

Aspects of community organization in
Caribbean stony corals (Scleractinia).

ABSTRACT

Stony corals (Scleractinia) are the ecological dominants on Caribbean coral reefs. These organisms are distributed in distinct zones over the reef profile. This pattern has been explained as the result of physiological demands but increasing emphasis is laid on ecological differences between the coral species and the predictability levels of the various habitats. However, striking anomalies are found in the occurrence of coral species and of reefs. These are in part caused by the diverse reactions of corals to the temporal and spatial heterogeneity of their environment. The continuity of the habitats is interrupted by factors such as epidemic disease, storms, outbreaks of competitions and human activities, the effect of which in turn depends on the composition of the coral community. The variations in coral response are caused by the evolution of different life histories such as displayed by Agaricia, Montastrea, Acropora and Madracis. These species differ in the way they reproduce, survive, regenerate, compete for space, their growth rates etc. Reefs and their distributive patterns are far from fully understood but the interaction of physiological requirements, life history characteristics, heterogeneity and recent history of the habitat, is of major importance in the explanation of community composition and the stage of reef development.

INTRODUCTION

Coral reefs are wide-spread throughout the Caribbean, ranging from Panama and Tobago in the south to Florida and the impoverished reefs of Bermuda in the north. Most Caribbean nations, the islands as well as the countries bordering on this sea, have reefs at least along parts of their coasts. Such coral reefs are increasingly exploited in commercial activities such as fisheries and tourism. Over-exploitation of the animal communities of reefs and damage through pollution and coastal development pose a serious threat to the continued existence of these systems.

Caribbean reefs are among the best developed in the world in terms of structure. The high accumulation rates of reefs, up to 12m/1000 years (Macintyre et al. 1977), allows them to considerably alter the relief of the sea bottom. The carbonate build-up of reefs results in various reef types which are traditionally called fringing reefs, barrier reefs and atolls, depending upon the distance to the shore or the presence of an island land mass. Recently (Adey and Burke 1977) the terms bench reefs and bank barrier have been introduced, based upon the geological history of the reef and its preexisting basement. Apart from differences in the major structure, there are smaller details in the physiognomy of a coral reef that vary from reef to reef. Over the reef profile, sloping from

the shore to the base of the living reef, features such as buttresses, sill reefs (e.g. Jamaica, Goreau and Goreau 1973), reef crests, spurs and grooves (e.g. Belize, Rutzler and Macintyre 1982) develop. The terms are not well defined but buttresses and canyons as well as spurs and grooves are arrangements of high coral ridges alternating with lower sand canals. Such series of ridges project into the sea at right angle with the reef crest or shore line. They are not the result of pre-existing structure or erosion but are constructional features (Shinn et al. 1981, 1982) built by the corals and associated organisms. Their occurrence appears to be related to the exposure of shallow reefs to wave energy (Burke 1982).

Many organisms partake in building the reefs but, although groups such as crustose coralline algae (Corallinaceae, Adey 1978) and hydrozoans (Millepora, Milliman 1969) can be locally significant, the contribution of the stony corals (Scleractinia) is of paramount importance. Reef-building coral communities extend from sea level to depth of 70 m (James 1977), while individual corals continue to greater depth of 80-100 m (Lang 1974, Bak 1975). At these great depths sclerospores may become a constructional component (Lang et al. 1975).

The prominent role of stony corals in reefs is such that they must be termed ecological dominants on Caribbean reefs. They are of vital importance and the reef and other reef organisms cannot exist without the corals. Corals are important in a trophic sense (Gladfelter, this volume), in the distribution and conservation of energy (= food, nutrients). Corals are certainly keystones in a structural sense. They built the habitat and are the environment for the other reef species.

