

THE PERSISTENCE OF BLACK-BAND DISEASE IN JAMAICA: IMPACT ON COMMUNITY STRUCTURE

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ABSTRACT

The distribution of black-band disease (BBD) and the fates of corals infected with BBD were quantitatively monitored in St. Ann's Bay, Jamaica over four years. Black-band disease was concentrated in the back reef and on shallow fringing reefs among the species *Diploria clivosa*, *D. strigosa*, *Montastraea annularis*, *M. cavernosa* and *Siderastrea siderea*; BBD was rare below 10 m. Between July 1991 and September 1995 BBD occurred on 342 corals within 20 sites (total area 6280 m²), representing 6.1% of the coral population. Infected corals appeared to be clumped and BBD was observed to spread from one coral to neighboring colonies, suggesting that this disease is highly infective. The abundance of BBD increased throughout 1992 and 1993, and a high incidence of BBD persists among the dominant coral species. In 1995, 65 corals had BBD, including 15 colonies observed with BBD in 1993. Large corals were rarely killed after one infection event. Instead, BBD corals were divided into two or more remnant colonies before the infection disappeared; a recurrence was observed later in the season or in subsequent years in 39 corals (11.4%). Overall 47.9% of the corals infected prior to 1995 have died. Black-band disease is contributing to a progressive elimination of massive corals from these reefs.

INTRODUCTION

Black-band disease (BBD) is a common affliction of massive reef-building corals caused by the cyanobacterium *Phormidium corallyticum* (Rützler and Santavy 1983). Black-band disease was first observed in Belize over two decades ago (Antonius 1973); BBD is now known to occur throughout the Caribbean (Garrett and Ducklow 1975; Rützler et al. 1983; Peters 1993), the Indo-Pacific (Antonius 1985a) and the Red Sea (Antonius 1988). While massive coral species are typically infected, BBD has been identified on acroporid corals from the Great Barrier Reef (Miller 1996). This disease may also occur on gorgonians and milleporids (Antonius 1985b; Feingold 1988).

Black-band disease characteristically forms a circular or crescent-shaped band that separates white, denuded skeleton from living coral. The disease community migrates across a coral's surface at a rate of up to 2 cm/day (Rützler et al. 1983). As the band progresses, recently exposed skeleton grades proximally into algal successional stages; filamentous algae colonizes regions closest to the band within days to weeks, followed by macroalgal turf and crustose algae (pers. obs.). BBD can kill an entire colony during one active season, or after a repeat infection the following year (Carlton and Richardson 1995). More often, BBD eliminates a patch of tissue and then disappears for a period of months to years (Bruckner et al. in press).

In most areas, 0.5-1.0% of the susceptible coral colonies are affected by BBD at a given time, with infections dispersed throughout the reef (Garrett and Ducklow 1975; Edmunds 1991). Reefs which experience substantial temperature variation are subject to a higher incidence of BBD during warm water months, and few or no infections when water temperatures fall below 25°C (Rützler et al. 1983; Antonius 1985b). Antonius (1988) observed an increase of BBD in industrialized areas, and found BBD-resistant species infected with this disease in polluted waters; he suggested that anthropogenic stressors are precursors to BBD outbreaks. Localized outbreaks have been reported from the Bahamas, Belize, the Cayman Islands, Florida (USA) and St. Vincent (Williams and Bunkley-Williams 1990; Peters 1993).

The incidence of BBD appears to be increasing, and this disease is considered an important factor in the decline of some coral reefs (Porter and Meir 1992). Therefore, on coral reefs subject to adverse environmental conditions, BBD may play an important role in restructuring the community and may be contributing to the demise of these reefs. In order to develop effective coral reef management strategies, high priority must be placed in determining the extent of BBD, and associations between BBD outbreaks and anthropogenic disturbances (Antonius 1995). This study examined the abundance of BBD, its

distribution in time and space, and patterns of disease spread on a coral reef system in Jamaica. Data is presented on coral loss due to BBD, and the short term modifications which have occurred on reefs where BBD has persisted for several years.

