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REGENERATION AND ASPECTS OF SPATIAL COMPETITION IN THE SCLERACTINIAN CORALS

AGARICIA AGARICITES AND MONTASTREA ANNULARIS

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ABSTRACT

Regeneration of corals was studied at the fringing reef on the southwest coast of Curacao. Three types of circular lesions were inflicted in situ on colonies of Agaricia agaricites and Montastrea annularis: 1 cm² tissue lesion, 1 cm² tissue + skeleton lesion, 5 cm² tissue + skeleton lesion. All lesions were surrounded by 10 cm living coral tissue. These artificial lesions were immediately colonized by fleshy algae. The second most important colonizers were clionid sponges. The regenerating coral tissue can overgrow the colonizing organisms. One regeneration mechanism was found in Agaricia agaricites and two different mechanisms were observed in Montastrea annularis.

Montastrea annularis grows over lesions faster than Agaricia agaricites. Both species recover small scars (1 cm²) much faster than large (5 cm²) ones. In Agaricia agaricites recovery was faster when only tissue was removed compared with damage to tissue + skeleton. In Montastrea annularis the opposite is the case. This has consequences for the impact of coral predators on different coral species.

KEY WORDS: Corals, Damage, Regeneration, Competition, Benthic Organisms, Curacao.

REGENERATION AND ASPECTS OF SPATIAL COMPETITION IN THE SCLERACTINIAN CORALS AGARICIA AGARICITES AND MONTASTREA ANNULARIS

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Introduction

The ability of Scleractinia to regenerate and repair their damaged colonies is a parameter of basic importance in many coral reef problems such as reef regeneration, impact of coral predators, effects of sedimentation, pollution and other adverse factors. This ability will depend on potential powers of regeneration as well as on the nature of the colonization of the new, bare skeleton by benthic organisms and the competitive capabilities of the corals. That regeneration of damaged coral colonies is possible has been demonstrated extensively (e.g. 1, 2). This work as well as recent research (3) emphasized the problems involved in skeletal regeneration.

The only observations dealing with the regeneration of superficial lesions on coral colonies are those of Fishelson (4). He gave qualitative records of phenomena occurring after numbers of colonies had partly lost their living tissue following desiccation. The degree of destruction of the tissue and the kind and degree of fouling of the bare skeleton determined whether colonies regenerated completely or partly or were totally destroyed.

In Curaçao exposure of reef corals to air is rare and ordinarily involves only the tips of branches of Acropora palmata and the upper parts of a few colonies of other species. Skeletal regeneration is common following damage induced by physical factors such as storms, gravitation etc. Field observations indicate that the most common causes of injury to living corals are sedimentation and predation. Infection with cyanophytes, reported to be a very important cause of coral mortality elsewhere in the Caribbean (5), is extremely rare in the Curaçao reefs. Sedimentation on living coral can result in death of the underlying living tissue, the degree of damage being dependent upon the size and amount of sediment particles, the species specific rejection capacity and the habitat (e.g. 6, 7). The effect of predation is difficult to assess but seems to be limited. Common coral predators in Curaçao are the gastropod Corallophila abbreviata, the polychaete Hermodice carunculata and, locally, the echinoid Diadema antillarum (8).

We are interested in the largely unknown effect on coral survival of scars caused by sedimentation or predation. The bare skeleton of the lesion is usually rapidly colonized by organisms competing with the corals for space. But there are no quantitative data available on either the relation between size or nature of a lesion and the rate of regeneration, or on the

competitive abilities of coral tissue and colonizing organisms.

This study is part of an attempt to determine the degree to which various environmental factors limit coral growth in situ.

