp.	4.2			*X. macrospiculata*	15.4
15 m fore reef SBB-S	42.0	48.7	*Acropora* spp.	17.5	44.3	11	*X. faraunensis*	19.9
			Montipora spp.	6.6			*X. umbellata*	15.9
			S. pistillata	4.6			*X. macrospiculata*	2.9
15 m fore reef SBB-N	74.2	56.8	*Goniopora* spp.	27.0	43.2	7	*X. obscuronata*	19.2
			S. pistillata	10.8			*H. ghardaqensis*	15.1
			Montipora spp.	7.0			*H. fuscescens*	9.4
20 m fore reef SSB-S	51.7	46.0	*Montipora* spp.	10.5	53.5	14	*X. faraunensis*	14.1
			Favites sp.	8.2			*X. macrospiculata*	10.0
			Acropora spp.	7.4			*X. obscuronata*	9.2
							X. nana	6.9
20 m fore reef SSB-N	77.45	42.8	*Acropora* spp.	12.6	56.9	12	*X. faraunensis*	27.0
			Montipora spp.	11.3			*X. obscuronata*	18.4
			Pavona varians	4.3			*X. verseveldti*	2.8
20 m fore reef MSS (below U-7)	58.7	62.5	*Montipora* spp.	21.1	35.1	8	*X. obscuronata*	12.0
			M. elephantotus	10.6			*X. faraunensis*	8.1
			Pavona varians	5.7			*X. nana*	3.0
			Acropora spp.	3.3			*X. biseriata*	3.0
30 m fore reef SBB-S	69.3	64.4	*Montipora* spp.	42.1	30.9	6	*X. faraunensis*	11.5
			Pavona varians	11.8			*X. obscuronata*	8.2
			Porites spp.	4.0			*X. nana*	5.2
			Acropora spp.	2.4			*X. verseveldti*	4.4
30 m fore reef MSS (below U-7)	62.8	51.8	*Pavona varians*	9.9	45.5	5	*X. faraunensis*	30.2
			P. crustacea	9.9			*X. nana*	7.4
			Montipora spp.	7.3			*X. macrospiculata*	5.6
			Acropora spp.	5.6				
10-11.5 m * fore reef MSS	30.4	93.1	*Acropora* spp.	38.6	4.8	3	*S. ehrenbergi*	3.8
			Montipora spp.	14.1			*P. fulvum fulvum*	0.9
			S. pistillata	9.4				
			Goniastrea spp.	3.6				

Tab. 5. Proportions of scleractinian and alcyonacean corals on 10 m transects at different depths on the reef near the Marine Science Station (MSS) and on the northern and southern fringing reef lining the 'Saudi Border Bay' (SSB-N, SSB-S), Aqaba.
*: Data KROLL (1990).

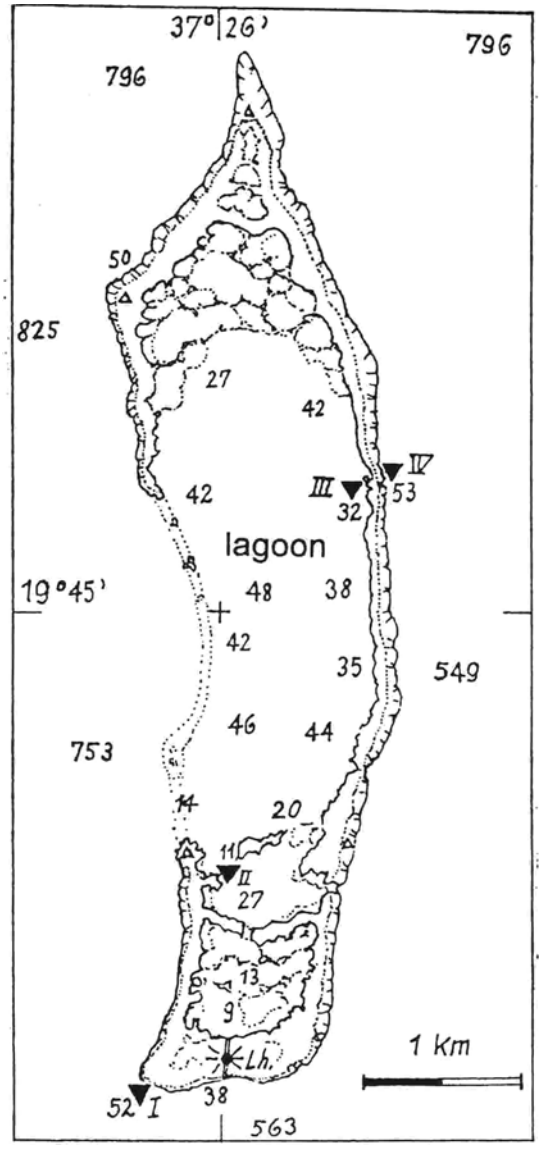


Fig. 21. Map of Sanganeb-Atoll near Port Sudan with location of test areas TQ I-IV (after MERGNER & SCHUHMACHER 1985a).

On Sanganeb-Atoll the reef flat is covered mainly by micro atolls of *Porites* sp. and *Stylophora pistillata* colonies. Notable quantities of soft corals first appear on the reef slope. The predominating Alcyonacea are here *Xenia* and *Sinularia* species (Pl. 31/3). The dominating scleractinians differ among the particular TQs, MERGNER & SCHUHMACHER (1985a) found as 'Leitarten' in TQ I: *Porites lutea*, in TQ II: *Lobophyllia corymbosa* and *Acropora hemprichi*, in TQ III: *Echinopora gemmacea*, and in TQ IV: *Acropora superba*, *Acropora corymbosa* and *Echinopora gemmacea*. The respective alcyonacean 'Leitarten' are *Xenia macrospiculata* in TQ I, none in TQ II, in TQ III *Sinularia* sp. and *Dendronephthya hemprichi*, and in TQ IV none. On the southern fore reef terrasse extending with an angle of 10 - 20° from 20 m down to about 30 m depth, alcyonaceans represent a high proportion of living cover (Table 6). *Xenia macrospiculata*, *X. obscuronata*, *Anthelia glauca*, *Sinularia* sp. and nephtheid species occupy 78.5% LC, whereas scleractinians reach only 6 % LC (Pl. 31/2).

Lagoonside reefs showed higher proportions of pulsating xeniid species (viz. *X. macrospiculata*, *H. ghardaqensis*) which correlates with higher rates of sedimentation in this area (Pl. 31/5-6).

4.2.1 The '*Xenia*-aspect'

Xeniid corals are the dominant Red Sea soft corals. Our investigations revealed a total of 31 species from 5 genera of Xeniidae in the Red Sea (viz. *Anthelia*, *Cespitularia*, *Heteroxenia*, *Xenia*, *Sympodium*) including one new record and two newly described species (REINICKE 1994). 15 species, mainly of the genus *Xenia* were found to occupy extended proportions of the living cover on reefs at Aqaba and on Sanganeb-Atoll (also reported from various other localities in the Red Sea) thus forming the '*Xenia*-aspect' in the species assemblages. They showed a distinct zonation pattern along the light gradient reflecting different modes of physiological adaptation to decreasing light-intensity (tested for 5 predominating species, see below). On Jordanian reefs the xeniid settlement reaches down to a depth of 40 m, exhibiting a bathymetric sequence as shown in Fig. 23 - viz. *X. macrospiculata* (*Xm*), *X. umbellata* (*Xu*), *H. ghardaqensis* (*Hgh*), *X. biseriata* (*Xb*), *X. obscuronata* (*Xo*), *X. faraunensis* (*Xf*), *X. nana* (*Xn*), *X. verseveldti* (*Xv*), *X. novaecaledoniae* (*Xnv*) with single colonies of *Heteroxenia fuscescens* (*Hf*) and patches of *Anthelia glauca* (*Ag*) and *Sympodium caeruleum* (*Sc*). On Sanganeb-Atoll (SSW-corner) the same bathymetric pattern was found to extend down to a depth of 70 m, with two additional species (*X. blumi* (Xbl), *X. crassa* (Xc)) overlying the shallow section between 2 and 15 m.

Experimental displacement of colonies from low to high light levels revealed photoadaptation to high illumination in zooxanthellae of *X. macrospiculata*, but no specific adaptations in those of *X. obscuronata* and *X. faraunensis*. In the reverse case, the density of zooxanthellae increased under reduced light conditions in *X. nana* and *X. novaecaledoniae* (details are given by REINICKE 1994).

4.3 Fluctuations in abundance of scleractinians and alcyonaceans

For the big flexible colonies of *Litophyton* sp. a rapid regeneration potential after damage by storm events has been described in the literature (TURSCH & TURSCH 1982). The data of *Xenia* species from the transects at Aqaba revealed comparatively high annual fluctuations for *X. umbellata* and *X. macrospiculata*, the dominating soft corals in reef sections between 5 and 15 m. *Xenia* species exhibiting a deeper range of distribution showed a higher constancy in the occupied space. In contrast, *Sinularia* and *Sarcophyton* colonies may persist over many years. Fluctuations in the Xeniidae ranged within 30-51 % SD of mean transect shares whereas scleractinians ranged 3-7 % SD with a maximum value of 18 % SD at 10 m depth (for details see REINICKE 1994).

It is noteworthy that the fluctuation in the xeniid cover is about 5-times higher than that of scleractinian cover

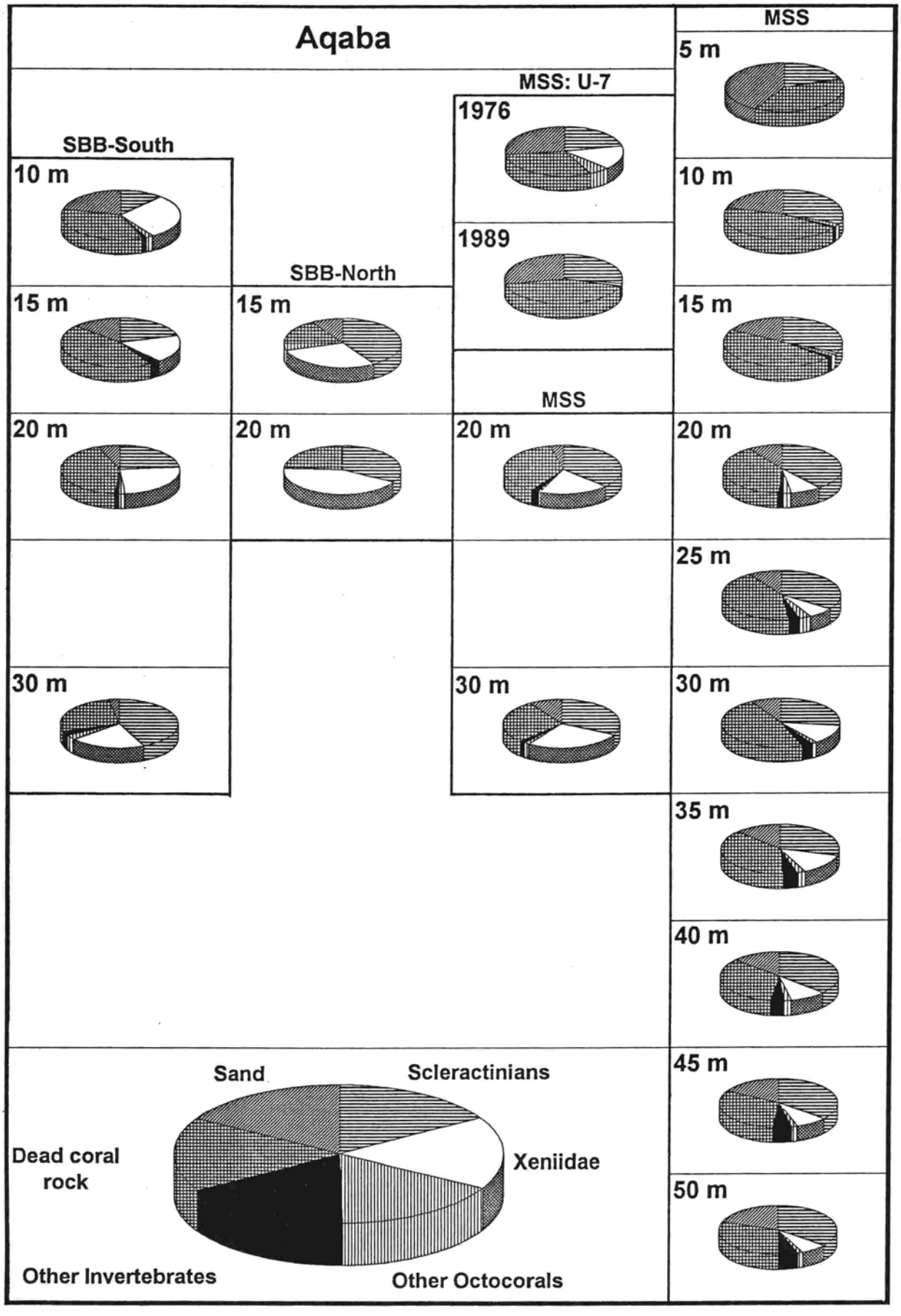


Fig. 22. Proportional composition of major categories of bottom coverage of 10 m transects at different depths at Aqaba. SBB = Saudi Border Bay, MSS = Marine Science Station.

depth [m] reef section	living cover [% LC]	Scleractinia [% LC]	dominant forms [% LC]		Alcyonacea [% LC]	number of species	dominant forms [% LC]	
5-6 m	84.3	25.3	*Acropora* spp.	10.3	73.0	6	*X. crassa*	30.1
outer reef slope			*Pocillopora* spp.	3.9			*X. blumi*	19.8
			Favites spp.	4.2			*L. arboreum*	10.8
			Porites spp.	1.3			Nephtheidae	5.7
			Pocilloporidae	9.1			*X. crassa*	22.4
10 m	69.4	21.9	*Montipora* spp.	6.3	84.9	19	*X. blumi*	13.3
outer reef slope			*E. gemmacea*	3.7			*X. biseriata*	11.7
			Porites spp.	2.1			*X. obscuronata*	10.6
			S. hystrix	5.6			*X. macrospiculata*	16.5
15 m	85.0	16.2	*Montipora* spp.	5.3	78.5	17	*X. obscuronata*	14.3
outer reef slope			*Porites* spp.	3.2			*X. crassa*	8.8
							A. glauca	7.7
			Pocilloporidae	2.6			*X. macrospiculata*	9.7
20 m	75.5	4.5	*Porites* spp.	1.7	69.3	11	*X. obscuronata*	14.3
fore reef			*Montipora* spp.	0.9			*Sinularia sp.*	10.3
							Nephtheidae	7.8
			Montipora spp.	21.8			Xeniidae	24.2
30 m	62.3	48.2	*S. pistillata*	13.0	47.0	12	*P. thyrsoides*	7.7
fore reef			*Favia* spp.	2.9			*Tubipora musica*	5.4
1980	47.0	50.4	*Porites lutea*	10.0	49.5	22	*X. macrospiculata*	37.1
TQ I: 6.5-11.5 m			*A. pharaonis*	9.0			*S.ehrenbergi*	2.8
outer reef slope								
TQ II: 3.0-7.5 m			*L. corymbosa*	38.9			*X. macrospiculata*	8.5
inner reef slope	57.6	85.3	*Porites lutea*	8.2	11.5	9	*S. ehrenbergi*	1.7
			A. hemprichi	5.5				
TQ IV: 7.5-11.5 m	55.2	85.6	*A. superba*	24.3	1.9	4	*X. macrospiculata*	1.8
outer reef slope			*P. verrucosa*	15.8				
1991	40.7	31.0	Poritidae	14.0	67.6	24	*X. crassa*	13.5
TQ I: 6.5-11.5 m			Acroporidae	7.4			*X. biseriata*	11.7
outer reef slope							*X. blumi*	8.2
TQ II: 3.0-7.5 m	58.1	69.9	*L. corymbosa*	35.5	26.4	18	*X. biseriata*	6.0
inner reef slope			*A. hemprichi*	11.7			*X. blumi*	5.0
			A. superba	30.6				
TQ IV: 7.5-11.5 m	55.5	76.2	*M. platyphylla*	9.9	6.4	4	*X. blumi*	5.7
outer reef slope			*A. corymbosa*	9.8				

Tab. 6. Proportions of scleractinian and alcyonacean corals on 10 m transects in different depths and in 5 x 5 m test squares on Sanganeb-Atoll.

