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REPORT

Rolf P. M. Bak · Gerard Nieuwland · Erik H. Meesters

# Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire

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**Abstract** Coral reefs are thought to be in worldwide decline but available data are practically limited to reefs shallower than 25 m. Zooxanthellate coral communities in deep reefs (30–40 m) are relatively unstudied. Our question is: what is happening in deep reefs in terms of coral cover and coral mortality? We compare changes in species composition, coral mortality, and coral cover at Caribbean (Curacao and Bonaire) deep (30–40 m) and shallow reefs (10–20 m) using long-term (1973–2002) data from permanent photo quadrats. About 20 zooxanthellate coral species are common in the deep-reef communities, dominated by *Agaricia* sp., with coral cover up to 60%. In contrast with shallow reefs, there is no decrease in coral cover or number of coral colonies in deep reefs over the last 30 years. In deep reefs, non-agaricid species are decreasing but agaricid domination will be interrupted by natural catastrophic mortality such as deep coral bleaching and storms. Temperature is a vastly fluctuating variable in the deep-reef environment with extremely low temperatures possibly related to deep-reef bleaching.

**Keywords** Deep coral reef · Global change · Bleaching · Coral reef temperature · Coral mortality · Long-term monitoring

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R. P. M. Bak (✉) · G. Nieuwland
Netherlands Institute for Sea Research (NIOZ),
P.O. Box 54, 1790 AB Den Burg,
Texel, The Netherlands
E-mail: rbak@nioz.nl
Tel.: +31-222-369541
Fax: +31-222-319674

E. H. Meesters
Alterra, P.O. Box 167, 1790 AD Den Burg, Texel,
The Netherlands

## Introduction

In the last century, introductions to ecological coral reef studies used to emphasize the unique high biodiversity of coral reefs in the marine environment. In this century the emphasis has clearly changed. There is the overwhelming concern that coral reefs are in worldwide decline through the activity of man. Coral bleaching, coral diseases, environmental degradation and over-fishing are listed as the prime factors (Grigg and Birkeland 1997; Rogers and Beets 2001; Bellwood et al. 2004; Feely et al. 2004). Large-scale studies, covering the range of reef provinces such as the Caribbean basin and the Great Barrier Reef, show how reefs are degraded and loose coral cover. For the Caribbean, Gardner et al. (2003) demonstrate, using 65 studies including 263 separate sites, that coral cover has been reduced from about 50 to 10% in the last 30 years. Bellwood et al. (2004) report a significant reduction in coral cover on the Great Barrier Reef. However, it is important to realize that the available data are practically limited to reefs shallower than 20 m.

Well-developed coral communities occur or occurred in deep (30–40 m) reefs (Goreau and Goreau 1973; Bak 1977; Macintyre et al. 1991; Vermeij and Bak 2004) but these reefs are neglected in the current debate. For the complete picture, to know how reefs stand today, studies should not be confined to shallow reefs. When the question is asked "Is the coral reef crisis upon us?" deep reefs should be included in our judgment. Of course, the problem is that there are extremely few quantitative data sets that allow an assessment of developments in deep reefs.

In this study we present long-term data (30 years) of developments of coral communities on reefs in the Netherlands Antilles, and we will use these data to study what is happening in deep reefs (30–40 m) in terms of coral cover, population dynamics, and coral mortality.

## Materials and methods

We use data from permanent quadrats that were first photographed in 1973 and frequently revisited and photographed over the last 30 years. The quadrats are arranged along four transects on the leeward coasts of the Netherlands Antilles. Transects I and II are located at Carmabi Buoy One, transect III is at Carmabi Buoy Two (Curaçao), transect IV is at Karpata (Bonaire, for details on all locations see van Duyl 1985). Along each transect, 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. All photographs of complete quadrats were supplemented by series of overlapping photographs of subsections of each quadrat. Negatives were printed to obtain contrast 20×26 cm photographs that were scanned and digitized to obtain maps of coral colony position, colony outline, and identity (Scion Image).

