LONG-TERM CHANGE IN CORAL COMMUNITIES ALONG DEPTH GRADIENTS OVER LEEWARD REEFS IN THE NETHERLANDS ANTILLES

R. P. M. Bak and G. Nieuwland

ABSTRACT

Reef slope coral communities were surveyed for long-term (20 years) changes in scleractinian coral cover, numbers of coral colonies and species richness, over the time intervals between the years 1973, 1983 and 1992. We compare such long-term structural changes in the communities at depths of 10, 20, 30 and 40 m. Our data are based on series of photographic records of permanent quadrats, a total of 36 m$^2$ reef bottom at each depth, along four transects on the leeward coasts of the islands of Curaçao and Bonaire. We summarize the changes in the permanent quadrats over time to demonstrate the main trends in the data set and, to understand the significance of the data for the reef community, test the results as effects of time and depth using mixed model ANOVAs. Changes in numbers of coral colonies and coral cover were a function of depth. Number of coral colonies decreased significantly at depths of 10, 20 and 30 m, but not at 40 m. Coral cover decreased significantly at 10 and 20 m, but not at 30 and 40 m. Diversity (species richness) decreased through the years independent of depth. There were no consistent differences between the two 10-year time-intervals. These results confirm earlier observations of coral mortality and spatial mobility which showed the deep reef (30, 40 m) as a much more constant environment than the relatively disturbed shallower reef (10, 20 m).

Two important terms in coral community dynamics are the species specific ecological strategies of the community components and environmental impact such as disturbances. To study the importance of both factors we started monitoring permanent quadrats on the reef bottom over depth in 1973 (Bak and Luckhurst 1980). Depth is a dominant gradient over reefs, incorporating variables such as turbulence, light and predation, and we were curious to see how community dynamic processes would vary over the reef with depth.

Ecological strategies of scleractinian coral species show an enormous range (Bak and Engel, 1979; Bak, 1983; Hughes and Jackson, 1985; Porter, 1987; Babcock, 1991; Meesters and Bak, 1993) and our first analysis of changes occurring in the quadrats after the first 5-year time-interval indicated that these ecological strategies are clearly reflected by the changes in the coral community (Bak and Luckhurst, 1980). A second result was that we found processes and phenomena on the deep reef (30, 40 m) to differ significantly from those in the shallower parts of the reef (10, 20 m).

Because we saw changes in the development of the coral communities and observed that these changes differed significantly in magnitude between depths, we became intrigued by the long-term development of our communities. The only long-term reef monitoring project known at that time was Connell’s study of quadrats in very shallow reef habitats on the Great Barrier Reef (Connell 1976, 1978) and it seemed expedient to continue our surveys on much deeper reef communities. Consequently our quadrats were photographed at least yearly between 1973 and 1992 (except 1984/1985).

There are extremely few similar quantitative data sets available that cover over 2 decades in deep reef communities (Dollar and Tribble, 1993). In this report we analyse change in the reef community in terms of species number, coral cover and numbers of colonies. We look at change in the coral communities from two
perspectives. The first is time: what is the direction of change over 2 decades, 1973–1983 and 1983–1992? The second is depth: is the rate and direction of change similar at 10, 20, 30 and 40 m depth on the reef slope?

METHODS

The permanent quadrats are arranged along four transects on the leeward coasts of the Netherlands Antilles. Transects I and II are at Carmabi Buoy 1, transect III is at Carmabi Buoy 2 (Curaçao), transect IV is at Karpata (Bonaire, for details on all locations see Duyl 1985). Along each transect four quadrats (3 × 3 m) are situated at depths of 10, 20, 30 and 40 m. Quadrats are marked at corners with stainless steel bars or small plastic floats.

The quadrats were photographed using a Nikonos camera, equipped with a UW Nikkor 15 mm f/2.8, picture angle 94°. Kodak 400 ASA film was used in all surveys. The photograph of the complete quadrat was supplemented by a series of detailed, overlapping photographs of the bottom. Negatives were printed to obtain contrasty 20 × 26 cm photographs. Photographs taken in December 1973, September 1983 and May 1992 were analysed for number and cover of coral species (projected surface area) using a CalComp Drawing Board II and a digitizer program (EDC, Agricultural University Wageningen).