(Fig. 24). A relative constancy of species composition and scleractinian cover was noted within four test squares on Sanganeb-Atoll over an 11 year period (Fig. 25). However, a significant decrease of *Sinularia* and *Dendronephthya* colonies occurred in TQ III.

5 ALCYONACEAN CORALS AND CORALLIVOROUS GASTROPODS AS IMPEDIENT FACTORS IN CALCIFICATION

G. B. Reinicke and H. Schuhmacher

5.1 Introduction

Reef growth depends predominantly on the calcification of scleractinian corals. Hence the 'untimely' death of the coral animal impedes the continuing deposition of calcium carbonate. Efficient space competitors, coral predators and parasites exert impedient influences. Some algae (*Dictyosphaera cavernosa*) and sponges (*Terpios* sp.) are known to overgrow and kill stony corals (e. g. Schuhmacher 1982). The starfish *Acanthaster planci* is a well known example of a coral predator.

In the Red Sea, alcyonacean corals are very striking candidates for efficient space competitors and corallivorous snails rank before the crown-of-thorns starfish as coral predators.

5.2 Xeniid corals

Soft corals, in particular xeniid corals seem to overgrow stony corals. This arises from the capability of the soft coral colonies to overtop neighbouring stony corals by hydraulic extension and to spread over open space rapidly by budding (Pl. 32/1). Direct experimental evidence, however, was found only in the case of the slender colonies of *Heteroxenia ghardaqensis*. They shaded and overgrew scleractinian colonies when fixed together on PVC-plates on the reef. Species attaining smaller colony size (viz. *X. macrospiculata*) surrounded but did not overgrow scleractinian colonies. The observation that in areas monitored for two years and longer the share of scleractinians remained stable and did not decrease in favour of abundant xeniid corals indicates that these xeniids fluctuate inversely to the open space (Fig. 24) and suggests that

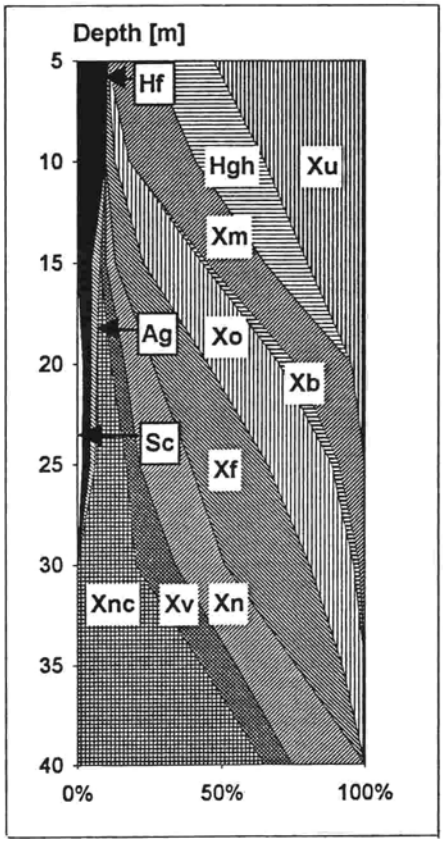


Fig. 23. Relative abundance pattern of Xeniidae species along the depth gradient on the reefs of 'Saudi Border Bay', Aqaba.

Ag: *Anthelia glauca*; Hf: *Heteroxenia fuscescens*; Hgh: *H. ghardaqensis*; Sc: *Sympodium caeruleum*; Xu: *Xenia umbellata*; Xm: *X. macrospiculata*; Xb: *X. biseriata*; Xo: *X. obscuronata*; Xf: *X. faraunensis*; Xn: *X. nana*; Xv: *X. verseveldti*; Xnc: *X. novaecaledoniae*.

xeniids are more significant as opportunistic colonizers of empty hard bottoms than as effective space competitors. There is no doubt, however, that a carpet of xeniid or other soft corals prevents the settlement of the larvae of hermatypic species and thus acts as a reef growth retarding element in the communities.

5.3 Coral feeding gastropods

Coral predators and parasites counteract the hermatypic role of scleractinian corals. By attacking the coral animal they reduce its potential for calcification. In the Red Sea, corallivorous gastropods are more important than the well known starfish *Acanthaster planci* (SCHUHMACHER 1994). The four most common corallivorous prosobranchs of the Red Sea *Drupella cornus* (Thaididae), *Coralliophila costularis*, *C. violacea* and *Quoyula madreporarum* (Coralliophilidae) remove or weaken the coral tissue in different ways and to a different extent.

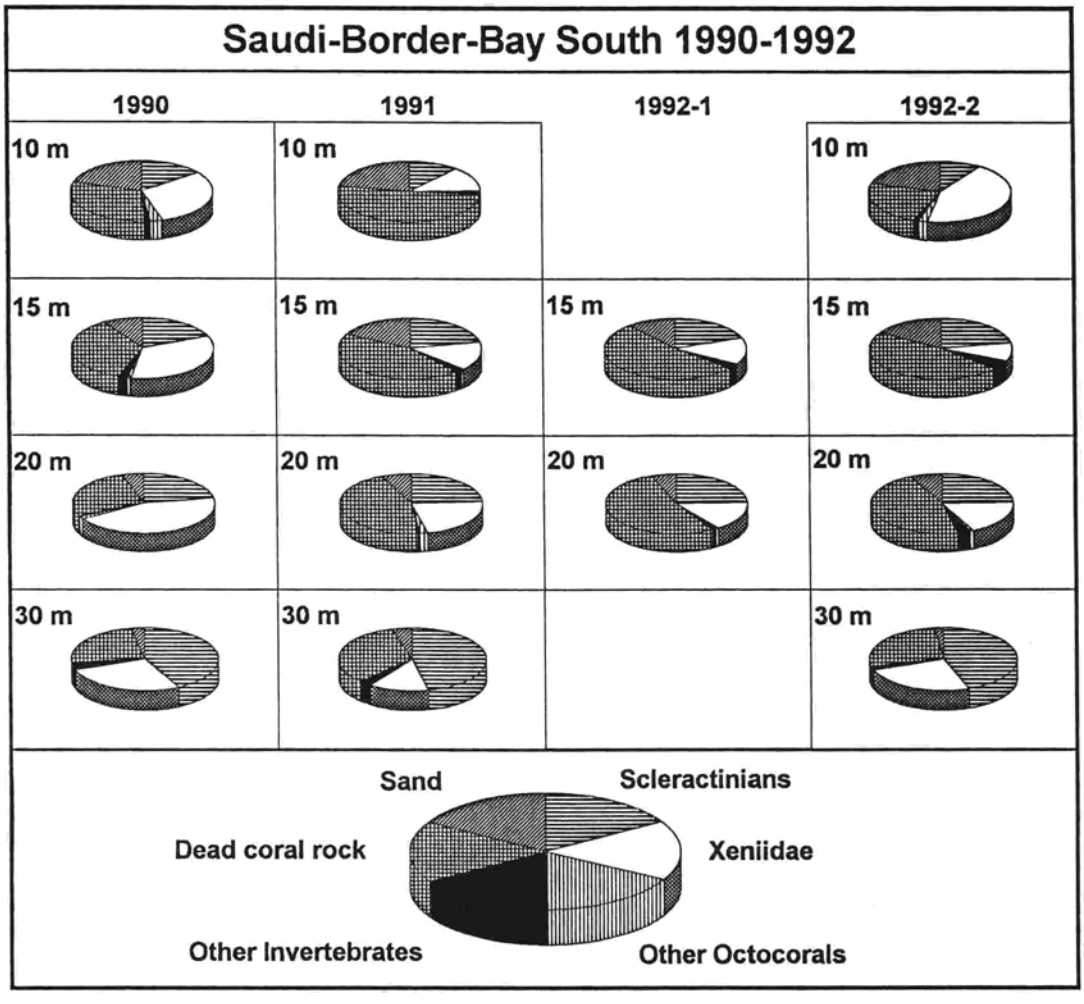


Fig. 24. Proportional composition of major categories of bottom coverage of 10 m transects at different depths over time in 'Saudi Border Bay', Aqaba. 1992-1 = March, 1992-2 = November.

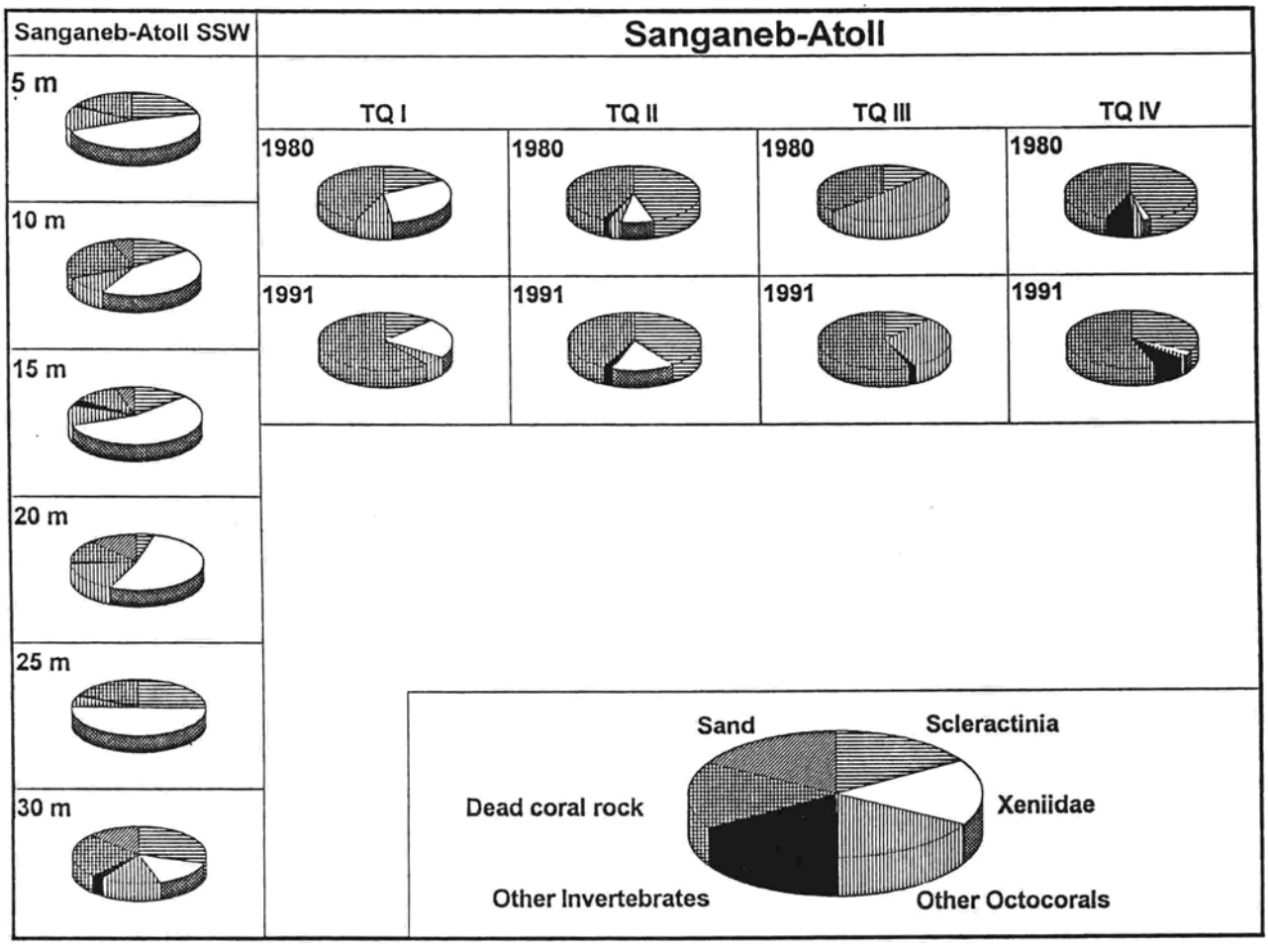


Fig. 25. Proportional composition of major categories of bottom coverage of 10 m transects at different depths in spring 1991 and of test squares (TQ) at some 10 m depth in spring 1980 and spring 1991, Sanganeb-Atoll.

Drupella cornus rasps off the coral tissue with a specially formed radula. After denuding a colony the gregarious animals move on to the next colony. In one incident a group of 7 snails removed the tissue of a head-sized *Stylophora pistillata* colony within 4 days. In another incident a group of 25 snails took 5 days to denude an *Acropora corymbosa* plate of approx. 0.4 m^2. Freshly killed colonies are easily detectable by their white skeleton (Pl. 32/2, 3).