MATERIALS AND METHODS

Description of study sites

St. Ann's Bay (18°27'N, 77°12'W) lies on Jamaica's north coast, east of Discovery Bay. The geomorphology of surrounding reefs are similar to descriptions for Ocho Rios, Jamaica (Goreau 1959). This system consists of a well-developed fringing reef with an emergent reef crest 200-500 m seaward of St. Ann's Bay, and a shallow reef terrace along the rocky shore at both ends of the bay (Fig. 1). Shallow reefs examined in this study have been severely degraded over the past two decades. A phase shift (Hughes 1994) from a reef dominated by coral to one with greater than 90% cover of macroalgae exists throughout the back reef. The brown coralline algae *Ralfsia* covers dead corals and limestone substrata, and continues to encroach on the remaining live *M. annularis* and *Diploria* corals. During the 1990's, *Diadema antillarum* began reinvading (1-3/m²) shallow fore reef sites. These sites (Channel, TI, FT) are also subject to sedimentation during storms, and are dominated by *S. siderea*, *M. annularis* and *M. cavernosa*; boring and encrusting sponges, fire coral and tunicates cover much of the dead coral. During September 1995 severe bleaching was observed at all depths; most scleractinian coral species and the hydrozoan coral *Millepora* were affected.

Monitoring program

Temporal abundance and spatial dispersion patterns of corals infected with BBD were examined on 13 fringing reefs near St. Ann's Bay, Jamaica. Disease frequency and progression was visually monitored using long-distance snorkeling and SCUBA surveys. Reefs were examined in July 1991, every 30 days from December 1991 to August 1993, and in September 1995. Weekly monitoring was conducted on four reefs which became heavily infected between December 1991 and August 1993.

All corals infected with BBD were tagged and photographed (Nikonos V) when first found. The disease interface was marked with one or two masonry nails inserted in the tissue-stripped skeleton immediately behind the band. Field observations recorded included length and width of the band, its location on the coral, the direction of disease spread and the general appearance of the coral. For each coral, one infection event refers to the period from initial infection to a time when the coral either dies or visible signs of BBD disappear. Reinfection is defined here as a reappearance of BBD after a period of dormancy.

Twenty non-overlapping study sites were established in December 1991 on four reefs (Lee, TI, FT and UC; 5 sites per reef) to follow the sequence of disease transmission, duration of BBD infections, and the impact on coral survival. Sites were patterned to conform to the reef topography and did not extend into non-coral areas; they encompassed approximately 10% of the total reef terrace. Each site consisted of a circular area (10 m radius, 314 m²) surrounding a central coral. The total number of uninfected or BBD infected colonies of the species *Diploria clivosa*, *Diploria strigosa*, *Montastraea annularis* species complex (*M. annularis* and *M. faveolata*; Weil and Knowlton 1994), *Montastraea cavernosa* and *Siderastrea siderea* was recorded within each site in 1992, 1993 and 1995. Progression of BBD was visually monitored in all sites at 7-14 day intervals between December 1991 and August 1993. BBD corals were photographed when first found, and at 30 day intervals between December 1991 and August 1993. All previously marked corals and newly infected BBD corals were photographed in September 1995.

Spatial pattern analysis

Within each site, the position (compass bearings and distance) of all corals infected with BBD was plotted relative to the central colony. T-square Index of Spatial Pattern (C) and Distance Index of Dispersion (I)

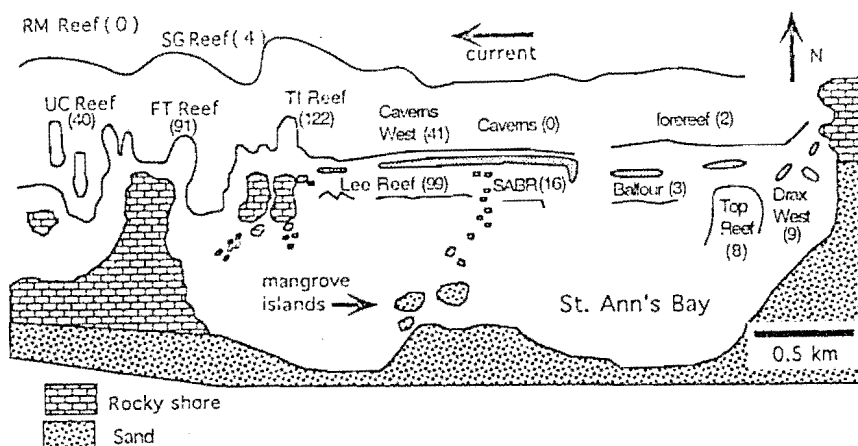


Fig. 1. Coral reefs examined for BBD, located near St. Ann's Bay, Jamaica. Numbers in parenthesis refer to the total number of corals infected with BBD between 1991 and 1995 for each reef.