All coral species were identified to species level except Madracis decactis and M. pharensis, which were grouped. Because both species are common, species richness presented in the Results section is a minimum value. Two of the Montastrea annularis morphs (Knowlton et al., 1992; Van Veghel and Bak, 1993) are common in the permanent quadrats (the columnar and the massive morphs). The third M. annularis morph, "bumpy" was very rare and it is grouped with the massive morph.

In addition to giving a description of the changes in the quadrats over time, we employed a three-way factorial mixed analysis of variance model to test for significance of changes in the reef communities at different depths (Sokal and Rohlf, 1981). Coral cover data and species richness were approximately normally distributed. Coral colony numbers were approximately normally distributed after one outlier was reduced to the next maximum value.

We use year, depth and transect effects to test for significance of changes in coral cover, numbers of colonies and species richness through the years. Year and depth are fixed main effects tested over the interactions year × transect and depth transect. The year × depth interaction was tested over the year × depth × transect interaction (see ANOVA Tables 1, 2, 3). Note that the random main effect

Table 2. Mixed model ANOVA on changes in coral cover at different depths with time

<table>
<thead>
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<th>Source of variation</th>
<th>df</th>
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<th>F</th>
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<tr>
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<tr>
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</tr>
<tr>
<td>Year</td>
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<td>2.98#</td>
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<tr>
<td>Depth × transect</td>
<td>9</td>
<td>490</td>
<td>11.02</td>
</tr>
<tr>
<td>Depth × year</td>
<td>6</td>
<td>276</td>
<td>6.21***</td>
</tr>
<tr>
<td>Transect × year</td>
<td>6</td>
<td>174</td>
<td>3.91</td>
</tr>
<tr>
<td>Depth × transect × year</td>
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# n.s. *** P < 0.005.
Table 3. Mixed model ANOVA on changes in number of coral colonies at different depths with time

<table>
<thead>
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<tbody>
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<tr>
<td>Transect</td>
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</tr>
<tr>
<td>Year</td>
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<td>713</td>
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<td>Transect × year</td>
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<tr>
<td>Depth × transect × year</td>
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<td>177</td>
<td>-</td>
</tr>
</tbody>
</table>

# n.s.
**P < 0.01.

and first order interactions, i.e., those with the factor transect included, use the three-way interaction as denominator in calculating the F-value.

RESULTS

Species Richness.—The initial number of coral species in the permanent quadrats varied from 16 to 5 from shallow to deep water. Species richness differed significantly (Table 1) at the different depths, highest numbers being reached at 20 m and lowest at the deep reef (Fig. 2). Numbers for each quadrat and changes in species richness are shown in Figure 1. Compared with 1973, the number of species is down in 1992 in all quadrats (but two) and at all depths. The main trend is for species richness to decrease in both time intervals, 1973–1983 and 1983–1992, and at all depths (Fig. 2, Table 1).

Abundant species, having densities >20 colonies at each depth (36 m²), generally showed a decrease in number of colonies but did not suffer species extinction in the quadrats. All species that had disappeared between the 1973 and the 1992 censuses belonged to species that had been relatively rare (densities <10 colonies at each depth). There was no obvious difference in this pattern between

Figure 1. Percentage change in species richness for each quadrat (1–16) at 10, 20, 30 and 40 m between 1973 and 1992. Number of species present in 1973 indicated at top of bars.
depths. Five rare species disappeared at 10 m, 3 at 20 m, 3 at 30 m and 4 at 40 m.

**Coral Cover.**—Coral cover varied initially from 27–77% in the 10 m quadrats, from 37–84% in the 20 m quadrats, from 22–66% in the 30 m quadrats and from 14–42% in the 40-m quadrats. There are enormous changes in the quadrat coral cover over time, up to 60% per decade. Differences in coral cover between the 1973 and 1992 surveys are shown in Figure 3 top. There is a clear difference between the shallow and the deep quadrats. At 10 and 20 m, cover has decreased in all quadrats but at 30 and 40 m cover was the same or increased. This pattern was the same for the 1973–1983 and the 1983–1992 time interval (Fig 3 bottom).

There were no obvious differences in patterns of change between the two decades (Fig. 4). The statistical analysis confirms that the changes in coral cover at the different depths through the years are significant for the communities (Table 2) and that cover has declined at 10 and 20 m (ANOVA F[2,3] = 5.94, 5.08, P < 0.05).