Coralliophila costularis has a more cryptic life-style, sitting at the base of a coral colony during daytime. At night, polyps are attacked and tissue pieces are sucked through the mouth and body wall. Large polyps, such as *Goniopora* sp., shrink and die after repeated attacks (Pl. 32/4). *Coralliophila violacea* is a sessile species, attached to *Porites* and *Synaraea* colonies (Pl. 32/5). The snails induce a very thin smooth aragonite layer as attachment scar. The surrounding coral tissue often appears pink indicating an early stage of necrotism. The mode of feeding is not yet clear. It seems likely that gastrovascular contents are taken in from the surrounding polyps.

The most careful exploitation of the coral polyps is exhibited by *Quoyula madreporarum* (Pl. 32/6). This species lives exclusively on *Stylophora*, *Seriatopora* and *Pocillopora* colonies. The snail forms a pedestal of 4-11 mm length with a peculiar wash-board surface (Pl. 32/7). The foot of the snail is firmly attached to the sculptured pedestal. This is formed of recrystallized coral aragonite. The surface of the coral's skeleton is dissolved by means of acidic mucus secreted from the snail's foot. The calcium carbonate is then deposited in laminar fashion onto the etched skeleton - suggestive of the botryoidal cement described by Aissaoui (1985). From the size and thickness of the pedestals it can be concluded that young snails may change their site whereas most of the adult animals no longer leave their attachment site. The snail feeds by carefully lowering its proboscis into the mouth of a coral polyp and sucking in the gastrovascular contents. This behaviour shows a very gentle exploitation of the surrounding coral polyps. The proboscis of the snail, which can be extended half the length of the animal, allows the feeding stress to be distributed. Nevertheless the coral tissue within reach of the proboscis gradually disintegrates and the snail has to build forward its pedestal accordingly.

An abundance of the four corallivorous gastropod species was counted on 10 m transects parallel to the reef edge and perpendicular to it on the upper fore reef at Aqaba and on Sanganeb-Atoll (for methodological details see Schuhmacher 1994). Furthermore, white feeding marks of *Drupella cornus* could be identified on pictures of earlier

records of 5 x 5 m quadrats at Aqaba and on Sanganeb-Atoll which are under long-term observation (for more data see SCHUHMACHER 1994). The occurrence of *Drupella cornus* is very patchy and seems to be restricted to shallow depths (< 15 m). Whereas the species accounts for some 1 % of coral death on average for the whole shallow reef part over the last decade, maximum values of nearly 30 % tissue depletion apply to some restricted sections of the Aqaba reef edge in 1992 and 1993. *Drupella* 'outbreaks', which mainly eliminated stands of *Acropora* and other fast-growing corals have been reported from the western Pacific (MOYER et al 1982, TURNER 1994). Whether denuded coral skeleton is due to *Drupella* attacks or due to natural death cannot be differentiated post mortem. The preferential elimination of fast-growing *Stylophora* and *Acropora* species may contribute to maintain an overall high coral diversity.

In comparison to the impact by *Drupella*, the parasitic *Coralliophila violacea* and *Quoyula madreporarum* are of minor significance. The attachment scars with their denuded periphery provide an entrance for boring organisms which may weaken the whole colony.

6 BIOEROSION BY GRAZING *DIADEMA* SEA URCHINS

D. K. KROLL

6.1 Introduction

The principal agents which chronically erode coral reefs are grazers and borers. Echinoids (e. g. *Diadema* spp.) have been recognized as important grazing bioeroders in many coral reef habitats, especially in the Caribbean region (HAWKINS & LEWIS 1982). But echinoid bioerosion is often highly variable among reefs and spatially within a given reef (BIRKELAND 1989). Published data are restricted to Pacific (BAK 1990) and Atlantic (GLYNN et al. 1979) reef regions and not transferable to the Red Sea reefs.

The most abundant invertebrate grazer on the reefs south of Aqaba is the echinoid *Diadema setosum* Leske. This sea urchin is a generalistic herbivore and shows a nocturnal feeding activity. During daytime *D. setosum* hides between coral rocks or forms aggregations against predators (Pl. 33/1). The urchins start foraging in the late afternoon, feeding on a variety of food items. Commonly

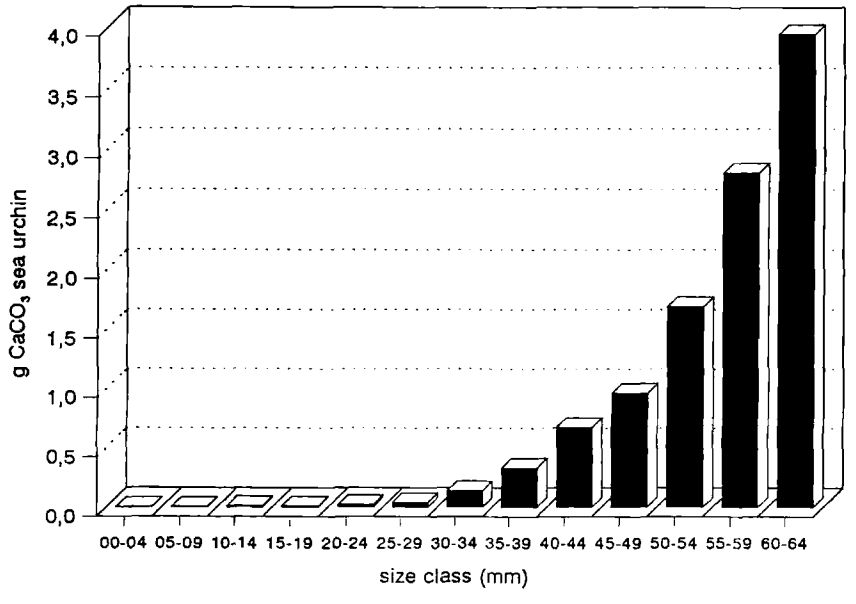


Fig. 26. Gut content (g $CaCO_3$ sea urchin^{-1}d^{-1}) of *Diadema setosum* in different size classes (mm).

Plate 32 Agents which impede calcification by scleractinians.

Fig. 1. *Porites* sp. colony surrounded by *Xenia macrospiculata* and *X. umbellata* colonies (a colony of *Sarcophyton ehrenbergi* on the right), Sanganeb-Atoll. Scale: 0.5 cm.

Fig. 2. *Drupella cornus*: Five specimens (*) have partly denuded a colony of *Acropora humilis*; Sanganeb-Atoll. Scale: 2 cm.

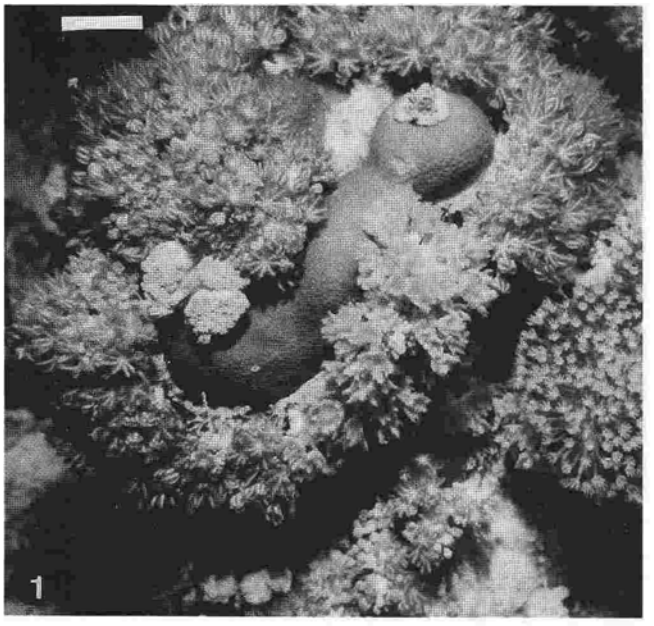
Fig. 3. Feeding front of *Drupella cornus* moving from left to right over an *Acropora hyacinthus* table. The white area is freshly denuded skeleton; older skeleton parts (far left) are settled by green algal turf. Arrows point to individual snails. Aqaba, south of Marine Science Station.

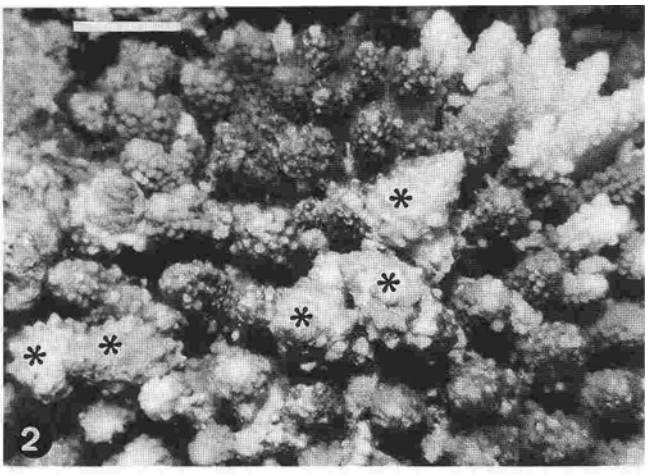
Fig. 4. *Coralliophila costularis*: Three individuals feed on *Goniopora planulata*; Aqaba. Scale: 2 cm.

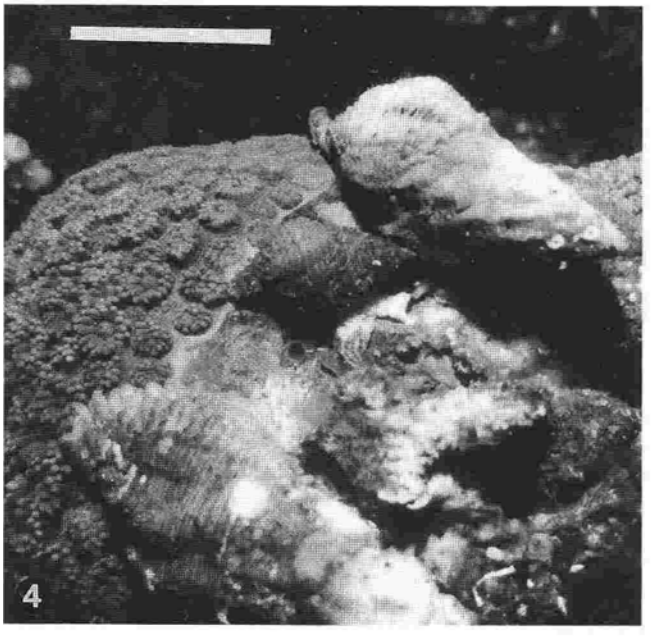
Fig. 5. *Coralliophila violacea*: Cluster of 9 snails attached to a *Porites* sp. colony. Note the wound marks around the left attachment sites; Sanganeb-Atoll. Scale: 1 cm.

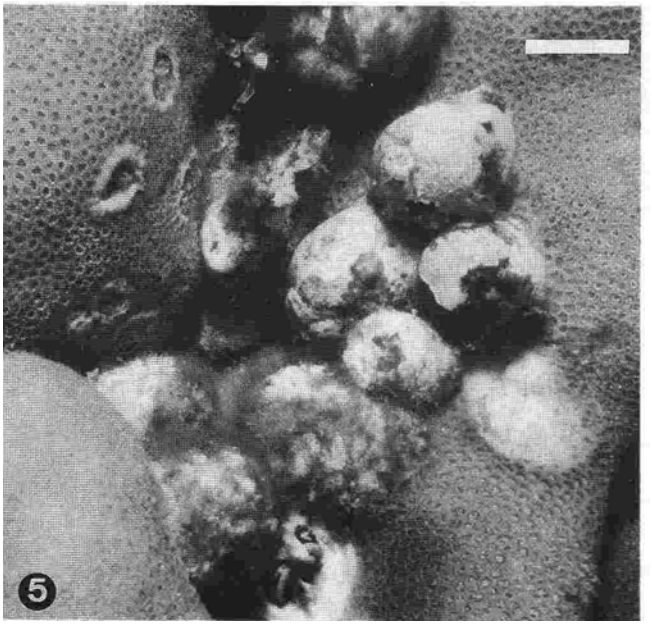
Fig. 6. *Quoyula madreporarum*: Pieces of living *Stylophora pistillata* with attachment scar (left), underside of the snail (center), snail attached to the host coral (right); Sanganeb-Atoll. Scale 1 cm.

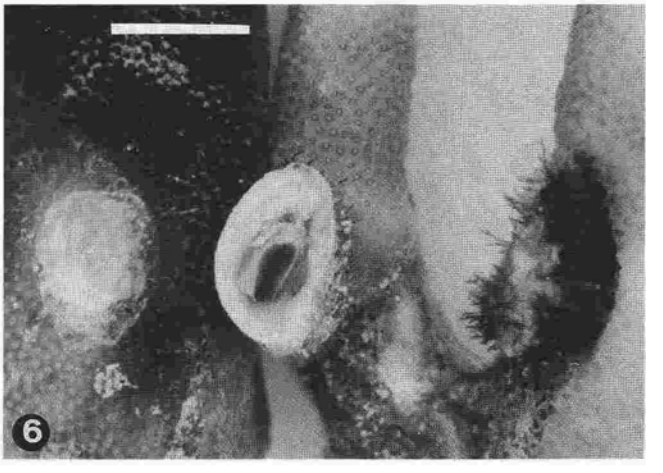
Fig. 7. *Quoyula madreporarum*: Skeleton of *Stylophora pistillata* with three attachment pedestals; note the dead area in the rear of the pedestals; Sanganeb-Atoll. Scale: 1 cm.

