

ATOLL RESEARCH BULLETIN

NO. 582

**LONG-TERM DECLINES IN CORAL COVER AT BONAIRE,
NETHERLANDS ANTILLES**

BY

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**ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
DECEMBER 2010**

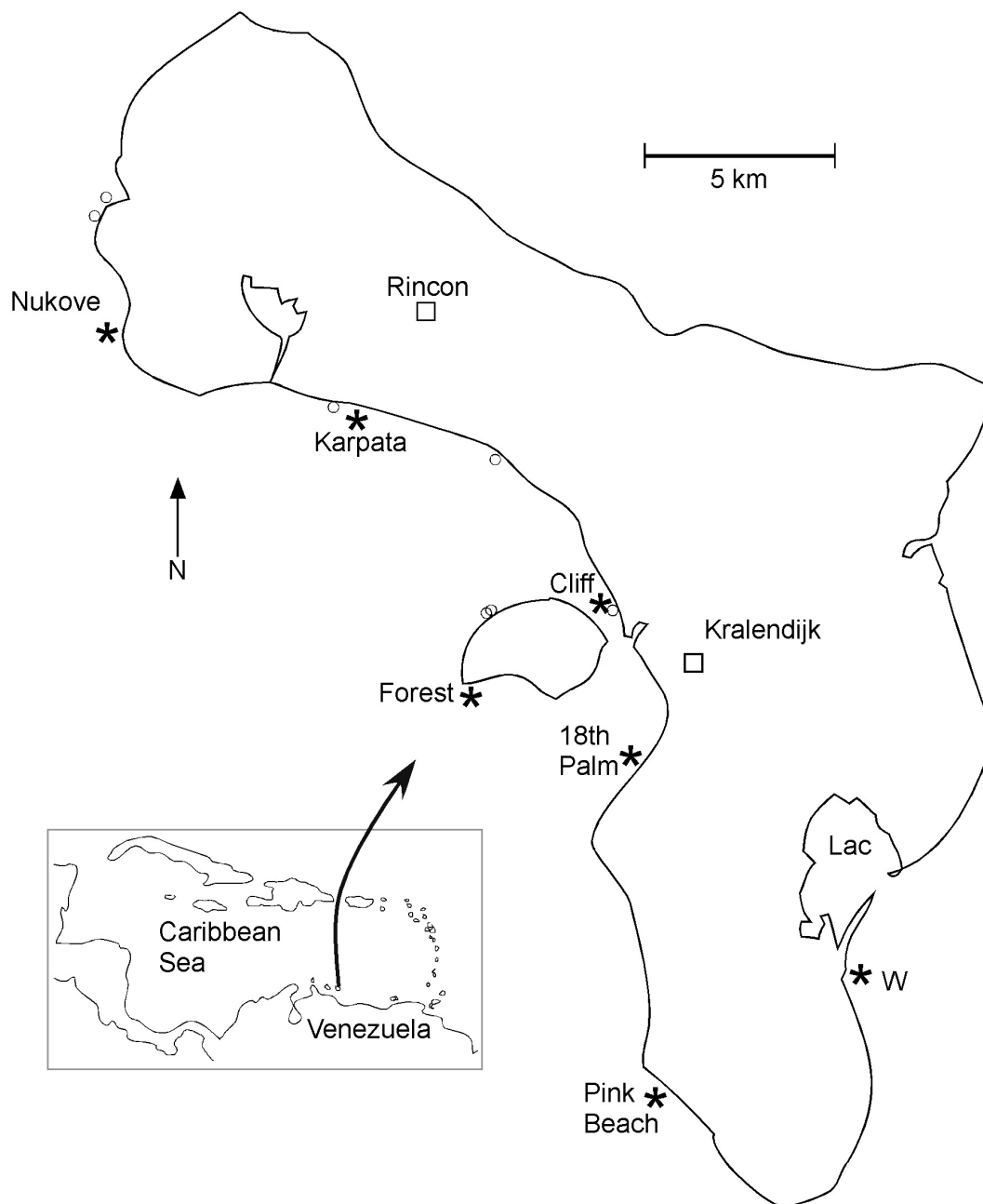


Figure 1. Location of sampling sites on Bonaire, Netherlands Antilles (stars). The town centers of Rincon and Kralendijk are indicated by squares. Open circles mark locations of additional historical sample sites, usually from a single time and depth (<15 m).

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M. DALE STOKES,^{1*} JAMES J. LEICHTER,¹ AND SALVATORE J. GENOVESE²

ABSTRACT

The reefs surrounding Bonaire have long been renowned for their high abundance and diversity of scleractinian corals and for their long-time status as a protected marine park. As part of a comprehensive study of the current status of Bonaire's reefs, a quantitative benthic community survey was conducted at 7 locations across depths from 10 to 30 m in early 2008. This showed mean coral cover ranging from 23.7% ± 3.8 (SE) to 38.4% ± 4.4 (SE) on the island's leeward shore and 1.6% ± 0.4 (SE) to 22.4% ± 3.6 (SE) on the windward shore. Percent cover of macrophytes and turf algae ranged from 41.7% ± 2.0 (SE) to 51.8% ± 3.0 (SE) on the leeward shore and 60.8% ± 4.1 (SE) to 82.7% ± 2.5 (SE) on the windward shore. Comparison of these results to earlier work from 1982 on the leeward shore and 1988 on the windward shore points to a significant, system-wide decrease in corals, increase in macroalgae and increase in the ratio of algae to corals. These observations point to significant degradation of reefs at a site often described as relatively 'pristine' in the Caribbean and highlight the sensitivity of coral reefs to anthropogenic and natural stresses even on well-protected islands.

INTRODUCTION

It is apparent that the health and biodiversity of coral reefs is in decline world wide (Jackson et al., 2001; Gardner et al., 2003; Bellwood et al., 2004; Cote et al., 2006; Knowlton and Jackson, 2008). In particular, Caribbean coral reefs show increasing degradation due to direct and indirect anthropogenic pressure and natural stresses (Mora, 2008). Fishing pressure, eutrophication from terrestrial development, loss of key species (e.g. *Diadema antillarum*, and framework corals such as *Acropora palmata* in the Caribbean), outbreaks of disease, bleaching, storm damage, temperature stress, habitat destruction and sedimentation, and their synergistic effects, have all increased both locally and globally (e.g. Harvell et al., 1999; Jackson et al., 2001; Gardner et al., 2003)

The Caribbean island of Bonaire in the Netherlands Antilles is known for its well-developed fringing reefs and high diversity (Scatterday, 1974; Ginsburg, 1994). The

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reefs surrounding the entire island, from sea level to 60 m depth, have been a protected marine park since ca. 1975, with restricted fishing, prohibitions on boat anchoring and spear fishing, and a support infrastructure of marine park personnel able to maximize compliance with regulations and minimize damage to the reefs by tourist activities (Dixon et al., 1993; Hawkins et al., 1999). For these reasons, Bonaire's contemporary reefs are often considered to be relatively pristine in comparison to those on other Caribbean islands (Dixon et al., 1993; Hawkins et al., 1999; Abel, 2003; Kramer and Bischof, 2003; Hawkins and Roberts, 2004).