In our analysis we compare the changes in community structure of the shallow reef (10 and 20 m quadrats, $n = 8$) with the deep reef (30 and 40 m quadrats, $n = 8$) over a 30-year period (1973–2002). We use Repeated Measures ANOVA (Quinn and Keough 2002) because the quadrats were repeatedly recorded in 1973, 1983, 1992, 1997, and 2002. Number of species and colony density are square root transformed, cover data are log-transformed. We studied residual and interaction plots to check graphically for violations of assumptions. All analyses were carried out with Systat (Version 10). The dominant coral genus in Caribbean deep reefs is *Agaricia* (Goreau and Goreau 1973; van den Hoek et al. 1978; Bak and Luckhurst 1980; Hughes and Jackson 1985), with *Agaricia lamarcki* or *Agaricia grahamae* as the dominant species. *A.lamarcki* is the most common and because the distinction between these two species based on morphological data is debatable (see Wells 1973; Cairns 1982) we group colonies of these species as *A.lamarcki*. To get information on deep versus shallow temperature fluctuation, temperatures were recorded at Carmabi Buoy One from 15th March 1999 to 5th Sept 2000 using SEAMON Mini temperature-loggers (Hugrun ehf. 1995–1998) at 15, 30, and 50 m depths.

## Results

### Number of colonies

Colony numbers differed between shallow and deep reefs when analysed over time (Fig. 1; significant interaction between depth and time; $F_{4,56} = 3.75$, $p = 0.009$). When analysed separately, we found that over the last three decades there has been a strong decrease ($F_{4,28} = 5.94$, $p = 0.001$) over time in the number of living coral colonies at the shallow reef while the decrease on the deeper reef was much less pronounced ($F_{4,28} = 3.24$, $p = 0.026$). The number of colonies present at the deep reef is more stable and, though there is a decrease between 1973 and 1983 ($F_{1,7} = 11.30$; $p = 0.012$), there is no significant difference between the number of colonies in 1973 and 2002 ($F_{1,7} = 2.84$, $p = 0.136$). In the deep reef, the number of colonies is lower than in the shallow reef. However, colonies at 30–40 m have a larger projected surface area than shallow reef corals (average 20% larger through time). Consequently, there is substantial coral cover at this depth (Fig. 2).

### Coral cover

There is a significant difference in the development of coral cover between the shallow and deep reef (depth–time interaction, $F_{4,56} = 3.861$ $p = 0.008$). Time has a significant effect on developments in the shallow reef ($F_{4,28} = 8.41$, $p < 0.001$) and 70% of the time effect can be accounted for by a linear decrease in coral cover. At 30–40 m cover does not differ significantly with time. Individual comparisons for each time interval, i.e. periods