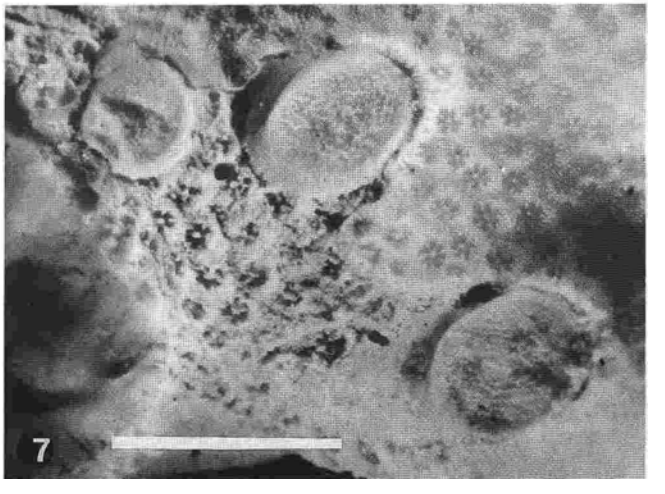












transect	size class (mm) 00-04	05-09	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	total
T-05	1	4	5	9	11	15	19	17	11	3	3	-	-	98
T-10	-	-	2	3	3	3	5	9	12	7	4	2	-	50
T-15	-	-	-	-	-	3	6	6	12	7	5	1	-	40
T-20	-	-	-	-	-	-	2	3	5	4	3	2	-	19
T-25	-	-	-	-	-	-	-	1	4	5	4	2	-	16
T-30	-	-	-	-	-	-	-	-	2	3	5	1	2	13
T-35	-	-	-	-	-	-	-	-	2	2	4	2	1	11
T-40	-	-	-	-	-	-	-	-	-	2	3	2	2	9
T-45	-	-	-	-	-	-	-	-	-	-	3	2	2	7
T-50	-	-	-	-	-	-	-	-	-	-	1	2	2	6
total	1	4	7	12	14	21	32	36	48	33	35	16	9	268

Tab. 7. Size distribution of *Diadema setosum* on transects (T-05 - T-50) near the Marine Science Station, Aqaba. Means of a census in autumn 1991 and in spring 1992.

they graze on the thin algal turf covering the coral rock scraping off the upper layer of the hard bottom, including endolithic algae and crustose corallines (Bak 1990). During the grazing of algae the urchins consume large quantities of calcium carbonate removed from the rocky substrate which is afterwards excreted as part of the fecal pellets (Pl. 33/3).

6.2 Materials and methods

At Aqaba ten 10 m belt transects about 150 m off the Marine Science Station were laid out on the reef between the reef flat and the deep fore reef down to 50 m (Fig. 19). Descriptions of this area are given by Mergner & Schuhmacher (1974, 1981).

Within the transects (each 10 m long x 50 cm wide) the maximum test diameters were measured of all sea urchins found on living and dead coral colonies and on sand. In addition, tagged *Diadema* specimens were studied in situ by time-lapse video camera in 10-minute intervals (Pl. 33/2).

From these two sets of data (viz. urchin density/substratum and cover of substratum) urchin densities were calculated for the area. Table 7 provides the average number of individuals per 5 m^2 of *D. setosum* in the transects. The census was done twice (autumn 1991 and spring 1992). To assess the quantity of carbonate eroded from the reef-framework by *D. setosum* 354 individuals were collected outside the test areas and grouped into 13 size classes (test diameters ranged 4-64 mm). The gut contents of each specimen were differentiated via calcium carbonate and ash-free dry weight.

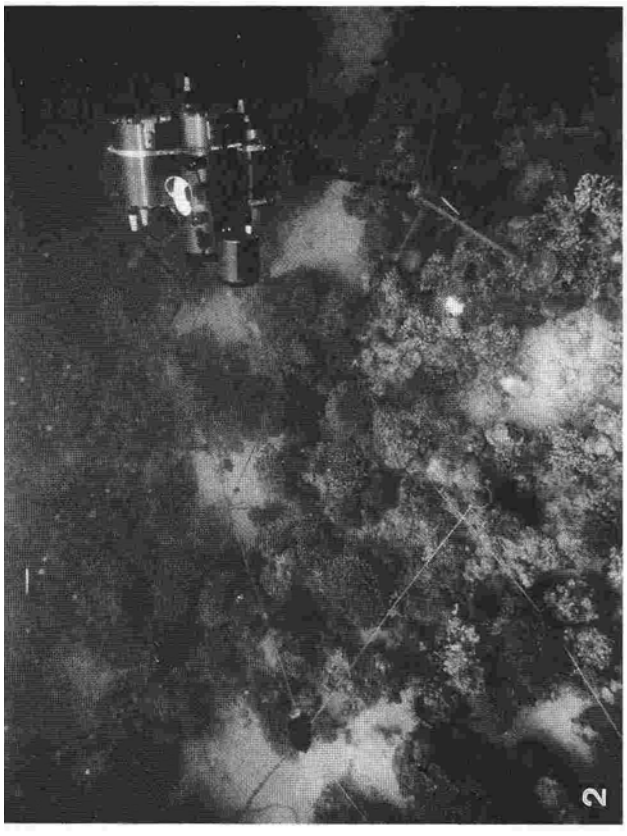
size class [a] (mm)	urchin density (5 m^{-2})	gut content (g $CaCO_3$ $urchin^{-1}$)	daily content of size class	daily erosion [b]
10-14	2	0.01	0.02	0.01
15-19	3	0.01	0.03	0.02
20-24	3	0.02	0.06	0.04
25-29	3	0.04	0.12	0.08
30-34	5	0.14	0.70	0.46
35-39	9	0.33	2.97	1.93
40-44	12	0.67	8.04	5.23
45-49	7	0.96	6.72	4.37
50-54	4	1.69	6.76	4.39
55-59	2	2.80	5.60	3.64
total daily erosion (g 5 m^{-2})				**20.17**

[a] maximum test diameter
[b] 35 % of pellet reworked material

Tab. 8. *Diadema setosum*. Daily reef-framework erosion (g . 5 m^{-2}) on transect T-10 near Aqaba.

Plate 33 *Diadema setosum* - a significant eroder at Aqaba reefs

Fig. 1. During the day *Diadema* sea urchins hide in small crevices or form aggregations against predators; Aqaba.
Fig. 2. During night tagged *Diadema setosum* has been studied in situ at 10-minute intervals by time-lapse video camera; Aqaba, fore reef U-7.
Fig. 3. Fecal pellets of *Diadema setosum* in situ (0.5 - 2 mm in size); Aqaba.
Fig. 4. Thin sections are reflecting the composition of *Diadema* fecal pellets (fragments of corals, coralline algae and sand grains). Scale: 1 mm.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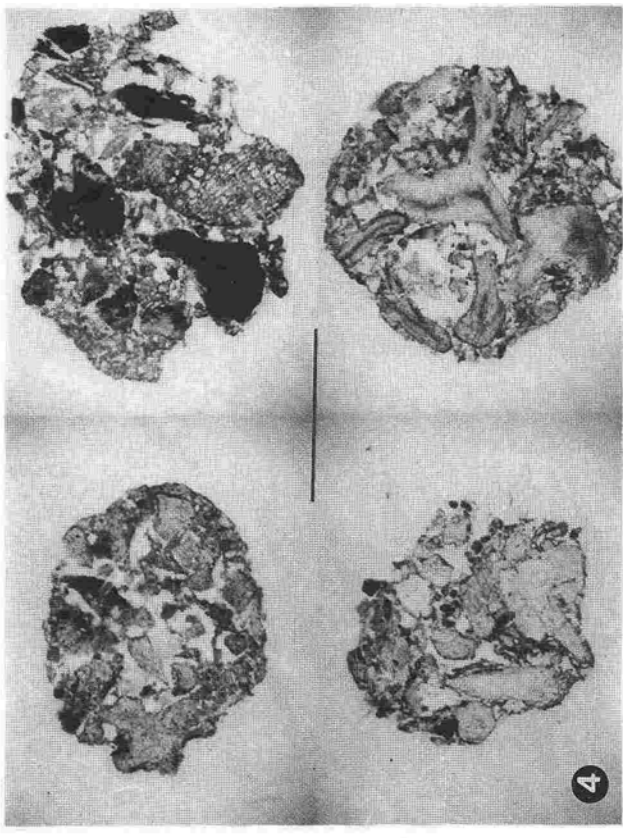
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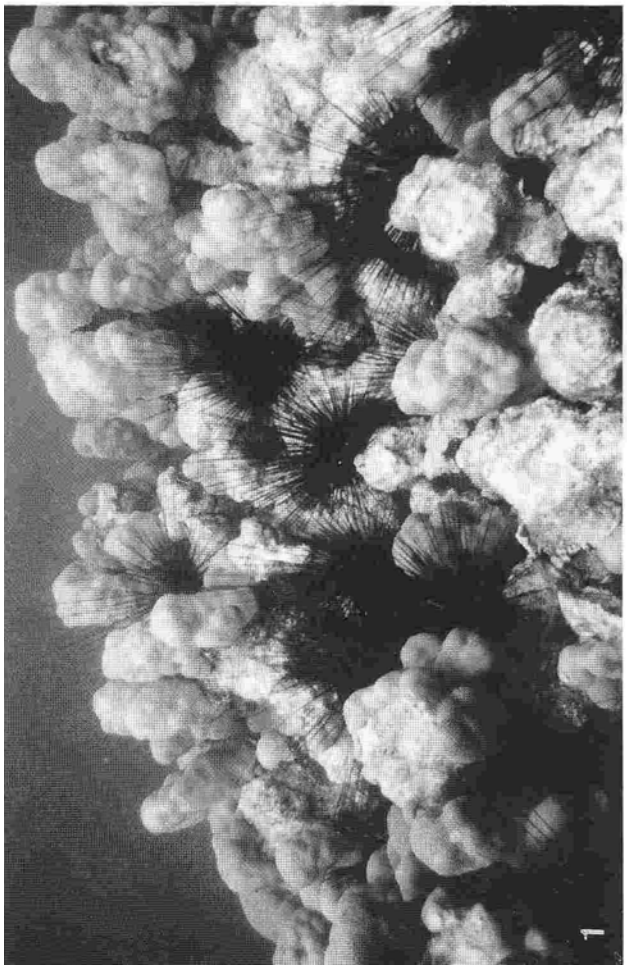
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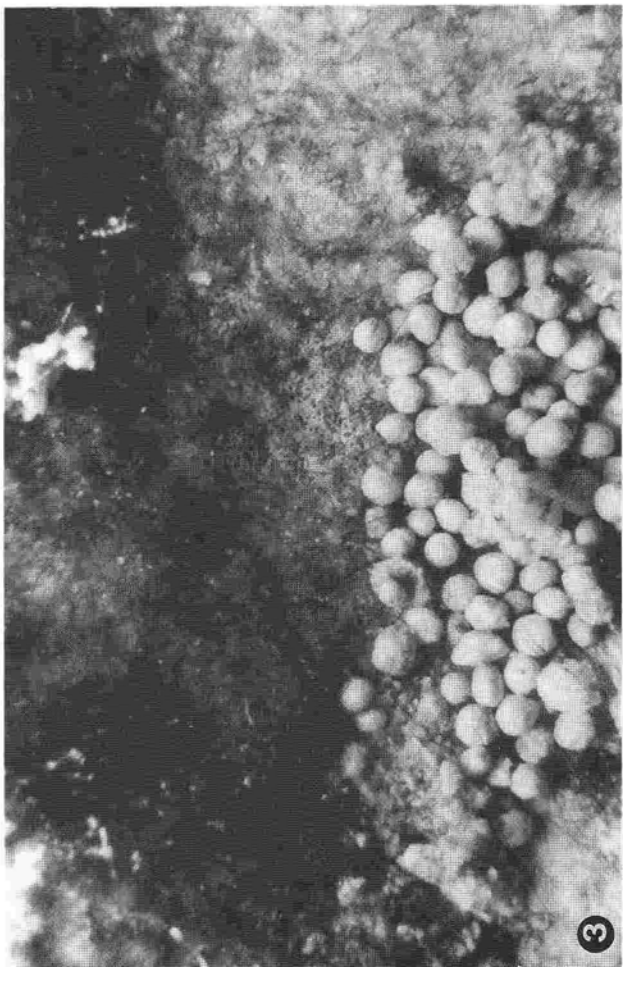
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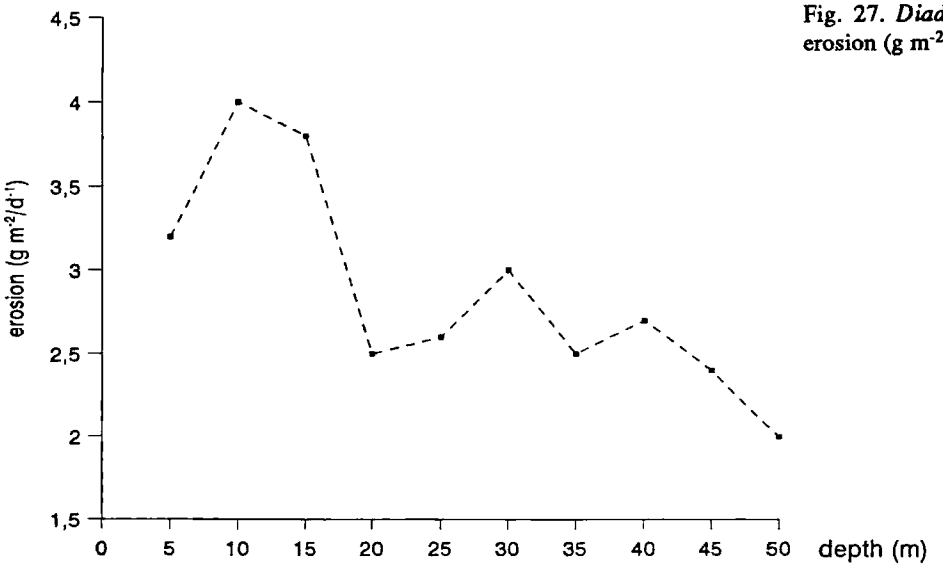


Fig. 27. *Diadema setosum*. Daily reef-framework erosion (g m^{-2}) at different depths.

6.3 Results

D. setosum shows a depth-related distribution pattern. The number of urchins decreases with increasing depth (e.g. approx. 20 individuals/m^2 at 5 m depth, 1 individual/m^2 at 50 m depth, see table 7). Small urchins (4-29 mm) were found only in the upper part of the reef. In the deeper part of the reef (40-50 m depth) big urchins predominate (50-64 mm).

Fig. 26 shows that the amount and composition of the gut content varied among different urchin size classes (0.01 - 3.94 g $CaCO_3$). The source of consumed carbonate (hard substratum or loose sediment) can be traced in the fecal pellets (HUNTER 1977, SCOFFIN et al. 1980). We checked at least 330 pellets by thin section (Pl. 33/4). The composition of the fecal pellets indicated a hard substratum origin for some 65 % of the carbonate particles, 35 % are derived from loose sediment particles.

Gut contents are known to vary quantitatively as well as qualitatively with urchin size. The total amount of bioerosion by *D. setosum* can be calculated by combining the data on the nature of the bottom coverage, sea urchin densities and size frequencies, the gut contents of the different urchin size classes and the origin of the gut carbonate. Table 8 illustrates the calculation for transect T-10 as an example. At 10 m depth the total erosion of the respective group of sea urchins amounts 20.2 g/5 m^2/d.

Together with the corresponding data for the other depths, we estimate a daily erosion of reef-framework (g/m^2/d) by *D. setosum*, as shown in Fig. 27.