Material and methods

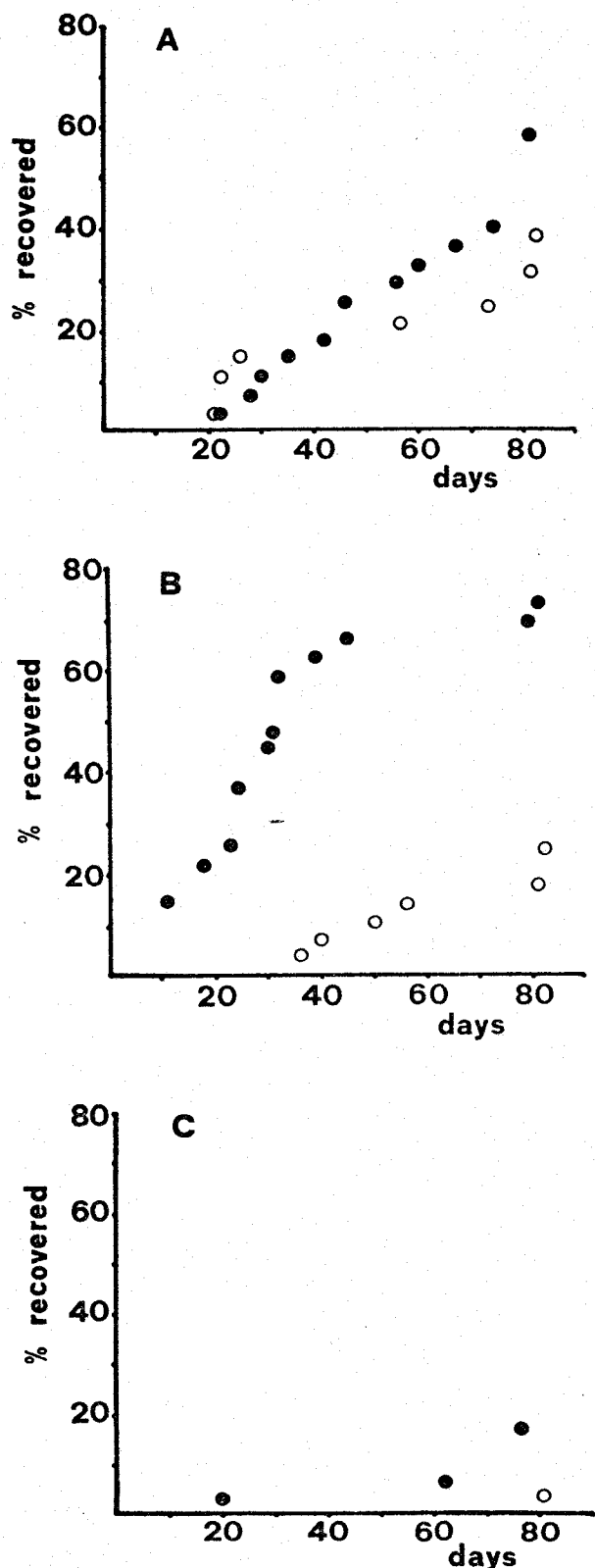
Our experiments and observations were done between March and July 1976 at the fringing reef on the southwest coast of Curaçao. Agaricia agaricites and Montastrea annularis, two species common on these reefs (9) as well as elsewhere in the Caribbean, were employed. The coral colonies were all located on a 150 m long stretch of reef, 700 m northwest of the entrance of Piscadera Bay. To exclude variations due to differences in the degree of exposure to water movement, sedimentation, light etc., the depth range of the experiments was restricted from 8 to 12 m.

On the living tissue of each species we made 3 series of 30 circular lesions. One series of lesions consisted of 1 cm² areas in the living coral tissue. A second series of the same size included removal of the tissue as well as the underlying superficial skeletal elements. In a third series the damage was inflicted to tissue and skeletal elements over a circular area of 5 cm².

The lesions were made by very carefully blowing clean the desired surface area with a fine jet of air, delivered from a SCUBA tank through a single hose Poseidon regulator. The second stage of the regulator was removed and a hollow needle mounted on the hose. The force of the air jet could be controlled with a wrench in the first stage of the regulator. Damage including tissue and skeleton was performed by scratching carefully with a knife the skeletal elements that protude above the coenenchymal surface. Subsequently skeletal elements (mostly septa) and tissue were blown away. The exact size of a lesion was controlled with a plastic templet in case of tissue damage, and the size was marked with a hollow punch when both tissue and skeleton had to be removed.