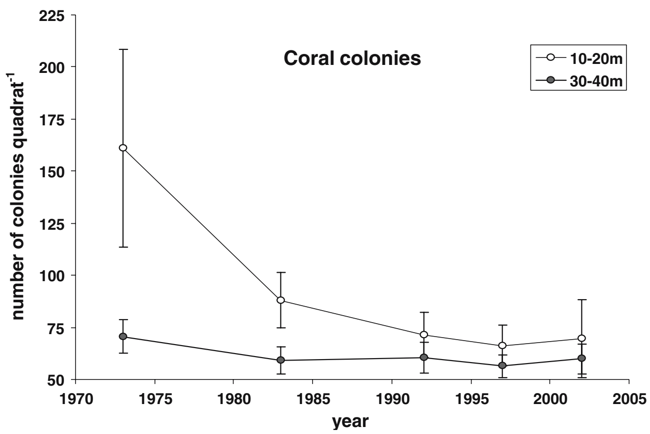



**Fig. 1** Number of coral colonies (mean ± 1SE) from 1973 to 2003 at two depths, 10–20 and 30–40 m

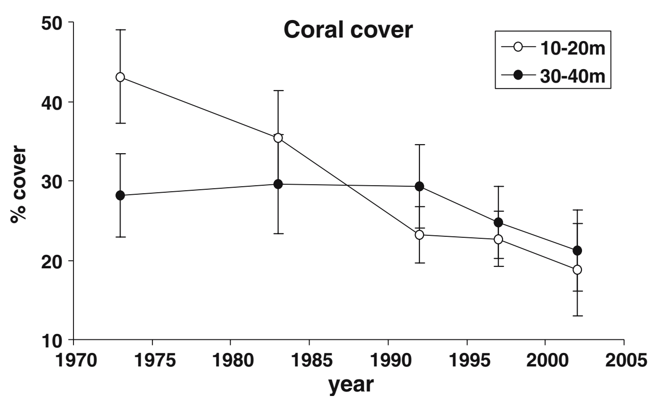



**Fig. 2** Coral cover (mean ± 1SE) from 1973 to 2003 at two depths, 10–20 and 30–40 m

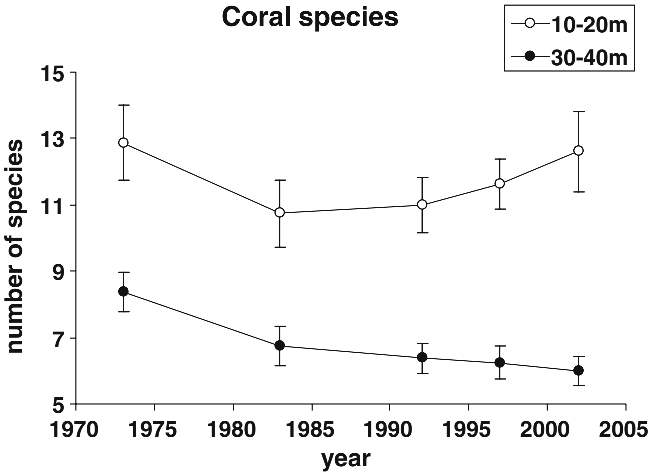



**Fig. 3** Number of coral species (mean ± 1SE) present at two depths, 10–20 and 30–40 m, from 1973 to 2003

between the different years of measurement, showed only that 1997 is significantly lower than 1992 ($F_{1,7} = 7.16$, $p = 0.032$). Change over the next time interval, between 1997 and 2002, was not significant ($F_{1,7} = 0.53$, $p = 0.491$).

### Coral species

The number of coral species is variable in the shallow reef though there is no decrease with time ($F_{4,28} = 1.70$, $p = 0.177$). The number of species is slowly but significantly ($F_{4,28} = 9.00$, $p < 0.001$) decreasing in the deep reef (Fig. 3). When we separate the agaricids, mainly *A.lamarcki*, from the other species (Fig. 4) we see a different trend between these two groups. There is no significant decline in the cover of *Agaricia* with time ($F_{4,28} = 0.87$, $p = 0.493$). However, the cover of other species, mostly species with non-flat, hemispherical colony surfaces such as *Diploria strigosa*,*Stephanocoenia michelinii*, and *Colpophyllia natans*, is decreasing with time ($F_{4,28} = 14.79$, $p < 0.001$).

## Discussion

The coral reef crisis (e.g. Bellwood et al. 2004) is driven by a variety of environmental changes all attributed to the activities of man. While a number of these changes will eventually be distributed throughout the oceans, much of the anthropogenic acute influence is at present limited to shallow water. The effects of shoreline development, physical destruction of corals, land-based changes such as increase in run off and pollution, artisanal fisheries and even global change such as ocean warming are at present largely limited to the most superficial layers of the ocean. The