CORAL DISTRIBUTION

Corals are distributed over reefs in certain patterns from shallow to deep water. Such a zonation of a Caribbean reef will show the following features:

1. Shore zone: In very shallow water occur a few hardy species with respect to temperature, salinity changes and dessication (Mayor 1918, 1924; Vaughan 1919; Wells 1932). The colonies are encrusting or semispheroid.
2. Acropora palmata zone: This is a zone of considerable wave action and the shape and size of the large branched A. palmata colonies will depend on exposure to wave force (Graus et al. 1977). The depth range of this species is influenced by water movement and it will occur in deeper water (to 12m) in more turbulent conditions (Glynn 1973, Bak 1975). Possible regulating mechanisms are exchange of gases, nutrients, waste products and (animal) food (Chamberlain and Graus 1975).
3. Acropora cervicornis zone: Seawards of the wave swept A. palmata zone loose sediments accumulate and this zone is dominated by a species particularly suited to such an environment. Little water movement is sufficient to prohibit the build-up of sediment on the tissues of the spindly branched A. cervicornis. The colonies grow in self-supporting clumps commonly resting on dead bases of branches, over the sandy substratum.

An interesting approach to zonation studies (Robert 1977) showed that the border between the A. palmata and the A. cervicornis zone coincided with the change from a wave force to a current force dominated reef habitat.

4. Head coral zone: Often dominated by Montastrea annularis.
5. Slope zone: Dominated by flattened shingle-shape colonies.

What the exact physiological requirements of the corals in these zones are or the limits of their physiological niche, is not very well known. The response of these corals to factors such as salinity or dissolved oxygen is not relevant to an explanation of the distribution, because such factors do not vary much and are rather uniformly distributed on the deeper reefs (Ott 1975, Dana 1976, Ohlhorst 1980). Food availability (zooplankton) is a possibly regulating factor. But recent studies showed no correlations between nutritional requirements of coral species and zonation pattern (Wellington 1982), and zooplankton densities appear to be spatially unpredictable over the reef (Ohlhorst 1980). The absence of such relations may be explained by the dependence of corals on other nutritional sources such as organic carbon produced and translocated by their endosymbiotic algae (zooxanthellae). Recent studies have concentrated on the interactions of the coelenterate coral host with these uni-cellular algae and the response of the coral algal unit to different light levels (see Gladfelter, this volume). Variations in the characteristics of the algae may be correlated with coral distributional patterns.

The zonation and occurrence of corals has traditionally been explained as the result of the physiological demands and the metabolic requirements of the particular coral species. But lately more emphasis has been laid on the ecological differences between species and the predictability level of the environment. Differences in life history characteristics between coral species, such as reproduction and regeneration rates, result in a variety of responses to stimuli of the biotic and abiotic environment. The variation in life history strategies is very well suited to elucidate the differences that are encountered between coral communities and is treated in more detail below.

The general coral zonation pattern appears obvious but there are striking exceptions in zonation and in the occurrence of coral reefs. Sometimes these can be related to the role of the corals in their environment and thus help to understand community organization. Or they are explained by the physiological response of the coral to a certain environment factor. An example of this is the occurrence of deep reef corals in turbid water at depths of only 1 m but at light intensities comparable to deeper water (Roos 1971). But sometimes these deviations are as yet inexplicable. A most intriguing example of the last category is the abrupt change from coral reef to non-coral reef rocky bottom. Such discontinuities occur on the north coast of Curacao and the same phenomenon has been described from Jamaica (Goreau 1969). In Curacao the reef, densely populated with corals and crustose coralline algae seems to engulf a rocky pavement. The pavement is only covered with crustose corallines,

Sargassum and a few scattered corals. There is no difference in environmental factors such as depth, water movement etc. on the reef and on the neighboring hard bottom. Why the hard bottom has not been colonized by dense coral growth is unknown. Goreau (1969) suggested that a certain "critical mass" must be reached before a true reef can develop. In Curacao the situation seems to indicate that the reef has internal controls which do not exist on the hard bottom a few meters away. How the critical mass concept has to be applied or what internal controls allow reef community development is not known.

Other variations to the general zonation model are in the discontinuity of coral communities along a coast: the Acropora cervicornis zone is absent at the southwest coast of Aruba where the Acropora palmata zone borders seawards on a dense growth of Montastrea annularis. But no M. annularis community is present at the eastern tip of the island where at the depth of the presumed head coral zone only scattered gorgonians and small corals occur. At Curacao and Bonaire the Acropora cervicornis zone is locally developed, alternating with long stretches of sandy bottom populated with gorgonians and few scattered corals.