In order to make a scar that could be used in the experiments, utmost care had to be taken to remove all tissue (a critical factor) from between the skeletal elements, and not to damage the surrounding tissue with too forceful blasts of air. The difficulties in this operation and in making circular lesions of exactly (error < 5 %) the same surface area, were the reasons that, even after practice, about 50 % of the lesions had to be discarded.

Coral colonies that looked perfectly healthy were selected. The living surface did not display



any discolouring or excessive dead spots. The size of the colonies was sufficient that at least a circular area of living tissue, not colonized by algae or sessile organisms, with radius of 10 cm was present around the lesion. The *Agaricia* colonies formed a very uniform sample, but the *Montastrea* colonies differed in colour (green and brown) and in shape of the colony (globular and columnar). Appearance and size of the colonies were recorded.

The individual colonies were marked with small, labelled underwater buoys. A few of these markers were lost, reducing the total number of lesions under observation at the end of the experimental period to 168. All lesions were checked weekly for the size of the lesion, nature of colonizing organisms and tissue regeneration characteristics. Observations on the majority of the lesions were discontinued after 84 days.

Results

The rates of regeneration of the scars are compared between the species and shown in Fig. 1. Evidently *Montastrea annularis* has a higher regeneration rate than *Agaricia agaricites*. Especially when the skeleton underlying the scar is also damaged, the regeneration process is much slower in *Agaricia*. Observations on the size of the scars confirm *Montastrea*'s higher capacity to cope with damage. In *Agaricia* 12 lesions (out of 85) were significantly enlarged (10 -1350 % of originally inflicted damage) after 84 days. In *Montastrea* only 2 lesions (out of 83) were enlarged (40 -100%).

It appears that different types of lesions influence the rate of regeneration strongly. Fig. 2a shows that *Agaricia* regenerates faster when the skeleton underlying the lesion is undamaged and only tissue is removed. Surprisingly, this is not the case in *Montastrea* (Fig. 2b). Regeneration is much faster in this species when both the tissue and the underlying skeleton are damaged.

Because the size of the colonies may influence the regeneration rate the size of the experimental colonies was noted. All *Agaricia* colonies formed vertical plates of approximately the same size. The colonies of *Montastrea* are assigned to three size classes: diameter < 40 cm, 40 cm < diameter < 60 cm, and diameter > 60 cm. Colonies of these size classes, which regenerated a tissue lesion in the experimental period,

Fig. 1 (left). Rates of regeneration of the two coral species expressed as percentage of lesions completely recovered. Open circles: *Agaricia agaricites*. Closed circles: *Montastrea annularis*. (A) 1 cm² tissue lesion. (B) 1 cm² tissue + skeleton lesion. (C) 5 cm² tissue + skeleton lesion. For *Agaricia agaricites* n = 28 (A), 28 (B) and 29 (C). For *Montastrea annularis* n = 27 (A), 27 (B) and 29 (C).