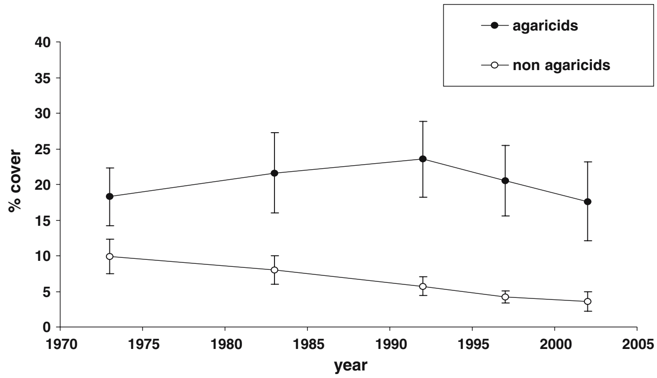


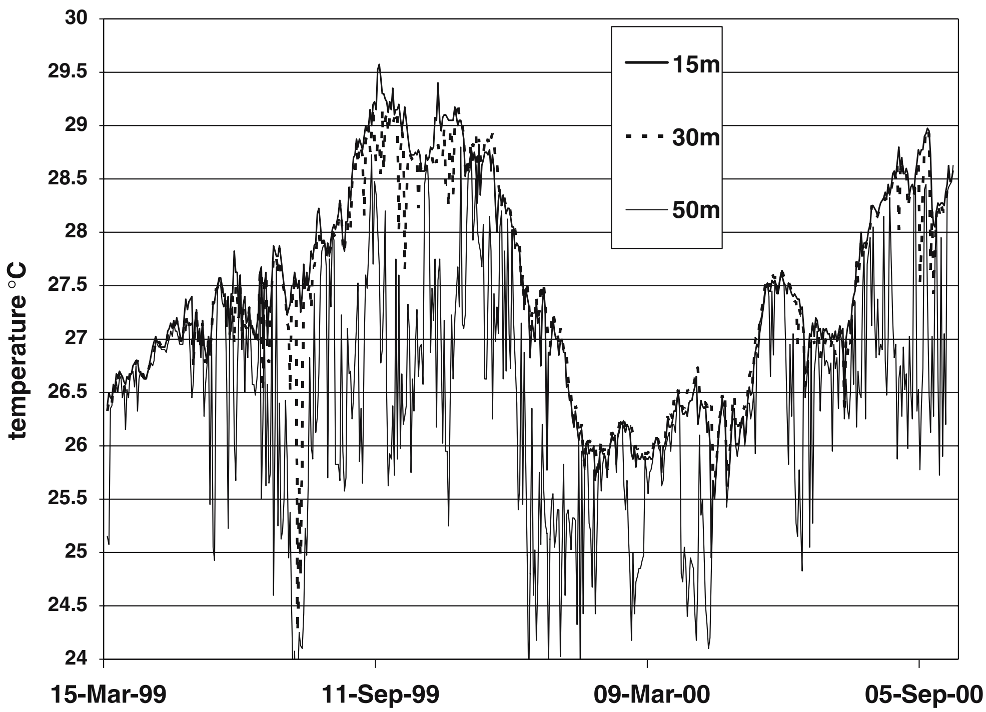

**Fig. 4** Cover (mean ± 1SE) of agaricid and non-agaricid corals in the deep reef, 30–40 m, from 1973 to 2003

development of the shallow reefs in our study reflects the deterioration in environmental conditions. Coral cover and numbers of coral colonies are decreasing, a trend that is in accordance with the process elsewhere in the Caribbean basin (Gardner et al. 2003) as well as in other main coral reef domains (e.g. Grigg and Birkeland 1997; Bellwood et al. 2004).