Coral communities also differ in the mean size of coral colonies and in the dominance of coral species; on some reefs, species such as Montastrea annularis reach large size, up to 4 m in diameter and height, while in another area along the coast all colonies are smaller than 1 m. The head coral zone is usually dominated by M. annularis but A. agaricites may be dominant or a consortium of other species. Patchiness appears to be a characteristic of reefs, reef corals and other reef organisms.

Some of the existing variation can be explained when we assume the reef habitat to be an unpredictable environment, subjected to disturbances of a varying frequency and intensity. In such a habitat the communities are unbalanced, not in equilibrium and the presence of species depends on the regulating impact of disturbance (see Connell 1976, 1978). When a pattern of succession (a change in species composition through time) of coral species and coral communities unfolds on a reef, disturbances will interrupt this process and cause a change in community composition. Succession on a reef would consist of two sequential phases:

1. a phase with an increase in species richness through time caused by the settlement of new species,
2. followed by a decrease in species numbers through factors such as competition.

Interruptions during the first phase will result in an abnormal low species number, while interruptions during the second phase will result in an abnormally high species number. The effect of a particular disturbance will depend on the characteristic of the corals such as on skeletal morphology or sediment rejection efficiencies. The mechanisms regulating a decrease in species number are uncertain (e.g. Bak et al. 1982, Bradbury et al. in press) but such impoverishment on older reefs has been observed (Grigg and Maragos 1974).

DISTURBANCE ON REEFS

Storms. the effects of storms is strongest in the shallow part of the reef and branched or otherwise fragile corals are more susceptible than others. Acropora palmata and A. cervicornis will in particular suffer through breakage. After breaking the living surfaces of the fragments will often die through mechanical damage and scouring of sand and rubble. The chance of survival is related to fragment size (Highsmith et al. 1980) and many fragments may survive.

Diseases. Most of the documented diseases of corals fall into one or two categories called: blackband diseases and whiteband diseases. Blackband disease affects mainly head corals such as Montastrea annularis and Diploria species. It seems to be more common in stressed habitats and outbreaks of this disease may be related to degradation of the environment (Antonius 1977). Whiteband diseases are epidemic in character. The disease sweeps over the reefs, affecting a high proportion of the colonies and killing most of these. It especially affects Acropora species. It is interesting to note that during a recent outbreak in some areas (Virgin Islands, see Gladfelter 1982) A. palmata was the main victim while on other islands (Bonaire, Curacao, Bak & Criens in press) the epidemic killed most of the A. cervicornis leaving the A. palmata reefs intact. There is evidence that the impact of this disease is enhanced by environmental stress. But epidemics certainly occurred in unstressed areas.

Competition. The importance of competition on reefs as a structuring force in community organization is a subject of current research. Some forms of composition such as with algae for space and light are undeniable and sometimes operate as disturbance. Under certain conditions, possibly changes in nutrient levels, algae can overgrow pristine reefs as shown by the occurrence of dying colonies of Agaricia agaricites under mats of the alga Dictyota (San Blas island, Bak pers. obs.). Of course similar phenomena have been documented for polluted reefs (Fishelson 1973, Banner 1974).

Predation. The influence of predators on corals in the Caribbean is disputed. No phenomena similar to the outbreak of Acanthaster planci, the crown of thorns, in the Indo-Pacific region have occurred. It is known, however, that common predators such as the fireworm Hermodice carunculata, the snail Coralliophila abbreviata and the sea urchin Diadema antillarum have a preference for certain coral species as favorite prey (Ott & Lewis 1972, Bak & van Eys 1975). The potential for an effect on community composition is present. It has been suggested that Coralliophila was important in the massive mortality of Acropora cervicornis in Jamaica following the passage of hurricane Allan (Knowlton et al. 1981).

