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CORAL COMMUNITY DECLINE AT BONAIRE, SOUTHERN CARIBBEAN

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ABSTRACT

We assessed the status of coral reef benthic communities at Bonaire, Netherlands Antilles, in December 2008 and January 2009 through ~5 km of photo transects taken at depths of 5, 10, and 20 m at 14 locations around the island. Univariate and multivariate analyses detected significant variation in benthic communities among depths and locations, as well as between leeward and windward sides of the island. Mean percentage cover of scleractinian corals ranged between 0.2% and 43.6% at the study sites and tended to be lowest at 5-m depth. The survey recorded 40 scleractinian coral species from 19 genera, within 10 families. Faviidae were by far the most abundant scleractinian family at all depths (predominantly *Montastraea* spp.), followed by Agariciidae at 20 and 10 m, and by Astrocoeniidae at 5-m depth. Macroalgal cover exceeded scleractinian coral cover at nearly all sites, averaging 34.9% (all samples pooled), compared with a pooled mean coral cover of 15.4%. Windward reefs were characterized by prolific growth of the brown algae *Sargassum* spp., and leeward reefs by growth of turf algae, *Dictyota* spp., *Trichogloeopsis pedicellata* (Howe) I. A. Abbott & Doty, and *Lobophora variegata* (Lamouroux) Womersley ex Oliveira. Damage from recent hurricanes was evident from the presence of toppled and fragmented corals, the movement of sand, and exposure of cemented *Acropora cervicornis* (Lamarck, 1816) rubble on the shallow reef platform. The combination of algal dominance and low to moderate coral cover are symptomatic of partly degraded reef systems, particularly as they coincide with elevated nutrients and reduced herbivory.

Massive region-wide loss of corals has been reported in the Caribbean, with declines of mean hard coral cover from ~50% to 10% since the 1970s (Gardner et al. 2003). In the late 1990s, the Atlantic and Gulf Rapid Reef Assessment (AGRRA) program reported Bonaire's coral reefs to be "healthy" relative to many other Caribbean reefs, characterized by higher than average coral cover, low mortality, low prevalence of diseases, low macroalgal abundance, and relatively high fish densities (Kramer 2003). Furthermore, in February 2008, Bonaire's coral reefs were designated as being the most pristine in the Caribbean by the National Oceanic and Atmospheric Administration (NOAA 2008). The present study demonstrates the first comprehensive, quantitative ecological study of leeward and windward coral reef benthic communities of Bonaire since the mass-mortality of the sea urchin *Diadema antillarum* (Philippi, 1845) in the 1980s (Lessios et al. 1984), the loss of acroporid reef corals from white band disease (Aronson and Precht 2001), and the hurricanes, Lenny (1999), Ivan (2004), and Omar (2008; Bries et al. 2004, Scheffers and Scheffers 2006, MDNAA 2008). The leeward fringing coral reefs of Bonaire have been described by several authors, including Scatterday (1974), Bak (1975, 1977), van Duyl (1985), Bak and Nieuwland (1995), and Bak et al. (2005). The aim of the present study is to provide quantitative data on the coral reef benthic communities of 14

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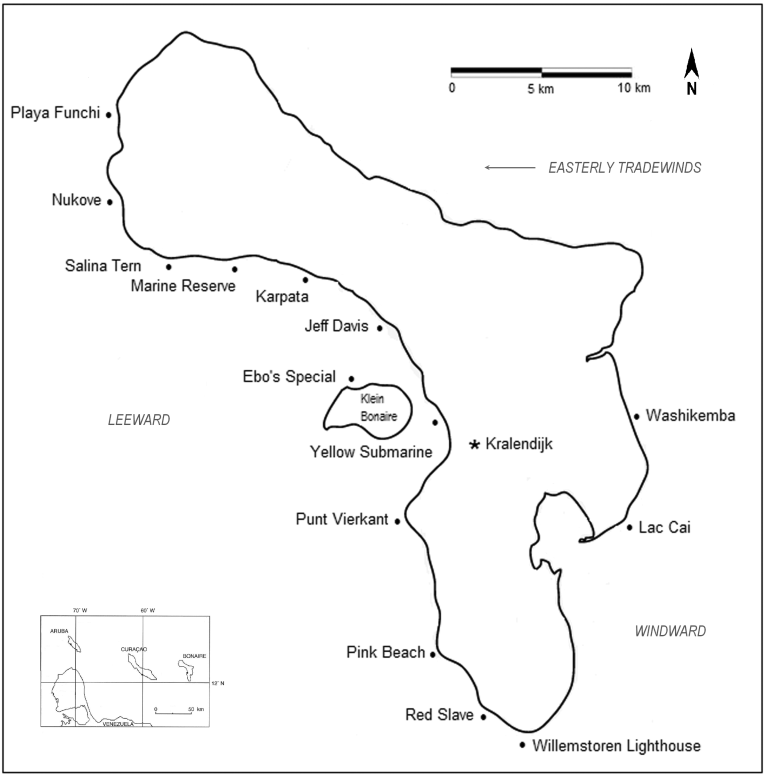

Figure 1. Map of the 14 study locations around the island of Bonaire, Netherlands Antilles, southern Caribbean. Locations Lac Cai and Washikemba are windward, all other locations are referred to as leeward.

study locations on leeward and windward fringing reefs of Bonaire, to determine their status in comparison with findings from previous studies, and to place the results in context with research conducted in the wider Caribbean region.

The Study Area.—The island of Bonaire is situated at 12°N and 68°W, 60 km off the coast of Venezuela in the Caribbean Sea (Fig. 1) and has been in existence since the Cretaceous, ~120 million ybp (Scheffers 2005). The climate in Bonaire is semi-arid, with annual precipitation of ~550 mm, and differs considerably from the typical Caribbean climate (Martis et al. 2001). Bonaire is situated in an area that experiences the lowest hurricane frequency in the tropical western Atlantic (Lugo et al. 2000). The Saffir-Simpson category four Hurricane Lenny in November 1999 was the first hurricane on record to pass the islands on a west to east track (Guiney 2000), followed by the category three Hurricane Omar in October 2008 (MDNAA 2008). Both hurricanes inflicted considerable damage to the leeward fringing reefs (Bries et al. 2004, MDNAA 2008).

The east and northeast coasts of the island are in the path of easterly trade winds (Bak 1975) and are exposed to consistent wave heights of 2–3.5 m above mean sea level (AMSL; van Duyl 1985). In contrast to the fringing reefs of other Caribbean islands, the reefs of Bonaire flourish mainly along the sheltered leeward coast, and show limited and patchy growth along the east coast (Scatterday 1974, van Duyl

1985). Most of the coastline along the leeward coast of Bonaire is exposed to waves < 1 m AMSL, with the most sheltered conditions in the Kralendijk area (van Duyl 1985).

Leeward fringing reefs are characterized by a submarine terrace with a width of between 20 and 250 m that gently slopes to a drop-off at ~5–15-m depth (van Duyl 1985). From there, a steeper slope (20°–50°) extends to depths of ~25–55 m, where the slope flattens and culminates in another drop-off at depths of 50–80 m (van Duyl 1985 and references therein). Over large areas, reefs are characterized by buttresses and spurs protruding from the drop-off and separated by sediment transport grooves (van Duyl 1985).

On the windward east coast of Bonaire, a gently sloping (10°–12°) platform extends to 30-m depth, ~250 m offshore (Scheffers et al. 2006). Coral reefs are restricted to the southeast of the island, extending as far north as Lac Cai (Fig. 1). Onshore deposits of coral reef fragments indicate that coral reefs used to flourish along the northeast coast of Bonaire. It has been suggested that reefs north of Lac Cai were extirpated by a series of strong wave events ending 4200 yrs ago that deposited reefs onshore and resulted in a phase shift to macroalgae dominated communities (Scheffers et al. 2006).

Materials and Methods

Sampling Design and Methods.—In December 2008 and January 2009, 2–3 mo after the reefs were exposed to waves from the category three Hurricane Omar, the coral reef benthic communities of 14 study locations (Fig. 1) were examined to provide detailed quantitative data on the status of benthic communities around the island of Bonaire. Study locations separated from one another were selected to minimize the potential effects of spatial autocorrelation. Due to adverse weather and access restrictions, only two locations could be surveyed on the trade wind exposed east coast of Bonaire. The remaining 12 locations were situated on the leeward west coast of Bonaire. Surveys were undertaken at depths of 5, 10, and 20 m at the locations to encompass communities on the shallow reef terrace and along the shallow and deep reef slope, respectively. Four randomly placed 30-m long replicate belt transects were photographed at each depth, totalling 12 transects across three depths at each location. At Washikemba, adverse weather and sea state conditions precluded diving at the 5-m depth. A total of 164 transects were surveyed using SCUBA. Photographs were taken using a Fuji Finepix F50fd digital camera in a Fuji WPFXF50 underwater housing, equipped with an Inon UWL105AD wide-angle lens, and one or two Inon D2000 S-TTL strobes. A 1-m long graduated stick was placed on the substratum along the transect line and a photograph was taken from above when the stick was completely visible in the LCD screen of the camera. Photographs were taken parallel to the substratum to avoid image distortion. The graduated stick was successively moved along the line and 30 sequential photographs were taken for each transect. A total of 4920 photographs resulted from these surveys.

Data Analysis.—Photographs were analysed using the image analysis software Coral Point Count with Excel® extensions (CPCe, Kohler and Gill 2006). Twenty random data points were overlaid onto each photograph and the category underlying each point was identified and recorded as biotic, encompassing scleractinian corals (see Harrison and Booth 2007 for definition), hydrocorals, gorgonians, sponges, macroalgae, coralline algae, and other benthos; or as abiotic, including dead coral and other substrata (cemented coral rubble, coral rubble, pavement, sand). All scleractinian corals were identified to species level. The transect data derived from the CPCe analysis were entered into a taxon abundance data matrix in Excel, tabulating species as rows and samples as columns. Mean percentage cover and standard errors of benthic categories were calculated for each depth at each location. Summary variables, mean species richness, and mean Shannon-Weaver diversity were calculated for each depth by location. Mean percentage cover of benthic categories, species richness, and Shannon-Weaver diversity were summarized for windward, leeward, and all sites at depths of 5, 10, and 20 m, and for all depths pooled.

