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Constancy and Change in Coral Reef Habitats Along Depth Gradients at Curaçao

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Summary. The cover of the main components of the substratum, their spatial relations as well as mortality of the most important living component (Scleractinia) were studied at the leeward reef of Curaçao, Netherlands Antilles. We used a point intercept method to analyse cover as well as change in spatial arrangement in sets of photographs of the same 12 quadrats (3 m × 3 m) taken in 1973 and 1978. Four quadrats were situated, along each of three transects, on the reef slope at depth of 10, 20, 30 and 40 m.

Cover was very constant in both living and non-living components over the study period. There was a small but significant change in coral cover caused by a decrease at 10 and 20 m.

Spatial arrangement of substratum components was subjected to changes equally large in living and non-living components. There was a significant difference in the magnitude of such changes between the shallower (10, 20 m) and the deeper quadrats (30, 40 m), the spatial rearrangement being much greater in the shallower habitats. In addition, there are important variations in the relative spatial change of the different coral species. The observed patterns of species that are more and less mobile through time, such as *Agaricia agaricites* and *Montastrea* spp. respectively, are related to life history phenomena such as recruitment and mortality.

Mortality of corals was studied using interval (8–10 months) sets of photographs. We found mortality to be high in colonies (≧30 cm diameter) of *A. agaricites* and low in *A. lamarcki* and *Montastrea* spp. Mortality of coral colonies in this size class is often catastrophic in character.

Our evidence indicates that community organization in deep coral reefs, both along the depth gradient and along the coast, is more influenced by spatial rearrangement of the substrata than has previously been recognized.

Introduction

Coral reefs and tropical rain forests are systems whose characteristics are frequently used to provide evidence for, sometimes conflicting, ecological theories on species diversity (Connell 1978). This is because, in their search for unifying theories that explain the relation between diversity of communities and the properties of the environment, ecologists tend to compare the supposedly more stable and more predictable high diversity coral reef communities and tropical rain forests with less diverse and purportedly less stable temperate systems. There are two main reasons why these comparisons are often unsatisfactory.

Firstly, although there are studies on diversity and species richness in coral reefs and tropical rain forests, little is known about their stability and the predictability of their environments (Farnworth and Golley 1974). This is especially true for coral reefs, the major exception being the studies of Connell (1973, 1976, 1978). However, this work is restricted to shallow reef habitats whose communities are more strongly effected by environmental variables, such as temperature, emergence and storms, than the deeper reefs.

Secondly, the concepts discussed are, at least in part, multi- or ill-defined (e.g. stability, Goodman 1975). In this paper we will not discuss the relative merit of the definitions and avoid the use of these terms. We are simply concerned with constancy and change in the main substratum components of coral reef habitats. Our data, which are quantitative, can then be used to discuss, in a general sense, stability and predictability on coral reefs.

The habitat that we studied, the leeward coast reef of Curaçao at depths of 10 m to 40 m, shows little variability in the most obvious environmental parameters. Temperature generally ranges from 26–28° C with a minimum and maximum of 24.5° and 28.8° C respectively recorded over a 24 month period (data collected 1977–78, Bak unpublished). Daylength varies 85 min during the year and mean sunshine/month ranged from 50.9–73.0% of possible maxima (Campbell stokes recorder, Meteorological Service data, 1971–72). Underwater light measurements, representing various submarine light and turbidity conditions, show less than 20% variation at any depth between 2 and 41 m (expressed as percentage of surface radiation, van den Hoek et al. 1978). The daily tidal range is small, about 30 cm (De Haan and Zaneveld 1959). Currents along the coast generally do not exceed 1 knot, but may infrequently reach a maximum of 2 knots (data 1971–72, Harbour Office). On this leeward coast, strong winds are rare. During a one year period, onshore winds with a velocity of more than 14 m/sec were recorded only 0.9% of the time (Meterological Service, 1971). Curaçao is outside the hurricane belt and therefore rough seas on the leeward coast are very infrequent. However, the effects of swell from distant storms striking this coast can have serious consequences for the shallow *Acropora* spp. reefs (De Buisonje 1974; Bak 1975). The influence of heavy seas on deeper reefs is essentially unknown.

We examined several rarely quantified parameters, mostly interrelated, in assessing constancy and change in the deeper reef environment. These factors cover the effect of slope, sedimentation, collapse of substrata and biomass removal.

This study was originally prompted by interest in the constancy and change of the deeper coral reef substrata and its influence

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on the associated resident reef fish communities. In addition, the research by one of us (Bak) on the life histories of the Scleractinia (the main structuring components of reefs) posed questions about the consequences of change in the substrata on life history phenomena, such as settlement of juveniles. From the opposite viewpoint, we were curious to know how certain characteristics of the life histories of corals, such as longevity, would influence the constancy of reef habitats.

We have sought answers to these questions by monitoring photographically, reef habitats at 3 locations and at 4 depths on the leeward coast of Curaçao for a period spanning 5 years.

Material and Methods

Study Area and Surveys

Our study sites were located 800–1,100 m west of Piscaderabaai (Fig. 1). They consitsted of 3 transects (I, II, III) perpendicular to the coast with quandrats (3 m × 3 m) roped off at depths of 10, 20, 30 and 40 m (Fig. 1). Each quadrat is designated by transect and depth (e.g. II–20, transect II, 20 m depth). Details of the substrata in these quadrats may be found in Luckhurst and Luckhurst (1978). Bak (1977) and Van den Hoek et al. (1978) have described the distribution of corals and algae in the vicinity of these transects. Due to the location of the transects (in the Carmabi study area), we are confident that we observed naturally occurring phenomena and not the results of human activities.

The quadrats were photographed using a Nikonos camera, equipped with an underwater super-wide angle lens (UW Nikkor 15 mm f/2.8. picture angle 94°). Kodak Tri-X (400 ASA) black and white film was used for all surveys. Light readings were taken with a Sekonic Marine Meter II. The negatives were printed to obtain contrasty 20 × 26 cm photographs. Resolution of these prints was very good: individual calices of corals such as *Montastrea cavernosa* (Linnaeus) could easily be distinguished.

The photographic surveys were made at intervals of 8–10 months, and at times when water clarity was considered sufficiently good to allow for high-quality prints. The 8 surveys were made on the following dates:

1973 – December
1974 – August
1975 – June
1976 – February, November
1977 – July
1978 – April, December.

Analysis of Substrata

As our interest was in longer term changes on the reef i.e. over a period of years and because many characteristics of the community suggest longer term phenomena rather than short term fluctuations (e.g. rate of coral growth), we compared our survey results in December 1973 with these in December 1978. Thus the results represent a change in the substratum of each quadrat over a period of 5 years.