Our data indicate that most factors that cause deterioration/destruction in the vulnerable shallow reefs are not yet effective at deep reefs. Deep reefs are connected to the more resilient environment of the deeper ocean. This is demonstrated by the limited influence of fluctuations in major environmental factors. Light is a variable of prime importance in coral biological function (e.g. Dunne and Brown 1996; Brown et al. 1999; Vermeij and Bak 2002) but variation in light intensity, be it through changes in cloud cover or turbidity, is a significant factor only in the shallow reef (e.g. see Vermeij and Bak 2002, 2004). The relative importance of the connection of reefs with the deeper ocean is also demonstrated when we consider temperature. Enhanced maximum seawater temperature is the major factor behind coral bleaching, a cause of significant circumtropical coral mortality (e.g. Brown et al. 1996; Hoegh-Goldberg 1999). However, increased maximum temperature appears to be most manifest in shallow water. Our temperature records and those of others (e.g. Leichter et al. 1996) show that the deep reef is bathed in waters originating in the deeper ocean. This is demonstrated by the frequency of cold-water influx in the deep-reef environment and the magnitude of the excursions in cold-water temperatures (Fig. 5).

What are the driving forces in the development of deep coral communities? The data indicate a slow space monopolization of the deep reef by agaricid corals. The change in cover of *Agaricia* over time is not significant but other species are slowly loosing cover (Fig. 4). The number of coral species is also slowly decreasing (Fig. 3). Nevertheless, total coral cover does not significantly decline over the three decades of observation. An explanation is that *Agaricia* species have a comparatively high linear growth rate, their plate/saucer-shaped colonies extending approximately 5 cm in diameter year

**Fig. 5** Seawater temperatures at 15, 30, and 50 m depth on the reef slope at Carmabi Buoy One, Curaçao, over an 18 month-time interval




(Bak 1976). There are at least two potentially major sources of coral mortality that can disrupt *Agaricia* space monopolization: coral bleaching and catastrophic sedimentation.

Coral bleaching and subsequent mortality is generally confined to reefs shallower than 20 m, but we have observed deep coral bleaching to occur in some reefs, away from our quadrats, in the period 1996–1998 (Meesters, Bak, unpublished results). The phenomenon is unmistakable: the reef slope deeper than 30 m seems to have a patchy covering of snow because the dominant large plating colonies of *Agaricia* species are totally white, having lost their endosymbiotic algae. There was substantial mortality among agaricids following the bleaching (Bak, unpublished results). The immediate causal factor of deep bleaching was not recorded but we know that extreme low temperatures occur in deep reefs (Leichter et al. 1996). Of course, usually extreme high temperature is identified as the forcing factor in bleaching, but cold-water influx has been recorded to cause bleaching on coral reefs (Roberts et al. 1982; Walker et al. 1982; Coles and Fadlallah 1991), possibly especially effecting *Agaricia* (J.C. Lang, personal communication). Low temperature, inferred to be connected with upwelling, was connected with bleaching in Bonaire deep reefs in 1992 (Kobluk and Kysenko 1994).

The second source of major coral mortality in deep reefs is catastrophic storm-generated sedimentation. Although, the direct physical effect of hurricane waves is limited to depths shallower than 10–15 m and coral debris is deposited not much deeper at the slope, fine sediment is transported over larger distances and will be deposited at the reef deeper than 30 m. Sediment rejection mechanisms are not very well-developed in corals such as agaricids (Bak and Elgershuizen 1976) and their flat or saucer-like colony shape does not facilitate sediment removal. This contrasts with other species that possess hemispherical colony shapes. These species will have higher survival rates. Fine sediment (mean grain size 100 $\mu$m) generated by hurricane Lenny (1999) killed nearly 40% of corals with flattened colony shape versus less than 5% of non-flat and hemispherical species (Bak, unpublished results) in affected sites.

Deep bleaching and storm generated sedimentation cause catastrophic mortality in the deep reef and because mortality is specifically affecting the dominating *Agaricia* species, it will prevent *Agaricia* space monopolization. If deep bleaching is indeed generated by cold-water upwelling against reef slopes then both causes of mortality are naturally occurring, i.e. in the sense that there is no relation with anthropogenic change of the environment. Impact of man in the deep reef appears still to be limited.

In conclusion, deep reefs do not necessarily show the same trend as shallow reefs. Shallow reefs are in the realm of the man-made environment while deep reefs are still in significant ecological processes part of a relatively undisturbed natural environment. Deep reefs are a neglected and understudied marine environment.

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