Linear mixed effects models (Pinheiro and Bates 2000) were fitted to the percentage cover, species richness, and Shannon-Weaver diversity index variables for scleractinian corals, and to macroalgae, sponge, and gorgonian cover. The 12 transects at each location were nested in their locations in a hierarchical random effects structure. The depth (5, 10, and 20 m) and aspect (leeward, windward) factors and their interaction were fitted as fixed effects. Non-significant effects ($P > 0.05$) were sequentially removed (interaction, largest P-value main effect, remaining main effect) and the model re-fitted at each step to obtain a reduced model for interpretation (the chosen fixed effects model). For the chosen fixed effects model for each variable, five model structures were compared for location level random effects: location varying in overall level only (intercept only for locations—one variance); in level over depths (location × depth with one common variance); in level at each depth (location × depth with three separate variances, one at each depth); in level over depths + aspect (location × depth with a common variance + in level over aspect with a common variance); in level over each depth + aspect (location × depth with three separate variances + in level over aspect with a common variance). For each variable, models with the chosen fixed effects structure and these random effects structures were fitted by restricted maximum likelihood (REML) and compared in terms of their Akaike Information Criteria (AIC) values (see Burnham and Anderson 1998). The random effects structure with the lowest AIC in each case was fitted together with the chosen fixed effect structure by maximum likelihood (ML) to obtain the final model estimates for each variable. The models were fitted using the Linear Mixed Models procedure in PASW Statistics v18.0.

Multivariate analyses were performed using PRIMER v6 (Clarke and Gorley 2006) to examine trends in the biotic (scleractinian corals, hydrocorals, gorgonians, sponges, macroalgae, coralline algae, other benthos) and abiotic (dead coral, cemented coral rubble, coral rubble, pavement, sand) data. Replicate transect data were used for all multivariate analyses except non-metric multidimensional scaling (nMDS) ordination for which mean biotic data (means across four replicate transects for each depth by location) were used to better visualize patterns in two dimensions. Separate Bray-Curtis similarity matrices were created from square root transformed transect data for biotic, coral, and abiotic categories. Means of replicate transect biotic data for each depth were subjected to cluster analysis and nMDS ordination. The taxa contributing to the dissimilarities of biotic communities among depths, between leeward and windward, and among nMDS groups of 60% similarity were identified using similarity percentage (SIMPER) breakdowns. Two-way nested analysis of similarity (ANOSIM) of depths nested within locations was performed for replicate biotic data to test for differences among depths nested in locations. Pairwise tests were conducted and global R values calculated using biotic replicate data (depths nested in locations). The BIOENV procedure was used to examine which environmental (depth, aspect) and abiotic variables best described the observed patterns in biotic communities. Correlation coefficients (Spearman) were calculated based on the similarity matrices of the biotic and environmental and abiotic data.

Results

Benthic Categories.—Macroalgae were the dominant (most abundant) category at 29 of the 41 study sites, and covered 34.9% ± 3.02 of the total area surveyed when all samples were pooled, followed by scleractinian corals (15.4% ± 1.60), gorgonians (7.7% ± 1.49), and sponges (7.5% ± 1.45; Table 1, Fig. 2). Only four of the 41 study sites were dominated by scleractinian corals; the 10-m depths at Saliña Tern and Willemstoren,

Table 1. Mean percentage cover of benthic categories, species richness, and Shannon-Weaver diversity of scleractinian corals at Bonaire summarized for leeward, windward, and all sites at depths of 5, 10, and 20 m, and for all depth samples pooled.

	5-m depth						10-m depth						20-m depth						All depth samples pooled					
	Leeward	SE	Windward	SE	Total	SE	Leeward	SE	Windward	SE	Total	SE	Leeward	SE	Windward	SE	Total	SE	Leeward	SE	Windward	SE	Total	SE
Mean cover																								
Scleractinian corals	9.47	1.70	1.75	0.16	8.24	1.47	19.70	1.90	8.87	0.99	18.15	1.77	21.04	1.57	4.17	0.65	18.63	1.44	16.73	1.72	5.56	0.69	15.37	1.60
Hydrocorals	1.08	0.33	0.13	0.08	0.94	0.28	0.87	0.20	0.96	0.28	0.88	0.21	0.48	0.18	0.04	0.04	0.42	0.16	0.81	0.23	0.43	0.15	0.76	0.22
Gorgonians	8.04	2.19	7.42	1.47	7.42	1.98	8.68	1.54	2.22	1.02	7.76	1.47	7.80	0.87	3.85	1.29	7.24	0.93	8.17	1.53	3.91	1.22	7.65	1.49
Sponges	1.54	0.56	0.04	0.04	1.32	0.48	6.93	1.24	0.88	0.52	6.06	1.13	16.84	3.00	1.31	0.46	14.62	2.64	8.43	1.60	0.88	0.40	7.51	1.45
Macroalgae	25.34	4.16	69.75	6.43	26.70	4.03	31.99	2.52	67.20	3.54	37.02	2.66	34.74	2.16	60.23	2.03	38.38	2.14	30.69	2.95	64.92	3.51	34.86	3.02
Coralline algae	1.05	0.45	0.00	0.00	0.90	0.39	0.61	0.27	0.69	0.20	0.62	0.26	0.93	0.70	0.00	0.00	0.79	0.60	0.86	0.47	0.28	0.08	0.79	0.43
Other benthos	0.93	0.24	4.58	0.84	1.13	0.26	2.73	0.74	7.67	1.35	3.43	0.83	4.23	0.86	2.38	0.48	3.96	0.81	2.63	0.61	4.94	0.90	2.91	0.65
Dead coral	3.64	2.31	0.00	0.00	3.12	1.98	2.90	1.03	1.37	0.42	2.68	0.94	1.44	0.33	0.06	0.02	1.24	0.29	2.66	1.22	0.57	0.18	2.41	1.10
Other substrata	48.91	5.02	16.33	4.54	43.09	4.63	25.60	3.55	10.15	1.51	23.39	3.26	12.51	2.20	27.96	1.07	14.72	2.04	29.01	3.59	18.51	1.94	27.73	3.39
Species richness																								
Scleractinian corals	4.96	0.69	3.25	0.25	4.83	0.66	9.98	1.01	9.00	0.56	9.84	0.95	13.19	0.77	6.50	0.87	12.23	0.79	9.38	0.83	6.85	0.62	9.07	0.80
Shannon-Weaver diversity																								
Scleractinian corals	2.11		1.30		2.13		2.16		2.21		2.23		2.48		2.48		2.50		2.52		2.45		2.55	

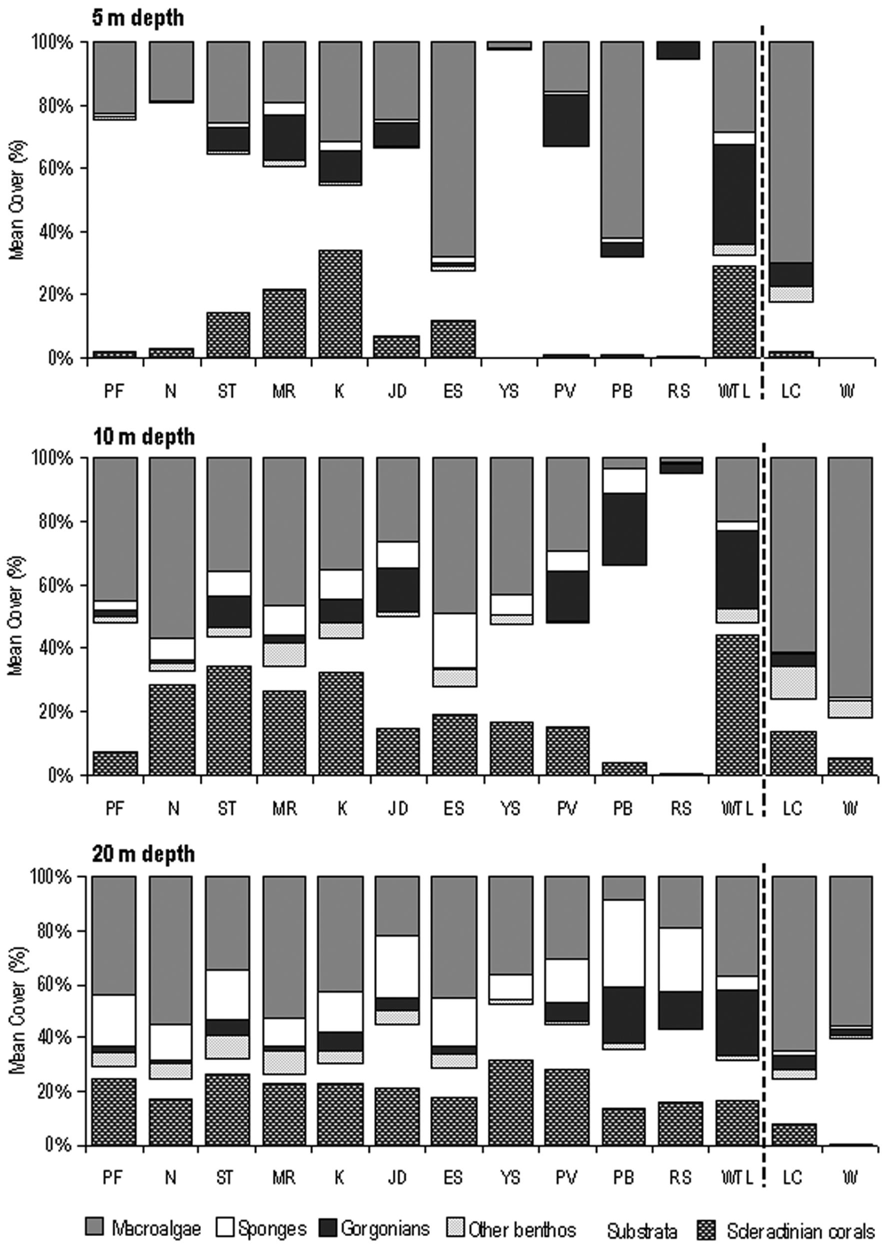

Figure 2. Stacked histograms of mean percentage cover of benthic categories scleractinian corals, macroalgae, sponges, gorgonians and other benthos at depths of 5, 10, and 20 m at 14 study locations around Bonaire, commencing with Playa Funchi in the northwest of the island and moving counterclockwise from leeward to windward. Scleractinian corals are plotted from the bottom, all other categories from the top. White space between bars indicates mean percentage cover of substrata. Locations to the right of the dotted line are windward. Codes for study locations: PF = Playa Funchi; N = Nukove; ST = Saliña Tern; MR = Marine Reserve; K = Karpata; JD = Jeff Davis; ES = Ebo's Special; YS = Yellow Submarine; PF = Punt Vierkant; PB = Pink Beach; RS = Red Slave; WTL = Willemstoren Lighthouse; LC = Lac Cai; and W = Washikemba.

and the 5-m depths at Marine Reserve and Karpata (Fig. 2). Mean coral cover ranged from a minimum of 0.2% ± 0.00 at the 5-m depth at Yellow Submarine up to 43.5% ± 1.59 at the 10-m depth at Willemstoren. While coral cover did not clearly correspond to a depth gradient across all locations, cover tended to be lowest at the 5-m depth (except Karpata and Willemstoren; Figs. 2, 3). Karpata was the only location where coral cover (33.4% ± 4.71 mean cover) reached its maximum at 5-m depth. Coral cover was generally highest in the south (Willemstoren) and along the northwest of Bonaire (between Saliña Tern and Karpata; Figs. 2, 3). At windward locations, mean coral cover ranged between 0.4% ± 0.08 and 13.5% ± 1.24, and was highest at 10-m depth. Mean coral cover across all windward samples pooled was only 5.6% ± 0.69, compared with 16.7% ± 1.72 mean cover at leeward locations (Table 1).