The analysis of the substratum was divided into 3 categories:

1. determination of changes in quadrat cover.
2. determination of changes in the spatial arrangement of substratum components.
3. nature and degree of coral colony mortality.

Quadrat Cover

We considered 12 components (Table 1) in our analysis of quadrat cover. We used cover rather than number of individuals both because the components are, or represent, sessile organisms and the majority of the individuals are colonial (or polystomal, Wells 1973). The selection was based on our interests as well as on our ability to identify each component on the prints. In the interpretation of the prints, we rigorously adhered to the following definitions:

1. Rock – all dead coral, not covered with sediment or not showing signs of animal occupancy.
2. Deep sediment – all sandy patches in which the surface relief did not reflect underlying rocky substrata.
3. Loose sediment – all other sediment including small sediment patches on rocky surfaces.
4. Coral fragments – the broken remains of the branched coral species *Madracis mirabilis* (Duchassaing and Michelotti) and *Eusmilia fastigiata* (Pallas).

All animals manifest other than the individual coral species and the categories, Coral-other and Sponge, were included in the category Invertebrates-other. This means that the estimation of coral cover is conservative because the latter category will include unrecognizable corals. Rock also included all organisms that were not discernable from rock, the most important of these being crustose coralline algae. These organisms may be assumed to play a role very similar to uncovered rocky surfaces at our depths (10–40 m) e.g. in respect to settlement of larvae. Very small and/or inconspicuous organisms such as turf algae, cirripedes, encrusting sponges and ectoprocts were not included in the analysis, except where they were large enough to be discernible and as such to be included in the category Invertebrates-other. We did not include Gorgonacea or Antipatharia in our analysis because these colonies are structurally flexible and their spatial position is frequently changed by prevailing currents and surge action. The substratum under the canopy of the colony was determined when necessary by detailed photographs and inspection.

The analysis of quandrat cover was conducted using a point sampling technique. Because the quadrats were heterogenous, we

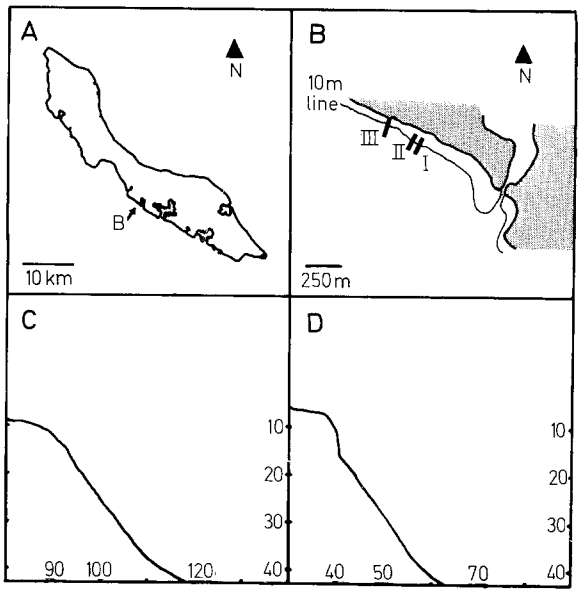

Fig. 1. A Map of Curaçao, Netherlands Antilles. Arrow indicates area around Piscaderabaai. **B** Location of study sites – transects I, II and III. **C** Reef profile of transects I and II. Vertical scale is depth (*m*) and horizontal scale is distance from shore (*m*). **D** Reef profile of transect III. Scales as in **C**

obtained a random sample by projecting a grid of 100 intercept points (10 rows, 10 columns) over each photograph to be analyzed (Kershaw 1964). This number of points gave repeatable estimates of cover within ±3%. All sampling points were located at least 30 cm inside the rope boundary. The cover data sets of 1973 and 1978 were compared to determine change in cover in the 5 year study period.

Spatial Arrangements of Components

In order to determine if there were spatial changes i.e. differences in the relative mobility and rearrangement of the components, we compared the position of the quadrat components in the two sets of photographs i.e. December 1973 and 1978. We placed a grid of 100 intercept points in precisely the same location on the December 1973 and December 1978 photographs. The small but inevitable effects of variation in camera position were overcome by use of a series of *in situ* reference points.

To obtain an index of spatial change, we compared the component present under each of the 100 different spatially localized points in 1973 with component present at the same point in 1978.

The index of absolute spatial change (I_A) was computed using the following formula:

$$I_A = \frac{(x-z)+(y-z)}{2}$$

where x = number of positions scored by a component in 1973
y = number of positions scored by the same component in 1978
z = number of x scored as still present in 1978.

The values of I_A thus represent the mean percentage change of a component and may range from 0 to 100. If the percentage quadrat cover of a component is taken into consideration, an index of relative spatial change (I_R) may be calculated using the following formula:

$$I_R = I_A \left(\frac{2}{C73+C78}\right) \times 100$$

where C73 = percentage cover of the component in 1973
C78 = percentage cover of the same component in 1978.

When the same sampling points are used in both analysis of cover and analysis of spatial change, the numerical values of C73 and C78 are identical with x and y.

Mortality of Coral Colonies

We recorded the mortality of the larger (≧30 cm maximum diameter, 30 cm is the size of a grid unit) colonies over the 5 year study period in order to relate the life history of the coral species to spatial change. All colonies of the above size were checked in 1973 and their condition noted. In the 1978 photographs, each of these colonies was checked for presence/absence and mortality of the living tissue. In the case of absence or mortality, we consulted the interval sets of survey photographs to determine if death or disappearance was gradual (the event spanning more than one survey interval) or catastrophic (death between two consecutive surveys).

Results

Cover of Quadrat Components

There are large differences between the quadrats in the cover of the various components (Tables 1–4). The total area covered by living components ranges from 20% or less (e.g. I-40, II-30) to more than 50% (e.g. III-10, III-20). About 80% of the living component is coral cover. Although there are changes in cover of the components over the 5 year study period, these are not related to cover per se. As some of the most significant changes

Table 1. Percentage cover of substratum components in 10 m depth quadrats (3 m × 3 m) at 3 transects in December 1973 and December 1978

Components	Transects						Total (mean)	
	I		II		III			
	'73	'78	'73	'78	'73	'78	'73	'78
Agaricia agaricites	0	0	2	2	1	1	1	1
A. lamarcki	0	0	0	0	0	0	0	0
Montastrea annularis	7	8	12	12	13	13	11	11
M. cavernosa	0	0	4	3	14	16	6	6
Meandrina meandrites	0	0	0	0	0	0	0	0
Coral – other	43[a]	24[a]	5	1	13	10	20	12
Sponge	0	2	0	4	5	4	2	3
Invertebrates – other	1	2	3	2	7	9	4	4
Rock	1	3	14	7	18	25	11	12
Loose sediment	7	12	8	12	16	18	10	14
Deep sediment	4	1	47	55	7	4	19	20
Coral fragments	37	48	5	2	6	0	16	17
All living components	51	36	26	24	53	53	43	38
All corals	50	32	23	18	41	40	38	30
All non-living components	49	64	74	76	47	47	57	62