These data prove that *Diadema setosum* accounts for considerable erosion of calcium carbonate on reefs, thus influencing the budget of growth and erosion in the reef area near Aqaba. In contrast to the coastal fringing reefs in the northern part of the Gulf of Aqaba not a single specimen of *D. setosum* was found on Sanganeb-Atoll.

Plate 34 Bioerosion experiments, Lee Stocking Island, Bahamas.

Fig. 1. Aerial view (looking west) of Exuma Islands and Lee Stocking Island (with 1 km air strip). Bahama bank is in background and to the left. Exuma Sound is to the right. Shallow water sites A to F are marked by upper tip of yellow triangles. Deep reef slope sites S, T, U and S', T', U' are marked by circles.

Fig. 2. Deep reef slope at 150 m water depth showing rock (talus block, age unknown) outcropping through sediment debris. Greenish color of rocks is due to living endolithic green algal infestation by *Ostreobium quekettii*. Northern transect, rock outcrop is approximately 50 cm in length.

Fig. 3. Experimental substrate types exposed for 5 months showing different quality and quantity of epilithic overgrowth that may influence endolithic colonization by microborers. Clockwise from left: coral (*Dendrogyra* sp.), shell (*Tridacna* sp.), shell (*Strombus* sp.), fine-grained limestone (Solnhofen lm. showing grazing traces made by a gastropod), coral (*Porites* sp.). In general, molluscan shell substrates show less epilithic colonization than the other substrates. Site N, windward side of the intertidal notch, low tide. Substrates are 1 x 1 cm.

Fig. 4. Intertidal notch with experimental substrates on PVC plate attached to the Pleistocene limestone surface of a small leeward island. Low tide, plate is 10 x 10 cm.

1
A
B
C
S
T
U
D
E
F

2

3

4

7 FACTORS CONTROLLING THE DISTRIBUTION OF MICROBORERS IN BAHAMIAN REEF ENVIRONMENTS

W. Kiene, G. Radtke, M. Gektidis, S. Golubic and K. Vogel

7.1 Introduction

The biological destruction of carbonate skeletal materials in coral reef environments (bioerosion) has an influence on the physical and biological character of reefs that is as important as biological construction. However, the environmental and ecological factors that control the processes of bioerosion are not as well understood as those that influence bioconstruction. As an attempt to assess bioerosion processes and the factors that control the distribution of the organisms that break down carbonate skeletons in reef environments, experiments that are exposing carbonate substrates to bioerosion are being conducted in reef and associated environments near Lee Stocking Island (Exuma Islands), Bahamas.

The bioerosion process involves a large number of organisms that bore and graze reef surfaces (Warme 1975, Bromley 1978, Hutchings 1986) and the experiments are assessing the interaction of these organisms and their impact. The initial focus of the study has been on microboring endolithic organisms. These microborers include a diverse assemblage of cyanobacteria, chlorophytes, rhodophytes and heterotrophs (fungi and bacteria, Golubic et al. 1975, Kobluk & Kahle 1978, Glaub 1994). Traces of these groups of microborers have a long geological history associated with reefs and as a result provide a valuable paleontological tool for reconstructing ancient reef environments and processes (Vogel 1993). These microbial organisms are rapidly established in carbonate substrates and, as a result, they constitute the first bioerosion process to occur on newly exposed carbonate substrates. In addition to their primary excavation of reef surfaces, microborers will also influence the erosion of surfaces by other bioeroding organisms, particularly grazers (Golubic et al. 1975, Torunski 1979, Bruggemann et al. in press). Therefore, the study of microborers is of considerable importance to the understanding of reef destruction and of the fossilization process of different reef building organisms and environments.

7.2 Methods

Factors related to water depth have been identified as important in controlling the distribution of microborers (Swinchatt 1969, Rooney & Perkins 1972, Golubic et al. 1975, Budd & Perkins 1980, Le Campion-Alsumard et al. 1982, Akpan & Farrow 1984, Vogel et al. 1987, Radtke 1991). Based on these earlier studies, the influences of water depth on light and hydrodynamic conditions were considered important to study when the experiments were designed. As a result, study sites were chosen at different water depths in windward and leeward locations near Lee Stocking Island (Pl. 34/1). By placing the experiments in these different sites they are also influenced by different water quality conditions that are fundamental to the distribution of reefs in the Bahamas (Neumann & Macintyre 1985, Kendall et al. 1990).

The sites are situated in three basic water depth ranges: intertidal, 2 to 30 m depth, and 100 to 275 m depth. Experiments have been placed in leeward intertidal conditions in an erosional notch of a small island (Pl. 34/4). The samples are subjected to conditions ranging from supratidal to just below lowest tide, a vertical range of 2 m (site N). To sample the endolithic community in this intertidal environment, experimental substrates (see below) are glued to 10 cm^2 PVC plates that are screwed to the Pleistocene limestone rock of the notch. These intertidal notches exist around all the islands of the Exumas. The leeward subtidal sites include a patch reef (site D) and a sandy site covered by sea grass (site E). Both these sites are at 2 m water depth. Windward sites include an *Acropora palmata* reef at 2 m water depth (site B), and two reef sites situated at 10 m (site F) and on the shelf edge at 30 m water depth (site C, Pl. 35/5). In addition, a site was established on a reef formed by large subtidal stromatolites (site A) that occur in a 6 m deep

Plate 35 Bioerosion experiments, Lee Stocking Island, Bahamas.

Fig. 1. Thin section of bored surface of an experimental substrate showing borings filled with tissue. Upper surface of substrate is marked by arrow. The depth of penetration is 300 µm, limestone substrate, 3 months exposure, scale bar: 100 µm.

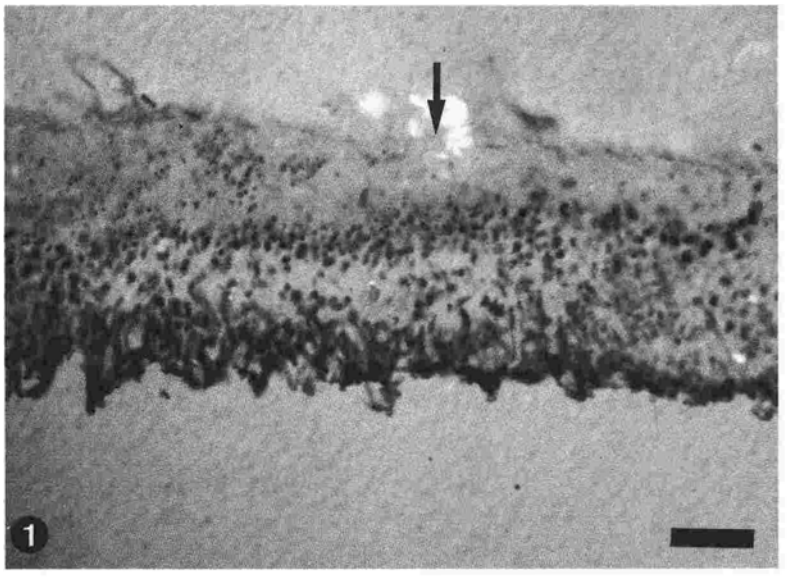
Fig. 2. Isolated species of *Solentia* from dissolved experimental substrate showing transition from green to red pigments (arrow) as filament penetrates deeper into substrate, site A, stromatolite reef, 6 m water depth, calcite substrate, 3 months exposure, scale bar: 50 µm.

Fig. 3. Deep reef slope experimental frames at 150 m. These frames are deployed and retrieved by submersible. Each frame contains plates holding 1 cm^3 microborer substrates and plates holding 5 x 5 x 2 cm *Porites* sp. coral blocks. Frame is 35 cm tall.

Fig. 4. Calcite crystal with *Phaeophila* sp. borings showing approximately 40% empty borings after 3 months of exposure. Site B, 2 m water depth, calcite substrate, 3 months exposure, scale bar: 50 µm.

Fig. 5. Experimental frame with PVC plates holding small (1cm^3) substrates for microborer studies and large (10 x 10 x 2.5 cm) *Porites* sp. coral blocks for boring-grazing interaction studies. Plates to right are newly deployed, while other plates have been exposed for 1 year. Site C, 30 m water depth, plates are 20 x 10 cm.

Fig. 6. Cast borings under light microscope (substrate dissolved) showing density of microboring in substrate surface ('bushes' and 'felts') after 3 months exposure. Limestone substrate, scale bar: 1 cm.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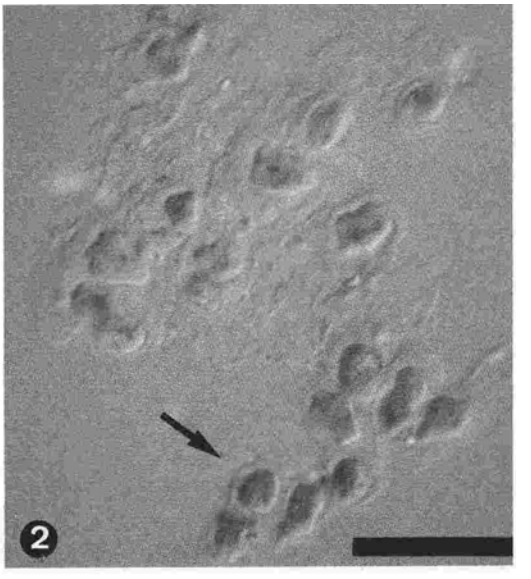
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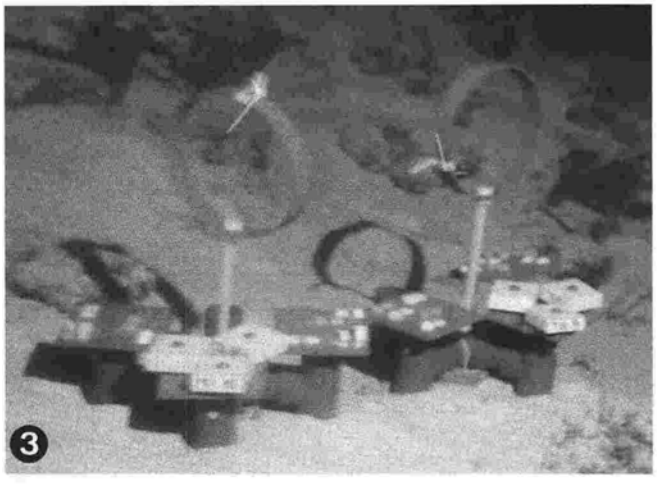
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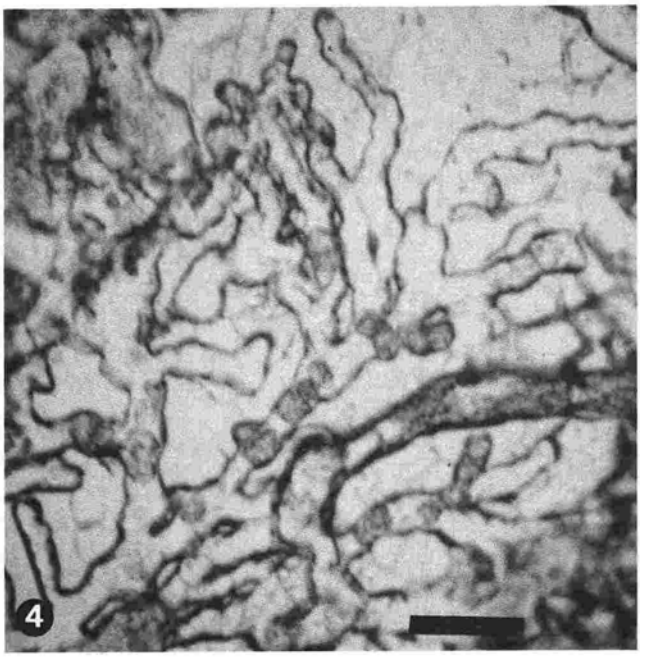
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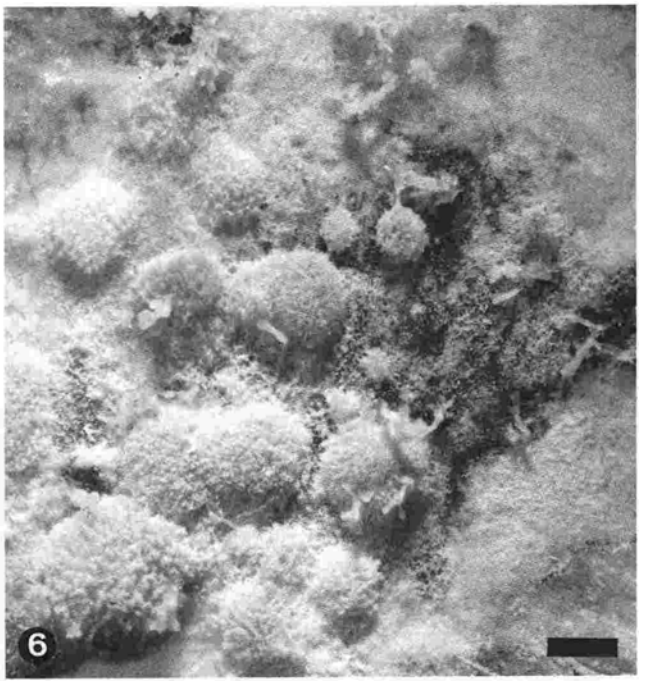
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tidal channel adjacent to Lee Stocking Island (DILL et al. 1986). Using a 2 person submersible based at Lee Stocking Island, experiments have also been established on the deep reef slope at 100, 150, and 275 m water depths (Pl. 35/3).

The substrate available to microborers was also considered important to bioerosion. PVC frames (Pl. 35/5) were constructed for exposing a variety of small $CaCO_3$ substrates (1 cm^3) at the different sites (Pl. 34/3). These substrates include a fine-grained homogeneous limestone (used because of its dense uniform character), clear calcite crystals (used because borers and their borings are easily observed after exposure in the experiments and calcite allows comparison of the results with other microborer studies that have used this substrate), and *Strombus* sp. mollusc shells (a dense substrate that occurs naturally at all the experimental sites and contains organic structures that may influence microboring in this substrate). Coral substrates have also been exposed, as well as sediment grains composed of 1 mm diameter ooids. These different substrates were glued to PVC plates that were easily mounted on the frames and removed at intervals from 1 week to 2 years that allowed the monitoring of the microboring community through time at the different sites. At collection times three or four replicates were collected of each substrate type, at each site. Three approaches have been taken to document the composition, distribution, and development of the microborer community at the experimental sites: 1) Casts of boring traces in the experimental samples are observed under SEM and provide a documentation of the cumulative effect of the microboring community and its composition through time. The casts are made by impregnating the dried sample with resin, and dissolving the carbonate substrate to reveal the filled borings of the microborers (Pl. 35/6, Pl. 36, Pl. 37/1-2, see GOLUBIC et al. 1970 and GOLUBIC et al. 1983 for more detailed descriptions of this technique). The casts observed under SEM also form the basis for the quantification of rates of boring by the endoliths. 2) Dissolution of the experimental substrates and identification of the remaining organics under a microscope provides a confirmation and detailed identification of the organisms that produce the traces seen in the SEM casts (Pl. 35/2). 3) As a basis for identifying the species that can occur in the experiments and the morphological development of their traces, the microborings in naturally occurring skeletal material from the experimental sites are also cast and observed under SEM (Pl. 37/3-6, see RADTKE 1993).