We recorded a total of 39 scleractinan coral species from 19 coral genera, within 10 coral families. The number of coral genera and families varied considerably between depths and between locations, with greatest variability of both variables occurring at the 5-m depth. The mean number of scleractinian coral species (species richness) per site (mean of four transects for each depth) ranged from 0.8 species (5- and 10-m depths at Red Slave) to 15.5 species (10-m depth at Willemstoren and 20-m depth at Karpata, Fig. 3). Mean species richness was consistently lowest at 5-m depth and followed a depth gradient at the 11 leeward locations between Playa Funchi and Red Slave, where it was highest at 20 m. At windward locations and Willemstoren Lighthouse, mean scleractinian species richness was highest at 10 m and lowest at 5-m depth (Fig. 3).

Faviidae were by far the most abundant scleractinian family at all depths, followed by Agariciidae at 20- and 10-m depths, and by Astrocoeniidae at 5-m depth. Highest mean cover of faviid species was recorded at the 10-m depth at Saliña Tern (29.1%), followed by the 10- (26.2%) and 5-m depths (25.4%) at Karpata. *Montastraea faveolata* (Ellis and Solander, 1786), *Montastraea annularis* (Ellis and Solander, 1786), *Agaricia agaricites* (Linnaeus, 1758), *Porites astreoides* Lamarck, 1816, and *Madracis mirabilis* Duchassaing and Michelotti, 1860 were the five most abundant scleractinian coral species. Rank order of abundance of species was highly variable (Fig. 3). While corals of massive and columnar growth forms tended to dominate, the branching coral *M. mirabilis* was common at depths to 10 m, and the encrusting *A. agaricites* was common at 20 and 10 m. With 13.3% ± 1.73 mean cover, *Agaricia tenuifolia* Dana, 1848 was a dominant species at the 10-m depth at Willemstoren and was only recorded at one other location, Lac Cai, on the windward side of Bonaire. Coral communities at Willemstoren differed from those of other locations in terms of species composition and abundance and were characterized by the occurrence of *Acropora palmata* (Lamarck, 1816), *A. tenuifolia*, *Siderastrea siderea* (Ellis and Solander, 1786), *Porites* spp., *M. faveolata*, *M. annularis*, and *Montastraea cavernosa* Linnaeus, 1767. Acroporidae were only rarely encountered during this study. *Acropora palmata* colonies were recorded at 5-m depth at Willemstoren (1.2% ± 0.82 mean cover), and at 10-m depth at Washikemba (0.8% ± 0.42 mean cover) and Lac Cai (0.3% ± 0.02 mean cover). *Acropora cervicornis* (Lamarck, 1816) was only recorded at 5-m depth at Saliña Tern and Ebo's Special, both registering a mean cover of 0.04% ± 0.04. Windward coral communities were characterized by massive and boulder growth forms, including *S. siderea*, *Diploria strigosa* (Dana, 1846), *P. astreoides*, *Diploria clivosa* (Ellis and Solander, 1786), *M. faveolata*, *M. cavernosa*, and *Meandrina meandrites* (Linnaeus, 1758).

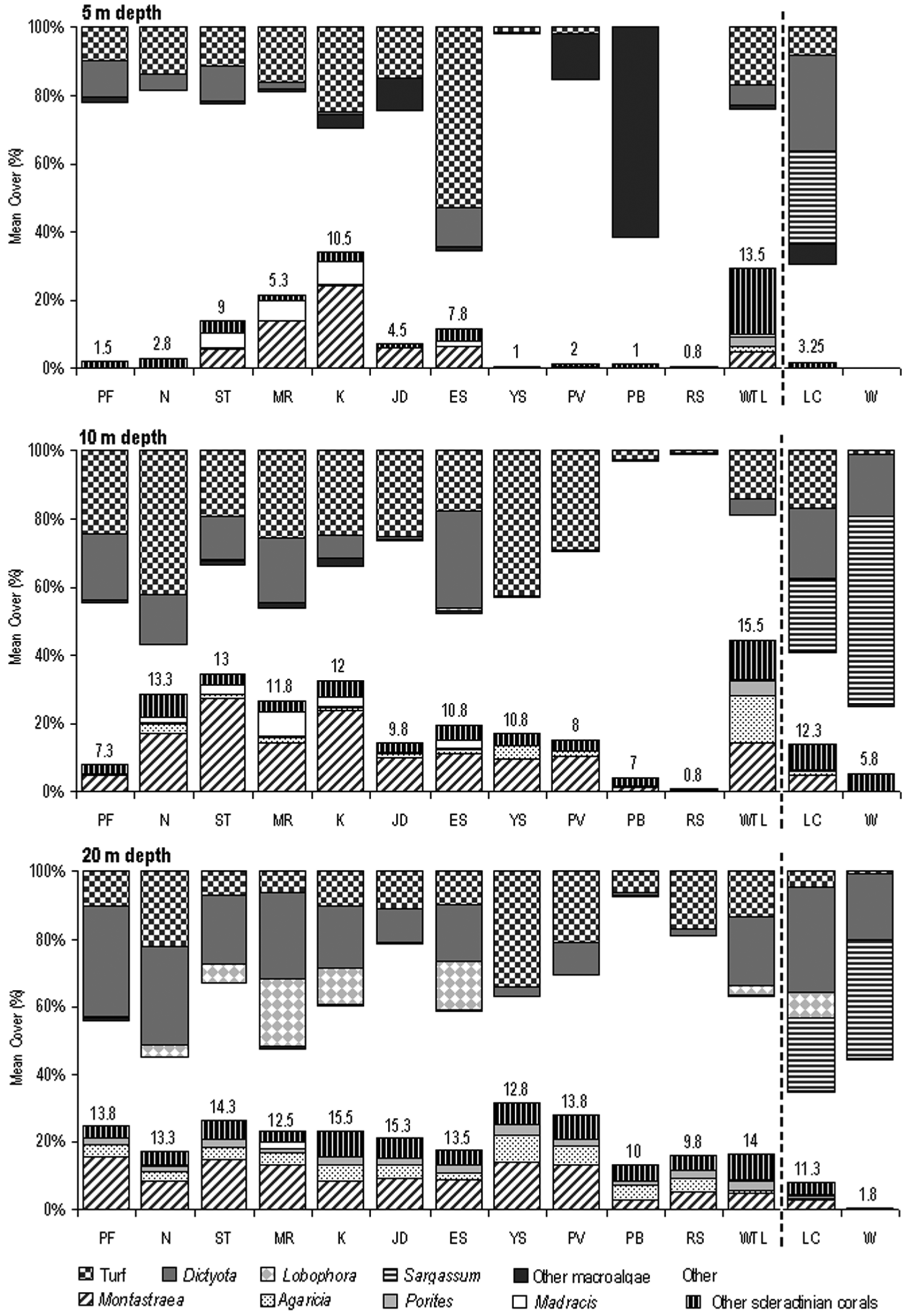

Figure 3. Stacked histograms of the four most abundant scleractinian coral and macroalgae genera at depths of 5, 10, and 20 m at the study locations around Bonaire. Scleractinian corals are plotted from bottom up, macroalgae from the top down. White space between bars indicates other benthic categories and substrata. Numbers above the coral bars indicate mean coral species richness for each site. Locations to the right of the dotted line are windward. Codes for study locations: PF = Playa Funchi; N = Nukove; ST = Saliña Tern; MR = Marine Reserve; K = Karpata; JD = Jeff Davis; ES = Ebo's Special; YS = Yellow Submarine; PF = Punt Vierkant; PB = Pink Beach; RS = Red Slave; WTL = Willemstoren Lighthouse; LC = Lac Cai; and W = Washikemba.

Mean macroalgae cover was highest at windward locations (64.9% ± 3.51 all windward samples pooled, Table 1), occupying up to 75.0% ± 2.63 cover at the 10-m depth at Washikemba (Fig. 2). Dominant algal categories included turf algae, *Dictyota* spp., *Trichogloeopsis pedicellata* (Howe) I. A. Abbott & Doty, and *Lobophora variegata* (Lamouroux) Womersley ex Oliveira on the leeward side, and *Sargassum* spp. on the windward side (Fig. 3). *Lobophora variegata* was mainly confined to depths > 15 m, with highest cover along the northwest coast between Nukove and Karpata, and at Ebo's Special on Klein Bonaire, reaching up to 20.1% ± 2.74 mean cover at the 20-m depth at Marine Reserve. An algal bloom of *T. pedicellata* (7.3% mean cover, leeward 5-m samples pooled) was observed on top of the exposed cemented rubble framework on the shallow reef platform and covered up to 61.8% ± 7.86 at Pink Beach. *Sargassum* spp. was the dominant category at windward sites, with a maximum mean cover of 54.8% ± 3.62 at the 10-m depth at Washikemba (Fig. 3).