[a] All *Madracis mirabilis*

Table 2. Percentage cover of substratum components in 20 m depth quadrats (3 m × 3 m) at 3 transects in December 1973 and December 1978

Components	Transects						Total (mean)	
	I		II		III			
	'73	'78	'73	'78	'73	'78	'73	'78
Agaricia agaricites	5	7	4	2	8	5	6	4
A. lamarcki	0	0	1	0	3	4	1	1
Montastrea annularis	1	1	3	0	3	3	2	1
M. cavernosa	1	1	1	1	6	9	3	4
Meandrina meandrites	3	2	7	6	14	6	8	5
Coral-other	25	19	17	19	13	9	18	16
Sponge	3	6	0	3	4	8	2	6
Invertebrates – other	6	4	6	9	7	8	6	7
Rock	21	27	31	31	19	18	24	26
Loose sediment	14	19	18	21	13	15	15	15
Deep sediment	10	6	12	8	10	10	11	8
Coral fragments	11	8	0	0	0	5	4	4
All living components	44	40	39	40	58	52	47	44
All corals	35	30	33	28	47	36	38	31
All non-living components	56	60	61	60	42	48	53	56

Table 3. Percentage cover of substratum components in 30 m depth quadrats (3 m × 3 m) at 3 transects in December 1973 and December 1978

Components	Transects						Total (mean)	
	I		II		III			
	'73	'78	'73	'78	'73	'78	'73	'78
Agaricia agaricites	0	0	1	1	6	3	2	1
A. lamarcki	7	5	6	5	24	30	12	13
Montastrea annularis	0	0	0	0	0	0	0	0
M. cavernosa	2	2	5	4	1	1	3	2
Meandrina meandrites	2	1	0	1	3	1	2	1
Coral-other	16	15	5	7	3	3	8	8
Sponge	0	0	0	1	3	5	1	2
Invertebrates – other	6	9	2	3	6	9	5	7
Rock	34	35	39	43	36	33	36	37
Loose sediment	20	21	21	20	18	15	20	19
Deep sediment	13	12	21	15	0	0	11	9
Coral fragments	0	0	0	0	0	0	0	0
All living components	33	32	19	22	46	52	33	35
All corals	27	23	17	18	37	38	27	26
All non-living components	67	68	81	78	54	48	67	65

Table 4. Percentage cover of substratum components in 40 m depth quadrats (3 m × 3 m) at 3 transects in December 1973 and December 1978

Components	Transects						Total (mean)	
	I		II		III			
	'73	'78	'73	'78	'73	'78	'73	'78
Agaricia agaricites	0	0	0	0	0	0	0	0
A. lamarcki	4	3	11	11	39	42	18	19
Montastrea annularis	0	0	0	0	0	0	0	0
M. cavernosa	0	0	1	1	0	1	0	1
Meandrina meandrites	0	0	0	0	0	0	0	0
Coral – other	8	5	7	5	5	3	7	4
Sponge	0	3	6	4	2	3	3	3
Invertebrates – other	6	2	0	1	4	9	3	4
Rock	43	37	48	43	33	31	41	37
Loose sediment	21	26	17	20	17	11	18	19
Deep sediment	18	24	10	15	0	0	9	13
Coral fragments	0	0	0	0	0	0	0	0
All living components	18	13	25	22	50	58	31	31
All corals	12	8	19	17	44	46	25	24
All non-living components	82	87	75	78	50	42	69	69

were in coral cover, we tested if the mean coral cover of a quadrat between 1973 and 1978 was correlated with the absolute change in coral cover between these years. There was no significant correlation ($r=0.326$, $p>0.1$).

The kinds of changes which occurred in the substrata are illustrated in a series of representative photographs (Figs. 2, 3). The magnitude of change in the cover of both living and non-living components is small (generally $<5\%$) (Tables 1–4). The larger changes are confined almost exclusively to the 10 and 20 m quadrats. At these depths, coral cover may change considerably e.g. in quadrat I-10, there was an 18% change in coral cover (Table 1). This change was due to the mortality of the coral *Madracis mirabilis* (see Fig. 2). In quadrat III-20, the 11% change was due mainly to the mortality of *Meandrina meandrites* (Linnaeus), although other species were also involved (Table 2). To test for significant changes in the cover of substratum components over the study period, we employed the Wilcoxon matched-pairs signed-ranks test. An examination of the data suggested that a comparison of the shallower quadrats (10 and 20 m) with the deeper quadrats (30 and 40 m) would be useful in establishing differences between the two depth ranges. In addition, comparisons were made with the data from all depths combined.

Due to the limiting conditions of the Wilcoxon test, only 2 comparisons were possible for the shallow zone; both were significant (loose sediment, $T=0$, $p<0.05$; all corals, $T=0$, $p<0.05$). No Wilcoxon comparisons were possible for the deep zone, but a sign test on the "All corals" category was not significant ($p>0.10$). Three of the Wilcoxon comparisons using the data from all depths combined were significant (Coral-other, $T=7$, $p<0.02$; Sponge, $T=7$, $p<0.02$; all corals, $T=8.5$, $p<0.02$). This latter value represents a significant decrease in coral cover, caused by decreases at the shallower depths (10, 20 m).

The quantitative changes in the cover of the various coral species differ. Apart from the large changes in *Madracis mirabilis* and *Meandrina meandrites*, the category Coral-other is more changeable than both the *Montastrea* species. An examination of the data from all quadrats combined (Table 5), shows that, in terms of cover, the reef habitat is remarkably constant over the depth range studied.

Spatial Arrangement of Components

The analysis of the spatial change of the various living and non-living components shows that there is a high degree of change in spatial arrangement (Tables 6–9). The combined effects of settlement, growth, dislodgement and death result in a considerable temporal instability of the living components. Variations in sediment quantity moving through the quadrat and changes in the direction of sediment channels and rivulets show up as changes in the presence of sediment on rock as well as in the size and abundance of deeper, sediment-filled basins.

The magnitude of total change (i.e. considering all substratum components) is very similar in quadrats at the same depth (Tables 6–9). In the 10 and 20 m quadrats total change ranges from 42 to 51, while at 30 and 40 m the range is only 16 to 33. The mean index of spatial change at the 2 shallower depths is significantly greater (Student's t-test, $t=7.691$, $p<0.001$) than the mean value for the deeper quadrats. In addition, there was a significant correlation between coral cover and the amount of spatial change (I_R) in the category All corals ($r=0.727$, $p<0.01$).