were used to examine patterning and dispersion of BBD corals. For each coral, calculations involved a comparison of the distance from the center of a study site to an individual coral (point to individual), and the distance to the nearest neighbor with BBD (individual to nearest neighbor). The value of C is approximately 0.5 for random patterns, significantly greater than 0.5 for clumped and less than 0.5 for uniform; the value I is approximately 2 for a random distribution, <2 for uniform, and >2 for clumped. The significance of C and I are obtained using a Z statistic and the probability table for a normal distribution (Ludwig and Reynolds 1988).

Effect of BBD on community structure

To obtain a detailed picture of the reef substrata in 1995, and to assess changes in coral abundance as a result of BBD, field observations were combined with photographs of individual BBD corals and transect data. Photographs of marked BBD corals taken in 1992, 1993 and 1995 were used to estimate the planar surface area of live tissue lost as a result of BBD, and the patch size of remnant coral isolates.

Coral cover and species abundance were estimated using a belt quadrat method. For each reef, adjacent quadrats (each 0.8 m²), along a 10 m line transect were photographed. Transect lines were oriented parallel to bathymetric contours, and did not extend into major sand channels, grooves or *Thalassia* beds. A minimum of two transects were performed on each reef (Lee Reef: rear zone, 1 m depth; FT Reef: shore zone, 4 m; TI Reef: mixed zone, 8 m; SG Reef: buttress zone, 18 m; RM Reef: fore-reef escarpment, 26 m). For each quadrat the number of coral species present, number of colonies of each species and percent cover was obtained. The planar surface area of all corals within quadrats, and sizes of individual BBD corals were determined by projecting 35 mm transparencies and digitizing images using Jandel Sigma Scan. When partial mortality was readily distinguishable, measurements were taken of the original colony, live tissue, exposed skeleton, and area of colonizing organisms. Percent coral cover was obtained by dividing the sum of coral cover values for all quadrats by the total number of quadrats sampled. Diversity statistics were calculated using the number of species and their abundance (H') and percent cover of each species ($H'c$). The evenness index (J') was also calculated for H' and $H'c$.

Statistical analysis

Seasonal variation in BBD abundance and frequency of new infections were examined with a G -test. Changes in abundance of live coral, incidence of BBD and coral mortality due to BBD were compared within a given site, between locations and between depths using a Student's t -test. One-way ANOVA was used to determine if differences existed between reefs for total coral cover, $H'c$, and coral density. To determine whether the number of corals which died between 1992 and 1995 varied between sites, a $R \times C$ Test of Independence (Sokal and Rohlf 1981) was performed using a chi-square test.

RESULTS

Spatial and temporal distribution

Between 1991 and 1995, black-band disease was identified on 342 scleractinian corals of five species on four shallow reefs (20 sites, 6280m²) near St. Ann's Bay, Jamaica. BBD was rare in July 1991 ($n=8$), with infections confined to the back reef (SABR and Lee Reef). The incidence of BBD increased dramatically in 1992 as infections spread throughout the back reef and to fringing reefs located west of Lee reef. The highest incidence of BBD occurred in August 1993 ($n=104$). In 1995, 65 corals were infected with BBD within 20 sites. Over four years, BBD affected <0.5% of the corals located east of Lee Reef. BBD occurred sporadically, and in low numbers (<1 coral/dive) on reefs below 10 m.

The appearance of new BBD infections was compared between seasons using data from 1992–1993, pooled into 3 month periods (J–M, A–J, J–S and O–D). Significant differences existed between seasons ($G=10.42$, $df=3$, $p<0.025$). The highest incidence of new infections (all species) were identified between July and September (33%) and the lowest number of new infections occurred between October and December (17.6%). Examination of separate species indicated significant differences between seasons for *Diploria* (pooled species), and *S. siderea* ($G=7.89$, $p<0.05$), and minor differences for *M. cavernosa* ($G=5.12$, $p<0.25$); no differences existed between seasons for *M. annularis* (mean=4.9, $sd=1.2$; $G=0.28$, $p>0.95$). The greatest number of new infections were found on *Diploria* (52.3%) and *S. siderea* (35%) between July and September. In contrast, *M. cavernosa* (40.2%) became infected most frequently between April and June (Fig. 2).