Despite the long-term protected status of Bonaire's marine ecosystem, there has been a significant decline in coral coverage in the recent decades. In the Netherlands Antilles, the mass mortality of *D. antillarum* (Bak et al., 1984; Greenstein, 1989; Carpenter and Edmunds, 2006; Debrot and Nagelkerken, 2006), coral bleaching events (Williams and Williams, 1990; Kobluk and Lysenko, 1994), diseases (Gladfelter, 1982; Meesters et al., 1997; Cervino et al., 2004; Nugeus and Bak, 2007), and recent storm damage (Kobluk, 1992; Bries et al., 2004; Scheffers and Scheffers, 2006) have all altered the ecosystem. And, recent increases in terrestrial development causing local eutrophication, sedimentation and direct physical damage to corals from a burgeoning local and tourist population are also thought to contribute to the changes in the reef community (Hawkins et al., 1999; Bak and Nieuwland, 2005; Bak et al., 2005; Uyarra and Cote, 2007; Jones et al., 2008). These changes highlight the tight coupling between terrestrial and shallow marine environments on small islands.

Bonaire has not received as intensive study as has the neighboring island of Curaçao. With the exception of the work by Bak and colleagues (Bak and Nieuwland, 1995; Bak et al., 2005), who sampled 4 photographic quadrats (3 x 3 m square) at a single site on Bonaire approximately every 10 years since 1973, there are very few historical, or island-scale data available. Other studies include detailed maps of the very shallow reef environment (< 15 m depth) before the mass *D. antillarum* mortality (van Duyl 1985), loss of acroporids primarily by white-band disease and storm damage (Kobluk and Lysenko 1992, see also Bak et al. 1984), and a few other more recent studies (e.g. Hawkins and Roberts, 2004; Carpenter and Edmunds, 2006; Green et al., 2008) that report some species assemblage information from single, unmarked locations and at depths < 15 m. There have also been some recent "rapid" reef assessment transect surveys from a few Bonaire locations circa 1997 and early 1999, at depths < 12 m (e.g. Kramer and Bischof 2003).

In this study we examine coral and algae coverage from 10 to 40 m depth, on a larger spatial scale (order 100's m) than previous studies, in order to compare with historical observations and form a baseline for future study. We have made use of overlooked data sets sampled in the 1980's (Stokes, Kobluk and Lysenko 1984) and 1990's on both the leeward and windward reefs and made surveys at identical locations in 2008. The windward site is an area of much lower anthropogenic impact because it is farther from the terrestrial development that is concentrated along the central, leeward coast of Bonaire. With these data we can ask whether similar patterns of species assemblage occur on leeward (more impacted) and windward (less impacted) sites, over a broad range of depths, and we can compare results with previous, more limited surveys.

METHODS

Site Description

The study was conducted on the leeward and windward fringing reefs of Bonaire, Netherlands Antilles (12°12' 25"N, 68°18' 25"W). Bonaire is situated in the La Blanquilla-Aruba island chain approximately 40 km east of Curaçao and approximately 85 km north of Venezuela and is separated from the South American continental shelf by the 1700 m deep Bonaire Trench (Fig.1). Detailed general descriptions of the leeward reefs of Bonaire can be found in Scatterday (1974), the works of Kobluk et al. (Kobluk and Kozlj, 1985; Kobluk and Lysenko, 1984; 1986; 1992; 1994) and van Duyl (1985). It should be noted that most of these general descriptions are of reef state before, or not long after, the Caribbean-wide die off of the urchin, *D. antillarum* in 1982-1984 (Lessios et al., 1984; Lessios, 1988; Greenstein, 1989; for a discussion of the regional effects of the *D. antillarum* die off in the Netherlands Antilles see Bak et al., 1984).

Contemporary Sampling

Transect sampling was conducted at sites spaced along the leeward coast at locations marked by the permanent Bonaire Marine Park moorings. From south to north, the sites were Pink Beach, 18th Palm, Cliff, Karpata, and Nukove (Figure 1). An additional location, Forest, was sampled on the south-western tip of Klein Bonaire. The Cliff sampling site was located approximately 100 m south of the present Marine Park mooring, directly overtop the previous "Aquahabitat" reef mapping survey location utilized by Kobluk and Lysenko in the 1980's and 1990's (Kobluk and Lysenko, 1984; 1986; 1992; 1994). One of the present authors (Stokes) was present during the Kobluck and Lysenko surveys and is familiar with location of the earlier sampling.

The windward sampling site (marked 'W' in Fig. 1) was located approximately 1 km south of the Lac Bay lagoon on the east coast of the island. Around most of Bonaire, the windward coast is typically formed from a limestone terrace fronting a vertical cliff into the sea and does not provide safe access from shore. Also, the windward shore typically experiences strong breaking waves, 2 to 3.5 m in height year round (van Duyl, 1985; Scheffers and Scheffers, 2006) due to the near-constant, strong, easterly trade winds (average speed, 6.7 ms⁻¹, DeBuissonje, 1974). Despite these restrictions limiting access, at a few locations along the south-east coast there are sections of shoreline that allow access to the fore reef on the few days per year when wave conditions are not extreme. The windward site 'W', is similar to other Bonaire windward reef locations that have been observed by the authors by small boat on occasions coincident with serendipitous drops in the trade winds.

In January 2008 benthic surveys were conducted by SCUBA diving to quantify coral and macroalgal abundance at 6 sites on the leeward side and 1 site on the windward side of the island. At each site, 3 separate, 50 m long transects, oriented parallel to the depth contours, were established at 5 m depth increments from 5 to 30 m (where the fore reef becomes dominated by a coralline sand plain). At 3 of the sites, (Forest, Karpata

and Nukove), where coral coverage extends deeper, transects were also conducted at 35 and 40 m depth. Along each transect, digital images were taken of 1 m² quadrats using a Nikon D70 digital camera in an Ikelite underwater housing with external strobes, attached to a rigid photo framer to provide consistent image scaling and lighting. Fifteen quadrat images were taken at approximately 3 m increments along each of the 3 transects, for a total of forty five, 1 m² images per depth, at 6 to 8 depths per site (270 images per site for those sites sampled to 30 m depth and 360 images per site for sites sample to 40 m depth).

Quadrat images were analyzed using the public domain NIH ImageJ software (Rasband, 2007) and Coral Point Count with Excel extensions (Kohler and Gill, 2006). For each image, the total surface coverage of primary reef-framework building corals, macrophytes, encrusting coralline algae, algal turf, sponges, gorgonians, *Millepora* sp. and sand was estimated from 200 overlaid random dots. The dominant corals measured included, *Montastrea annularis* complex, *M. cavernosa*, *Agaricia* sp., *Siderastrea siderea*, *Porities* sp. and other scleractinian species, mainly *Diploria* sp., *Colpophyllia natans*, *Eusmilia fastigiata*, *Stephanocoenia michelini*, *Madracis* sp. and *Meandrina meandrites*. Because of the difficulty in differentiating some coral species based on morphology, we have pooled the *M. annularis* morphotypes (Knowlton et al., 1992; van Veghel and Bak, 1993), and the *Agaricia* species (Wells, 1973) into their respective groups. For this analysis we considered macrophytes to be fleshy species greater than 2 cm; the primary taxa were *Dictyota* sp., *Styopodium* sp., *Padina* sp., *Lobophora variegata*, and *Turbinaria* sp. Algal turf included a variety of small filamentous species as well as cyanobacteria and diatoms. The sponges identified included *Aiolochoxia crassa*., *Aplysina* sp., *Agelas* sp., *Callyspongia* sp., *Xestospongia* sp., *Neofibularia nolitangere*, *Ectyoplasia* sp., *Diplastrella* sp., *Clathria* sp., *Ulosa ruetzleri*, *Cliona* sp., and *Aka* sp.. Identified gorgonians included *Muricea* sp., *Gorgonia* sp., *Pseudopterogorgia* sp., *Erythropodium* sp., *Plexaura* sp., *Pseudoplexaura* sp., and *Eunicea* sp..