7.3 Results

7.3.1 Distribution of microborers

One of the most important controls on microborer colonization so far identified is the type of substrate (Pl. 34/3). Of the different substrates used in the experiments, the limestone substrate is more densely colonized at all sites than the other carbonate substrates studied (Pl. 36/3, 4). The least colonized are the calcite crystals (Pl. 36/1, 2). After only three months, casts of the borings show that the limestone substrates from the shallow subtidal sites to 30 m have 70% of their surfaces bored by microendoliths, while calcite crystals have less than 40% of their surfaces colonized. Although the community within the different substrates are similar, variation in the depth of penetration (Pl. 35/1, Pl. 36/2, 5), and density of boring by the community causes these differences.

It appears from the data, that different microborer communities distinguish the three basic water depth ranges sampled by the experiments (Fig. 28). Cyanobacteria (Pl. 35/2, Pl. 37/1) dominate in the intertidal notch. The chloro-

Plate 36 SEM images of microborings in experimental substrates from Lee Stocking Island Bahamas.

Fig. 1. Borings of *Phaeophila* sp. and *Solentia* sp. (arrow) in calcite showing lower density than that occurring in other substrate types (see Pl. 36/3). This lower density is typical for calcite. Site C, 30 m water depth, calcite crystal, after 12 months exposure, SEM image (68102).

Fig. 2. Side view of cast borings in calcite showing 'allomorphic' adaptation of borings to the calcite rhombohedral crystal structure. Site C, 30 m water depth, calcite crystal, after 12 months exposure, SEM image (68113).

Fig. 3. SEM image of cast borings showing an example of the intensity to which experimental substrates can be colonized by microborers. *Solentia* sp. 'bush' (upper right corner) and undetermined 'felt'. Site C, 30 m water depth, limestone substrate, after 3 months of exposure, SEM image (49715).

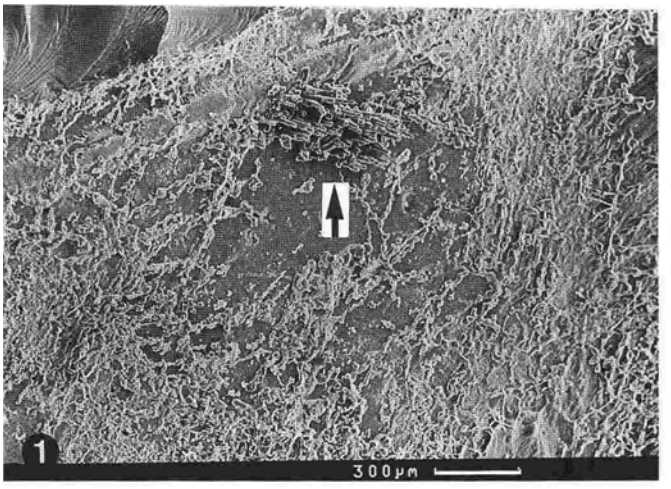
Fig. 4. 'Network' of the chlorophyte *Phaeophila* sp. (thick borings) and the cyanobacteria *Plectonema* sp. (thin borings). Same substrate as Fig. 5. Site C, 30 m water depth, limestone substrate, after 12 months exposure, SEM image (67908).

Fig. 5. Side view of cast borings showing depth of penetration by *Phaeophila* sp. (original upper surface of experimental substrate faces down in this view). Large boring to right is cast of *Ostreobium brabantium*. Site C, 30 m water depth, limestone substrate, after 12 months exposure, SEM image (67948).

Fig. 6. Ooid (dissolved) showing diverse microborer casts (central borer is *Hyella racemus* AL-THURKAIR, GOLUBIC & ROSEN) This diversity of borings is a reflection of the unknown length and history of exposure of naturally occurring substrates at the experimental sites. SEM image (60917).

Fig. 7. Cast of ball-shaped microborer showing hollows created by early (within 3 months) diagenetic centripetally growing needle cement (now dissolved). Site A, stromatolite reef, 6 m water depth, limestone substrate, SEM image (49765).

Fig. 8. Close-up of ball-shaped microborer shown in Fig. 7 with hollows created by dissolved needle cement. Site A, stromatolite reef, 6 m water depth, limestone substrate, after 3 months exposure, SEM image (49766).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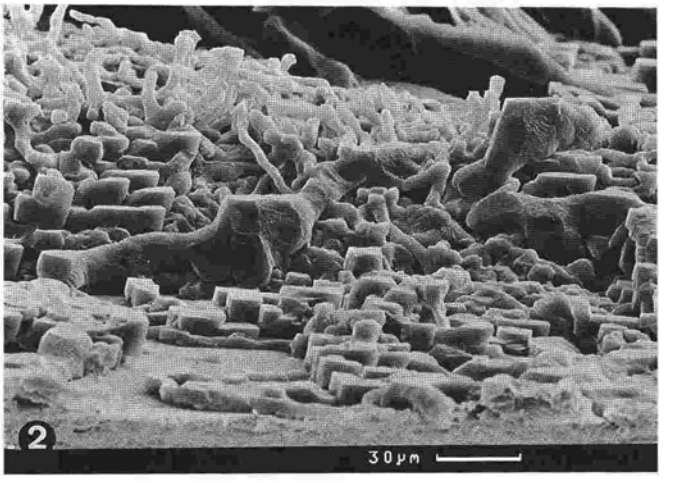
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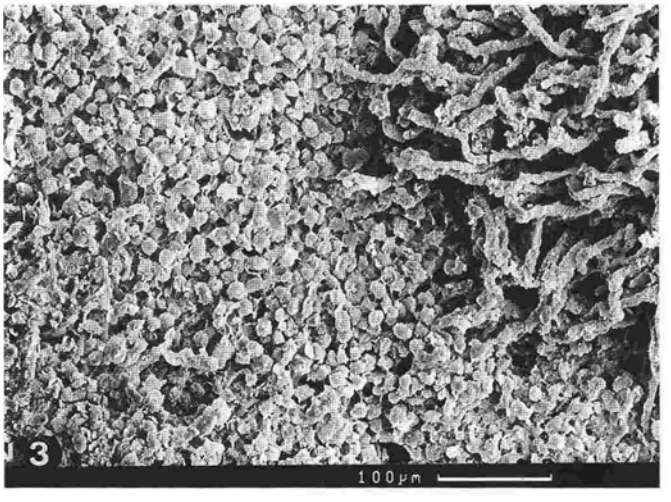
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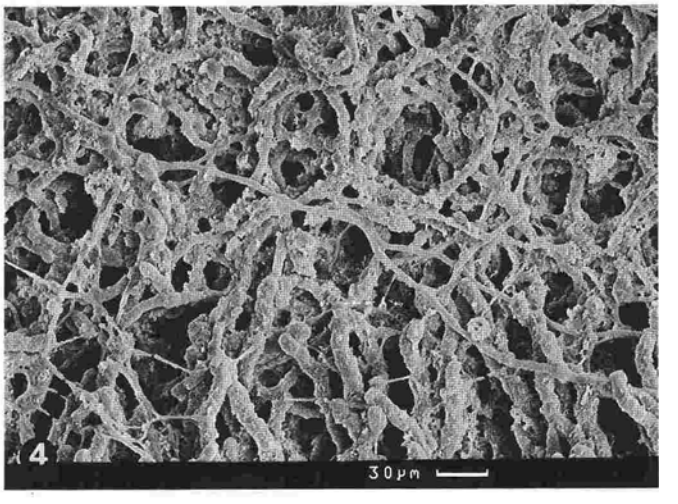
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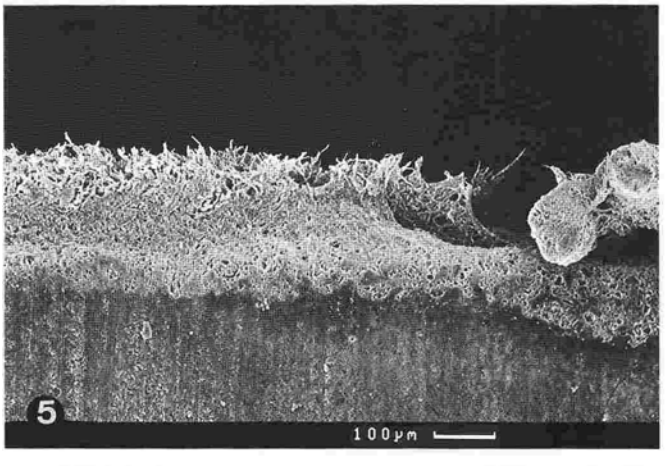
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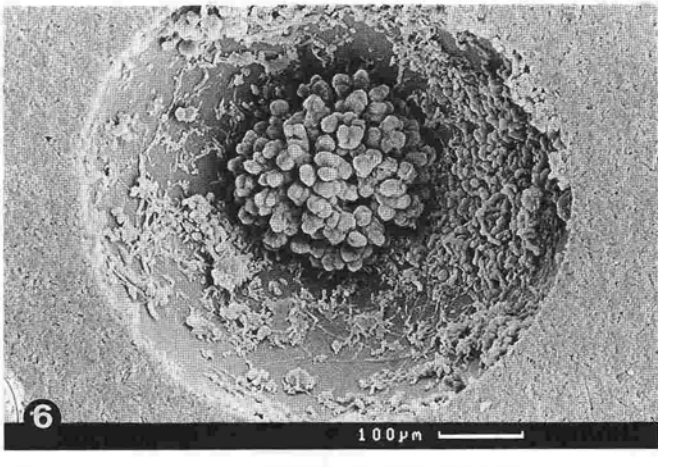
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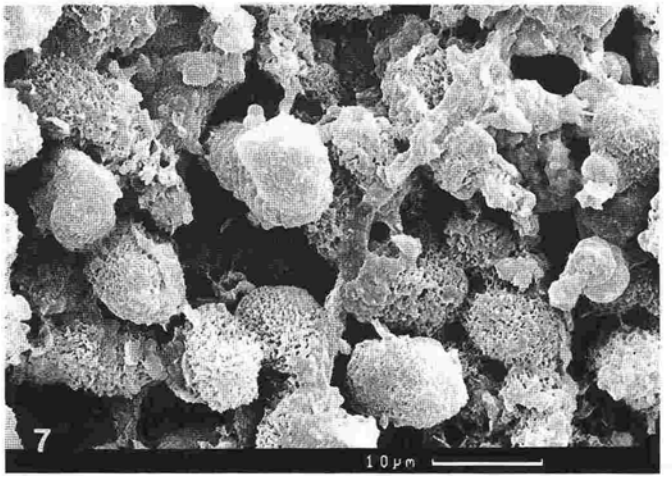
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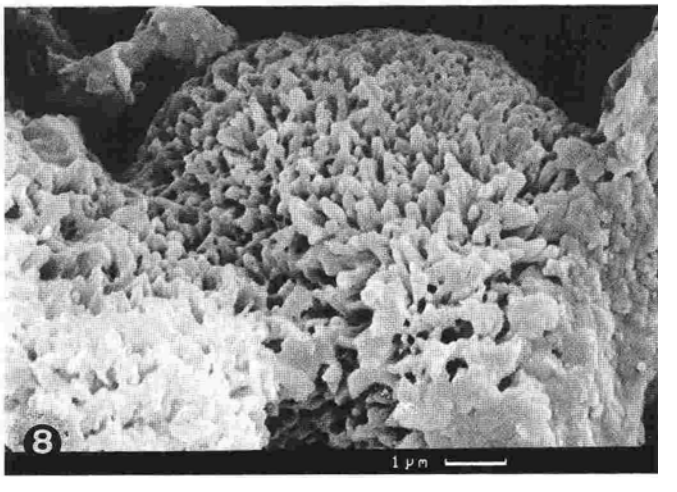
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phyte genus *Phaeophila* (Pl. 35/4, Pl. 36/1, 2, Pl. 37/4) and the cyanobacteria genera *Solentia* (Pl. 35/2, Pl. 36/1, 3), *Hyella* (Pl. 37/1) and *Plectonema* (Pl. 36/4) dominate the sites from 2 to 30 m water depth. The deep reef slope from 100 to 300 m is dominated by the chlorophyte genus *Ostreobium quekettii* (Pl. 34/2, Pl. 37/2), as well as borings by fungi (Pl. 37/6) and bacteria.

One of the first organisms to colonise the experimental substrates is *Phaeophila* sp. (Pl. 35/4, Pl. 36/1, 4). This green alga is found in samples exposed for 1 week and its colonization increases up to 6 months. However, after 12 months its abundance in samples remains constant or possibly decreases while the abundance of *Ostreobium quekettii* (Pl. 37/2) increases. Of the shallow water sites, only site C (30 m) shows *O. quekettii* in abundance in the experimental samples before 1 year. Boring heterotrophs can occur in samples after 1 month, but they do not occur abundantly until after 1 year of exposure.

One of the most significant changes with time as the endolithic community develops is the turnover in borers. Boring traces, when found in substrates, are not always occupied. In as little as 3 months, vacated *Phaeophila* sp. borings occur (Pl. 35/4). After 1 year, approximately 40% of the *Phaeophila* sp. borings in a substrate are vacated. These vacated borings can be empty, occupied by new borers, or filled with diagenetic materials (Pl. 36/7, 8), even after 3 months.

In addition to these dominating patterns, there are a large number of microborers that occur in the experimental and natural substrates in the subtidal sites from 2 to 30 m, but their presence at a site, at a particular time, seems to be randomly determined. These organisms, that begin to appear in the experiments after 4 weeks, are dominated by species of cyanobacteria. The cyanobacteria genera *Plectonema*, *Solentia*, *Hyella* and *Mastigocoleus* can be present in a substrate at any time after 4 weeks, but their variability in recruitment to the experimental and natural substrates make differences between the sites and sampling periods for these endoliths difficult to identify. For example, borings by *Phaeophila* sp. occupy 90% of sample surfaces after 3 months at site E with little variability between replicate experimental limestone substrates. However, the remaining 10% of the surfaces show large differences between replicate samples in the density and the types of borings present. Identifying differences between the samples and the sites is further complicated by difficulties in identifying species in cast. For instance, the genus *Hyella* (Pl. 36/6, Pl. 37/1) has several species and these species could have site specific distributions, but identification of the different species is not yet possible in the cast and difficult with light microscopy.