Gorgonians tended to be more abundant along the southwest and south of Bonaire, where they represented the dominant benthic category at the 5-m depths at Punt Vierkant, Red Slave, and Willemstoren, and at the 10-m depths at Pink Beach and Red Slave (Fig. 2). Highest mean gorgonian cover of 31.8% ± 3.80 was recorded at the 5-m depth at Willemstoren. Mean cover of sponges tended to increase with depth and sponges occupied up to 32.1% ± 4.57 mean cover at the 20-m depth at Pink Beach. Sponges were the dominant category at the 20-m depths at Pink Beach, Red Slave, and Jeff Davis (Fig. 2).

Dead coral cover averaged 2.4% ± 1.10 of the bottom cover (all samples pooled) and was highest at 5-m depth at leeward sites (3.6% ± 2.31 mean cover, Table 1). Similarly, mean abundance of the category "other substrata" was also highest at leeward 5-m sites (48.9% ± 5.02 mean cover, Table 1) and was mainly composed of sand.

General Linear Mixed Effects Models: Tests of Significance of Fixed and Random Effects.—Tests of significance of fixed and random effects from linear mixed effects models revealed significant differences ($P \leq 0.05$) between depths (fixed effect) for scleractinian coral cover ($P = 0.011$; mean ± SE = 2.5 ± 3.36 at 5 m, 12.8 ± 3.42 at 10 m, 13.3 ± 1.92 at 20 m), for scleractinian coral species richness ($P = 0.000$; 4.5 ± 1.08 at 5 m, 10.4 ± 1.06 at 10 m, 12.8 ± 1.06 at 20 m), and scleractinian Shannon-Weaver diversity ($P = 0.000$; 0.92 ± 0.14 at 5 m, 1.55 ± 0.14 at 10 m, 2.00 ± 0.14 at 20 m; Table 2). Significant differences were detected between leeward and windward locations (fixed effect) for scleractinian coral ($P = 0.000$; 17.0 ± 1.60 leeward, 2.0 ± 3.49 windward) and macroalgae cover ($P = 0.000$; 30.1 ± 2.71 leeward, 64.9 ± 7.30 windward). Significant interaction between the fixed effects of depth and aspect was detected for sponge cover ($P = 0.046$), which increased significantly with depth on the leeward (1.5 ± 1.30 at 5 m, 7.4 ± 1.30 at 10 m, 16.8 ± 1.30 at 20 m), but not on the windward side (0.04 ± 4.51 at 5 m, 0.9 ± 3.19 at 10 m, 1.3 ± 3.19 at 20 m; Table 2).

Significant variation over locations for measures taken at the different depths (random effect) was observed for scleractinian coral species richness [$P = 0.002$; variance ± SE (based on squared difference between observed and estimated means) = 5.20 ± 1.69], scleractinian coral Shannon-Weaver diversity ($P = 0.000$; 0.24 ± 0.06), macroalgae cover ($P = 0.000$; 252.3 ± 58.53), gorgonian cover ($P = 0.003$; 16.0 ± 5.44), and sponge cover ($P = 0.000$; 16.4 ± 4.52), with the variances well described by a common estimate in each case. The variation over locations for scleractinian coral cover re-

Table 2. Tests of significance of fixed and random effects from mixed effects models for scleractinian coral cover, species richness, and Shannon-Weaver diversity; and macroalgae, gorgonian, and sponge cover. Significance at P ≤ 0.05.

Variable	Fixed effects	F	dfN	dfD	P	Random effects	Wald Z	P
Scleractinian coral cover	aspect	17.826	1	23.341	0.000			
	depth	5.264	2	31.116	0.011	location × depth 5 m	2.451	0.014
						location × depth 10 m	2.561	0.010
						location × depth 20 m	2.239	0.025
						residual	7.842	0.000
Species richness	depth	38.707	2	26.517	0.000	location × depth	3.076	0.002
(Scleractinia)						location × aspect	2.092	0.036
						residual	7.842	0.000
Shannon-Weaver diversity	depth	15.317	2	41.000	0.000	location × depth	4.252	0.000
(Scleractinia)						residual	7.842	0.000
Macroalgae cover	aspect	20.074	1	41.000	0.000	location × depth	4.311	0.000
						residual	7.842	0.000
Gorgonian cover						location × depth	2.944	0.003
						location × aspect	2.278	0.023
						residual	7.842	0.000
Sponge cover	aspect	12.116	1	41.000	0.001			
	depth	4.473	2	41.000	0.017	location × depth	3.626	0.000
	depth × aspect	3.330	2	41.000	0.046			
						residual	7.842	0.000

corded at the different depths was also significant, but was better described by separate variances for each depth. Although the variation was significant at all depths, less variation of coral cover over locations was observed at the 20-m depth (113.4 ± 46.28 at 5 m, 136.7 ± 53.37 at 10 m, 24.9 ± 11.13 at 20 m). In addition to these location by depth effects, significant variation over locations was observed for measures taken at the leeward and windward aspects for scleractinian coral species richness (P = 0.036; 9.52 ± 4.55) and gorgonian cover (P = 0.023; 43.6 ± 19.15). Only one variance was estimable for these locations by aspect effects, because there was only one pair of means to be compared. The biotic nature of differences among locations, depths, and aspect is outlined below.

Community Level Analysis.—Comparisons of benthic community patterns show that at Bray-Curtis similarities of 60% and 70%, the 41 study sites grouped together in nine and 17 distinct groups, respectively (Fig. 4). At 60% similarity, the 27 sites in Group A (see Fig. 4 for group composition) clustered mainly due to cover of turfing algae, sponges, *Dictyota* spp., gorgonians, *M. faveolata,* and *M. annularis* (Table 3). All sites in Group A, except the 10-m depth at Playa Funchi, had a mean coral cover of ≥ 10%. *Sargassum* spp. and *Dictyota* spp. caused the five windward sites to cluster in Group B. Similarities between the two sites in Group C were caused by turfing algae, *Dictyota* spp., and *Millepora* spp. The two 5-m sites in Group D clustered due to gorgonians, *T. pedicallata*, and turfing algae (Table 3). The remaining five sites had a mean coral cover of ≤ 3.6%. The 5-m depth at Yellow Submarine was

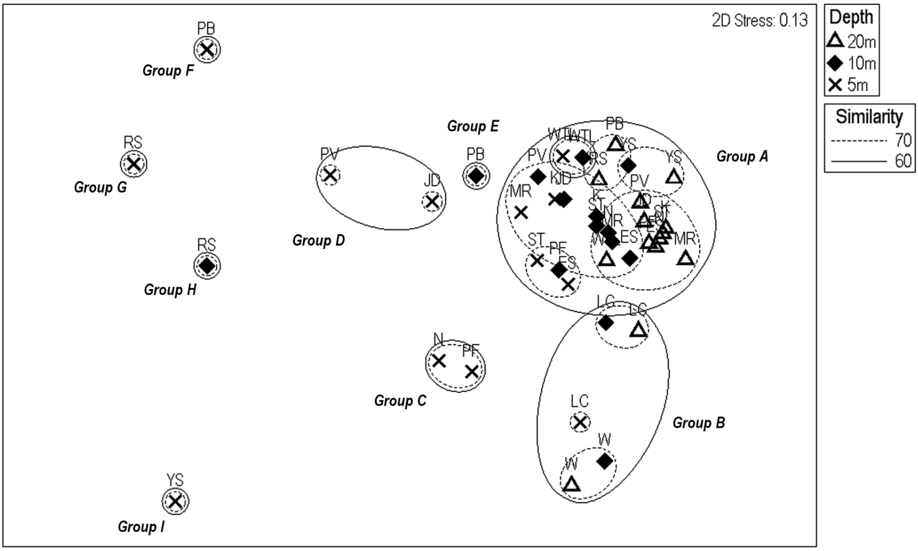

Figure 4. nMDS plot based on Bray Curtis similarity of square root transformed mean biotic data from 41 study sites around Bonaire, arranged by depth. Means are derived from four replicate transects each at depths of 5, 10, and 20 m at the 14 study locations. Crosses = 5 m; solid diamonds = 10 m; triangles = 20 m depth. Overlay clusters based on 60% and 70% Bray-Curtis similarity. Groups A to I based on 60% Bray-Curtis Similarity. Codes for study locations: PF = Playa Funchi; N = Nukove; ST = Saliña Tern; MR = Marine Reserve; K = Karpata; JD = Jeff Davis; ES = Ebo's Special; YS = Yellow Submarine; PF = Punt Vierkant; PB = Pink Beach; RS = Red Slave; WTL = Willemstoren Lighthouse; LC = Lac Cai; and W = Washikemba. Stress = 0.13.

dominated by sand and had the lowest mean biotic cover (2.3%) of all sites. The 5-m depth at Pink Beach was characterized by an algal bloom of *T. pedicellata* (61.8% mean cover). Generally, the 5-m sites tended to be the most dispersed, showing that communities varied considerably at this shallowest depth. Increasing stress levels of 0.06, 0.08, and 0.11 for separate nMDS plots for depths of 20, 10, and 5 m, respectively, and decreasing average similarity within depth groups (62.14%, 51.67%, 34.57%) from deep to shallow in SIMPER also indicate increasing variability with shallower depths.

The 20- and 5-m depths were the most dissimilar (66.22%), followed by 10- and 5-m depths (62.15%), and by 20- and 10-m depths (49.76%), with macroalgae, sponges, and gorgonians contributing between 42.51% and 46.36% of the differences between depths. Varying abundances of *M. annularis*, *M. faveolata*, *M. franksi*, *A. agaricites*, *M. cavernosa*, and *Stephanocoenia intersepta* (Lamarck, 1816) caused the main difference in coral communities between depths. Mean cover values of sponges, *Dictyota* spp., *L. variegata*, gorgonians, *M. franksi*, *A. agaricites*, *M. cavernosa*, *S. intersepta*, and *P. astreoides* were higher at 20-m depth. Turf algae, *M. annularis,* and *M. faveolata* were more abundant at the 10-m depth. Biotic communities at 5-m depth were characterized by high abundance of turf algae, *T. pedicellata*, gorgonians, *Dictyota* spp., *Millepora* spp., and *M. annularis*.

Groups F and I were the most dissimilar (91.43%), and Groups D and E were the least dissimilar (50.94%) in a SIMPER analysis of nMDS groups based on 60% Bray-Curtis similarity (see Fig. 4 for group composition). Macroalgae contributed between 15.6% (Groups A and C) and 43.7% (Groups C and D) to the first 60% of differences

Table 3. SIMPER analysis summary showing the biotic categories contributing ~80% of the similarities of sites in groups A–D based on 60% similarity in nMDS ordination. See Figure 4 for group composition.