Historical Sampling and Data

Historical data quantifying the coral and macroalgal distributions at both the Cliff and windward sites have been included for comparison with the contemporary sampling. Because the survey techniques varied in the previous studies, they are outlined briefly below.

In 1988, one of the authors (Stokes) collected benthic survey data at the windward site. This included 6 parallel transects separated 10 m apart running perpendicular to the reef slope from 3.1 m to approximately 40 m depth. At 3.1 m (10 ft) depth intervals an 8 m² quadrat was sampled and the surface area of all hermatypic corals, gorgonia and algae (pooled as fleshy macrophytes, turf, and encrusting coralline algae) was calculated from linear dimensions of colonies measured to the nearest cm with a flexible tape. Species identification and the dimensional measurements were performed *in situ*, with macrophyte samples collected for later laboratory identification as required.

Kobluck and Lysenko collected extensive coral and algae distribution data at multiple sites along the leeward coast from the late 1970's through the early 1990's (Kobluck and Lysenko, 1984; 1992; 1994). Unfortunately most of this extensive dataset was lost after their untimely deaths in the mid 1990's before it had been comprehensively published. However, comparative summary data of some benthic species distributions from the Cliff, "Aquahabitat", site remain from their extensive in situ mapping project terminated in 1982 (Kobluck and Lysenko, 1984). In that project, 3 contiguous grids (each approximately 226 m² in size) were constructed over the entire 10 to 40 m depth range of the reef slope, and the position and dimension of every sessile organism 1 cm or larger within the grid quadrats mapped by hand on calibrated plexiglass slates. The mapped data were reassembled into a large-scale mosaic, checked for accuracy against a larger scale photo mosaic of the same area, and then digitized for analysis on an Apple III computer. It should be noted that the data reported by Kobluck and Lysenko are the absolute number of individual organisms and surface area coverage over several hundred m², not a statistical subsampling. They counted and measured the entire population of organisms (1 cm or larger) over many hundreds of square meters of reef -- a monumental task.

Statistical Comparisons

In making statistical comparisons we seek to use the simplest, most robust methods to elucidate the large differences evident in the data. This is appropriate because of the limitation in the historical datasets available for comparison and because of the differences in the survey techniques used to calculate the percent area coverage of the benthic organisms. Despite the introduction of small biases in the coverage estimates using the point transect, photographic quadrat and *in situ* quadrat sampling, large differences in coverage means can be tested for significance (Chiappone and Sullivan, 1991, Nadon and Stirling, 2006, Leujak and Ormond, 2007).

For the contemporary data, the means and standard errors of the percent cover for each taxonomic group, total hard corals, the total algae (fleshy macrophytes and algal turf), and the ratio of total algae to total hard corals, were calculated from the $n = 45$ quadrats for each depth (3 transects at each depth) for both the Cliff and windward sampling sites. Because the historical data was collected in approximately 10 foot depth intervals, not the 5 m depth intervals used in the contemporary sampling, the data from the closest 10 foot depth contour was used for comparison, i.e. 15 m compared to the 15.2 m (50 ft) historical samples, 25 m compared to 24.4 m (80 ft) historical sample. Statistical comparisons were then made between the contemporary and historical datasets. All percent cover data were arcsine-squareroot transformed prior to statistical comparisons and critical p values of 0.05 were used to assess significance except where noted below. For the historical data from the Cliff site (Kobluck and Lysenko 1984) an overall mean for coral and algal cover across depths was calculated from the individual values reported at each depth. One-sample t -tests were used to compare the means for coral and algal cover from 2008 across all sample quadrats at all depths to the 1982 mean value. This is a test of the null hypothesis of no difference between the mean of the sample distribution for 2008 and the overall mean value of the population for 1982 (where the census included the entire population). The mean density of sponges measured in each of the

quadrats across all sampling depths in 2008 was similarly compared to the overall mean density of sponges from 1982 by one-sample t-test. Density data were log transformed prior to statistical comparison.

For the windward site, where data from multiple transects and quadrats are available in both the contemporary and the historical datasets, two-way ANOVAs with factors Year and Depth were used to assess significance of differences in both the coral and the algae cover. Only data from depths that matched to within 1 m in both the contemporary and the historical were used in this analysis. An F max test was used to assess homogeneity of variance and in cases where variance differed among groups the critical p-value for significance of the main effects was adjusted downwards following Underwood (1997). Within the specific sampling depths two-sample t-tests were also used to assess the significance of differences between 1988 and 2008. For these tests a Bonferroni correction to the critical p-value was used to reduce the probability of Type-1 error for the multiple tests run across the sampling depths.

RESULTS

In 2008 coral and macroalgal cover varied from about 2 to 42 %, and about 8 to 70% respectively (Fig. 2). The lowest percent coral coverage was typically found at those depths and locations having primarily a loose sand / rubble substrate (i.e. the shallowest depths at Nukove, Forest and Cliff), and the coralline sands off Pink Beach. As shown in Figure 3, at the Cliff site the estimated total mean coral coverage in 2008 (mean coverage = 29.9 % \pm 1.6 SE) was significantly lower ($t_{1,74} = -7.284$, $p \ll 0.001$) than in 1982 (mean coverage = 42.3 %) and the total mean algae coverage in 2008 (mean coverage = 46.4 % \pm 1.5 SE) was significantly higher ($t_{1,74} = 32.269$, $p \ll 0.001$) than in 1982 (mean coverage = 6.4 %). The specific comparisons at each depth showed significant differences for both coral and macrophyte coverage at all depths except for the coral coverage at 15 m ($t_{1,15} = 0.13$, $p = 0.05$). Across depths at this site the percent coral coverage decreased 10 to 40 % from 1982 to 2008 while the percent algae coverage increased approximately 40 to 50%. The 1997 data (which only cover 8 to 12 m depth) also indicate an increase in algae coverage compared to 1982 at these shallow depths.

At the windward site (Fig. 4) the total mean coral coverage in 2008 ranged from 1.6 % \pm 0.4 (in the very high wave energy swash zone) to 22.4 % \pm 3.6 (mean \pm SE). In 1988 the total mean coral coverage ranged from 13.3 % \pm 2.7 to 63.9 % \pm 9.3 (mean \pm SE). Due to unequal variance among groups (determined by F max test) the critical p value to assess significance was adjusted downward to 0.0001. Two-factor ANOVA indicated significant effects of year ($F_{1,1} = 42.4$, $p \ll 0.0001$) and depth ($F_{1,8} = 5.5$, $p \ll 0.0001$) on the coral percent coverage. There was no significant interaction effect between depth and year. Comparing the differences in coral coverage between 1988 and 2008 at the sampling depths, indicate significant differences at the 5, 10, 15, and 20 m depths ($p < 0.0056$). The total mean algae coverage in 2008 at the windward site ranged from 60.8 % \pm 4.1 to 82.7 % \pm 2.5 (mean \pm SE). In 1988 the total mean algae coverage ranged from 17.0 % \pm 4.5 to 53.0 % \pm 8.9 (mean \pm SE). Due to unequal variance among