Bioerosion. This is not only an important factor in the general accumulation of reef bodies and sediments but also in the survival and mortality of coral colonies. The sea urchin Diadema antillarum is an important eroder of bases of living corals. While the dead base is eroded the living part is continuing to grow and increase in mass and the result is a weakened structure. Such colonies are much easier dislodged and destructed. They will not reach the size of intact colonies. Because Diadema populations can vary strongly in density along coasts (e.g. Bauer 1980)

and because certain species such as Montastrea annularis and Colpophyllia natans (which grow potentially to large size) are conspicuous victims of their grazing behavior they exert a strong influence on colony size in coral communities (Bak unpubl. obs.).

Human Interference. The activity of man covers a large spectrum of disturbing influences on reefs (Johannes 1975). Human interference may result in the death of reefs, or may stress reef communities so much that diseases and bacterial infections or changes in the biology of coral species such as in fecundity, may change the community structure (e.g. Dodge & Vaisnys 1977; Bak 1978; Ducklow & Mitchell 1979; Loya & Rinkevich 1980). The impact of pollution can vary through the year with changing environmental conditions. For example, thermal pollution will be most effective during the months with highest sea temperatures. Of course the impact of agents of pollution varies with depth, the shallower zones being generally most affected.

However, to mention that disturbing agents, such as those listed above do halt community development, set back successional sequences and change the structure of coral populations is only to illuminate one side of the interaction structure. On the other side there is a characteristic feedback from the coral population. To what degree a disturbance affects a coral community and in which direction the change will be, depends not only on the disturbing agents but on the species composition and the constructional qualities (e.g. size of colonies) of the affected community.

LIFE HISTORY CHARACTERISTICS IN CORALS

It is obvious that corals react differently to disturbances. At a certain disturbance level, e.g. a moderate storm, a community of branched or otherwise fragile corals would be much more affected than a community consisting for hundred percent of large Montastrea annularis colonies. To understand this spectrum of reactions we can consider the changes in a fairly typical Caribbean reef community consisting of a mixed coral assemblage of some 15 to 20 species. These changes are caused by small disturbances, occurring while environmental factors are considered stable, over a five year period. Table 1 shows the spatial change of the main bottom components of the reef. Spatial change is expressed as I_R and reflects the extent to which a component remained at the same place or changed position on the bottom. The values of I_R range from 0 (= no change in position over 5 years), to 100 (= all positions changed, see Bak & Luckhurst 1980 for details). It appears that the coral species vary highly in their "mobility", some are subjected to much more change than others. Such characteristics are indicative for the different life histories employed by the different species in the community. For example Agaricia agaricites proved to be an unstable coral in the community (Table 1, $I_R=56$) and the same study showed that this was related to the extraordinary high mortality in this species. Over 5 years 64% of the larger A. agaricites died (Table 2, Bak & Luckhurst 1980). These values are in marked contrast with those of Montastrea annularis which is spatially stable (Table 1, $I_R=13.6$) and has a low mortality (Table 2). But while A. agaricites may be relatively easily wiped out, it is very abundant as a small colony. This is a consequence of the survival of small remnants of larger colonies

(Lewis 1974, Bak & Engel 1979, Bak & Luckhurst 1980, Hughes and Jackson 1980), but is mainly caused by its extreme efficiency as a recruiter through sexually produced larvae (Table 3). Of course this prolific settlement complements the extensive mortality resulting in the pattern of high spatial mobility. The abundance of A. agaricites as a juvenile recruit is balanced by a relatively great vulnerability. A. agaricites is poor in sand sediment removal from its horizontal surfaces (Bak and Elgershuizen 1976) and lesions in the living tissue regenerate badly, especially if the skeleton is damaged, and such prolonged lesions carry a higher risk of invasion by organisms such as excavating sponges (Bak et al. 1977; Bak & Steward-van Es 1980). In A. agaricites energy appears to be allocated to reproduction and settlement rather than to maintenance and survival. Within the species this strategy is carried to the extreme limits by the form humilis (van Moorsel 1981).