The relative importance of change in living and non-living components at each depth may be analyzed by relating it to total change. If the I_R values of living and non-living components are expressed as a percentage of total I_R (total change), clear differences are found. At the three shallowest depths (10, 20 and 30 m), change in non-living components is respectively 9, 19 and 15% greater than in the living component. In contrast, at 40 m depth this pattern is reversed with the living component showing 4% greater change than the non-living.

There is considerably more spatial change in some categories than in others, i.e. some components are mobile than others. This is true both for the living and the non-living components. For example, the non-living component Deep sediment, which was more confined to basins and large depressions, shifted less

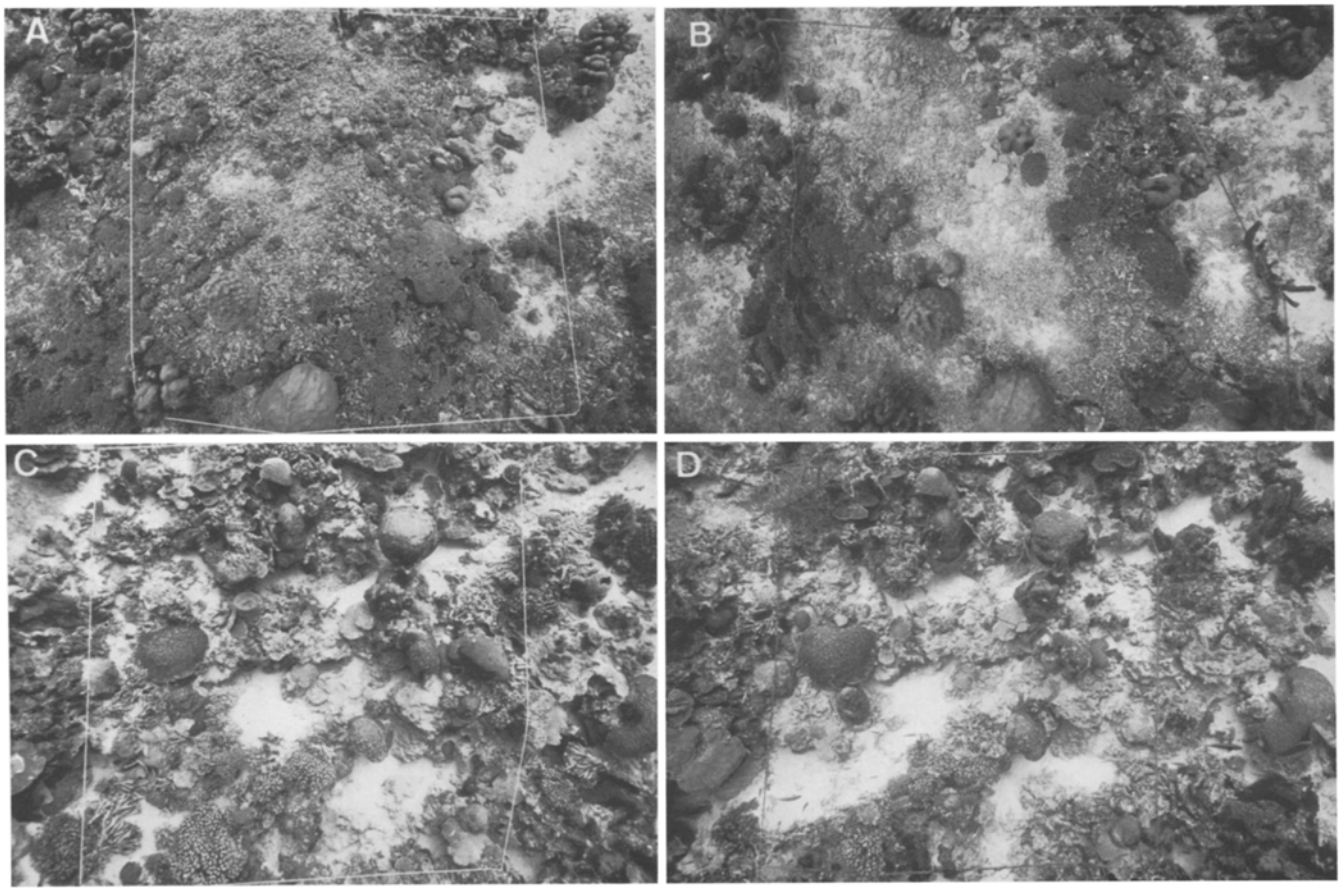

Fig. 2A–D. Appearance of quadrats (3 m × 3 m) at depths of 10 m (**A, B,** quadrat I-10) and 20 m (**C, D,** quadrat I-20) in December 1973 (*left*) and December 1978 (*right*). Note destruction of *Madracis mirabilis* in I-10 and collapse of coral heads (*middle right*) in I-20

over the quadrats than the relatively thin layer of "Loose sediment" which was continuously covering and subsequently exposing rocky surfaces. In the living portion of the quadrat substrata, the corals as a group, appeared to be more stable, i.e. less mobile, than other living components. The I_R values for "All corals" for the 10, 20, 30 and 40 quadrats are respectively 37.4, 38.3, 18.9 and 18.4. These values are low when compared with the same values for non-coral invertebrates (Sponges and Invertebrates-other) – 73.8, 51.8, 46.7 and 35.4.

Although few I_R values are available for comparison between the individual coral species due to the quadrat cover limitation (5% or greater), there are marked differences between the species. The 2 species of *Montastrea* are characterized by low I_R values – *M. annularis* (Ellis and Solander) (13.6) and *M. cavernosa* (8.3), as is *Agaricia lamarcki* Milne Edward and Haime (mean 13.2) (Tables 6, 8, 9). In contrast, *A. agaricites* (Linnaeus) has a high I_R (56), while *Meandrina meandrites* and the category Coral-other score intermediate values, 33.8 and a mean of 40.5 respectively.

Mortality of Coral Colonies

The percentage of the larger (≧30 cm max. diameter) coral colonies that disappeared, died completely or suffered a mortality of ≫50% of the initial living surface is shown in Table 10. The reason that the last category, colonies largely but not completely dead, is included in these data is that in some species, e.g. *Agaricia agaricites* and *Porites astreoides* Lamarck (Lewis 1974) and *Meandrina meandrites* (this paper), large portions of colonies often die but small remnants may survive. There were remarkable differences between the various species. *Montastrea annularis, M. cavernosa* and *Agaricia lamarcki* showed a relatively low mortality in this size group, while mortality was very high in *A. agaricites. Meandrina meandrites* and the category Coral other take an intermediate position.