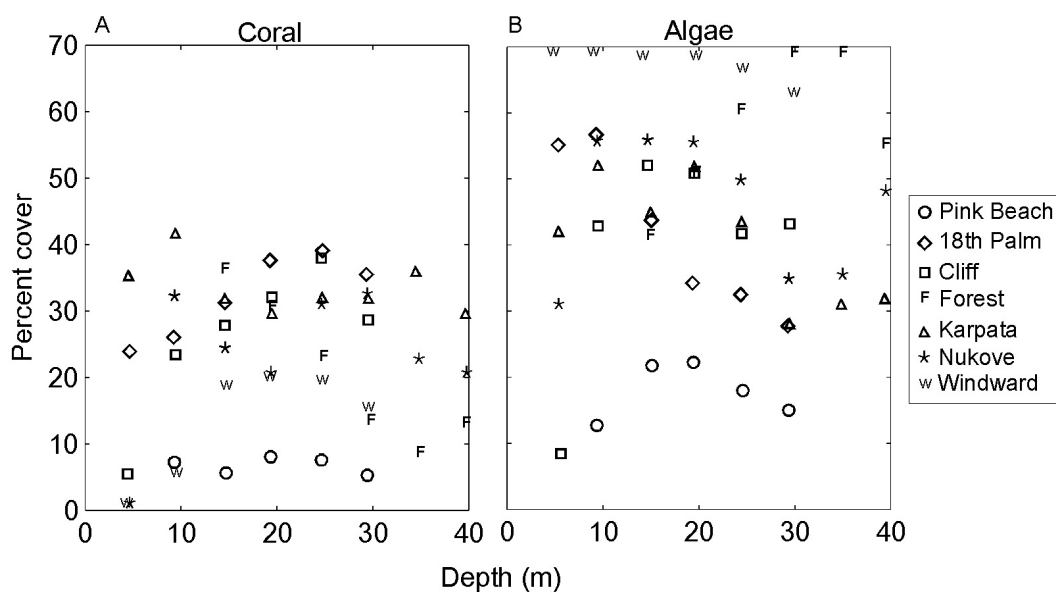


Figure 2. Mean percent coverage of A) hard coral and B) algae as a function of depth at the Bonaire sample sites in 2008. For clarity standard errors are not plotted but are presented in Table 1 along with details of sample sites.

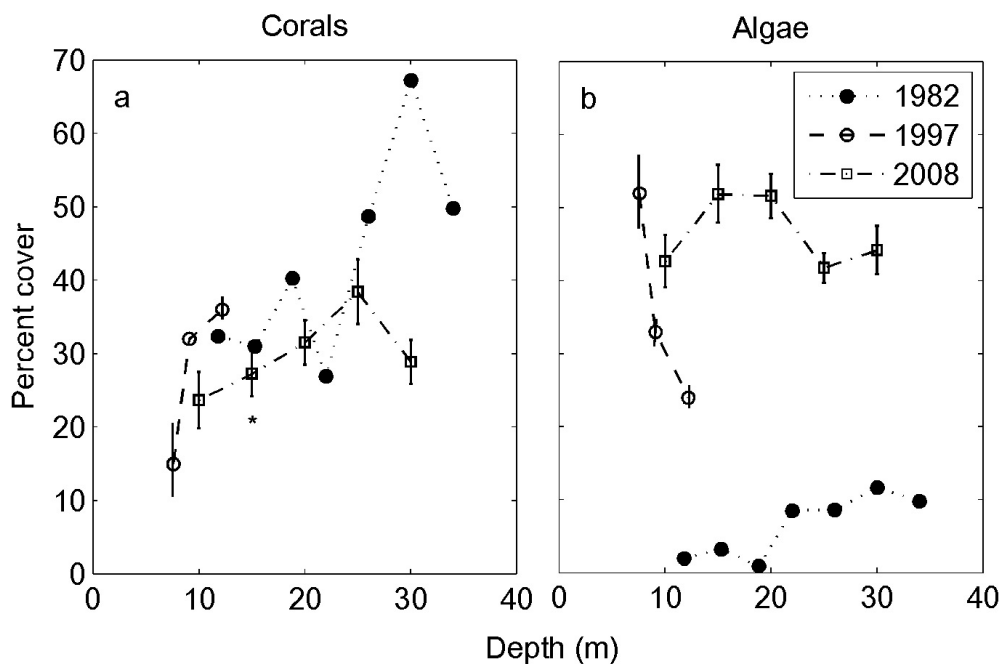


Figure 3. Percent coverage of A) hard coral and B) algae as a function of depth at the Cliff site for 3 time periods. Data from 1982 are shown in solid circles, 1997 in open circles (Reef Check, K. Handschuh pers com) and 2008 in open squares. The error bars for the 1997, 2008 data represent ± 1 SE. 1982 data generated from Kobluck and Lysenko (1984). Differences in coral cover are significant at all depths except 15 m (indicated by an asterisk).

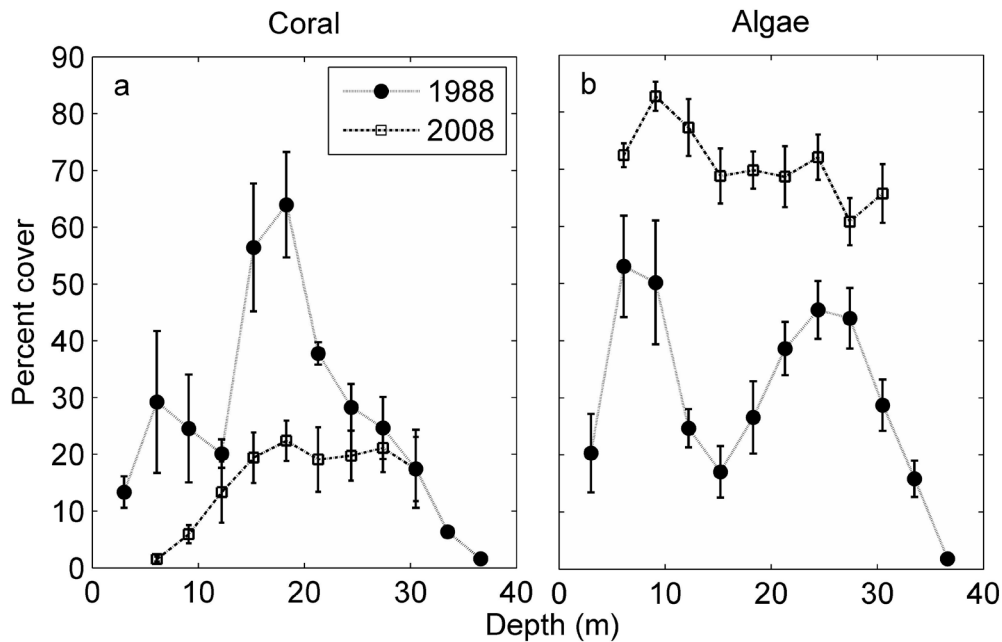


Figure 4. Percent coverage of A) hard coral and B) algae as a function of depth at the windward site from 1988 and 2008. Data from 1988 are shown in solid circles and data from 2008 shown in open squares. Error bars represent ± 1 SE

groups (determined by F max test) the critical p value to assess significance was adjusted downward to 0.0003. Two-factor ANOVA showed a significant effect of year ($F_{1,1} = 152.9$, $p < 0.0001$) on the algal percent coverage. Comparing the differences in algae coverage between 1988 and 2008 at the sampling depths, indicate significant differences at all depths ($p < 0.0056$).