The strategy of Montastrea annularis is in many aspects the opposite: Montastrea has few recruits (Table 3) but survival is good as shown by regeneration efficiency, (Bak et al. 1977), mortality is low (Table 2) and colonies can reach a high age and a great size. This view of Montastrea is confirmed by its spatial stability on the reef, having an Index of spatial change four times as low as Agaricia agaricites (Table 1). Under the current conditions both species can persist in the same habitat. This is shown by the lack of change in cover over the 5 year period (Table 4). The environment is changing (unpredictable) enough for A. agaricites to persist through colonization. Table 1 shows bare rock, a necessary resource for settlement, to be a spatially changing bottom component, while Table 4 demonstrates the continuity of this resource through time. This means that there is continually new rock uncovered and available for settlement by an opportunistic species such as A. agaricites. On the other hand, the habitat is not so unpredictable that a stable coral such as M. annularis cannot persist.

Distinctively different life histories are employed by the branched Acropora species. A. palmata is rare as a sexually produced juvenile (Table 3) but it is successful in asexual proliferation (Bak & Criens in press). This is in accordance with the high regeneration rate of lesions (Bak unpubl.) and the high growth rate (Bak 1976; Gladfelter et al. 1978). Such characteristics are easily understood with regard to the habitat of A. palmata on the shallow reef. Colonies are very exposed to turbulence and breakage of parts of colonies occurs under normal conditions (Bak 1976, Fig. 7). Occasionally storms will destroy colonies and whole A. palmata assemblages, but A. palmata is well-adapted to such disturbances and may actually need these to survive locally (van Duyl in prep.). A. cervicornis is more fragile and occurs in deeper water than A. palmata but the life strategy is very similar.

In these coral species extensive fragmentation with subsequent regeneration of colonies will result in a decrease of genetic variation in the population. This may be a double-edged sword: it facilitates survival of the species through enhanced chances of cementation to other fragments, which will result in greater stability. On the other hand it may be the reason why the Acropora species are so susceptible to epidemic diseases. Vegetative reproduction in Acropora increases the chance of local maintenance of a population but the potential to colonize other reefs is reduced.

Local persistence is also enhanced by the lack of antagonistic reactions (e.g. Hildemann *et al.* 1975) between the two species (Bak & Crieens 1982). Fragments of *A. palmata* and *A. cervicornis* fuse easily. Well-developed communities of the two species are highly co-occurrent (van Duyl in prep.) and intra-generic fusion will be of advantage in survival.

Madracis mirabilis resembles the *Acropora* species in some respects. Living in deeper water as assemblages of clumped colonies or in nearly monospecific fields, this fragile branched species is less susceptible to wave action. But even in the absence of storms the colonies are subjected to considerable disturbance and the species can suffer a 50 percent reduction in cover over a few years (Bak & Luckhurst 1980). Continuing observations show the survivorship of colony fragments to be good (Bak & Crieens in press; Bak pers. obs.). This despite the relatively low growth rate and although the fragments of *M. mirabilis* cannot enhance their stability through fusion. Stability is increased through the interference of the characteristic sponge fauna of *M. mirabilis*. These organisms cover the lower, dead, parts of the branches and their attachment to the substrata gives the *Madracis* fragments a reasonable stability in the relatively calm water conditions of this habitat.

A potentially important life history aspect in corals is their ability to compete with other coral species for space, because they vary in their competitive abilities such as extra-coelenteric digestion of neighbors through the mesenterial filaments. They can be ranked in an aggressive hierarchy (Lang 1970, 1971, 1973), with dominant species killing subordinate species: e.g. *Montastrea annularis* would kill *Acropora palmata* which would kill *Agaricia agaricites* which would kill *Madracis mirabilis*. If such a process could unfold on the reef, one species or a few species would persist through time while the subordinates would be eliminated. This would ultimately, when not interrupted, result in a climax community of dominant aggressive species. However, subordinates may maintain themselves through rapid growth and overgrow the more aggressive species. Competition through overgrowth and shading has shown to be of importance in rapidly growing corals on shallow Pacific reefs (Connell 1976, 1978). Recently the existence of yet another coral interaction mechanism, sweeper tentacle development, has been demonstrated (Richardson *et al.* 1979; Wellington 1980; Bak *et al.* 1982). Such elongated tentacles are developed in response to extra-coelenteric attack and used in counter-attack. Employing sweeper tentacles subordinate corals are able to reverse the initial dominance-subordinate relationship. An additional complicating factor in interspecific coral interactions is the role of epifauna. Vagile animals such as small crabs can occupy the lesions resulting from the coral interaction and damage the unaffected attacker (Bak *et al.* 1982). Reversal of interaction patterns in Caribbean corals is shown in Fig. 1.