Category	Average abundance	Average similarity	Sim / SD	Contrib %	Cum %
Group A: average similarity 59.89%					
Turfing algae	4.31	11.95	2.75	19.95	19.95
Sponge	3.01	7.40	2.48	12.36	32.31
Dictyota spp.	3.01	6.43	1.44	10.74	43.06
Gorgonian	2.49	5.24	1.28	8.76	51.81
Montastraea faveolata	2.04	4.82	2.02	8.05	59.87
Montastraea annularis	1.71	3.50	1.15	5.85	65.72
Other biota	1.32	3.16	2.25	5.28	70.99
Agaricia agaricites	1.23	2.61	1.33	4.35	75.35
Porites astreoides	1.05	2.34	1.56	3.90	79.25
Millepora spp.	0.77	1.69	1.21	2.82	82.07
Group B: average similarity 65.94%					
Sargassum spp.	5.51	20.12	3.15	30.51	30.51
Dictyota spp.	4.82	18.21	6.04	27.61	58.13
Other biota	2.09	6.66	4.17	10.11	68.23
Gorgonian	1.68	4.21	1.23	6.39	74.62
Turfing algae	1.99	4.09	1.13	6.20	80.82
Group C: average similarity 59.50%					
Turfing algae	3.07	20.20	2.04	33.95	33.95
Dictyota spp.	2.41	13.87	1.52	23.32	57.26
Millepora spp.	1.27	11.09	2.50	18.64	75.90
Porites astreoides	0.58	5.32	3.04	8.94	84.84
Group D: average similarity 65.58%					
Gorgonian	3.28	20.23	2.80	30.85	30.85
Trichogloeopsis sp.	3.14	17.52	1.68	26.72	57.56
Turfing algae	2.42	10.37	1.95	15.81	73.38
Sponge	1.02	5.81	3.27	8.86	82.23

between nMDS groups. The brown algae *Sargassum* spp. only occurred at windward locations (Group B) and contributed between 17.4% (Groups B and A) and 25.4% (Groups B and C) to the differences between nMDS groups (Table 4). Together with *Dictyota* spp., turf algae, sponges, and gorgonians, *Sargassum* spp. accounted for 48.0% of the dissimilarities between leeward and windward locations. Scleractinian corals contributed 13.5%, 14.3%, and 22.8% to the first 60% of differences between Groups A and B, A and D, and A and C, respectively (Table 4).

Two-way nested analysis of similarity (ANOSIM) of depths nested in locations for replicate data identified significant differences (P = 0.001) among depths across all location groups and very limited overlap of biotic communities (R = 0.863). Although biotic communities between location groups showed considerable overlap (Global R = 0.255), they still differed significantly (P = 0.001). Pairwise location comparisons (depths nested in locations and based on Bray-Curtis Similarity) show that biotic communities of windward locations Washikemba and Lac Cai were most clearly separated (R > 0.5) from other locations (Table 5). Community composition at Willemstoren Lighthouse showed limited overlap with communities

Table 4. SIMPER analysis summary showing the biotic categories contributing ~60% of differences between nMDS Groups A–D. See Figure 4 for group composition.

Category	Mean % cover	Mean % cover	Av Diss	Diss/SD	Contrib %	Cum %
Average dissimilarity 59.49%	Group A	Group B				
Sargassum spp.	0.00	5.51	10.34	3.21	17.39	17.39
Turf algae	4.31	1.99	5.02	1.33	8.44	25.83
Sponge	3.01	0.76	4.13	1.64	6.94	32.77
Dictyota spp.	3.01	4.82	3.98	1.27	6.68	39.45
Gorgonian	2.49	1.68	3.08	1.28	5.18	44.64
Montastraea annularis	1.71	0.18	3.00	1.30	5.04	49.68
Montastraea faveolata	2.04	0.62	2.98	1.54	5.01	54.68
Agaricia agaricites	1.23	0.18	2.02	1.48	3.40	58.08
Lobophora spp.	0.70	0.78	1.92	0.89	3.23	61.31
Average dissimilarity 63.06%	Group A	Group D				
Trichogloeopsis sp.	0.05	3.14	7.24	2.14	11.48	11.48
Dictyota spp.	3.01	0.00	6.72	1.72	10.66	22.14
Turf algae	4.31	2.42	5.62	1.39	8.91	31.05
Sponge	3.01	1.02	4.56	1.57	7.23	38.28
Gorgonian	2.49	3.28	3.88	1.40	6.15	44.43
Montastraea faveolata	2.04	0.63	3.42	1.59	5.43	49.86
Montastraea annularis	1.71	1.29	2.96	1.28	4.69	54.55
Agaricia agaricites	1.23	0.10	2.61	1.58	4.14	58.69
Other biota	1.32	0.28	2.40	1.67	3.81	62.50
Average dissimilarity 63.31%	Group A	Group C				
Gorgonian	2.49	0.05	6.19	1.45	9.78	9.78
Sponge	3.01	0.68	5.80	1.71	9.16	18.94
Turfing algae	4.31	3.07	5.02	1.15	7.92	26.87
Dictyota spp.	3.01	2.41	4.87	1.34	7.69	34.56
Montastraea faveolata	2.04	0.09	4.82	2.08	7.61	42.17
Montastraea annularis	1.71	0.00	4.40	1.37	6.95	49.12
Agaricia agaricites	1.23	0.00	3.04	1.65	4.80	53.92
Other biota	1.32	0.56	2.19	1.40	3.46	57.38
Montastraea cavernosa	0.89	0.00	2.15	1.41	3.39	60.77
Average dissimilarity 65.42%	Group C	Group B				
Sargassum spp.	0.00	5.51	16.63	2.85	25.41	25.41
Dictyota spp.	2.41	4.82	7.51	1.51	11.48	36.89
Turf	3.07	1.99	5.83	1.29	8.91	45.80
Gorgonian	0.05	1.68	4.71	1.64	7.21	53.01
Other biota	0.56	2.09	4.37	2.00	6.67	59.68
Millepora spp.	1.27	0.45	2.70	1.45	4.13	63.81
Average dissimilarity 66.29%	Group C	Group D				
Gorgonian	0.05	3.28	14.00	2.83	21.12	21.12
Trichogloeopsis sp.	0.57	3.14	11.55	1.81	17.43	38.55
Dictyota spp.	2.41	0.00	9.65	1.83	14.55	53.10
Turf	3.07	2.42	7.77	1.45	11.72	64.82
Average dissimilarity 73.6%	Group D	Group B				
Sargassum spp.	0.00	5.51	14.86	3.06	20.19	20.19
Dictyota spp.	0.00	4.82	12.65	5.78	17.19	37.38
Trichogloeopsis sp.	3.14	0.25	7.79	1.91	10.58	47.96
Gorgonian	3.28	1.68	4.83	1.44	6.56	54.51
Other biota	0.28	2.09	4.62	2.65	6.28	60.80

Table 5. Resuts of pairwise tests between locations performing two-way nested ANOSIM for biotic transect data. Codes for study locations: PF = Playa Funchi; N = Nukove; ST = Saliña Tern; MR = Marine Reserve; K = Karpata; JD = Jeff Davis; ES = Ebo's Special; YS = Yellow Submarine; PF = Punt Vierkant; PB = Pink Beach; RS = Red Slave; WTL = Willemstoren Lighthouse; LC = Lac Cai; and W = Washikemba.

	PF	N	ST	MR	K	JD	ES	YS	PV	PB	RS	WTL	LC	W
PF														
N	–0.33													
ST	–0.06	–0.04												
MR	–0.07	–0.07	–0.22											
K	0.19	0.04	–0.19	–0.22										
JD	0.26	0.04	0.00	–0.19	–0.11									
ES	–0.15	–0.26	0.04	0.00	0.22	0.19								
YS	0.17	0.04	0.26	0.26	0.26	0.11	0.22							
PV	0.19	0.15	0.00	0.11	–0.04	–0.22	0.19	0.00						
PB	0.33	0.33	0.44	0.41	0.44	0.15	0.48	0.22	–0.11					
RS	0.30	0.33	0.30	0.33	0.37	0.11	0.48	0.26	0.00	0.07				
WTL	0.52	0.37	0.48	0.67	0.52	0.52	0.59	0.48	0.33	0.48	0.44			
LC	0.67	0.67	0.78	0.78	0.89	0.81	0.81	0.44	0.63	0.56	0.56	0.93		
W	0.75	0.92	1.00	1.00	1.00	1.00	1.00	0.17	0.83	0.33	0.25	1.00	0.67	

at other locations. *Sargassum* spp. contributed most to the dissimilarity between windward and leeward locations, and gorgonians were important in distinguishing Willemstoren Lighthouse from other locations. Biotic communities at the remaining 11 locations showed considerable overlap, with five location pairs recording identical communities (R = 0) and the majority of pairs producing R ≤ 0.26. Negative R values (close to zero) were identified for 15 location pairs, indicating patchiness of communities and greater dissimilarity within than among location pairs (Chapman and Underwood 1999).

The results of BIOENV analysis reveal that the combination of the environmental and habitat variables, depth, aspect, and hard and soft substrata, best described (0.736) the patterns observed in the biotic data. Abiotic variables alone poorly explained (correlation coefficients between 0.246 for depth and 0.434 for soft substratum) the patterns observed in benthic communities.

Discussion

Status of Bonaire's Coral Reef Benthic Communities.—Findings of the present study are consistent with results from other recent benthic studies from the Netherlands Antilles (Bak and Luckhurst 1980, Bak and Nieuwland 1995, Bak et al. 2005, Nagelkerken et al. 2005). The combination of low to moderate coral cover and algal dominance at the vast majority of sites raises concerns about the status of Bonaire's coral reefs. Although the results from the present study are not directly comparable to earlier surveys due to differences in survey locations and methods, Bonaire's coral reefs have experienced considerable decline in coral cover and species richness since the 1970s and 1980s (e.g., Bak 1977, van Duyl 1985, Bak and Nieuwland 1995, Bak et al. 2005; Table 6). Bak and Nieuwland (1995), for instance, documented mean coral cover of 27%–77% and 11.75 coral species at 10-m depth, and 37%–84% mean cover and 14.25 species at 20-m depth in 1973.

Table 6. Compilation of published benthic studies of Bonaire and the wider Caribbean.