The changes in coral and macroalgae cover are highlighted in Figure 5 showing the ratio of total algae to total coral cover. A ratio less than 1 indicates greater coverage of coral than algae. In 1982 the ratio ranged from 0.02 to 0.47 indicating a spatial dominance of coral at the Cliff site. However, in 2008, the ratio ranged from 1.9 to 2.8 indicating a two to three fold greater coverage by algae across the depths. In 1997, the ratios at 8 to 12 m depth, were intermediate. Indeed, as evinced in Fig. 5A, macrophytes dominated coral coverage at all the sites sampled with ratios from approximately 1 to 8. At the windward site, in 1982, the values ranged from 0.3 to 2.5 depending on the depth (mean = 1.42 ± 0.18 SE), showing a greater proportion of algae across depths than at Cliff. In 2008, the algae to coral ratio at the windward was much larger than in 1988 ranging from 5.1 ± 1.1 to 21.3 ± 2.8 (mean \pm SE), showing a 2 to 20 fold greater coverage of macroalgae than of coral. The patterns in percent coral coverage at the Cliff site (Fig. 3) are detailed by coral taxonomic grouping in Figure 6A. In 1982 the species composition was dominated by *Agaricia* sp. particularly at depths >15 m. Additionally, coral coverage was broadly distributed across a range of other coral species. In 2008, in addition to an overall decrease in total percent coverage the formerly dominant *Agaricia* sp. exhibited reduced coverage at all depths. In addition, the *Siderastrea* sp., *Porities* and ‘Other’ species were much reduced or absent. Only the *M. annularis* complex and *M. cavernosa* show coverage similar to 1982 levels.

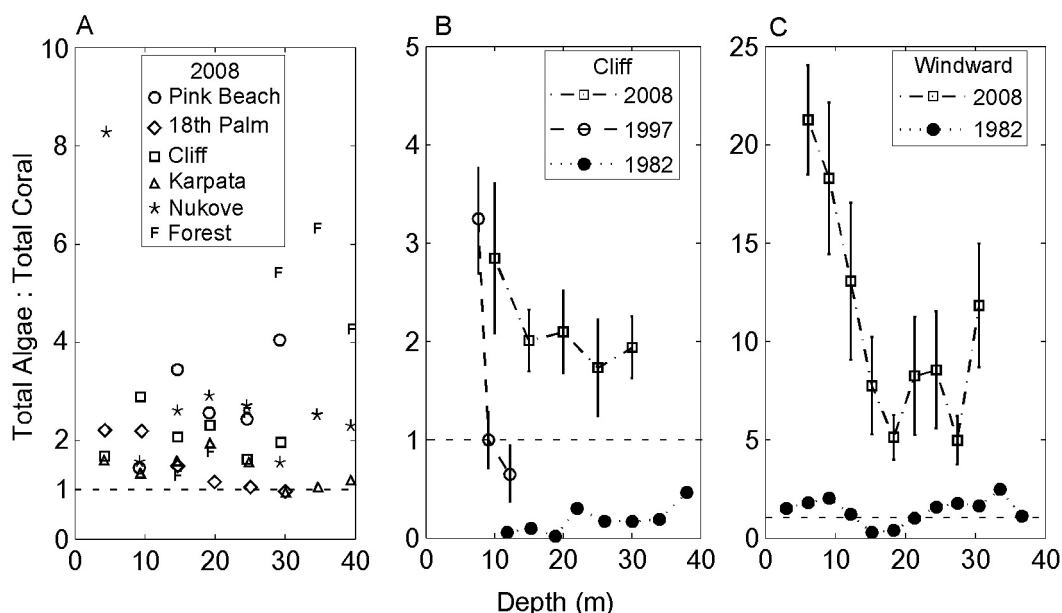


Figure 5. Ratio of total algae to total coral coverage as a function of depth at A) all sites, B) at the Cliff site in 1982 (solid circles), 1997 (open circles) and 2008 (open squares), C) at the windward site in 1982 (solid circles) and 2008 (open squares). Error bars represent ± 1 SE. Note the difference in y-axis scaling between the Cliff and windward sites.

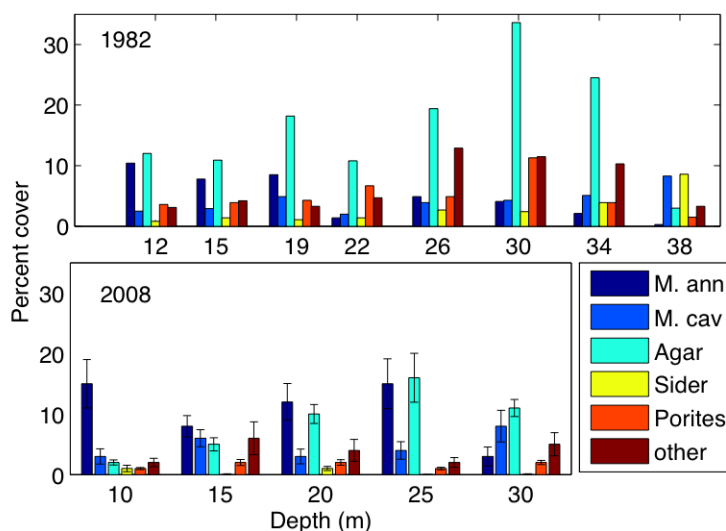


Figure 6A. Mean percent cover of dominant scleractinian coral species or taxonomic group as a function of depth at the Cliff site for 1982 and 2008. Legend indicates *Montestrea annularis* complex (M. ann), *M. cavernosa* (M. cav), *Agaricia* sp. (Agar), *Siderastrea siderea* (Sider), *Porities* sp. (Porites), and other species, primarily *Diploria* sp., *Colpophyllia natans*, *Eusmilia fastigiata*, *Stephaocoenia michelini*, *Madracis* sp. and *Meandrina meandrites* (Other). 1982 data generated from Kobluck and Lysenko (1984). Error bars represent ± 1 SE.

At all sites in 2008 (Fig. 6B) *Agaricia* sp. was dominant at depths greater than about 20 m while *M. annularis* complex and *M. cavernosa* were most dominant at shallower depths. The Karpata site had the greatest coral coverage for nearly all species at all depths, while the lowest coverage was found at Pink Beach. The latter site is a