It appears that many variables interfere in competition for space and the ultimate result of superior competitors, domination of the coral community and monopolization of space, will be a very time consuming process. Indeed the time scale involved for competition to become a structuring force in communities may easily exceed the time interval between larger and smaller disturbances.

CONCLUSION

The interaction of environmental factors, coral physiology, interruptive forces and life history characteristics determines the character of a coral community in situ, is of necessity a general statement. We do recognize some of the effects of these factors in coral reefs. However, their variations in magnitude and interaction level over the reef and along the coast, are still not well understood. In view of this incomplete understanding of coral reefs, the world-wide degradation of reefs should concern us gravely. Research on these vulnerable systems must be encouraged while prudence should be a key word in the management of reefs.

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Table 1. Spatial change of substratum components, with a mean cover of 5% or greater per depth, at 10, 20, 30 and 40 m. I_R = index of relative spatial change.

Components	Depth			
	10m	20m	30m	40m
	I_R	I_R	I_R	I_R
<u>Agaricia agaricites</u>	-	56	-	0
<u>A. lamarcki</u>	0	-	14.4	11.9
<u>Montastrea annularis</u>	13.6	-	0	0
<u>M. cavernosa</u>	8.3	-	-	-
<u>Meandrina meandrites</u>	0	33.8	-	0
Coral - other	62.5	35.3	22.5	41.8
Sponge	-	-	-	-
Invertebrates - other	-	58.5	38.3	-
Rock	59.1	50.8	24.1	20
Loose sediment	60	56.7	37.4	25.4
Deep sediment	29.2	28.4	30	22.7
Coral fragments	51.6	-	0	0
All living components	43.2	41.3	25	22.6
All corals	37.4	38.3	18.9	18.4
All non-living components	47.4	49.9	29.1	21.7
Total change per quadrat	45.7	46	27.7	22

Table 2. Mortality of coral colonies (≥ 30 cm maximum diameter) between December 1973 and December 1978. Values expressed as % of N for each component. Mortality-other, includes colonies with mortality of $>50\%$ in living surface.

Components	N	<u>Catastrophic mortality</u>		<u>Mortality-</u>	<u>Total</u>
		<u>disappearance</u>	<u>skeleton</u>	<u>other</u>	<u>Mortality</u>
		<u>between two</u>	<u>still</u>		
		<u>consecutive</u>	<u>present</u>		
		<u>censuses</u>			
<u>Agaricia agaricites</u>	11	27	0	36	64 ⁺
<u>A. lamarcki</u>	47	2	0	9	11
<u>Montastrea annularis</u>	22	14	0	0	14
<u>M. cavernosa</u>	22	5	0	9	14
<u>Meandrina meandrites</u>	21	10	5	24	38
Coral - other	38	21	0	21	42
Total	161	11	1	14	26

+ Arithmetic discrepancies are due to rounding errors

Table 3 - Percentage of the juveniles of different coral species per depth in Curacao. Total gives for each species the percentage of total sample (n = 919).