An examination of the duration of the processes of mortality and disappearance showed a large proportion of these events to be relatively (compared to the potential life span of Scleractinia) short term phenomena (Table 10). "Catastrophic" mortality (a process which starts and finishes within the interval between two consecutive surveys) accounts for 45% of all coral colony mortality. If we exclude the colonies which still had some living tissue remaining and consider only the totally dead or absent colonies ($n=26$), it appears that 69% of the colonies died through catastrophic events, while only 31% survived more than one survey interval.

A comparison of the number of catastrophic mortalities that were accompanied by the disappearance of the coral skeleton with the number which left the coral skeleton in situ, showed a nearly 100% incidence of the former phenomenon (Table 10). This indicates that collapse of substrata and dislodgement of corals were much more important factors than predation in coral mortality. Predation would result in the dead coral skeleton remaining in

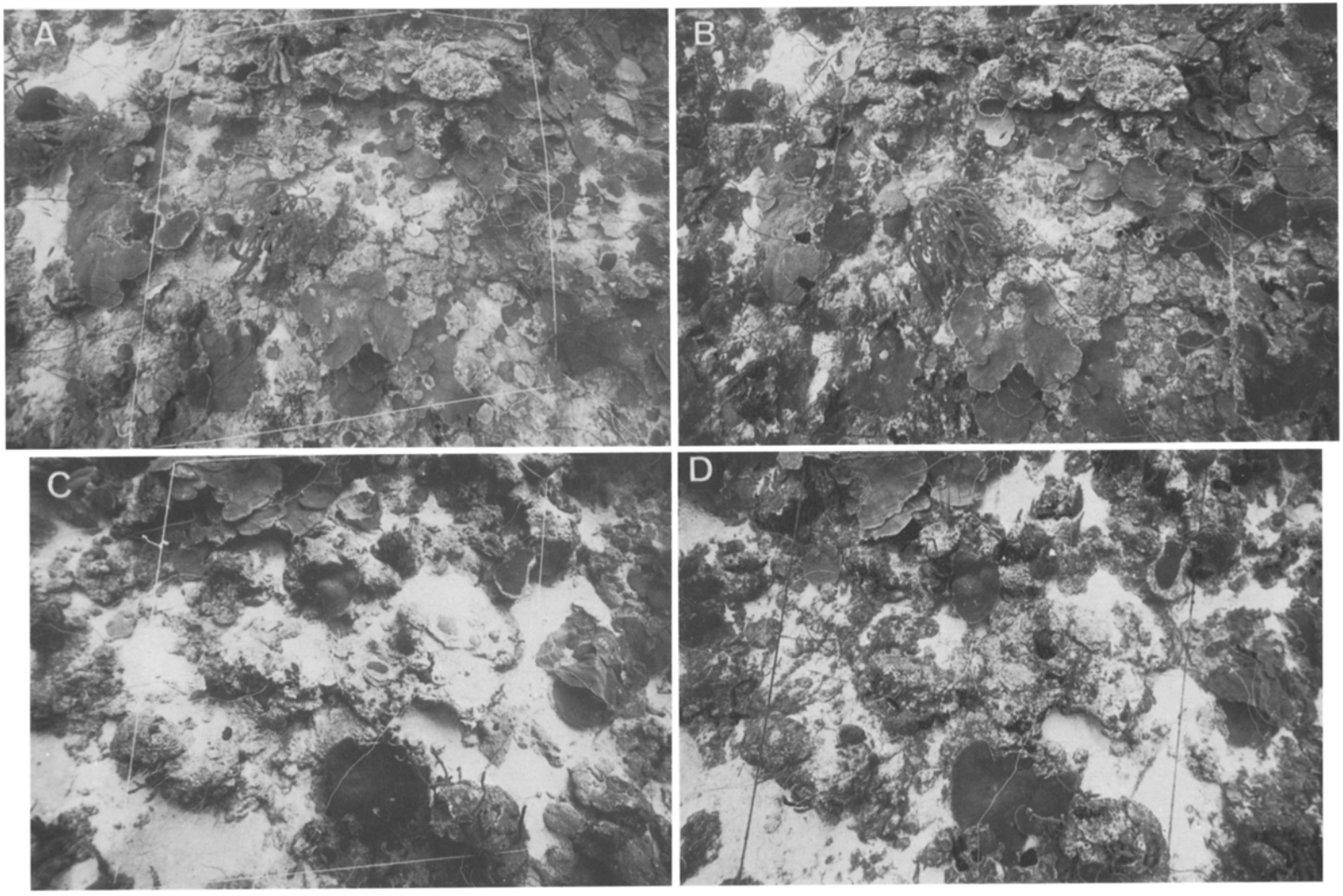

Fig. 3A–D. Appearance of quadrats (3 m × 3 m) at depths of 30 m (**A, B,** quadrat III-30) and 40 m (**C, D,** quadrat II-40) in December 1973 (left) and December 1978 (*right*). Note growth of *Agaricia lamarcki* colonies (*upper right*) in III-30 and appearance of dislodged coral (*upper middle*) in II-40

Table 5. Comparison of mean percentage cover by substratum components for all quadrats ($N=12$) between December 1973 and December 1978

Components	'73	'78
Agaricia agaricites	2	2
A. lamarcki	8	8
Montastrea annularis	3	3
M. cavernosa	3	3
Meandrina meandrites	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

place. Although dead coral skeletons are more easily infested by excavating sponges etc., the rate of such processes exceeds the 8 months interval period.

The relationship of depth to the two modes of mortality (Table 11), shows that catastrophic mortalities are much more common in the shallower reef habitats (10 and 20 m), whereas processes of longer duration are most common at intermediate depths (20 and 30 m). There is relatively low mortality of either kind in the deepest quadrats (40 m).

Discussion

The high degree of constancy in cover but considerable spatial change can be interpreted to mean, that in these habitats there is a high stability (sensu lato) in terms of substratum cover, but low stability in terms of the spatial arrangement of the mosaic of substratum components. This last phenomenon, the instability of spatial arrangement, is closely related to the predictability, or rather, unpredictability of the environment. It appears to us that, in the literature, diversity is too often used to explain and demonstrate stability and predictability in (reef) environments. In addition, predictability is frequently inferred from the species composition or size of individuals or colonies, while the processes shown to be important in this study, spatial arrangement through dislodgement and collapse of substrata and changes in sediment flow, are not quantified. Our data indicate that "a temporal mosaic exists as a result of different time spans elapsing after the creation of small open spaces following disturbances" (Grassle 1973). When the size and frequency of appearance of these spaces are used as a measure of environmental predictability, as Grassle (ibid.) suggests, then our reef habitats, especially at 10 and 20 m, are highly unpredictable.