Reference	Location	Method and design	Period	Benthic communities
Scatterday 1974	Bonaire	Qualitative description of zonation patterns at two sites.	1970s	Coral zonation: *Diploria clivosa* zone, *Acropora cervicornis* zone, *Acropora palmata* zone, *Montrastraea annularis* zone.
Bak 1975	Netherlands Antilles	Qualitative description of zonation patterns.	1970s	Coral zonation: Shore zone, *A. palmata* zone (1–4 m), barren zone (3–4.5 m), higher diversity area (4–35 m).
Bak 1977	Curaçao	Two transects (normal to shore) at one site.	1970s	Coral cover of 8%–45% at 0–40 m depth; 20% cover at 5–5.6 m, 40% at 10–10.4 m, and 30% at 19–22 m depth.
Van Duyl 1985	Bonaire	Aerial photograps and submarine surveys along the leeward coast.	1981–1983	Coral cover of 20%–40% at 29% of the survey area, and of > 40% at 29% of survey area at 0–10 m depth.
Van Duyl 1985	Curaçao	Aerial photograps and submarine surveys along the leeward coast.	1981–1983	Coral cover of 20%–40% at 25% of the survey area, and of > 40% at 9% of the survey area at 0–10 m depth.
Bak and Nieuwland 1995	Curaçao and Bonaire	Four permanent quadrats (3 × 3 m) each, at three sites in Curaçao and at one site in Bonaire.	1973–1992	In 1973: Coral cover of 27%–77% and 11.75 coral species at 10 m depth, and 37%–84% cover and 14.25 species at 20 m depth. In 1992: 25%–73% decline in cover on 1973 levels.
Bak et al. 2005	Curaçao and Bonaire	As above (see Bak and Nieuwland 1995).	1973–2002	Decline of coral cover from ~43% (1973) to ~19% (2002) at 10 and 20 m and from ~28% to ~21.5% at 30 and 40 m depth. Species richness declined from ~12.8 to ~12.7 at 10 and 20 m depth, and from ~8.5 to ~6 species at 30 and 40 m.
Nagelkerken et al. 2005	Curaçao	Point intercept along transects (normal to shore) at nine sites.	1973–2003	Coral cover declined from 52.2% (1973) to 21.7% (2003) at depths of 3 to 36 m.
Sandin et al. 2008	Curaçao and Bonaire	10 quadrats (2 m^2) at each of five sites in Curaçao and six sites in Bonaire.	Not specified	Coral cover of 26.6%, macroalgae cover of 26.1%, and cover of turf algae of 32.5% at 20 m depth.
Hughes 1994	Jamaica	Not specified.	1977, 1993	Coral cover declined from 52% (1977) to 3% (1993) and macroalgae increased from 4% to 92%.
Gardner et al. 2003	Caribbean	Meta analysis. 263 sites.	1977–2002	Coral cover declined from ~50% (1977) to ~10% (2002).
Kramer 2003	Caribbean	Atlantic and Gulf Rapid Assessment at 302 sites.	1997–2000	Coral cover of 26% Caribbean wide and ~46% at Bonaire. Macroalgae cover of 23% Caribbean wide and of < 15% at Bonaire.
McClanahan and Muthiga 1998	Belize	Line transects at five sites.	1970, 1997	Coral cover declined from 80% (1970) to 20% (1997), and macroalgae increased from 20% to 80%.
Andréfouët and Guzman 2005	Caribbean Panama	Remote sensing and rapid snorkel assessments at Kuna Yala coral reef.	2001	Coral cover of 22.8% at < 5 m, 26.5% at 10 m, 27.4% at 15 m, and 19.7% at > 20 m depth. Macroalgae cover of 63%.
Coelho and Manfrino 2007	Little Cayman	Atlantic and Gulf Rapid Assessment using line transects at nine locations.	1999–2004	Coral cover declined from 26.5% (1999) to 16.3% (2004).
Bruno et al. 2009	Caribbean	Meta analysis. 120 sites.	1996–2006	Mean coral cover of 15.9%; mean macroalgae cover of 40% (> 25% at 30% of sites, > 50% at 73% of sites)
Present study	Bonaire	Four replicate photo transects each at 5, 10 and 20 m depth, at 14 locations.	2008–2009	16.7% and 5.6% mean coral cover, 9.4 and 6.9 mean coral species richness, and 30.7% and 64.9% macroalgae cover at leeward and windward locations, respectively.

The most striking difference between the results of the present study and the studies of Scatterday (1974), Bak (1975, 1977), and van Duyl (1985) is the widespread absence of the previously dominant shallow water species, *A. palmata* and *A. cervicornis*. In the early 1980s, the *A. palmata* and *A. cervicornis* groups of communities (see van Duyl 1985) commonly occurred at 0.5–6 m and 1–10 m depths, respectively, but these were rarely encountered in the present study. The decimation of the tall, three dimensional *A. palmata* colonies has changed the biophysical structure of many Caribbean reefs, as they have been replaced by slower-growing species, which typically rest much closer to the substrata (Pandolfi and Jackson 2006).

Mean coral cover of 16.7% ± 1.72 (all leeward samples pooled) recorded in the present study is slightly lower than in other recent studies from Bonaire and Curaçao that recorded mean coral cover between 18% (Bak et al. 2005) and 22% (Nagelkerken et al. 2005), and identified a reduction in coral cover from 43% and 58% recorded in 1973, respectively. These results are inconsistent with the findings of the AGRRA assessment in the late 1990s (Kramer 2003), which found that Bonaire's coral reefs were among the "healthiest" in the Caribbean, with 46% mean coral cover at Bonaire, compared with 26% mean cover Caribbean wide (possible causes are discussed below). Mean coral abundance recorded in the present study corresponds with the 10%–25% mean cover recorded in the wider Caribbean region (see Table 6) and is consistent with 15.9% ± 1.0 mean coral cover and 40.0% ± 2.1 macroalgal cover identified by Bruno et al. (2009) in a meta-analysis of 120 Caribbean sites.

A Combination of Chronic and Acute Disturbances.—It has been suggested that coral cover at Bonaire and Curaçao has decreased significantly due to physical, biological, and anthropogenic disturbances (Bak and Luckhurst 1980, Bak and Nieuwland 1995). Bonaire's coral reefs have been exposed to chronic stress from coastal development, urbanization, discharge of sewage into coastal waters (Bak and Nieuwland 1995), nutrient pollution (Wieggers 2007), and declines in fish stocks (Wilkinson 2004, Alvarado et al. 2007). Furthermore, Bonaire's normally sheltered leeward coral reefs have suffered acute damage from three severe hurricanes in the past decade (Bries et al. 2004, Scheffers and Scheffers 2006, MDNAA 2008). The Saffir-Simpson category four Hurricane Lenny in 1999 was the first storm in the 113-yr record of Atlantic tropical cyclones that took an extended west to east track (Guiney 2000) and severely impacted Bonaire's normally sheltered leeward coast with up to 6-m waves (Guiney 2000, Bries et al. 2004). The leeward reefs of Bonaire were severely damaged (Bries et al. 2004), and were impacted again by the category five Hurricane Ivan in 2004 (Scheffers and Scheffers 2006) and the category three Hurricane Omar in October 2008, which also took a west to east track (MDNAA 2008). Coral communities that develop in sheltered environments tend to be more fragile and vulnerable than corals in wave-stressed habitats (Witman 1992), which can lead to severe mortality when storm events occur (van Duyl 1985). Gardner et al. (2005) found that the abundance of corals decreased by ~17% Caribbean-wide in the year after a hurricane and that coral reefs took a minimum of 8 yrs to recover. When the reefs were surveyed for the present study, only 2–3 mo after Hurricane Omar, storm damage was evident in the form of toppled and fragmented corals, the movement of sand, and exposure of cemented *A. cervicornis* rubble on the shallow reef platform, and an algal bloom of *T. pedicellata* on top of the exposed cemented rubble framework. As many dead coral colonies had been overgrown by algae and other taxa by the time surveys were conducted (and were hence coded to other benthic categories), mean dead coral cover recorded in the present study is likely to underestimate mortality caused by Hurricane Omar.

Coral Communities.—Considerably fewer scleractinian coral species (39) were recorded in the present study than the 47 and 57 species documented by Scatterday (1974) and Bak (1977) for Bonaire and Curaçao, respectively. The increase in coral species richness with depth at leeward locations is consistent with the findings of Bak (1977), who identified that the upper slope zone at depths between 15 and 30 m was most species rich and represented a transition zone of shallow and deeper reef species. The disharmonic patterns of coral distribution detected in the present study are in contrast with the long term pattern of persistence in relative abundance through time of the Pleistocene record (Pandolfi and Jackson 2006) and may be a product of the recent disturbance regime, whereby the reefs were exposed to disturbances more frequently than the time interval required for recovery (Grigg 1983).

Macroalgae and Other Benthos.—The increasing dominance of macroalgae on Caribbean reefs has become a widespread occurrence in recent decades (e.g., Hughes 1994, Gardner et al. 2003, Bruno et al. 2009) and was also observed on the reefs of Bonaire. *Lobophora variegata* is reported to have spread in the Caribbean during extensive coral degradation (Mumby et al. 2007, Nugues and Bak 2008), and significant increases from 5% at 20- and 30-m depths to 25% and 18%, respectively, were recorded in permanent quadrats in Curaçao between 1998 and 2006 (Nugues and Bak 2008). The increase is thought to have occurred as a consequence of coral mortality from storm impacts, disease, and coral bleaching.

Coral-algal interactions need to be viewed in the context of the prevalent grazing intensity and nutrient regime in an area (Nugues and Bak 2006). Monitoring has shown that between 2003 and 2007, mean biomass of scarid parrotfish on Bonaire's reefs steadily declined from 7000 to 4000 g 100 m^{-2} (Alvarado et al. 2007), and a 2006 nutrient survey suggests that Bonaire's reefs are at or beyond the threshold of nutrient pollution (Wieggers 2007). Effects of nutrient enrichment and reduced herbivory interact (Scheffer et al. 2001, Jompa and McCook 2002, Littler and Littler 2007) and may operate synergistically to alter communities (Scheffer et al. 2001). Once chronic human impacts have undermined resilience, pulses of mortality, such as that caused by a hurricane, can trigger a transition to macroalgal dominance (Littler and Littler 2007, Scheffer et al. 2008, Hughes et al. 2010) and increased abundance of other life forms such as soft corals and sponges (Norström et al. 2009). Mean sponge and gorgonian cover recorded in the present study was more than three times the mean cover on Curaçao (Nagelkerken et al. 2005). Aggressive overgrowth of scleractinian corals by the colonial ascidian, *Trididemnum solidum* (Van Name, 1902), has been recorded at Bonaire (Sommer et al. 2010) and neighboring Curaçao (Bak et al. 1996).