Coral Species	D E P T H				% Total Sample
	3-9m	9-17m	17-26m	26.37m	
<u>Stephnanocoenia michelini</u>		2.6	3.9	6.7	3.4
<u>Madracis decactis</u>		2.6	0.5	2.6	1.4
<u>Madracis mirabilis</u>	0.8				0.2
<u>Madracis pharensis</u>		0.5	0.5	2.6	1.0
<u>Acropora</u> sp.	0.8				0.2
<u>Agaricia agaricites</u>	77.8	61.7	45.6	39.9	56.1
<u>Agaricia lamarcki</u>		1.0	2.4	12.7	4.5
<u>Agaricia grahamae</u>				0.8	0.2
<u>Leptoseris cucullata</u>		12.4	19.0	8.6	9.4
<u>Siderastrea siderea</u>	0.8			1.1	0.5
<u>Porites astreoides</u>	9.5	3.6	9.3	9.3	8.2
<u>Porites porites</u>	1.6	0.5			0.5
<u>Diploria strigosa</u>	1.2				0.3
<u>Manicina/Colpophyllia</u> sp.	0.4	1.6	1.0		0.7
<u>Montastrea annularis</u>	1.2				0.3
<u>Montastrea cavernosa</u>		0.5		1.1	0.4
<u>Meandrina meandrites</u>	2.4	4.1	8.7	9.7	6.3
<u>Dichocoenia stellaris</u>				0.4	0.1
<u>Mussa/Scolymia</u> sp.				0.8	0.2
<u>Mycetophyllia ferox</u>		0.5			0.1
<u>Eusmilia fastigiata</u>	0.8	5.2	8.7	3.4	4.2
<u>Millepora</u> sp.	2.8	3.1	0.5		1.5
Unidentified				0.4	0.1

Table 4 - Comparison of mean percentage cover by coral reef substratum components between December 1973 and December 1978. Cover determined over 108 m², at depths 10-40m.

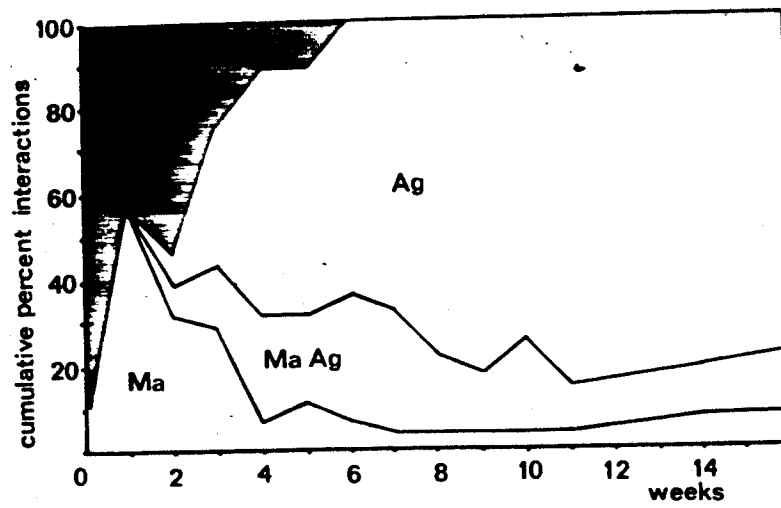
Components	'73	'78
<u>Agaricia agaricites</u>	2	2
<u>A. lamarcki</u>	8	8
<u>Montastrea annularis</u>	3	3
<u>M. cavernosa</u>	3	3
<u>Meandrina meandrites</u>	2	1
Coral - other	13	10
Sponge	2	4
Invertebrates - other	4	6
Rock	28	28
Loose sediment	16	18
Deep sediment	13	12
Coral fragments	5	5
All living components	38	37
All corals	32	28
All non-living components	62	63

FIGURE LEGEND

Fig. 1. Reversal of dominance-subordinate relationships in pairs of coral colonies. Shading indicates no interaction.

- A. Madracis mirabilis suffers initial mortality in contact with Agaricia agaricites, but increasing mortality occurs in Agaricia after the first week. Ma = Madracis subordinate, Ma Ag = both species damaged, Aq = Agaricia subordinate, n = 28 pairs.
- B. Initially mortality occurs only in Madracis mirabilis, but Montastrea annularis suffers increasing mortality after the first week. Ma = Madracis subordinate, Ma Mo = both species damaged, Mo = Montastrea subordinate. n = 29 pairs.

A



B