During a single infection event multiple regions on individual corals became infected (Fig. 3), and infections spread among closely associated corals. T -square analysis (pooled species and individual species) revealed that BBD infections were clumped ($C \geq 0.904$; $Z \geq 3.997$, $p<0.001$). In addition, clusters of BBD infections (pooled species) were uniformly distributed throughout the study sites (Distance Index of dispersion; $I \leq 1.49$).

Community characteristics and BBD impact

The dominant massive coral species showed a significant decrease in colony abundance between 1992 and 1995 (paired t -test, $t=3.1$, $df=79$, $p<0.0025$) in permanent sites (Table 1). The number of corals which died differed between reefs ($R \times C$ Test of Independence, $G=124.4$, $df=9$, $p<0.001$). A higher proportion of *M. annularis* (48.7%) and *Diploria* spp. (55.4%) died in the back reef (Lee Reef). Total mortality of *M. cavernosa* (8.8%) and *S. siderea* (16.6%) was lower; the majority of these species which died were from TI and FT reefs. Few corals (2.2%) died on UC reef during this period.

Analysis of BBD distribution among individual species revealed that colonies of *M. annularis* (morphotype I and II), *D. clivosa* and *D. strigosa* were most frequently infected in the back reef; the majority (>95%) died by 1995. In contrast, *M. cavernosa* and *S. siderea* had a