Community Level Analysis.—Biotic communities generally tended to separate by aspect (leeward and windward) and by depth in nMDS ordination, with heterogeneity increasing at the shallower sites. Greater exposure of shallow water communities to physical, biological, and anthropogenic disturbance (Bak and Luckhurst 1980, Huston 1985, Bak and Nieuwland 1995) may have contributed to their variability.

Biotic communities between Playa Funchi and Punt Vierkant showed the greatest degree of overlap. Communities along the northwest coast were characterized by high cover of macroalgae (*Dictyota* spp., turf algae, and *L. variegata*) and high abundance of species from the *M. annularis* species complex, *M. mirabilis* (at 5- and 10-m depths), *A. agaricites,* and *P. astreoides* (at 20-m depth). Large "pagoda style" (van Duyl 1985) *M. faveolata* colonies were abundant along the reef slope at Playa Funchi and Nukove. Coral cover of between 13.6% and 33.4% at 5-m depth at Saliña Tern, Marine Reserve, and Karpata was comparatively much higher than at other locations, and was mainly composed of *M. annularis*, *M. mirabilias,* and *M. faveolata*. Toppled and fragmented corals, overgrown by algae, were commonplace on the reef slope along the northwest coast. Gorgonians were less abundant than along the southwest coast of Bonaire, where they represented the dominant benthic category at a number of 5- and 10-m sites. Their pliable growth forms tend to make soft corals less vulnerable to sedimentation than hard corals (Schleyer and Celliers 2003), making them well adapted to the more turbid conditions along the southwest coast of Bonaire, where large sandy patches occur and a moderate current runs from the southwest. The great accumulation of sand (> 80% mean cover) to depths > 10 m at Red Slave may be attributable to the strong energy gradient operating in the northeast trade wind setting at the southwest fringe of Bonaire (Roberts 1983).

Although we did not directly measure wave energy, we hypothesize that exposure plays a major role in structuring biotic communities between leeward and windward locations. Consistent waves of 2–3.5 m and oceanic swell (van Duyl 1985) have likely precluded substantial coral community development at 5-m depth along the windward coast. Grigg (1998) proposed that scour, abrasion, and breakage prevented long-term reef accretion at sites in Hawaii with extremely high wave energy and that wave energy was modulated by depth. We recorded the highest mean windward coral cover was 10-m depth. Van Duyl (1985) suggested that high algal cover and whiplash from plants moved by strong wave action negatively impacted coral settlement and juvenile coral survival on the windward fringing reefs of Bonaire. Although extremely high wave energies likely have prevented substantial reef accretion on the windward coast, coral communities have flourished in the high wave energy environment at Willemstoren Lighthouse, which is exposed to waves of between 1.5 and 2 m (van Duyl 1985). Willemstoren had the highest mean coral abundance and species richness of all surveyed locations, and differed from the other locations in coral community structure.

The results of our study raise concerns about the status of Bonaire's coral reef benthic communities and show that even reefs formerly regarded as the most pristine reefs in the Caribbean have experienced coral community decline and ecological shifts in the past few decades. The combination of low to moderate coral cover and algal dominance at the majority of sites are symptomatic of partly degraded reef systems, particularly as they coincide with elevated nutrients (Wieggers 2007) and reduced herbivory (Alvarado et al. 2007). Bonaire's coral reefs were surveyed only 2–3 mo after the occurrence of Hurricane Omar, and the impacts from that hurricane were still evident along leeward reefs. The extreme variability detected at all spatial scales may be a product of the recent disturbance regime that has precluded recovery of these reef communities.

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Appendix. Mean percentage cover of benthic categories, species richness, and Shannon-Weaver diversity of scleractinian corals summarized for leeward, windward, and all sites at depths of 5, 10, and 20 m, and for all depth samples pooled.

	5-m depth						10-m depth					
	Leeward		Windward		Total		Leeward		Windward		Total	
		SE		SE		SE		SE		SE		SE
Mean cover												
Acropora palmata	0.10	0.07	0.00	0.00	0.09	0.06	0.00	0.00	0.40	0.23	0.06	0.03
Acropora prolifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agaricia agaricites	0.12	0.04	0.00	0.00	0.10	0.03	1.27	0.28	0.19	0.06	1.12	0.25
Agaricia fragilis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agaricia grahamae	0.01	0.01	0.00	0.00	0.01	0.01	0.08	0.06	0.00	0.00	0.07	0.05
Agaricia tenuifolia	0.10	0.05	0.00	0.00	0.08	0.04	1.10	0.14	0.47	0.33	1.01	0.17
Agaricia undata	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01
Agaricia lamarcki	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01
Colpophyllia natans	0.05	0.03	0.00	0.00	0.04	0.03	0.62	0.27	0.27	0.12	0.57	0.24
Dendrogyra cylindrus	0.03	0.03	0.00	0.00	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Dichocoenia stokesi	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.01
Diploria clivosa	0.33	0.11	0.46	0.23	0.32	0.11	0.08	0.06	0.48	0.25	0.13	0.09
Diploria labyrinthiformis	0.21	0.13	0.00	0.00	0.18	0.11	0.16	0.08	0.08	0.06	0.15	0.08
Diploria strigosa	0.56	0.12	0.71	0.25	0.53	0.12	0.44	0.18	0.77	0.26	0.49	0.19
Eusmilia fastigiata	0.01	0.01	0.00	0.00	0.01	0.01	0.19	0.10	0.04	0.04	0.17	0.09
Madracis decactis	0.04	0.02	0.00	0.00	0.04	0.01	0.02	0.01	0.06	0.04	0.02	0.02
Madracis mirabilis	1.48	0.51	0.00	0.00	1.27	0.44	1.40	0.47	0.06	0.04	1.21	0.40
Meandrina meandrites	0.05	0.02	0.08	0.05	0.04	0.02	0.17	0.08	0.06	0.04	0.15	0.08
Montastraea annularis	3.24	0.96	0.00	0.00	2.77	0.82	6.00	1.10	0.38	0.23	5.19	0.98
Montastraea cavernosa	0.11	0.06	0.04	0.04	0.10	0.06	0.54	0.18	0.29	0.10	0.50	0.17
Montastraea faveolata	1.86	0.84	0.00	0.00	1.59	0.72	5.41	0.95	1.97	0.36	4.92	0.87
Montastraea franksi	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.09	0.00	0.00	0.12	0.08
Mussa angulosa	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.01	0.01
Mycetophyllia aliciae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mycetophyllia ferox	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00
Mycetophyllia lamarckiana	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.01
Other *coral*	0.04	0.03	0.00	0.00	0.04	0.03	0.05	0.03	0.02	0.02	0.04	0.03
Porites astreoides	0.51	0.14	0.00	0.00	0.44	0.12	0.76	0.25	0.42	0.15	0.71	0.24
Porites divaricata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Porites furcata	0.04	0.02	0.00	0.00	0.04	0.02	0.10	0.04	0.00	0.00	0.08	0.03
Porites porites	0.18	0.13	0.00	0.00	0.16	0.11	0.40	0.14	0.04	0.02	0.35	0.13
Siderastrea radians	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00
Siderastrea siderea	0.31	0.13	0.46	0.14	0.30	0.12	0.57	0.24	2.76	0.50	0.88	0.28
Solenastrea bournoni	0.01	0.01	0.00	0.00	0.01	0.01	0.05	0.03	0.02	0.02	0.04	0.03
Solenastrea hyades	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.01
Stephanocoenia intersepta	0.01	0.01	0.00	0.00	0.01	0.01	0.07	0.05	0.04	0.04	0.07	0.05
Tubastraea coccinea	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00

Appendix continued.

	20-m depth						All depth samples pooled					
	Leeward		Windward		Total		Leeward		Windward		Total	
		SE		SE		SE		SE		SE		SE
Mean cover												
Acropora palmata	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.16	0.09	0.05	0.03
Acropora prolifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agaricia agaricites	3.32	0.59	0.04	0.02	2.85	0.51	1.57	0.30	0.09	0.03	1.39	0.27
Agaricia fragilis	0.02	0.02	0.00	0.00	0.02	0.02	0.01	0.01	0.00	0.00	0.01	0.01
Agaricia grahamae	0.24	0.10	0.00	0.00	0.20	0.09	0.11	0.06	0.00	0.00	0.10	0.05
Agaricia tenuifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.07	0.19	0.13	0.38	0.07
Agaricia undata	0.09	0.06	0.00	0.00	0.07	0.05	0.03	0.02	0.00	0.00	0.03	0.02
Agaricia lamarcki	0.33	0.14	0.15	0.10	0.30	0.14	0.11	0.05	0.06	0.04	0.10	0.05
Colpophyllia natans	0.67	0.28	0.29	0.07	0.61	0.25	0.44	0.19	0.23	0.08	0.42	0.18
Dendrogyra cylindrus	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01
Dichocoenia stokesi	0.00	0.00	0.04	0.04	0.01	0.01	0.01	0.01	0.02	0.02	0.01	0.01
Diploria clivosa	0.07	0.07	0.08	0.08	0.07	0.07	0.16	0.08	0.32	0.18	0.18	0.09
Diploria labyrinthiformis	0.03	0.02	0.02	0.02	0.03	0.02	0.14	0.08	0.04	0.03	0.13	0.07
Diploria strigosa	0.60	0.29	0.60	0.20	0.60	0.28	0.53	0.20	0.69	0.23	0.55	0.20
Eusmilia fastigiata	1.03	0.31	0.06	0.02	0.89	0.27	0.41	0.14	0.04	0.03	0.37	0.13
Madracis decactis	0.02	0.01	0.04	0.02	0.02	0.01	0.03	0.01	0.04	0.03	0.03	0.01
Madracis mirabilis	0.20	0.12	0.04	0.04	0.18	0.11	1.03	0.36	0.04	0.03	0.91	0.32
Meandrina meandrites	0.42	0.17	0.25	0.06	0.40	0.15	0.21	0.09	0.14	0.05	0.20	0.09
Montastraea annularis	0.93	0.31	0.04	0.02	0.80	0.27	3.39	0.79	0.17	0.10	2.99	0.71
Montastraea cavernosa	2.09	0.43	0.63	0.27	1.88	0.40	0.91	0.22	0.38	0.16	0.84	0.21
Montastraea faveolata	4.35	0.77	0.71	0.24	3.83	0.69	3.87	0.85	1.07	0.24	3.53	0.78
Montastraea franksi	2.61	0.69	0.06	0.06	2.25	0.60	0.92	0.26	0.03	0.03	0.81	0.23
Mussa angulosa	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01
Mycetophyllia aliciae	0.09	0.05	0.00	0.00	0.08	0.05	0.03	0.02	0.00	0.00	0.03	0.02
Mycetophyllia ferox	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Mycetophyllia lamarckiana	0.00	0.00	0.06	0.06	0.01	0.01	0.01	0.01	0.03	0.03	0.01	0.01
Other *coral*	0.17	0.08	0.02	0.02	0.15	0.07	0.08	0.05	0.02	0.02	0.08	0.04
Porites astreoides	2.01	0.44	0.54	0.15	1.80	0.40	1.09	0.28	0.38	0.12	1.01	0.26
Porites divaricata	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Porites furcata	0.01	0.01	0.00	0.00	0.01	0.01	0.05	0.02	0.00	0.00	0.04	0.02
Porites porites	0.01	0.01	0.00	0.00	0.01	0.01	0.20	0.09	0.02	0.01	0.18	0.08
Siderastrea radians	0.02	0.02	0.00	0.00	0.02	0.01	0.01	0.01	0.00	0.00	0.01	0.01
Siderastrea siderea	0.50	0.19	0.25	0.15	0.46	0.18	0.46	0.19	1.30	0.29	0.56	0.20
Solenastrea bournoni	0.03	0.02	0.00	0.00	0.02	0.02	0.03	0.02	0.01	0.01	0.02	0.02
Solenastrea hyades	0.02	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.01
Stephanocoenia intersepta	1.14	0.29	0.23	0.13	1.01	0.27	0.41	0.12	0.11	0.07	0.37	0.11
Tubastraea coccinea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix continued.