As for differences among the various coral species: all species declined in cover in the shallower part of the reef (10–20 m), except *Colpophyllia natans*, which showed an increase. Some species decreased in proportion to the overall decrease in coral cover (e.g., *Madracis mirabilis*), some decreased more than average (e.g., *Agaricia agaricites*). At the deep reef there was a clear increase of *A. lamarcki*.

**Number of Colonies.**—There was also a decrease in number of colonies. There are two important aspects to this decrease. Firstly, it was much greater in the shallower part of the reef, up to 60% at 10 and 20 m, than in the deep reef, up to 30% at 30 and 40 m (Fig. 5 top). Change in number of coral colonies varied at depths through the years (Table 3). Numbers decreased significantly at 10, 20

![Figure 2. Model of change in number of species at each depth from 1973 to 1992 (R² = 0.968, P < 0.001).](image-url)

and 30 m but not at 40 m (ANOVA $F_{[2,3]} = 324.95, 5.74, 7.89, P < 0.000, P < 0.05, P < 0.05$, respectively). Secondly, much of the severe reduction in coral colony numbers in the shallowest part of the reef, at 10 m, was confined to the period 1973–1983 (Figs. 5 bottom, 6).
Figure 4. Model of the change in coral cover at each depth from 1973 to 1992 ($R^2 = 0.954$, $P < 0.001$).

Over all depths abundant species (densities >20 colonies each depth) declined in numbers (77% of the species). Abundance was maintained in 18% of these species and increased in 4%.

**DISCUSSION**

Although the reefs of the Netherlands Antilles are fairly rich in species for the Caribbean, species lists giving approximately 55 species (Bak, 1975), quantitative surveys over the reef slope from 10–40 m give typically 15–19 species for 5-m-wide belt transects (Bak, 1977). Apparently our permanent quadrats, with a species richness of up to 17 species in 1973, reflected the diversity of the area. The data show that there is a consistent decrease in species in the time interval 1972–1992 (Fig. 1), the effect not being significantly dependent on depth (Table 1).

Rare species became extinct in the quadrats, abundant species became less abundant (except for deep *Agaricia lamarcki*). Quadrats at all depths lost 3–5 species while only one species shows up as a new recruit in 1992 (*A. lamarcki* at 10 m). Similar loss of rare species from coral reef permanent quadrats has been reported for shallow reefs in the Florida Keys (Porter and Meier, 1992).

The change in coral cover over time for each depth is summarized in Figure 4. Bak and Luckhurst (1980) noticed that over the period 1973–1978 cover of reef bottom components was remarkably constant. After a period of 20 years our conclusion must be different. There is a significant decrease in coral cover through both decades but the pattern is depth dependent (Table 2). Is this simply because our perspective has changed or is there a change in processes and mechanisms? It should be noticed that this decline in cover is not caused through a bias towards high cover localities in original site selection (D’Elia et al., 1991; Hughes, 1992). Locations with high cover are indeed more likely to decline but we avoid this
problem because our series includes sites at all depths with low to very low original coral cover (14 to 37%).

It appears that at 10 and 20 m depth coral cover has significantly decreased (ANOVA $F_{2,31} = 5.94, 5.07$ respectively, $P < 0.05$). Bak and Luckhurst (1980) noticed that change, in terms of spatial rearrangement of bottom components and coral mortality, is much more a phenomenon of the shallow (10, 20 m) than the deep reef (30, 40 m). They show the deep reef to be a more constant environment than shallower depths where physical and biological disturbances will be more pronounced. Figure 4 demonstrates that significant change in cover is limited to the shallower part of the reef and remains approximately level at 30 and 40 m.

Very different things are happening at the various depths. Shallow, at 10 and 20 m coral cover and number of colonies decreased but this is not the case at 30 and 40 m. Deep, numbers of colonies stayed roughly level but also coral cover stayed level or seemed to increase. This is mainly the result of growth of the dominant coral at these depths, the large foliaceous Agaricia lamarcki. Eleven species occur in all quadrats at 40 m, none of those, except A. lamarcki, covering more than 3% of the reef bottom. A. lamarcki does increase from 18% (1973) to 29% (1992). During the same time interval these quadrats lose four species (36%). The suggestion that A. lamarcki is monopolising space at 40 m seems reasonable because locally, in some of the quadrats, this species is exceeding 60% cover.