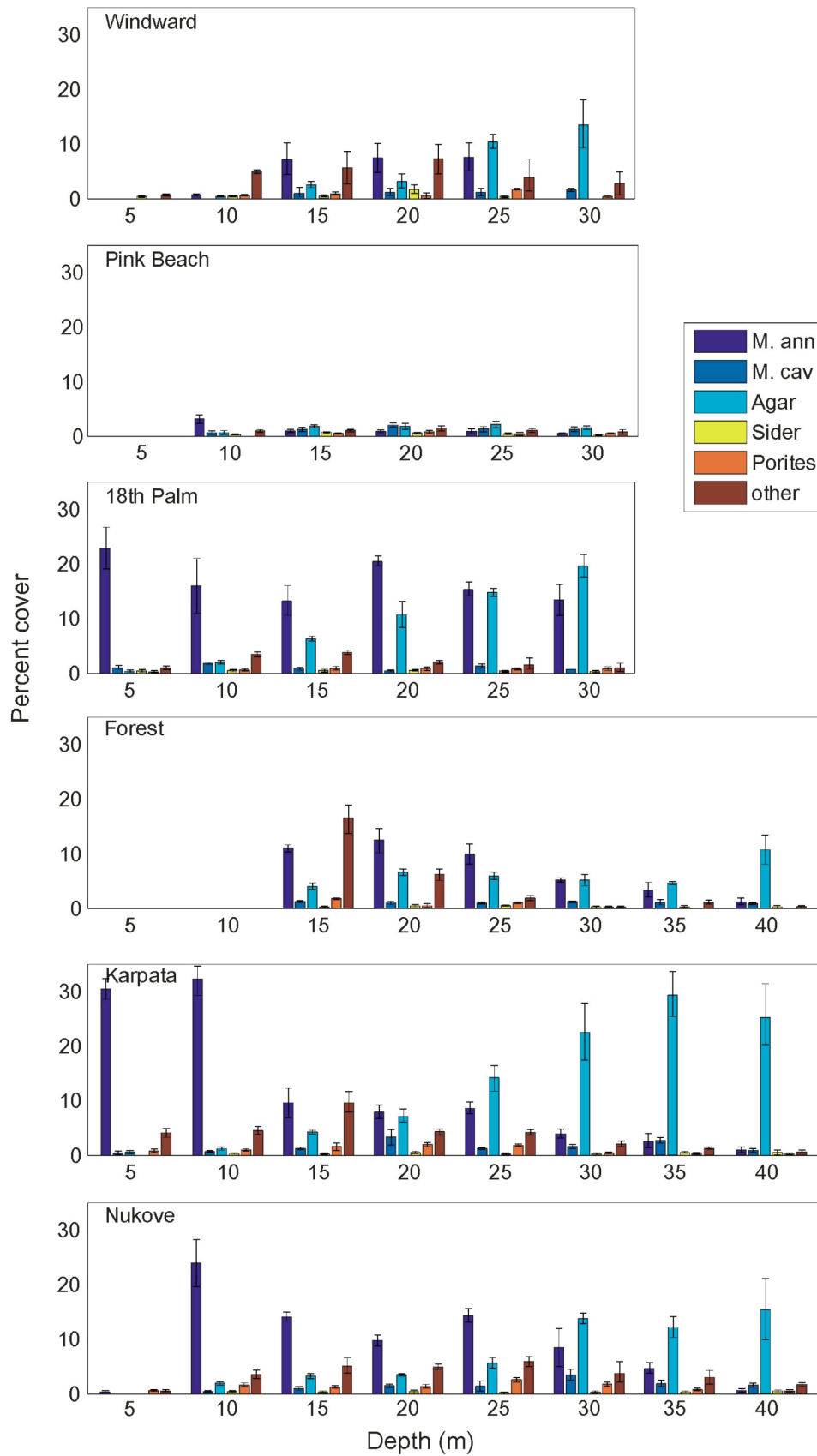


Figure 6B. Mean percent cover of dominant scleractinian species at other Bonaire sites sampled in 2008. Same legend as in 6A.

location with a shifting sand substrate extending off shore and has large numbers of gorgonians and sponges interspersed with isolated hard coral outcroppings.

It is significant to note that at all sites during the 2008 surveys we observed a large number of the massive coral colonies particularly *M. annularis*, *M. cavernosa*, *Colpophyllia natans* and *Diploria sp.* showing clear evidence of disease and partial mortality. In 2008 many formerly large coral colonies were reduced to a patchwork of live tissue and dead areas colonized by turf and macro algae and other fouling organisms. It should be further noted that the *Acropora* and *Eusmilia* zones that dominated the reef at depths shallower than about 10 m in the historical studies (e.g. van Duyl 1985) were almost entirely absent in 2008.

Figure 7 shows the density of individual sponges at the Cliff site in 1982 and 2008. In 1982, there were 3.0 to 10.4 individuals per m², in 2008 this had increased to 6.9 ± 1.2 to 22.9 ± 2.4 (mean ± SE) individuals per m². The overall difference in the number of sponges across all depths is statistically significant ($t_{1,74} = -40.98$, $p \ll 0.001$), and this increase is particularly dramatic at 25 and 30 m depth. The 1982 data only includes sponge density; however, for 2008 mean sponge density at each depth was tightly correlated to mean sponge percent cover ($r^2 = 0.81$, $p = 0.037$, $n = 5$). In 2008, the mean percent sponge cover at the 30 m site was 11.2 ± 2.1 (mean ± SE) suggesting that sponges are now an important spatial occupant whereas it is likely that in 1982 they occupied less than 1 to 2 % of the area.

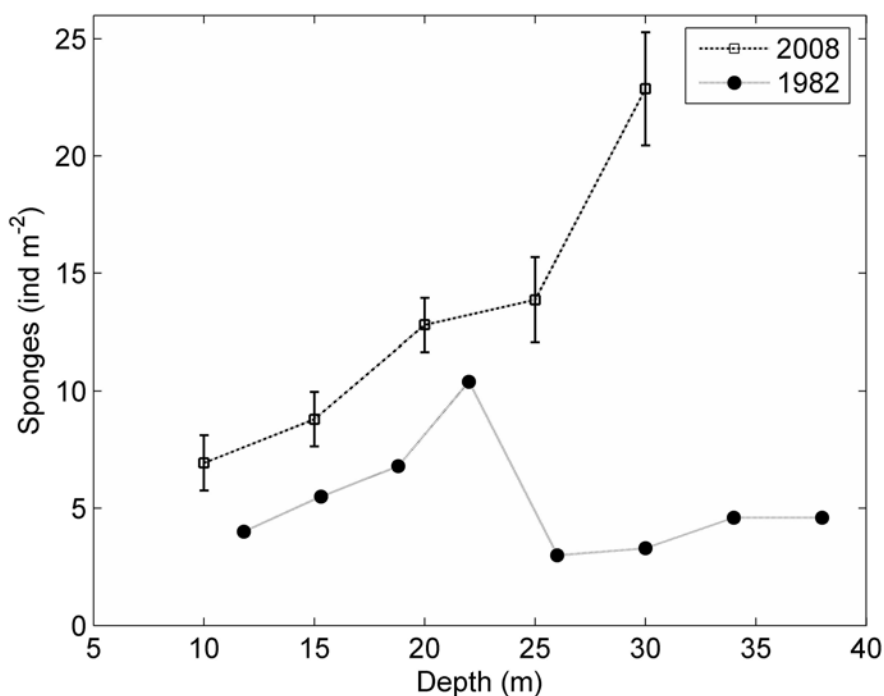


Figure 7. Density of sponges (the number of individuals m²) as a function of depth. Data from 1982 are shown in solid circles and data from 2008 shown in open squares. Sponge species include *Aiolochoxia crassa*, *Aplysina sp.*, *Agelas sp.*, *Callyspongia sp.*, *Xestospongia sp.*, *Neofibularia nolitangere*, *Ectyoplasia sp.*, *Diplastrella sp.*, *Clathria sp.*, *Uloa ruetzleri*, *Cliona sp.*, and *Aka sp.*. Error bars represent ± 1 SE. 1982 data generated from Kobluck and Lysenko (1984).

DISCUSSION

Comparison to Historical Data

As shown in Table 1, there is very limited data available to place the 2008 survey results into a historical context. The coral coverage summary data that is available tends to be of limited spatial scope and at shallow depths (~ 10 m). The shallow shelves along parts of Bonaire's leeward coast have been strongly impacted by recent storm damage (Kobluk, 1992; Bries et al., 2004; Scheffers and Scheffers, 2006) and by the loss of the once dominant Acroporid community (Gladfelter, 1982; Meesters et al., 1997) that existed in very shallow water and was, therefore, difficult to sample adequately. Line point transect data of coral and algae distribution were collected at the Cliff site in 1997 by the non-profit Reef Check organization (data courtesy of K. Handschuh) for a Caribbean wide, rapid coral reef health assessment program. Corals were identified and the presence of algae or sand along 50 m length line point transects surveyed at 7.6, 9.1 and 12.2 m depths and then used to estimate percent coverage. In addition 6 locations on the north end of the island were surveyed in 1999 using rapid coral reef assessment, AGRRA, protocols (10 m modified line point count transects, Ginsburg et al. 1998). Bak and colleagues (Bak and Engle, 1979; Bak and Luckhurst, 1980; Bak et al., 1984; 2005; Nugues and Bak, 2008) have collected a photo time series (1973 - 2002) of reef community structural change from a revisited set of permanent quadrats on Bonaire at Karpata. At this location, single 3 x 3 m quadrats at 10, 20, 30 and 40 m depth were photographed at approximately decadal intervals and the number of species and coral coverage were calculated (Bak et al., 2005). As reported by Bak et al. the percent coverage data was pooled into two depth bins, 10 m + 20 m (their shallow) and 30 m + 40 m (deep) and then combined with 3 similar sites in Curaçao. Hawkins et al. (1999) reported the percentage of live coral coverage in 1994, calculated from photographed quadrats at 10 m depth at 3 'heavily used' dive sites along Klein Bonaire as well as within two reserves, restricted from public access, along the northwest coast (adjacent to and west of the Karpata site).