	5-m depth						10-m depth					
	Leeward		Windward		Total		Leeward		Windward		Total	
		SE		SE		SE		SE		SE		SE
Millepora spp.	1.08	0.33	0.13	0.08	0.94	0.28	0.87	0.20	0.96	0.28	0.88	0.21
Gorgonians	8.04	2.19	7.42	1.47	7.42	1.98	8.68	1.54	2.22	1.02	7.76	1.47
Sponges	1.54	0.56	0.04	0.04	1.32	0.48	6.93	1.24	0.88	0.52	6.06	1.13
Dictyota spp.	3.86	1.73	28.29	2.74	5.33	1.68	9.00	1.85	19.58	0.88	10.51	1.71
Trichogloeopsis spp.	7.26	1.37	0.21	0.08	6.24	1.18	0.03	0.03	0.27	0.12	0.07	0.04
Halimeda spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.01
Lobophora variegata	0.00	0.00	0.17	0.12	0.01	0.01	0.03	0.02	0.33	0.14	0.08	0.04
Other Macroalgae	0.70	0.38	4.08	0.38	0.89	0.35	0.69	0.48	0.08	0.08	0.61	0.42
Padina spp.	0.00	0.00	2.29	0.54	0.17	0.04	0.00	0.00	0.42	0.15	0.06	0.03
Sargassum spp.	0.00	0.00	26.83	2.82	1.92	0.20	0.00	0.00	37.82	4.09	5.40	0.58
Turfing algae	13.52	2.69	7.88	3.29	12.15	2.54	22.22	2.66	8.68	1.76	20.29	2.53
Coralline algae	1.05	0.45	0.00	0.00	0.90	0.39	0.61	0.27	0.69	0.20	0.62	0.26
Anemones	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.02	0.01	0.01
Other	0.89	0.23	4.58	0.84	1.09	0.25	1.67	0.49	7.63	1.36	2.53	0.62
Trididemnum solidum	0.05	0.03	0.00	0.00	0.04	0.02	1.05	0.33	0.02	0.02	0.90	0.29
Dead coral	3.57	2.28	0.00	0.00	3.06	1.95	2.71	0.99	1.37	0.42	2.52	0.90
Dead gorgonian	0.07	0.06	0.00	0.00	0.06	0.05	0.19	0.09	0.00	0.00	0.17	0.07
Rubble	5.93	2.05	0.04	0.04	5.09	1.76	3.25	1.26	0.06	0.02	2.80	1.08
Cemented Rubble	14.71	3.92	0.00	0.00	12.61	3.36	0.36	0.23	0.21	0.11	0.34	0.22
Pavement	0.00	0.00	15.71	4.69	1.12	0.33	0.01	0.01	7.18	0.75	1.03	0.11
Sand	28.27	4.91	0.58	0.36	24.27	4.24	21.97	3.33	2.70	1.24	19.22	3.04
Summary by categories												
Scleractinian corals	9.47	1.70	1.75	0.16	8.24	1.47	19.70	1.90	8.87	0.99	18.15	1.77
Hydrocorals	1.08	0.33	0.13	0.08	0.94	0.28	0.87	0.20	0.96	0.28	0.88	0.21
Gorgonians	8.04	2.19	7.42	1.47	7.42	1.98	8.68	1.54	2.22	1.02	7.76	1.47
Sponges	1.54	0.56	0.04	0.04	1.32	0.48	6.93	1.24	0.88	0.52	6.06	1.13
Macroalgae	25.34	4.16	69.75	6.43	26.70	4.03	31.99	2.52	67.20	3.54	37.02	2.66
Coralline algae	1.05	0.45	0.00	0.00	0.90	0.39	0.61	0.27	0.69	0.20	0.62	0.26
Other benthos	0.93	0.24	4.58	0.84	1.13	0.26	2.73	0.74	7.67	1.35	3.43	0.83
Dead coral	3.64	2.31	0.00	0.00	3.12	1.98	2.90	1.03	1.37	0.42	2.68	0.94
Other substrata	48.91	5.02	16.33	4.54	43.09	4.63	25.60	3.55	10.15	1.51	23.39	3.26

Appendix continued.

	20-m depth						All depth samples pooled					
	Leeward		Windward		Total		Leeward		Windward		Total	
		SE		SE		SE		SE		SE		SE
Millepora spp.	0.48	0.18	0.04	0.04	0.42	0.16	0.81	0.23	0.43	0.15	0.76	0.22
Gorgonians	7.80	0.87	3.85	1.29	7.24	0.93	8.17	1.53	3.91	1.22	7.65	1.49
Sponges	16.84	3.00	1.31	0.46	14.62	2.64	8.43	1.60	0.88	0.40	7.51	1.45
Dictyota spp.	15.65	1.41	25.17	2.14	17.01	1.51	9.50	1.67	23.56	1.75	11.22	1.68
Trichogloeopsis spp.	0.00	0.00	0.00	0.00	0.00	0.00	2.43	0.47	0.15	0.06	2.15	0.42
Halimeda spp.	0.01	0.01	0.02	0.02	0.01	0.01	0.00	0.00	0.02	0.02	0.01	0.01
Lobophora variegata	4.80	0.77	3.88	0.47	4.67	0.73	1.61	0.26	1.72	0.27	1.62	0.26
Other Macroalgae	0.29	0.16	0.19	0.12	0.27	0.15	0.56	0.34	0.93	0.16	0.60	0.32
Padina spp.	0.00	0.00	0.08	0.05	0.01	0.01	0.00	0.00	0.66	0.19	0.08	0.03
Sargassum spp.	0.00	0.00	28.25	1.42	4.04	0.20	0.00	0.00	31.79	2.77	3.88	0.34
Turfing algae	14.00	1.84	2.65	0.53	12.38	1.65	16.58	2.40	6.10	1.57	15.30	2.30
Coralline algae	0.93	0.70	0.00	0.00	0.79	0.60	0.86	0.47	0.28	0.08	0.79	0.43
Anemones	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Other	2.38	0.68	2.38	0.48	2.38	0.65	1.64	0.47	4.92	0.90	2.04	0.52
Trididemnum solidum	1.85	0.43	0.00	0.00	1.59	0.37	0.98	0.26	0.01	0.01	0.86	0.23
Dead coral	1.30	0.33	0.06	0.02	1.12	0.29	2.52	1.20	0.57	0.18	2.29	1.07
Dead gorgonian	0.14	0.09	0.00	0.00	0.12	0.08	0.14	0.08	0.00	0.00	0.12	0.07
Rubble	0.78	0.47	0.04	0.04	0.67	0.40	3.32	1.26	0.05	0.03	2.92	1.11
Cemented Rubble	0.00	0.00	12.42	0.93	1.78	0.14	5.02	1.39	5.05	0.42	5.03	1.27
Pavement	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	6.02	1.25	0.74	0.15
Sand	11.73	1.93	15.48	1.69	12.27	1.89	20.66	3.39	7.39	1.25	19.04	3.13
Summary by categories												
Scleractinian corals	21.04	1.57	4.17	0.65	18.63	1.44	16.73	1.72	5.56	0.69	15.37	1.60
Hydrocorals	0.48	0.18	0.04	0.04	0.42	0.16	0.81	0.23	0.43	0.15	0.76	0.22
Gorgonians	7.80	0.87	3.85	1.29	7.24	0.93	8.17	1.53	3.91	1.22	7.65	1.49
Sponges	16.84	3.00	1.31	0.46	14.62	2.64	8.43	1.60	0.88	0.40	7.51	1.45
Macroalgae	34.74	2.16	60.23	2.03	38.38	2.14	30.69	2.95	64.92	3.51	34.86	3.02
Coralline algae	0.93	0.70	0.00	0.00	0.79	0.60	0.86	0.47	0.28	0.08	0.79	0.43
Other benthos	4.23	0.86	2.38	0.48	3.96	0.81	2.63	0.61	4.94	0.90	2.91	0.65
Dead coral	1.44	0.33	0.06	0.02	1.24	0.29	2.66	1.22	0.57	0.18	2.41	1.10
Other substrata	12.51	2.20	27.96	1.07	14.72	2.04	29.01	3.59	18.51	1.94	27.73	3.39