There was not much difference in changes between the two decades, at least at this scale. The only striking difference is that the decrease in number of colonies at 10 m between 1973–1983 levels off during the last decade (Fig. 6). Because coral cover continued to decrease (Fig. 4) and because there was no sign of an influx of coral recruits the colonies must suffer partial mortality and get smaller.
Partial mortality has been recognized as a factor influencing colony numbers in other declining coral communities (Porter and Meier, 1992).

There are a series of well-known/hypothetical causes for the degradation of coral reefs. These include coral bleaching, competition, diseases and environmental change. Coral bleaching only occasionally occurs on reefs at depths greater than 10 m, e.g., in Curacao it has been seen in *Agaricia lamarcki* as deep as 40 m. The species most susceptible to bleaching in the Netherlands Antilles is *Montastrea annularis* (Meesters and Bak, 1993), which was only common in quadrats at 10 m. Here cover in *M. annularis* changed from 10% to 12% to 7% (1973 to 1983 to 1992). These are not very dramatic changes and we conclude that coral bleaching was not the major cause of mortality in our permanent quadrats.

Mass mortalities of the herbivorous sea urchin *Diadema antillarum* (Lessios et al., 1983) occurred on the reefs of Curacao in October 1983 (Bak et al., 1984) and reduced urchin densities by 97-100%. This resulted in a significant increase of thallose algae (De Ruyter van Steveninck and Bak 1986; Carpenter 1985). Such algae compete with sessile reef invertebrates for space and relaxing herbivorous grazing pressure can ultimately result in the demise of coral communities (Hughes 1989; Hughes et al., 1987). However, although algae such as *Lobophora variegata* and *Dictyota* spp. may have increased on our reefs, coral colonies are not being obviously overgrown.

Another common competitor for space on our reefs is the compound ascidian *Trididemnum solidum* (Bak et al., 1981; Duyl et al., 1981). We hypothesize that a possible increase in the abundance of the ascidian is related to eutrophication and are in the process of investigating changes in abundance of this organism along the leeward Curacao coast since 1978.

Hurricanes are rare in this area of the Caribbean, but hurricane Joan swept the islands in 1988. The possible impact of this storm must be analysed in our photographic records from 1986 and 1989. However, for our purpose here it is sufficient to note that we observe generally the same pattern in the 1973/1983 and the 1983/1992 intervals. Where the pattern differed, e.g., the relatively large decline in colony numbers at 10 m, this is in the first decade, i.e., the period without hurricanes. Apparently the hurricane has not been decisive in setting the pattern of decreasing coral cover and colony density.

Factors such as diseases are unlikely to be important. White-band disease is practically limited to the *Acropora* species and these are only common at depths shallower than 10 m along these coasts (Bak and Criens, 1981; Duyl, 1985). Black-band disease is rare on these reefs.

The most likely factor in the degradation of the shallow part of the reef is “coastal development.” The effects of urbanisation and the development of the tourist industry include the discharge of larger quantities of sewage into coastal waters and artificial beach construction. Water column characteristics will change. An indication of the rôle of eutrophication is the relatively high densities of bacteria over the reef, up to $10^6$ cells·ml$^{-1}$ (Bak and Nieuwland, unpubl.). The production and functioning of the reef pelagic microbial community is presently under investigation.

Theoretically the possibility remains that the changes we observed in the upper part of the reef are not anthropogenic in origin but are part of natural, cyclic phenomena. Comparative studies of our quadrats and similar quadrats at the untouched reefs at the upcurrent, eastern tip of the islands will help to address this point. It is clear, however, that even though on a geological scale we may see a small part of a cycle, in terms of coral community dynamics the development appears completely unidirectional. On a geological scale reefs wax and wane but
the continuous decrease demonstrated during the last two decades in the 10-m, 20-m reef will, if persistent, within decades result in total decay of the coral communities.

**Conclusions**

Over the last two decades coral cover and number of coral colonies significantly decreased in coral communities studied in the upper part (depths 10 and 20 m) of the reefs of Curacao and Bonaire. Such changes were largely absent in the deep reef (30, 40 m).

Relatively rare species disappeared and diversity (species richness) decreased at all depths. The same trends were observed during the time intervals 1973–1983 and 1983–1992. If the continuous decreases observed over the last 20 years persist, the coral communities at 10, 20 m will have decayed within decades.

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**Literature Cited**


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