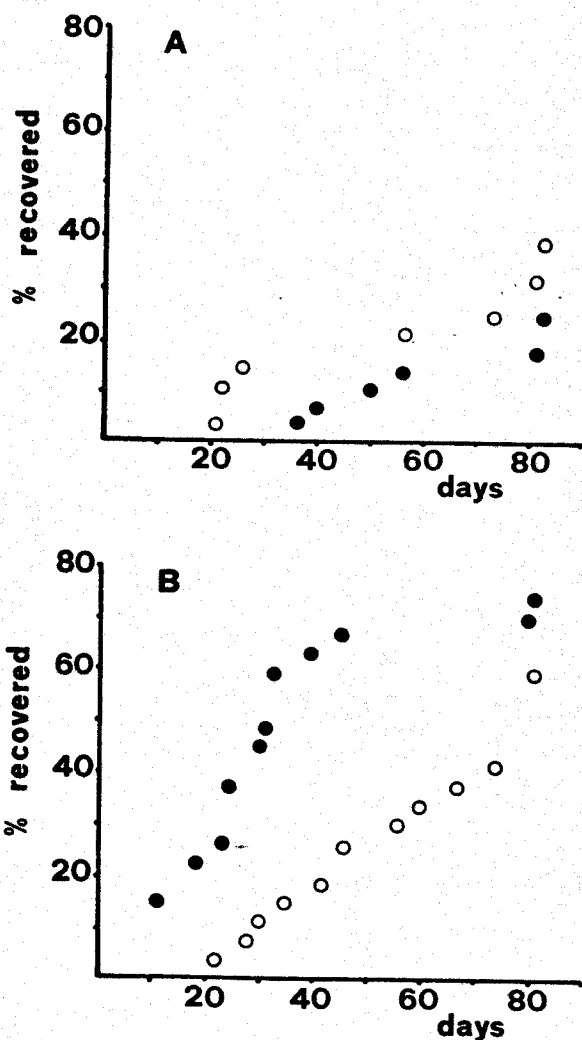


Fig. 2. Comparative rates of regeneration of 1 cm tissue and tissue + skeleton lesions. Open circles: complete recovery of tissue lesion. Closed circles: complete recovery of tissue + skeleton lesion. (A) *Agaricia agaricites* n (t) = 28, n (t+s) = 28. (B) *Montastrea annularis* n (t) = 27, n (t+s) = 27

did so in respectively 72.3 (57 %), 38.0 (67 %) and 45.2 (71 %) days on average. The numbers in brackets give the percentage of the corals that recovered within 84 days. It appears that the smallest sized colonies regenerated significantly more slowly than the larger ones (t test, $p < 0.02$). No differences are found between the size classes when the recovery periods for the tissue-skeleton lesions are compared.

The two species employed different strategies to overgrow the scars. In *Agaricia agaricites*, after regeneration and activation of the

peripheral coral tissue, the septa between the surrounding calices and the lesion elongate. The outgrowth of the tissue ridge, followed by the newly calcified skeleton does stay clear of the lesion. The regenerated skeleton forms a dome-shaped roof over the damaged surface. The closing of these structures takes relatively much time. Fig. 3a shows that the covering of the last 25 % of the scar takes more than 33 % of the recovery time. The algae that have colonized the lesion