Apart from the "traditional" environmental parameters (mentioned in the Introduction) and from instances in which perturbations are outstanding and readily noticed, such as extremely low tides (Loya 1972, Fishelson 1973) or hurricanes (Glynn et al. 1964, Connel (1973, 1978), stability or predictability is seldom measured on coral reefs. The use of such parameters would classify these habitats as relatively predictable (sensu Slobodkin and Sanders 1969). However, when traditional parameters are quantified and related to coral distribution on well-developed reefs, it has been shown that these "macro" factors (apart from light) do not explain the structure of coral reefs very well (Ott 1975, Dana 1976).

When cover in the individual quadrats is compared, it appears that, although there was a very high stability in cover through time, this stability was less at 10 and 20 m than at 30 m and 40 m. Nevertheless, the fluctuations are minor when compared to published data on the stability of coral cover. Connell (1973) observed in shallow reef habitats at Heron Island (Great Barrier Reef), that the area covered by living coral varied by a factor

Table 6. Spatial change of substratum components in 10 m depth quadrats (3 m × 3 m) at 3 transects between December 1973 and December 1978 (Abs = absence, App = appearance, since December 1973 census; I_A = index of absolute spatial change, I_R = index of relative spatial change; see text for details)

Components	Transects									Total (Mean)			
	I			II			III						
	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	I_R[a]
Agaricia agaricites	0	0	0	1	2	1.5	1	0	0.5	1	1	0.7	–
A. lamarcki	0	0	0	0	0	0	0	0	0	0	0	0	0
Montastrea annularis	2	2	2	1	1	1	2	1	1.5	2	1	1.5	13.6
M. cavernosa	0	0	0	0	0	0	1	2	1.5	0	1	0.5	8.3
Meandrina meandrites	0	0	0	0	0	0	0	0	0	0	0	0	0
Coral – other	26	12	19	5	0	2.5	10	7	8.5	14	6	10	62.5
Sponge	0	2	1	0	4	2	3	3	3	1	3	2	–
Invertebrates – other	1	1	1	3	1	2	4	7	5.5	3	3	2.8	–
Rock	0	2	1	13	7	10	10	9	9.5	8	6	6.8	59.1
Loose sediment	4	7	5.5	6	10	8	5	11	8	5	9	7.2	60
Deep sediment	2	0	1	10	17	13.5	3	2	2.5	5	6	5.7	29.2
Coral fragments	16	25	20.5	5	2	3.5	3	0	1.5	8	9	8.5	51.6
All living components	29	17	23	10	8	9	21	20	20.5	20	15	17.5	43.2
All corals	28	14	21	7	3	5	14	10	12	16	9	12.7	37.4
All non-living components	22	34	28	34	36	35	21	22	21.5	26	31	28.2	47.4
Total change per quadrat			51			44			42			45.7	45.7

[a] Index calculated only for those components with a quadrat cover of 5% or greater

Table 7. Spatial change of substratum components in 20 m depth quadrats (3 m × 3 m) at 3 transects between December 1973 and December 1978 (Abs = absence, App = appearance, since December 1973 census; I_A = index of absolute spatial change, I_R = index of relative spatial change; see text for details)

Components	Transects									Total (Mean)			
	I			II			III						
	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	I_R[a]
Agaricia agaricites	2	2	2	3	1	2	5	4	4.5	3	2	2.8	56
A. lamarcki	0	0	0	1	0	0.5	1	2	1.5	1	1	0.7	–
Montastrea annularis	0	0	0	3	0	1.5	1	0	0.5	1	0	0.7	–
M. cavernosa	0	1	0.5	0	0	0	1	3	2	0	1	0.8	–
Meandrina meandrites	2	0	1	2	1	1.5	8	0	4	4	0	2.2	33.8
Coral other	12	7	9.5	5	6	5.5	5	1	3	7	5	6	35.3
Sponge	1	1	1	0	2	1	1	6	3.5	1	3	1.8	–
Invertebrates – other	5	3	4	3	6	4.5	1	5	3	3	5	3.8	58.5
Rock	4	13	8.5	15	13	14	15	16	15.5	11	14	12.7	50.8
Loose sediment	7	11	9	8	12	10	8	5	6.5	8	9	8.5	56.7
Deep sediment	3	2	2.5	5	4	4.5	1	1	1	3	2	2.7	28.4
Coral fragments	10	6	8	0	0	0	0	4	2	3	3	3.3	–
All living components	22	14	18	17	16	16.5	23	21	22	20	17	18.8	41.3
All corals	16	10	13	14	8	12	21	10	15.5	17	9	13.2	38.3
All non-living components	24	32	28	28	29	28.5	24	26	25	25	28	27.2	49.9
Total change per quadrat			46			45			47			46	46

[a] Index calculated only for those components with a quadrat cover of 5% or greater

Table 8. Spatial change of substratum components in 30 m depth quadrats (3 m × 3 m) at 3 transects between December 1973 and December 1978 (Abs = absence, App = appearance, since December 1973 census; I_A = index of absolute spatial change, I_R = index of relative spatial change; see text for details)

Components	Transects									Total (Mean)			
	I			II			III						
	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	I_R[a]
Agaricia agaricites	0	0	0	1	1	1	2	0	1	1	0	0.7	–
A. lamarcki	2	0	1	0	1	0.5	2	6	4	1	2	1.8	14.4
Montastrea annularis	0	0	0	0	0	0	0	0	0	0	0	0	0
M. cavernosa	0	0	0	1	0	0.5	0	0	0	0	0	0.2	–
Meandrina meandrites	1	0	0.5	0	0	0	2	0	1	1	0	0.5	–
Coral – other	2	1	1.5	1	4	2.5	2	1	1.5	2	2	1.8	22.5
Sponge	0	0	0	0	0	0	3	4	3.5	1	1	1.2	–
Invertebrates – other	1	4	2.5	2	3	2.5	1	3	2	1	3	2.3	38.3
Rock	7	6	6.5	12	9	10.5	11	8	9.5	10	8	8.8	24.1
Loose sediment	6	7	6.5	6	12	9	6	7	6.5	6	9	7.3	37.4
Deep sediment	2	3	2.5	10	3	6.5	0	0	0	4	2	3	30
Coral fragments	0	0	0	0	0	0	0	0	0	0	0	0	0
All living components	6	5	5.5	5	9	7	12	14	13	8	9	8.5	25
All corals	5	1	3	3	6	4.5	8	7	7.5	5	5	5	18.9
All non living components	15	16	15.5	28	24	26	17	15	16	20	18	19.2	19.1
Total change per quadrat			21			33			29			27.7	27.7

[a] Index calculated only for those components with a quadrat cover of 5% or greater

of 2 to 3 over a period of 7 years. Glynn (1976) studying the effects of extremely low tides in Panamá (Pacific reefs) found coral cover to decrease by a factor of 2.5 in 15 months. Our data span a 5 year period and it is clear that there are no comparable changes in cover in the reef habitats that we studied.