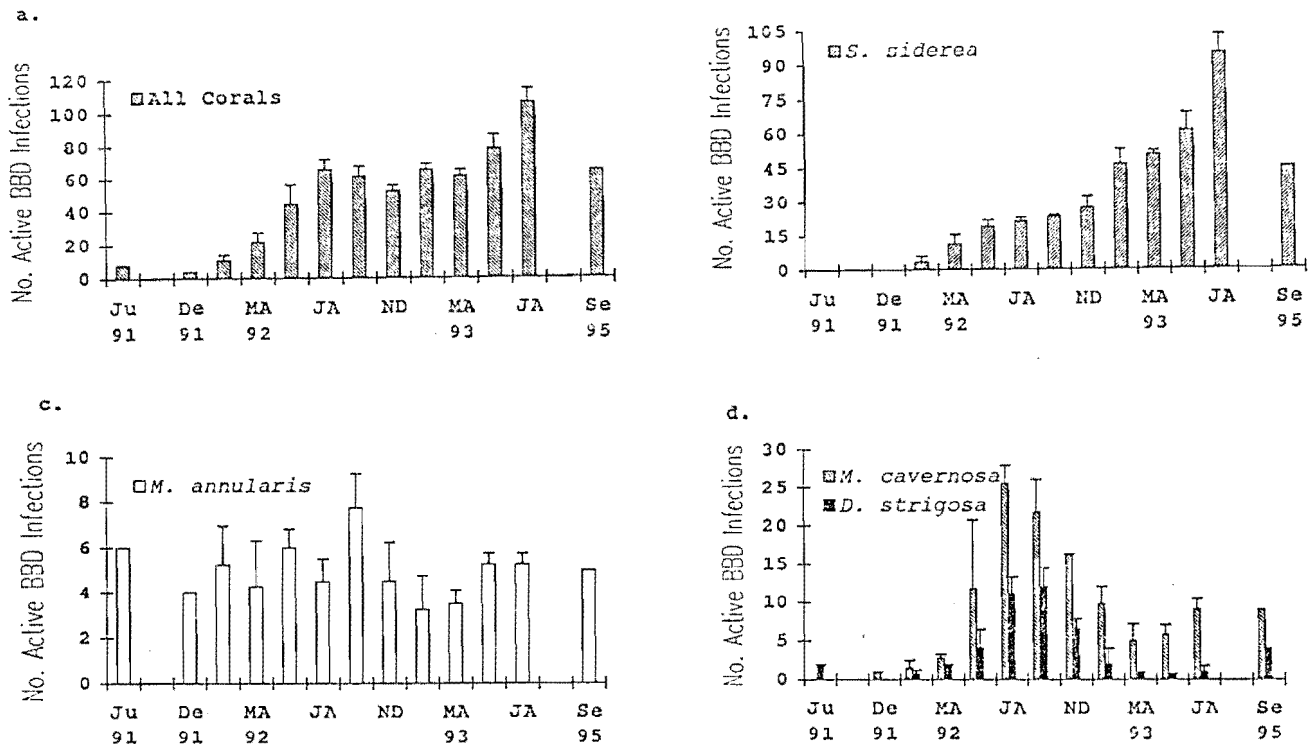


Fig. 2: Temporal variation of BBD infections within 20 sites (6280 m² total area) in St. Ann's Bay, Jamaica. Data for July 1991, December 1991 and September 1995 are from single surveys. Between January 1992 and August 1993 reefs were surveyed at 14 day intervals; each bar indicates the mean incidence of BBD from four surveys. (a) total number of infections on all species; (b) BBD on *S. siderea*; (c) BBD on *M. annularis* (morphotype I and II are pooled); (d) BBD on *M. cavernosa* and *D. strigosa*. Corals were infected with BBD for a mean of 4 months (max=15.5).

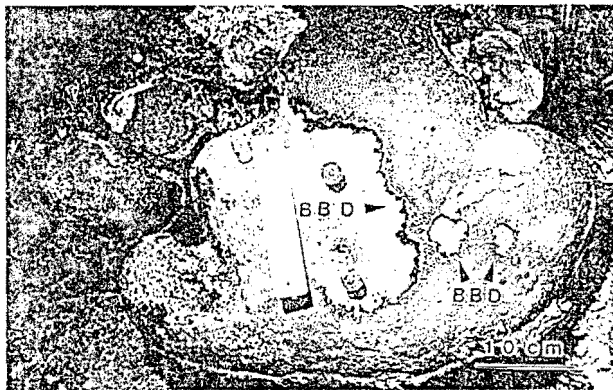


Fig. 3: *Siderastrea siderea* with black-band disease (BBD) photographed on 7/4/92. BBD has infected three separate areas on this coral. This coral died in 1993.

higher incidence of BBD on FT and TI reefs. Individual colonies of these species are larger, and more than 65% were alive in 1995. Total coral counts from 20 sites (pooled for each reef) demonstrate that no significant differences in density exist between the fore reef and back reef for *M. annularis* and *Diploria* spp. (*t*-test, *p*>0.05); *M. cavernosa* and *S. siderea* were more abundant on the fore reef, however (*p*<0.001).

Of those corals infected with BBD, small colonies (mean=239 cm², *sd*=106, *n*=34) died after one infection event, within 1-8 months (mean=3.3, *sd*=2.24). Larger colonies were reduced in size, and often divided into physiological isolates. These corals were infected for up to 15.5 months (mean=4.5, *sd*=2.8); in addition, 11.4% exhibited a reactivation of BBD after a period of dormancy. Plots of size frequency show consistent decreases in the number of large colonies of *S. siderea* and *M. cavernosa*. Colonies of *S. siderea* (infected in 1992 or 1993, alive in 1995) lost 49.9% (*sd*=27.3) of their tissue, with a decline in mean colony area from 2736 cm² to 883 cm² (*t*=12.41, *df*=92, *p*<0.005); 93 colonies consisted of 153 remnant patches of tissue in 1995. Colonies of *M. cavernosa* declined in size by 68% (*sd*=20.7), with a

Table 1: Reduction in coral abundance on four reefs (five 314 m² sites per reef) in St. Ann's Bay, Jamaica between Feb. 1992 and Sep. 1995. Uninfected corals are compared with corals which have been infected with BBD and died. *Diploria strigosa* and *Diploria clivosa* have been pooled. RE = colonies with a reappearance of BBD after a period of dormancy.

species	Uninfected			BBD Infected						Dead BBD corals			
	1992	1995	Loss	92	93	95	RE	Total	%	92	93	95	Tot
<i>S. siderea</i>	2160	1791	17%	50	147	43	21	217	9.5	0	3	94	97
<i>M. cavernosa</i>	1745	1609	9%	41	25	13	8	62	3.4	5	5	11	21
<i>M. annularis</i>	1348	1115	17%	17	12	5	6	33	2.4	9	4	14	26
<i>Diploria</i> sp	301	229	24%	20	6	4	4	27	8.2	6	3	11	20
Total	5564	4744	15%	118	190	65	39	342	6.1	19	15	130	164

decrease in mean size from 2123 cm² to 469 cm² ($t=17.59$, $df=47$, $p<0.005$); 48 colonies have been subdivided into 74 patches of tissue. The smallest measured area of live tissue is 7.5 cm² (Fig. 4).