Physiological responses have been identified that may relate to light conditions. A noticeable difference occurs in the color of *Solentia* sp. that corresponds to the reduced light intensity, caused by overgrowing epiliths or the depth it has penetrated into a substrate. The deepest filaments of these colonies within substrates are more red in color than portions that are near the surface when they are isolated from the substrates by dissolution (Pl. 35/2). This color shift by this cyanobacteria suggests a change in pigment composition in response to decreasing light levels with depth within substrates or shading by epiliths.

Microborings identified by cast show the greatest diversity in the natural shell substrates collected at the experimental sites (for details, see RADTKE 1993). However, the length of time these shells were exposed to microborer recruitment may have varied substantially. Therefore, these substrates provide only samples of the organisms that can potentially occur in the experiments (Pl. 37/3-6).

The ooid sand grains also show a high diversity of borings under SEM (Pl. 36/6). Observation of ooids from the sediment deposits around Lee Stocking revealed that the experimental ooids most likely contained borings be-

Plate 37 Examples of microborings in casts from experimental and naturally occurring substrates, Lee Stocking Island, Bahamas.

Fig. 1. *Hyella caespitosa* BORNET & FLAHAULT with deeply penetrating borings. Cast, experimental substrate (*Strombus* sp.), site D, 2 m water depth, 4 weeks exposure, SEM image (74905).

Fig. 2. Boring of *Ostreobium quekettii* BORNET & FLAHAULT. Experimental substrate (Calcite), site T, northern transect, 140 m water depth, 6 months of exposure, SEM image (67530).

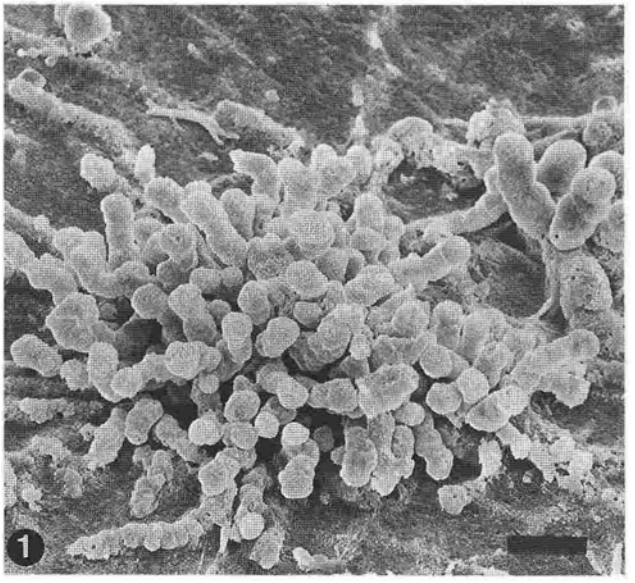
Fig. 3. A single boring of the green algae *Codiolum polyrhizum* (LAGERHEIM) KORNMANN in naturally occurring substrate (bivalve mollusc shell). This form has not yet been discovered in the experimental samples. Site C, 30 m water depth, SEM image (4814).

Fig. 4. Borings by the green alga *Phaeophila engleri* REINKE with different morphological development stages (transition from small to large boring chambers) that can occur in this species. Natural substrate (*Macoma constricta*), site D, 2 m water depth, SEM image (4822).

Fig. 5. Borings made by 'Conchocelis', the endolithic stage of the red alga *Porphyra* sp. (arrow) associated with boring made by *Phaeophila engleri* REINKE (larger borings). 'Conchocelis' has been discovered only once in the experimental substrates. Natural substrate (*Periglypta listeri*), site B, 2 meters water depth, SEM image (5206).

Fig. 6. Boring fungus *Lithopythium gangliiforme* BORNET & FLAHAULT. Natural substrate (*Tellina* sp.), site F, 10 m waters depth, SEM image (1305).

Scale bar for all Figs. is 20 µm.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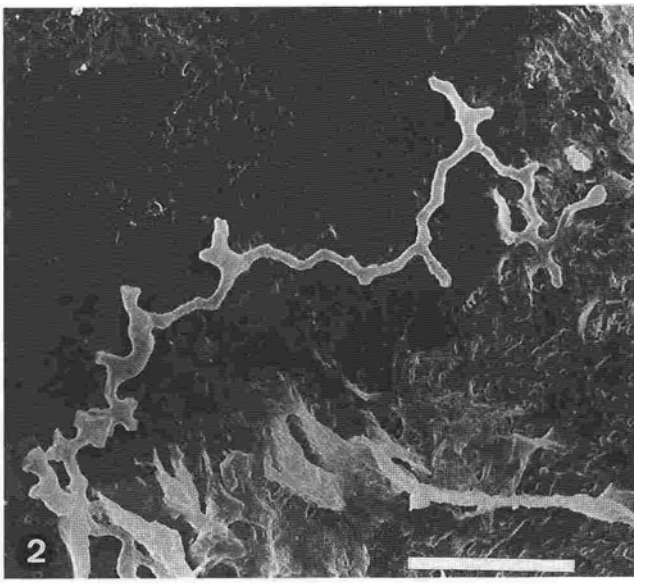
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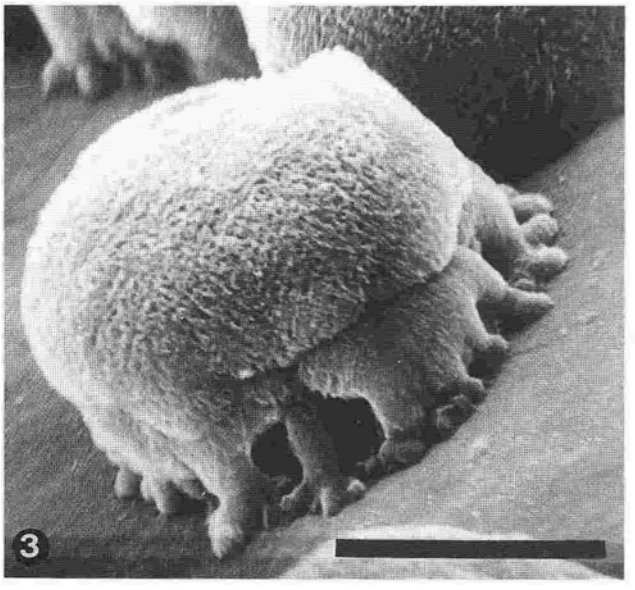
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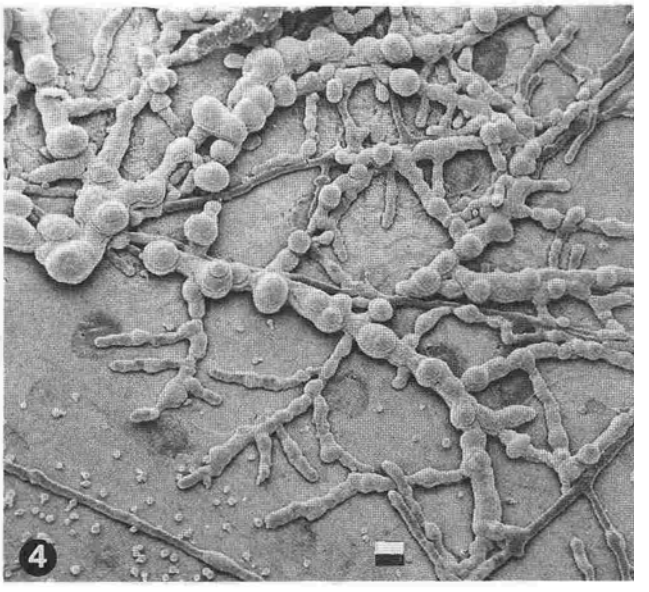
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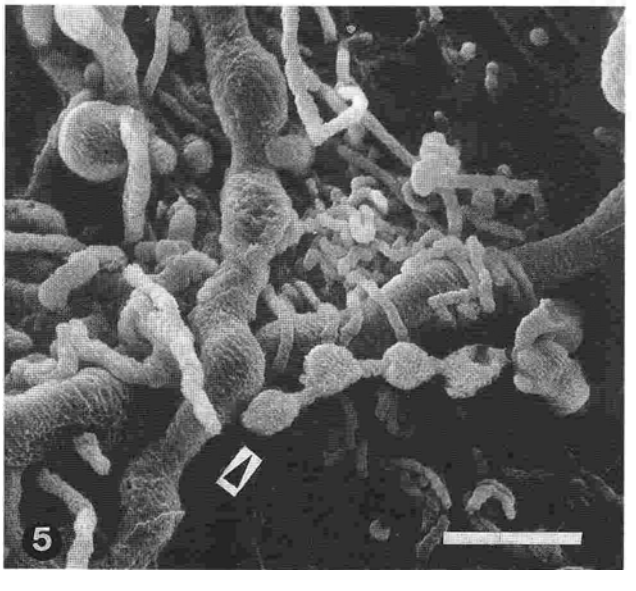
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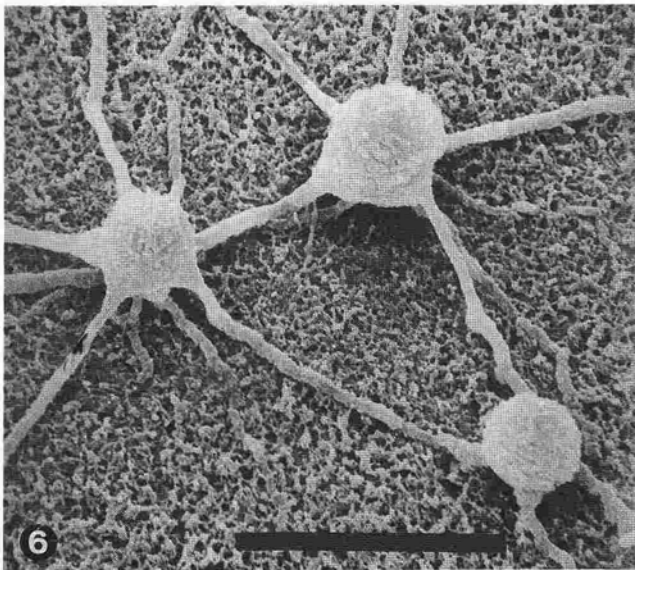
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fore they were exposed and causes the highly diverse assemblage of borings seen in the experimental grains. In addition, the coral substrates have so far presented problems for identifying microborers in the casts. The natural pores and the borings occurring in the septal walls within these substrates are both filled with resin during preparation. Observing the casts of the borings under SEM is therefore impaired. Because of these problems with ooids and coral in the experiments, the results presented here do not include data from these substrates. However, it is hoped that further development of analytical techniques will allow future results from the experiments to include these substrates.

7.3.2 Rates of microboring

The microscopic size and the endolithic habitat of microborers presents challenging problems that must be overcome in order to measure their rate of excavation within reef substrates (Pl. 36/4). A technique has been established that has created a classification system that can be applied to the SEM study of boring casts of the experimental substrates that gives quantitative results.

Microboring traces can be classified into several basic types based on their morphology, density of colonization, and depth of penetration in the experimental substrates (Pl. 36/3-5). Each of these boring types have relatively standard excavation densities and depths of penetration. By mapping SEM overview photographs (Pl. 35/6) and classifying areas with these different density-depth factors, a rate of excavation and a measure of the contribution by different endoliths to the rate of bioerosion is possible.

The results so far show that differences in substrate colonization and the depth of penetration within the different substrates have a major influence on the rate of carbonate removal by the microboring community. The high density of colonization in the homogeneous limestone can reach a depth of 300 µm (Pl. 35/1, Pl. 36/5) and this substrate shows the highest excavation rates (up to 100 g/m^2/3 months). Molluscan shells are bored to a maximum depth of 30 µm and show intermediate excavation rates (up to 20 g/m^2/3 months). Calcite crystals are the least excavated (Pl. 36/1). Boring depths in calcite are less than 10 µm (horizontal boring networks, Pl. 36/2) and show rates of 0.5 g/m^2/3 months or less. Differences in boring rates are also seen between different water depths. In the shallow water experiments from 2 to 30 m water depth, the maximum rate of microboring can be reached in 3 months (100 g/m^2/3 months), while colonization rates are very slow in deep water sites (less than 0.5 g/m^2/3 months). Colonization in the notch after 3 months ranges from the maximum in substrates at the low tide level to no excavation in substrates exposed to supratidal conditions (wet only during storms). The rates of excavation are not maintained through time. After 3 months, the rate of excavation is reduced. This is particularly true in the subtidal sites in less than 30 m of water where *Phaeophila* sp. borings are abundant in the experimental samples, but a large proportion of these borings are vacant after 3 months (Pl. 35/4).

7.4 Discussion

These experiments continue in the Bahamas and the results presented here represent the initial phase of our assessment. As additional data are obtained, the results may be modified. From the results obtained so far, clearly a complex variety of factors will control the composition of the microborer community found at a given location at any time. In particular, the differences in colonization between the different types of substrate are notable. Possible reasons for this variability between substrate types are differences in surface texture, density, or the translucency of the material being bored.

The influence of different substrates on microborer colonization has been recognized in previous work by Perkins & Tsentas (1976) and Le Campion-Alsumard (1978). Large differences in endolithic colonization between the different substrates is of considerable importance to bioerosion in different reef environments since the composition of coral reef surfaces is extremely heterogeneous both within and between different habitats. In addition, the changing nature of reef builders through geological history will have presented different kinds of substrates for colonization by endoliths (Vogel 1993). Therefore, the evolution of microborers and their presence in ancient reef environments may have been strongly influenced by the changing nature of reef substrate through geological time. The process of diagenetic infilling not only of microborings (Bathurst 1966, Alexandersson 1972, Kobluk 1977, Kobluk & Kahle 1978, Harris et al. 1979), but also of macroborings (Scoffin 1972, Ginsburg & Schroeder 1973, Kiene 1988), forms an important aspect of the preservation of carbonate skeletons in reef environments and to the way that these skeletons contribute to reef growth and the fossilization process. Therefore, the interaction of reef frameworks with bioerosion processes through geological time may have influenced the preservation of different fossil reef builders.