These limited historical data restrict a robust statistical comparison to only the Cliff, Karpata, and windward sites. At these locations it is clear that the coverage of massive, hermatypic corals at those locations has significantly declined since 1982. The percent coral coverage at all the locations surveyed in 2008 tend to be lower than nearby historical survey sites and show relatively low coverage along much of the leeward coast to about 30 m depth.

The historical and contemporary data compared here used different survey methodologies. For a detailed discussion of transect techniques and comparison with quadrat sampling see Chiappone and Sullivan, (1991), Nadon and Stirling, (2006), and Leujak and Ormond, (2007). The absolute accuracy of the different methods for providing estimates of benthic coverage varies with the technique used and either length of transect or number of quadrats sampled (Nadon and Stirling, 2006; Lam et al., 2006; Leujak and Ormond, 2007). The power to detect change between the data sets then depends on the sample number and the abundance/size of the substrates surveyed. The

Table 1. Percent coral coverage in Bonaire from 2008 and available historical data. Sampling depth, site location and sampling protocol are indicated. All coverage data shown as mean % \pm SE, except Green et al (2008) and Kramer and Bischof (2003) which show mean % \pm SD.

Date	Location	Sampling Protocol	% Coral Coverage (mean % \pm se)							Reference	
			5 m	10 m	15 m	20 m	25 m	30 m	35 m		40 m
2008	Nukove Kampata Forest Cliff	Photoquadrat transect (50 m)	0.5 \pm 0.2 36.2 \pm 2.6	33.8 \pm 3.4 42.1 \pm 4.5	24.7 \pm 2.5 31.4 \pm 3.8	21.6 \pm 1.8 29.5 \pm 0.9	30.5 \pm 3.6 32.8 \pm 2.1	32.8 \pm 2.7 31.1 \pm 6.6	23.0 \pm 2.4 36.8 \pm 2.2	20.0 \pm 6.2 29.6 \pm 5.3	present study
1988	18th Palm Pink Beach Windward		5.86 \pm 3.0 25.7 \pm 4.4	26.6 \pm 3.9 27.9 \pm 3.1	30.1 \pm 3.1 31.3 \pm 3.4	35.6 \pm 3.4 37.5 \pm 2.8	38.5 \pm 4.4 39.8 \pm 1.6	31.6 \pm 3.1 36.5 \pm 3.9	7.6 \pm 1.7		
	Windward		1.6 \pm 0.4 14.7 \pm 1.6	6.7 \pm 0.7 28.5 \pm 8.0	5.8 \pm 1.3 19.4 \pm 4.4	8.6 \pm 1.4 20.2 \pm 4.5	7.4 \pm 1.3 19.7 \pm 5.6	4.2 \pm 0.7 17.4 \pm 5.6			
2004	Kampata	Photoquadrat transect (40m)	5 m 8 \pm 4 (mean % \pm sd)					27.1 \pm 3.7	21.4 \pm 6.4		Green et al. (2008) & Carpenter & Edmunds (2006)
2003	Kampata	single 3x3 m photoquadrat			10+20 m ~19 \pm 5					30+40 m ~22 \pm 4	Bak et al. (2005) figure 2
1996		at 10, 20, 30, 40 m depths,			~23 \pm 3					~25 \pm 4	
1993		10 and 20, 30 and 40 m			~24 \pm 3					~29 \pm 4	
1983		depths pooled with 3 Curacao			~36 \pm 4					~30 \pm 5	
1973		Curacao photoquadrats			~44 \pm 5					~38 \pm 4	
1999	Barcadera Carl's Jam Habitat	AGRAA protocol, line point transect (10 m)		~10 m 42.5 \pm 11.0 52.0 \pm 14.0							Kramer & Bischof (2003)
	Kampata			56.0 \pm 47.5							
	Twin Peaks W. Klein			44.0 \pm 8.5 47.0 \pm 12.5 41.5 \pm 9.5							
1997	Cliff Forest 18th Palm	Reef Check point transect (50 m)	7.6 m 32.0 \pm 10.8 49.0 \pm 7.0 26.0 \pm 17.0	9.1 m 30.3 \pm 2.2	12 m 29.3 \pm 3.5 60.0 \pm 6.0 48.5 \pm 6.5						K. Handschuch pers. com.
1994	Jerry's Jam Siagbaai Carl's hill Boca Canon Forest Kampata	Photoquadrat transect (110 m)	10 m ~40 \pm 4 ~61 \pm 5 ~38 \pm 5 ~53 \pm 5 ~40 \pm 5 ~52 \pm 5								Hawkins et al. (1999) figure 2
1982	Cliff	Photomosaic	11.8 m 32.4		15 m 31.0			25 m 48.7	30 m 67.0	35 m 49.7	38 m 25.0 Kobluck & Lysenko (1984)

contemporary photo quadrats used in the 2008 surveys (45 per depth, with 200 point counts per frame) provide high statistical power for comparison, but the comparative power of the historical data sets (with smaller sample sizes) is much less. In general line transects methods tend to overestimate some substrates while photoquadrats slightly underestimate them, while mapping methods like that used by Kobluck and Lysenko at the Cliff site, are the most accurate (Leujak and Ormond, 2007). Despite the potential bias introduced by the different sampling methods used in the historical surveys, reasonable comparisons can be made between the data sets if the analysis is restricted to the more abundant substrate types (in this case the primary frame-building corals and groups like macrophytes, sponges etc. rather than rarer classes). Considered in this way, even comparisons with the Reef Check data in Table 1, with limited line point transect sampling, can provide an estimate for the large changes in percent coverage seen here (requiring at least about an absolute 12% change in coral coverage to be minimally detectable Lam et al. 2006; Luejak and Ormond, 2007).

Bonaire Reef Degradation

The deterioration of coastal environmental conditions due to natural and anthropogenic stresses has led to a decline in coral reef health worldwide. In the heavily populated Caribbean the combined effects of coastal development, agricultural land use, climate change, artisanal and industrial over-fishing have led to massive changes in adjacent coral reef communities (Gardener et al., 2003; Mora, 2008). Marked declines in coral cover have also been reported on islands with limited human population suggesting the importance of climate change and non-point source stresses on reefs with limited direct anthropogenic stress (Coelho and Manfrino, 2007). The fringing reefs surrounding the entire island of Bonaire and Klein Bonaire, despite their being a protected marine reserve since ca 1975, appear to be rapidly transitioning to a degraded state similar to that found at other Caribbean islands. The island's long history of marine park protection has probably helped slow the deterioration. However, characterizing current state of Bonaire's fringing reefs as 'pristine' is perhaps only tenable when comparing their current state to that on other, severely impacted Caribbean islands, rather than to the state of Bonaire's reefs as recently as two decades ago.