The highest variation in our study occurred in the I-10 quadrat which is dominated by *Madracis mirabilis*. It was not clear why this fragile branched species, living in a relatively benign environment (compared with coral species which depend heavily on asexual propagation such as *Acropora palmata*), should allocate resources to growth and maintenance rather than to the production of recruits (Bak and Engel 1979). This study shows that *M. mirabilis* is also subjected to considerable disturbance. Similar changes in cover have been observed in other *M. mirabilis* beds (Bak,

Table 9. Spatial change of substratum components in 40 m depth quadrats (3 m × 3 m) at 3 transects between December 1973 and December 1978. (Abs. = absence, App. appearance, since December 1973 census; I_A = index of absolute spatial change, I_R = index of relative spatial change; see text for details)

Components	Transects									Total (Mean)			
	I			II			III						
	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	Abs.	App.	I_A	I_R[a]
Agaricia agaricites	0	0	0	0	0	0	0	0	0	0	0	0	0
A. lamarcki	1	0	0.5	1	0	0.5	4	7	5.5	2	2	2.2	11.9
Montastrea annularis	0	0	0	0	0	0	0	0	0	0	0	0	0
M. cavernosa	0	0	0	0	0	0	0	1	0.5	0	0	0.2	–
Meandrina meandrites	0	0	0	0	0	0	0	0	0	0	0	0	0
Coral – other	5	1	3	3	2	2.5	3	0	1.5	4	1	2.3	41.8
Sponge	0	0	0	2	1	1.5	1	2	1.5	1	1	1	–
Invertebrates – other	3	1	2	0	1	0.5	0	3	1.5	1	1	1.3	–
Rock	12	6	8	14	4	9	8	3	5.5	11	4	7.8	20
Loose sediment	4	9	6.5	4	11	7.5	0	0	0	3	7	4.7	25.4
Deep Sediment	0	8	4	1	6	3.5	0	0	0	0	5	2.5	22.7
Coral fragments	0	0	0	0	0	0	0	0	0	0	0	0	0
All living components	9	2	5.5	6	4	5	8	13	10.5	8	6	7	22.6
All corals	6	1	3.5	4	2	3	7	8	7.5	6	4	4.7	18.4
All non-living components	16	23	19.5	19	21	20	8	3	5.5	14	16	15	21.7
Total change per quadrat			25			25			16			22	22

[a] Index calculated only for those components with a quadrat cover of 5% or greater

Table 10. Mortality of coral colonies (≧30 cm maximum diameter) in all quadrats between December 1973 and December 1978. Values expressed as % of N for each species. Mortality – other and total mortality include dead colonies with small living remnants (see text)

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

[a] Arithmetic discrepancies are due to rounding errors

Table 11. Analysis of coral colony mortality (≧30 cm maximum diameter) in all quadrats by depth. Mortality-other and total mortality include dead colonies with small living remnants. (see text) Values expressed as % of total sample size

Depth (m)	*N*	Catastrophic mortality	Mortality–other	Total Mortality
10	9	19	2	21
20	19	24	21	45
30	10	0	24	24
40	4	2	7	9
Total	42	45	55	100[a]

[a] Arithmetic discrepancy due to rounding errors

pers. obs.). Factors responsible include predation by *Diadema antillarum* Philippi (Bak and Van Eys 1975) and the excavation of shallow depressions in *Madracis* beds by the Ocean Triggerfish, *Canthidermis sufflamen* (Mitchell), (Bak, pers. obs.). Clearly, the fragile nature of the colonies makes them highly susceptible to these biological as well as to physical factors such as the passage of dislodged coral heads through the bed.

The analysis of spatial change revealed that there was far more spatial change in the shallower (10 and 20 m) quadrats than in the deeper quadrats (30 and 40 m). This may be due in part to the influence of storms on the shallower parts of the reef. One of us (Luckhurst) has observed extensive damage to beds of *Acropora cervicornis* (Lamarck) at a depth of 21 m on the south coast of Puerto Rico after the passage of hurricane David. However, such extreme conditions are not known on the leeward coast in Curaçao.

An examination of the indices of change shows the horizontal homogeneity of the habitats as evidenced by the similarity in index values at each depth (Tables 6–9). The values (total change) for 10 and 20 m (I_R range – 42 to 51) are significantly greater than those for 30 and 40 m (I_R range – 16 to 33). This confirms the relatively greater constancy (stability) of the deeper reefs. In the deepest quadrats (40 m), there is a relatively higher mobility in the living components than in the non-living. The categories Sediment and Rock in the shallow quadrats are as mobile as the category Coral-other, but in the deeper quadrats, this latter category is more mobile. Clearly, physical factors such as water movement are of less influence in the deeper quadrats.

A continous change in the cover of non-living components such as Sediment and Rock must have implications for the settling and survival of the juvenile benthos. These are stochastic patterns

of natural disturbance that will reduce competition and favor, with respect to settlement, those species with frequently or continuously available larvae, such as the coral *Agaricia agaricites* (Van Moorsel 1980) and the ascidian *Tridemnum solidum* (Van Name) (Van Duyl per. obs.), rather than larvae of highly competitive species. In this sense there may be, at least at the level of juvenile benthos, an analogue to certain phenomena in the acquisition of living space by guilds of reef fishes (Sale 1978). It is also important to realize that although the category Rock is spatially changing, the cover of rocky substratum is constant (Table 5). In other words, there is predictability in the amount of rock available for settlement in time, but not in space. The resource space is continually covered and renewed – a temporally varying mosaic. As a result, in these habitats and at this scale, space may not be the extreme limiting resource it is purported to be on coral reefs.

There is no increase in the species richness of corals with depth which corresponds to an increase in the predictability of the environment. Bak (1977) and Luckhurst and Luckhurst (1978) working respectively in the vicinity of the transects and in the quadrats themselves, found species richness to be lowest at 40 m. This is probably due to the fact that only a minority of the coral species is adapted to the local light regime.