The controlling influence of light is obviously of particular relevance since the majority of microboring species are photoautotrophs. The quantity and quality of light are both important in determining species composition, character and abundance (Golubic et al. 1975). The shift in pigment composition of *Solentia* sp. with depth within the substrates has been reported for a number of cyanobacteria (Le Campion-Alsumard 1978) and exemplifies the sensitivity of certain microborers to light conditions. The dominance of *Ostreobium quekettii* in the deep slope sites shows the ability of this organism to live in low light conditions. This occurrence of *Ostreobium quekettii* in deep water environments has been observed by Fredj & Falconetti (1977), Lukas (1978), Le Campion-Alsumard et al. (1982), and Akpan & Farrow (1984). *Ostreobium quekettii* not only lives in these deep water environments, but also lives deep within coral skeletons beneath live coral tissue (Kanwisher & Wainwright 1967, Lukas 1974, Highsmith 1981) where light levels are reduced.

As has been shown for larger macroboring organisms in studies of bioerosion on the Great Barrier Reef (Hutchings

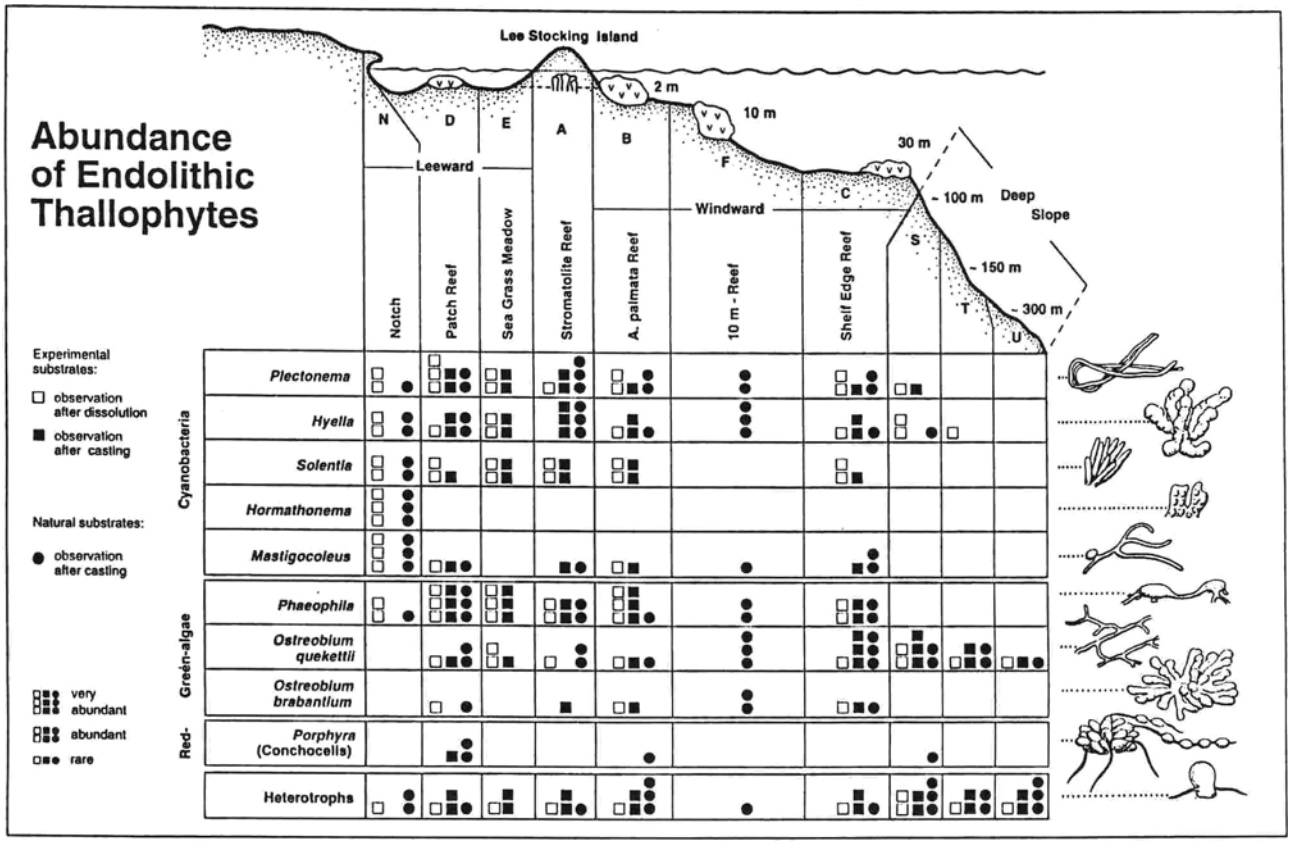

Fig. 28. Initial results of the distribution of different microborers (rows, with characteristic boring traces illustrated to the right) identified from dissolution (light microscopy) and casting (SEM) of experimental substrates, and casting (SEM) of naturally occurring molluscan shell substrates from the experimental sites (columns) near Lee Stocking Island, Bahamas. Site N is several sites within the 2 m intertidal range of the erosion notch that surrounds a small leeward Island. Sites D, E, B, F, and C are shallow windward and leeward reef sites from 2 to 30 m water depth. Site A is a reef formed by large subtidal (6 m water depth) stromatolites in a channel adjacent to Lee Stocking Island. Sites S, T, and U are windward deep reef slope sites at 100, 150 and 275 m water depth respectively. These data are based on up to 3 replicate samples from each site exposed for time periods ranging from 1 week to 24 months. The three methods have not been applied fully to all sites (column N, E and, F) and differences between sites should not be considered statistically significant. The data are relative abundances based on the scale shown to the left. Identification of the different *Hyella* and *Solentia* species from casts is tentative.
Three basic zones can be characterized by their microborers: 1) the intertidal notch dominated by cyanobacteria, 2) shallow water reef sites dominated by cyanobacteria and the green alga genus *Phaeophila*, and 3) the deep reef slope dominated by the green alga *Ostreobium quekettii* and heterotrophs (fungi and bacteria).

et al. 1992), the results suggest the microboring community contains species that are early boring colonists that establish rapidly in newly available substrates. These first colonists are from the genus *Phaeophila*. They have a short generation time and the individuals or colonies turn over rapidly, leaving behind only the record of their presence in their boring traces. With time, these early borers are replaced or joined by slower growing but long lived species, such as *Ostreobium quekettii*, that may eventually dominate the endolithic community. The early colonization and subsequent presence of unoccupied borings produced by *Phaeophila* sp. in experimental substrates has also been recorded by Kobluk & Risk (1977) (see Lukas 1979 for a re-examination of their endolith identification). Chazottes et al. (1994) have also found that *Ostreobium quekettii* is a late colonizer in experiments conducted in French Polynesia. Since *O. quekettii* favors low light conditions, its delayed growth may be a response to decreased levels of light within substrates as epilithic colonization develops with time. Its appearance in experimental samples from the 30 m site before the other shallow water sites may be a response to lower light levels at this site. Bacteria and fungi are also slow to colonise the experimental substrates. As heterotrophs, these borers require the organic resources of the early-colonizing, autotrophic borers. Heterotrophic borers may also attack organic structures that exist in skeletal material. As the substrate becomes bored by both algae and fungi, these organic structures become more accessible to heterotrophs. The development of epilithic algae communities on reefs surfaces can be influenced by many factors (Berner 1993), and this is likely to be true for endoliths. Whether the succession of different microborers seen in the experiments is purely a response to changing light conditions and nutrient resources in the substrates, or a response to many other ecological factors, remains unanswered.

Interpreting the development of the microboring community through time from only the traces left behind in dead or fossil skeletal material is a complicated task that requires more detailed understanding of the life history,

boring morphology, and environmental controls on endolithic organisms than is known at present. However, the results suggest that with longer exposure of a substrate to microborer recruitment, the greater chance there is that a species will establish in the substrate, and thus, a greater diversity of boring traces will be preserved. This is particularly evident in the higher diversity of borings in samples of natural substrates (mollusc shells and ooids), collected from the sea floor, than that found in the experimental substrates. Since the natural substrates have likely been exposed to borer recruitment for longer periods than the experimental substrates, the cumulative effect of random borer recruitment through time has been to preserve a greater diversity of traces made by the microborers.

The rates of boring measured so far are in agreement with those obtained with other techniques used in previous studies of microborer bioerosion in reef environments (KOBLUK & RISK 1977, TUDHOPE & RISK 1985, PEYROT-CLAUSADE et al. 1994, CHAZOTTES et al. 1994). Although these rates represent removal of dissolved carbonate, the greatest impact of these rates will be in how the rate of excavation will influence the subsequent erosion by other organisms. In shallow water, the long term erosion rate will be determined by grazing erosion caused by animals such as parrotfish that feed on endolithic algae (KIENE 1985, 1988, BELLWOOD & CHOAT 1990, KIENE & HUTCHINGS 1994). BRUGGEMANN et al. (in press) show that the rate of bioerosion of reef substrates by these fish is controlled by the density of boring by endolithic organisms that form a major part of the diet of these grazers. He found that the rate of grazing bioerosion for a particular reef habitat is a function of the density of bioeroding fishes and the amount of microborer infested substrate that is present.

7.5 Future Studies

It has been the focus of our study to try and unravel some of the factors that control the distribution of bioerosion processes. In a continuing effort to do this we are further refining our sampling techniques and data collection procedures that will provide a more detailed understanding of the microboring community and its impact on bioerosion in reef environments. The distribution of bioerosion by grazers and macroborers at the study sites will be assessed in the study of coral blocks that have been exposed for 2 to 3 years in experiments conducted parallel with the microborer study (Pl. 35/5). These macro-erosion experiments are comparable to ongoing studies being conducted in the Red Sea, to previous studies by PEYROT-CLAUSADE et al. (1994) and CHAZOTTES et al. (1994) in French Polynesia, and to previous bioerosion experiments on the Great Barrier Reef (KIENE 1985, 1988, KIENE & HUTCHINGS 1994).

The study of the morphometric development of borings made by the different endolithic species is being conducted. It is hoped that this study will provide a basis for identifying different species from very similar boring traces, such as those made by the different cyanobacteria species. This may further refine the distribution patterns by these species that have so far proven difficult to recognize. In addition to the Bahama studies, the impact of nutrients on bioerosion and the role of bioerosion on the nutrient pathways of reefs is being investigated at One Tree Reef on the GBR (from Sept. 1993). This major program, co-ordinated by Australia's Great Barrier Reef Marine Park Authority, is evaluating the effect of controlled introduction of nitrogen and phosphorous on a variety of reef organisms and processes (STEVEN & LARKUM 1993). An important aspect of this evaluation is the impact of nutrients on net calcification and reef growth. By monitoring bioerosion processes within these experiments, it is hoped that insight will be gained on how enriched nutrient conditions change reef erosion processes and alter rates of reef accretion. The rapid colonization of substrates by microborers suggests that the response of these endoliths may provide a valuable early indicator of water quality decreases in reef environments that result from elevated nutrients.

The investigations in the Bahamas and the Great Barrier Reef are focusing attention on bioerosion not only as a destructive function on reefs, but also as an essential part of the incorporation, alteration, and transfer of inorganic and organic materials within the coral reef ecosystem. With this focus, bioerosion is proving to have a fundamental role in building the highly diverse biological and geological character of reefs today and in the past.

8 GENERAL CONCLUSIONS

This compilation of diverse studies allows some preliminary conclusions to be drawn that have relevance to broad issues of reef development and provides direction for further studies. The two contributions on coral growth show the importance of light in controlling rates of calcification. However, adaptations that modify energy intake by particular corals can compensate for reduced light conditions and such modifications can be further altered by local environmental conditions. The data show the importance of considering conditions imposed by bathymetry and latitude when comparing coral calcification and growth rates. The variability of ecological conditions in shallow water can impose significant effects on coral growth. In addition, rates of coral growth in the northern Red Sea appear to be higher than observed on reefs in the Atlantic and Pacific at similar latitude. These data stress the need for additional understanding of the regional conditions that influence coral growth in the Red Sea.

Translating coral growth into reef growth requires, in part, a comprehension of the community of other calcifying and non-calcifying organisms within a given reef area. It is crucial to realize the impact of ahermatypic organisms such as soft corals in competing with reef constructors for available space. However, the role of spatial and temporal variability in ahermatypic cover in the model of reef carbonate budgets remains poorly understood. A soft coral carpet may react 'neutrally' with regard to reef growth, while open space can be the site of colonization by reef constructors or the site of destruction by reef destroyers.

Over the last decade the proportion of scleractinians have remained relatively stable at Aqaba and on Sanganeb-Atoll. On the other hand, the proportion of soft corals to open space has varied considerably at these sites over the same period. It is noteworthy when comparing the role of open space on a reef that xeniids are completely absent in some reef regions (e.g. Persian Gulf, Maldives).

'Outbreaks' of coral predators, such as the starfish *Acanthaster planci* or the gastropod *Drupella* can have a significant impact on creating open space on a reef and quantitatively halt calcification by coral tissue. The duration of the impact of such predation is, at the very least, several years and can significantly disrupt patterns of coral growth. These coral predators, and soft corals that may colonize the open spaces they create, do not leave fossil traces on the reef surface that have been recognized (the pedestal of *Quoyula madreporarum* is an exception). It is therefore particularly difficult for geologists to consider these influences when reconstructing reef dynamics of the past.

The traces produced by bioeroders may have some application to determining the history of open space on a reef. Reef surfaces subjected to grazing by *Diadema* or other grazers may preserve their respective traces. The removal of carbonate by such bioerosion can have a significant impact on reef budgets. The impact of grazing erosion on the development of borer populations within reef surfaces may provide insight into the intensity of carbonate removal from fossil reef surfaces. Borers, particularly microborers, are widespread geographically and occur in a wide range of reef habitats. Unlike corals, microborers have probably been a constant member of the reef community throughout geological history. The further study of their distribution and ecology on living reefs may provide valuable clues to depth, nutrient conditions, and substrate history of Holocene and older reef deposits.

The compilation of research efforts presented here has not defined the entire range of controls on Holocene reef growth. However, it has shown that integration of data from a wide range of disciplines is necessary to understand the factors that influence the incorporation and transformation of calcium carbonate on coral reefs. Combining data on the distribution and rates of carbonate construction and destruction and their environmental and ecological controls within different reef environments is a useful approach to investigating the development of reefs. The result is a wider view of the function and variability of the different components within the reef carbonate economy. The interdisciplinary collaboration among reef scientists required to gain this view will provide better understanding of the environmental changes faced by reef communities in the past, today, and in the future.

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