Coral coverage on the windward, Cliff, and Karpata locations has decreased by as much as 50% depending on the depth and location. The mean percent coral coverage across the Caribbean is thought to be about 10% (Gardner et al., 2003), and while the coral coverage on Bonaire in 2008 averaged approximately 30% at the leeward site, and is still much higher than the Caribbean average, this is less than half of what it was in the 1980's when some leeward sites had > 80% coral coverage. The approximately 50% or more reduction in coral coverage is comparable to the drastic reduction in coverage recognized earlier on unprotected reefs worldwide (Gardner et al., 2003; Bellwood et al., 2004). The decrease is most evident at depths < 25 m on the windward site. The deeper sampling locations on the windward site, at the base of the fore reef, had similar percent coral coverage to that measured in 1988.

A shift in the dominant, shallow water scleractinian species to *Porities asteroides* has been reported for the Caribbean (Green et al., 2008), however, in that study, historical data for Bonaire were not available for comparison to their measured 1.3 % coverage in 2004. As noted in this study, at both the Cliff and windward sites, the percent coverage of *Porities sp.* has decreased from 10 to 30 m depth along with all other scleractinian species. The Green et al. (2008) data are based on a single 40 m transect at 5 to 6 m depth, shallower than in this or Bak et al. studies along the fore reef. Thus, it is difficult to extend their conclusions beyond the shallowest waters once dominated by Acroporids and *M. annularis* complex (Scatterday, 1974, Kobluk and Lysenko, 1984).

Across all depths, at both Cliff and the windward site, there has been a dramatic increase (2 to 20 fold) in the coverage of macroalgae, where it now dominates the substrate. A similar dramatic increase in the macrophyte, *Lobophora variegata*, has been observed in Curaçao (Nugues and Bak, 2008). The most likely cause of this increase in algal abundance is the marked and lasting reduction in abundance of *D. antillarum* since 1982-84 coupled with the loss in live coral cover. Although some small patches of *D. antillarum* are now present in shallow water (Carpenter and Edmunds, 2006; authors' pers. obs.) there are presently few urchins below approximately 10 m depth. Before the die off, most sites around Bonaire and Curaçao had high densities of *D. antillarum*, often exceeding 50 individuals m⁻² (Bak et al., 1984; Greenstein, 1989). Grazing conchs, which primarily consume algae and seagrasses in shallow sandy areas have also been largely extirpated from Bonaire, but were once abundant as evidence by large shell mounds at several locations around the island. Grazing fishes, notably parrotfish (Scaridae) and surgeonfish (Acanthuridae) still appear to be relatively abundant around Bonaire (Auster et al., 2005; and authors' pers. obs.) and this abundance is probably enhanced by the relatively limited (although certainly not absent) fishing pressure around the island. It is difficult to know what fish abundances were in the past, but in the absence of urchins the present fish densities in Bonaire do not appear to be sufficient to keep macroalgae abundance low at depths deeper than 10 m. An additional important consideration for Bonaire is that the entire area of reef development occupies a steep and narrow shelf, typically no more than a few hundred meters wide from the shoreline. This narrow shelf is likely to offer relatively few natural refuges from which adult fish populations could support high recruitment of herbivorous species. The paucity of natural mangrove habitat around much of Bonaire is similarly likely to contribute to a lack of natural refuges and habitats for juvenile herbivorous fish.

On Curaçao, the aggressively spreading, colonial tunicate *Trididemnum solidum*, has shown a 900% increase in hard bottom coverage, overgrowing scleractinian corals (Bak et al., 1996). In our 2008 surveys *T. solidum* was present in low densities at the Cliff site (< 1%), however, farther along the coast to the north and west at Karpata and Nukove, it is a dominant and spreading component of the benthos with densities rivaling the increase in coverage reported in Curaçao, and smothering many massive coral colonies (Fig. 8). The apparent success of *T. solidum* as well as the significant increase in the density of sponges at the Cliff site, lends support to speculation that filter feeding organisms capable of exploiting bacteria and other small particulates may be out-competing scleractinian corals in environments impacted by coastal development.

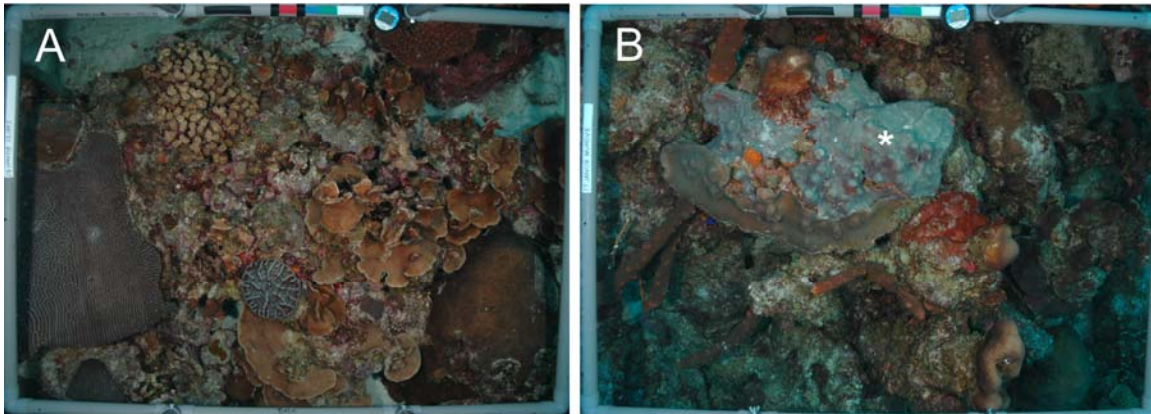


Figure 8. Photo quadrat images from 20 m depth showing a mixed hard coral assemblage at the Cliff site (A) and Nukove site (B). A large colony of the invasive tunicate, *Trididemnum solidum*, is indicated by the white star. Diseased coral polyps, and overgrowths by algae and filamentous cyanobacteria are also evident.

For the shallow portions of the reef (depth < 20 m) at the Cliff and Karpata site the changes from 1982 are largely in agreement with Bak et al. (2005) who described data from 1973 to 2003 on coral abundance across depths from permanent photo quadrats at 3 sites in Curacao and the single site in Bonaire. Bak et al. showed decreases in coral density and cover at 10 and 20 m, however they also showed smaller rates of change at deeper sites at 30 and 40 m. They concluded that the under-studied deep reefs might, to some extent, be protected from shallow water anthropogenic stresses. At both sites, coral and algal cover at depths > 20 m now appear to also have decreased significantly. Across all depths at the 7 sites sampled in this contemporary survey, including Karpata, the percentage of coral coverage is much less than reported in historical surveys. Thus, it appears that the decline in coral and increase in algae is now extending into deeper waters, suggesting that the proximate causes and impacts of these changes are not limited to shallow depths.

The reefs of Bonaire appear to be following a trajectory of degradation similar to other Caribbean reefs (Gardner et al., 2004). Despite its long-term status as a protected marine park, and even on the undeveloped windward coast, major changes in reef species assemblages are evident. Because the developed area of the island has been relatively small until recently, the timing of degradation relative to other Caribbean islands may have been delayed. The capacity for coral recovery is unknown. However the presence of 20 - 40% live coral coverage in a few locations suggests that coral populations might recover if the proximate causes of the present decline are identified and mitigated.

ACKNOWLEDGEMENTS

We thank our colleagues Dr M. Patterson and Dr A. Trembanis for their assistance during the 2008 fieldwork as part of the NOAA Ocean Exploration Program. We also thank researcher divers O. Rutten, D. Lüsse, as well as S. Patterson for their field assistance in Bonaire. Z. Boudreau assisted with analysis of benthic photos. Additional support was provided by B. Bowker, W. Stark, the Toucan Dive Resort and the Bonaire National Marine Park manager, R. de Leon. This project was funded via NOAA Office of Ocean Exploration grant, OE 2007-086

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