There are significant differences in spatial mobility, expressed as I_R, between the living components. Firstly, at the two depths for which sufficient data are available (20, 30 m), spatial change is relatively low in corals compared with other living components. Secondly, there are considerable differences in the mobility of the various coral species. *Agaricia agaricites* is spatially very mobile, while *A. lamarcki* as well as *Montastrea annularis* and *M. cavernosa* are relatively very stable species. *Meandrina meandrites* and the category Coral-other take an intermediate position. Spatial change reflects processes of settlement, survival, growth and mortality. A species, such as *A. agaricites*, has the highest percentage of settlers out of the juvenile coral population (Bak and Engel 1979) and probably a relatively low rate of survival (Bak and Elgershuizen 1976; Bak et al. 1977) and a high mortality (this paper). At the other end of the spectrum, are the *Montastrea* species with generally few settlers, better survival and low mortality. Other species are arranged between these extreme life history strategies, although in species such as *Acropora palmata* life history phenomena are not so linearly ranked. Our data on coral mortality (Table 10), confirm this pattern of generally r and K selected strategies.

Mortality of large colonies is lowest in the most constant environment and higher at shallower depths where both physical and biological disturbances are more pronounced. (Table 11). Common grazers, such as *Diadema antillarum* and parrotfishes (Scaridae) are more abundant on the shallow reef. Grazing by these organisms means rasping or biting off the underlying coral rock, causing a higher bioerosion of the bases of the living corals at the shallower depths. In combination with the effects of clionid sponges, this will result in a greater susceptibility of collapse and dislodgement. The upper, living part of the coral colony increases in weight due to continuing calcification and this effect will be particularly prevalent in larger colonies. Under these circumstances colonies will be especially liable to collapse in the shallower quadrats which are more exposed to both bioerosion and surge action. The importance of catastrophic mortality (Table 10) confirms earlier observations on growth and life history processes in stony corals (Bak 1976).

Although we noticed some cases in which corals were interfering and competing for space aggressively (sensu Lang 1973), this defensive action does not result in mortality of whole colonies. Functional dominance (e.g. Yodzis 1978) does not appear to be very important in the habitats we studied. A fair amount of opportunism is advantagenous in these highly spacially mobile environments. This is why *Agaricia agaricites* is such a common coral on these reefs as opposed to other assemblages at the same depth in which *Montastrea annularis* is the dominant species (Bak 1975). In this later type to reef, in which *Ag. agaricites* is an unimportant, rare or absent species, spatial change should be low. On other kinds of reefs with different dominance patterns functional dominance may be an important feature of community organization. These are testable predictions which may show the coral reef as a tropical marine shallow water habitat to be more variegated in community organization than previously thought.

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References

Bak RPM (1975) Ecological aspects of the distribution of reef corals in the Netherlands Antilles. Bijdr Dierk 45:181–190

Bak RPM (1976) The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Neth J Sea Res 10:285–337

Bak RPM (1977) Coral reefs and their zonation in the Netherlands Antilles. AAPG Studies in Geology 4:3–16

Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. *In*: DL Taylor (Ed) Proceedings of the Third International Coral Reef Symposium, Vol. 1 University of Miami Rosenstiel School of Marine and Atmospheric Science

Bak RPM, Elgershuizen JHBW (1976) Patterns of oil-sediment rejection in corals. Mar Biol 37:105–113

Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar Biol 54:341–352

Bak RPM, van Eys G (1975) Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia (Berl) 20:111–115

De Buisonjé PH (1974) Neogene and quarternary geology of Aruba, Curaçao and Bonaire. Martinus Nijhoff, The Hague, Holland

Connell JH (1973) Population ecology of reef-building corals, *In:* OA Jones and R Endean (eds), Biology and geology of coral reefs Biology 1, Vol 2. Academic Press, New York, p 205–245

Connell JH (1976) Competitive interactions and the species diversity of corals. *In:* GO Mackie (ed), Coelenterate ecology and behaviour, Plenum Press, New York p 51–58

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science, New York 199:1302–1310

Dana TF (1976) Reef-coral dispersion patterns and environmental variables on a Caribbean coral reef. Bull Mar Sci 26:1–13

De Haan D, Zaneveld JS (1959) Some notes on tides in Annabaai Harbour, Curaçao, Netherlands Antilles. Bull Mar Sci 9:224–236

Farnworth EG, Golley FB (1974) Fragile ecosystems. Springer Verlag, New York

Fishelson L (1973) Ecological and biological phenomena influencing coral-species composition on the reef tables at Eilat (Gulf of Aquaba, Red Sea). Mar Biol 19:183–196

Glynn PW (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol Monogr 46:431–456

Glynn PW, Almodóvar LR, Gonzáles JG (1964) Effects of hurricane Edith on marine life in La Parguera, Puerto Rico. Carib J Sci 4:335–345

Goodman D (1975) The theory of diversity-stability relationships in ecology. Quarterly Review Biology 50:237–266

Grassle JF (1973) Variety in coral reef communities. *In:* OA Jones and R Endean (eds) Biology and geology of coral reefs, Biology 1, Vol 2. Academic Press, New York, p 247–270

Kershaw KA (1964) Quantitative and dynamic ecology. London: Edward Arnold

Lang JC (1973) Interspecific agression by scleractinian corals. 2. Why the race is not only to the swift. Bull Mar Sci 23:260–279

Lewis JB Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. *In:* Proceedings of the Second International Coral Reef Symposium, Vol 2. p 201–206 AM Cameron, BM Cambell, AB Cribb, R Endean JS Jell, OA Jones, P Mather and FH Talbot. (eds) Great Barrier Reef Committee, Brisbane, Australia

Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar Biol 13:100–123

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. Mar Biol 49:317–323

Ott B (1975) Community patterns on a submerged barrier reef at Barbados West Indies. Int Revue ges Hydrobiol 60:719–736

Sale PF (1978) Chance patterns of demographic change in populations of territorial fish in coral rubble patches at Heron Reef. J Exp Mar Biol Ecol 34:233–243

Slobodkin LB, Sanders HL (1969) On the contribution of environmental predictability to species diversity. Brookhaven Symp. in Biol 22:82–93

Van den Hoek C, Breeman AM, Bak RPM, van Buurt G (1978) The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles. Aquatic Bot 5:1–46

Van Moorsel GWNM (1980) Planulation and settlement of the stony coral *Agaricia agaricites*. Proc Assoc Is Mar Labs Carib 15th Meet Abstract (Jamaica University of the West Indies)

Wells JW (1973) What is a colony in anthozoan corals? *In:* (RS Boardman, AH Cheetman, AG Coates, WA Oliver and FM Bayer) (eds) Animal colonies. Dowden Hutchinson and Ross, Stroudsburg, Pensylvania, p 29

Yodzis P (1978) Competition for space and the structure of ecological communities. Springer Berlin, Heidelberg, New York

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