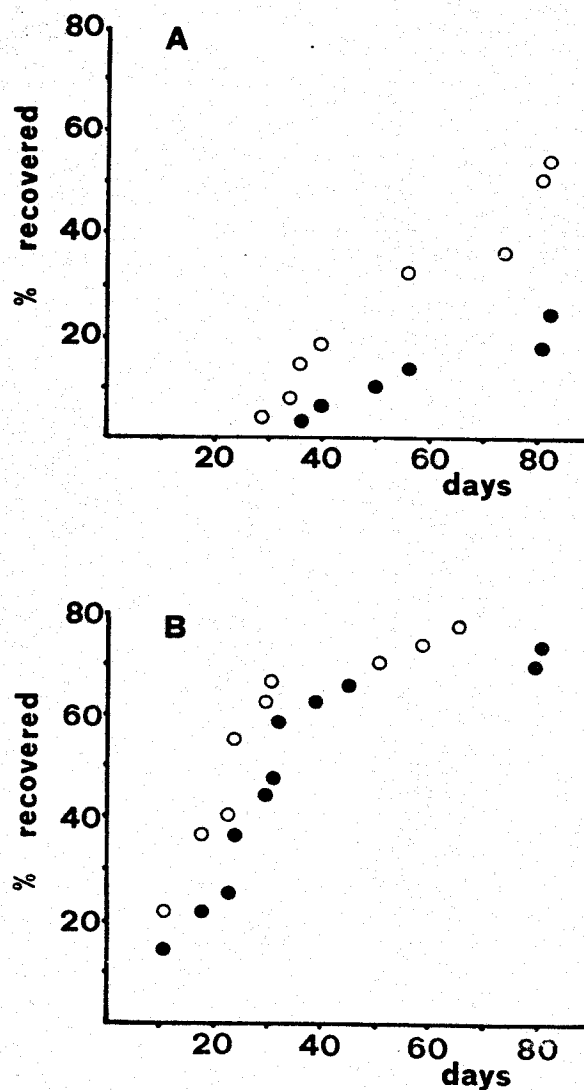


Fig. 3. Regeneration rates of tissue + skeleton lesions to 75 % and 100 % recovery of lesion respectively. Open circles: 100 % recovery of lesion. Closed circles: 75 % recovery of lesion. (A) *Agaricia agaricites* n (75 %) = 28, n (100 %) = 28. (B) *Montastrea annularis* n (75 %) = 27, n (100 %) = 27

protrude through the final opening in the regenerated skeleton and seem to retard the complete closure of the structure.

Montastrea annularis showed two different modes of regeneration. In one half of the colonies the coral tissue grows rapidly over the lesion. This vigorous tissue growth is activated by all surrounding polyps. In this process of rapid overgrowth the remnants of old calices often become occupied by the new polyps. In these colonies we never saw small polyps. A seemingly undifferentiated tissue layer showed, on the next weekly observation, polyps that are the same size as the original polyps.

The second half of the Montastrea colonies displayed another process of regeneration which is characterized by much slower recovery. Polyps which were partly damaged at the edge of the inflicted lesion regenerate and elongate their septa to the center of the lesion. Between these elongated septa, initially small, new polyps are formed which in their turn elongate their septa towards the center of the lesion. Regenerating Montastrea colonies were never observed to form chambers under the regenerated skeleton and there is no disproportional time lag between approximate and total closure of the lesion. In contrast with Agaricia the last 25 % coverage of the scar takes 25 % of the total recovery time (Fig. 3b).

In both species the tissue around the lesion may expel zooxanthellae. This results in a light-coloured spot in the tissue that sometimes remains visible for weeks after the complete regeneration of the scar.

Fresh lesions are colonized within a few days with fleshy algae. The resulting algal turf acts as a sediment trap. Consequently the scars become covered with dense algal-sediment mats. The second most abundant colonizing organisms are burrowing sponges (clionids). We observed the first clionids on the lesions 12 days after infliction of the damage. Agaricia lesions were more heavily colonized with clionids than lesions on Montastrea during the experimental period. We suggest this is caused by the slower recovery of this species as compared to Montastrea. This explanation is supported by the variation in number of settled sponges on the different types of lesions, which reflects the different lengths of time available for settlement (Table 1). Some of the sponges were overgrown by algae and corals in the experimental period. The only other colonizers observed were encrusting sponges (2 times), anemones (1) and Bryozoa (2).

Discussion

Our previous field observations as well as data in the literature (e.g. 10) suggested that the efficiency of coral species in competition with organisms colonizing the bare skeleton is very low. Supposedly, colonization of a scar means that this part of the skeleton is dead.

Table 1. Number of clionid sponges observed to settle on the various types of lesions. (Ag: Agaricia agaricites; Mont: Montastrea annularis; t: tissue, 1 cm²; t+s: tissue and skeleton, 1 cm²; t+s.5: tissue and skeleton 5 cm²)

	Ag			Mont		
	t	t+s	t+s.5	t	t+s	t+s.5
no. clionids	5	10	13	2	1	11

This dying of parts of the colony could only be prevented by rapid tissue growth of the corals to cover the wound before settlement of other organisms occurred.

In our experiments we found all lesions to be colonized. Total recovery in the most rapidly regenerating lesions (Montastrea, tissue + skeleton damaged) took 11 days. This time interval allows ample time for algal colonization. However, the corals appear to be quite able to overgrow the colonizing algae. Fishelson (4) also noted that corals are able to overgrow algae that colonized dead parts of the skeleton.

The larger lesions (5 cm²) were the slowest to recover. Less than 20 % of the lesions recovered during the time of the experiment. Observations on 10 lesions in Montastrea annularis after 170 days showed that, compared with the last check (84 days), 4 colonies displayed no further recovery and 6 colonies overgrew an additional 15 -90 % of the original scar.

Connell (10) suggested how the size of the lesion might be of consequence. He thought the amount of materials and energy that can be supplied by the lesion-surrounding coral tissue to be of critical importance in regeneration. Loya (3) found damage to be more detrimental to very small colonies than to larger ones. In the present experiments we find a significant difference in regeneration rate between tissue lesions on small and larger colonies of Montastrea annularis. However, in case of damage to the tissue as well as the underlying skeleton no difference is found between the size classes. This argues against the potential rate of tissue regeneration as being the limiting factor in regeneration in this case. The difference between the rates of recovery of tissue + skeleton lesions and tissue lesions in Montastrea suggests that different factors are of prime importance in the regeneration of the different types of lesions. This phenomenon may be related to similar reactions to light and heavy damage (including skeletal elements) in Plexaura flexuosa. Lang da Silveira and van 't Hof (11) observed in this species regeneration rates to be slow when only the outer and middle rind was removed, compared with the regeneration of lesions that include also the removal of the axial sheath (inner layer of spiculae). Lack of reports on the reactions of colonial Anthozoans to various forms of damage

precludes interpretation of these data.

We found no indications of differences in the regeneration rates between the different morphological forms of Montastrea annularis. Nor could we assign either of the two regeneration processes displayed by this species to a particular form.

The effect that damage has on the condition of coral colonies appears to depend on a large number of factors. The various species react differently, the type of damage is a basic variable, the size of the colony is important, as is the nature of the colonizing organisms. Glynn (12) reports that a Cliona transplanted on a scar in Siderastrea tissue overgrows the coral. We found Agaricia agaricites and Montastrea annularis able to compete successfully with clionids. It appears that in Montastrea fewer sponges settled and that these were more easily overgrown than in Agaricia. In addition, in both species, fewer sponges settled on the 1 cm² lesions and these were more easily overgrown than those on the 5 cm² lesions. This phenomenon is correlated with the time available for settlement and growth of the clionids. Small sponges will be overgrown, larger ones can maintain themselves.

It must be noted that generalizations on the competitive abilities of corals must be avoided. Previous observations (13) support the view that relations between corals and other benthic reef organisms should be studied at the species level.

The location of the lesion on the coral colony is of importance. Ott & Lewis (14) observed no regeneration when patches of Montastrea tissue had been removed by Coralliophila abbreviata. This snail removes tissue patches on the boundary of dead skeleton and living tissue. These patches are subsequently colonized by algae. All lesions we studied were surrounded by living tissue and though the lesions were also colonized by algae a considerable percentage of the lesions recovered. Finally, adverse conditions in the environment may impair the competitive abilities of corals (15, 16).

Our results show that predators can have different effects on different coral species. For instance predation by Diadema antillarum on Agaricia agaricites would cause relatively more serious damage than predation by Coralliophila abbreviata. The first predator scrapes off parts of the skeleton underlying the tissue, while the second one sucks off the tissue without damage to the skeleton. Montastrea annularis, on the other hand would recover sooner from predation by Diadema, because skeletal damage apparently accelerates tissue regeneration.

In conclusion, the corals studied are efficient competitors, pushing and overgrowing organisms that colonize lesions on their dead skeletons. The most important colonizers, settling within a few days, are fleshy algae. A secondary role is played by clionid sponges which settle within two weeks. Different coral species show different regeneration rates and regenerate relatively more slowly or faster depending on the type of damage inflicted.

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