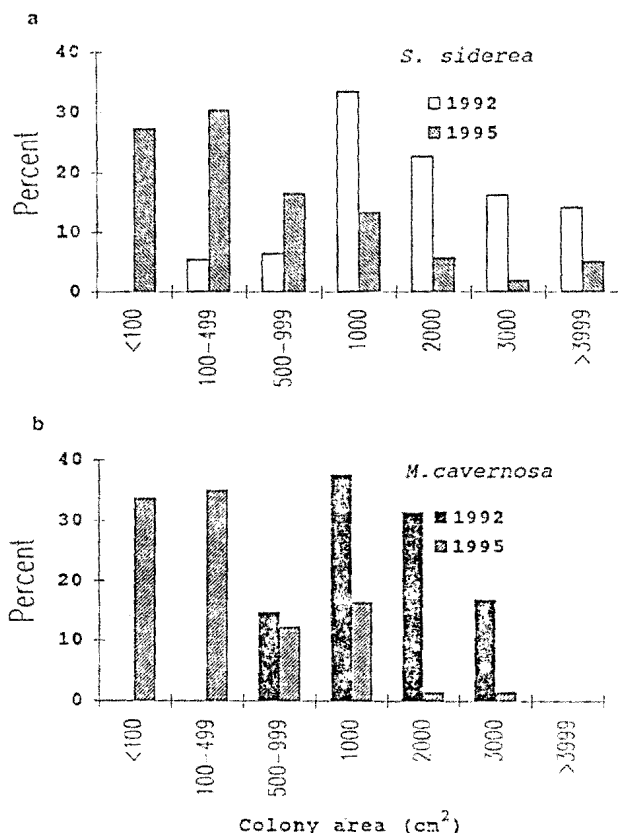


Fig. 4: Size distributions (planar surface area) of corals infected with BBD prior to 1995. Data was pooled from 20 sites and is presented as the percentage each size class contributes to the total. (a) original area of *S. siderea* in 1992 ($n=93$) and tissue remaining in 1995, after BBD disappeared; (b) size of *M. cavernosa* in 1992 ($n=48$) and in 1995.

Blocks of reef photographed along line transects at 5 depth contours were used to estimate coral abundance, species diversity and appearance of individual corals (Table 2). Coral diversity (H') increased from the back reef to the fore reef (SG), decreasing slightly on the fore reef escarpment (RM). Species richness and evenness (J') follows this pattern. With the exception of SG, reef coral cover was positively correlated to H' . SG reef was characterized by a high density of small corals, while FT, TI and RM are dominated by a low density of large colonies of few species. On RM reef *Agaricia* were lumped as a single genera, thus H' must be regarded with caution. In all photoquadrats, macroalgae occupied >40% of the substrata (42-91%); algal overgrowth of corals was most pronounced on Lee and SG reefs. Live *S. siderea* (37.7%) and *M. cavernosa* (35.3%) colonies from FT and TI photoquadrats had been reduced in size, and often were subdivided into several physiological isolates; exposed skeleton was colonized by sponges (26.4%), tunicates (4.1%), other cnidarians (especially *Millepora complanata*) (9.9%) and algal turf (59.6%). On reefs severely impacted by BBD (Lee, TI and FT) >85% of the live coral cover consists of the three genera most frequently infected with BBD.

Table 2: Comparison of BBD abundance and coral cover from 5 reefs near St. Ann's Bay, Jamaica. Percent cover is followed by total number of corals which became infected between 1992-1995 (in parenthesis). No BBD was observed on RM reef. Cover was determined planimetrically from adjacent photoquadrats taken in 1995.

	Reef Depth	Lee (1m)	FT (4m)	TI (8m)	SG (18m)	RM (26m)
<i>S. siderea</i>		1.1(53)	8.4(58)	13.4(83)	1.5(2)	0
<i>M. cavernosa</i>		0.1 (4)	1.1(29)	2.4(29)	2.2(1)	0.9
<i>M. annularis</i>		2.8(36)	1.1 (3)	0.7 (5)	6.3(1)	3.6
<i>Diploria</i>		1.2(22)	0.8 (0)	0.1 (2)	1.5(0)	0.7
Other		0.1 (0)	2.0 (1)	2.3 (9)	10.3(0)	16.6
Total:						
coral cover (%)		5.3	12.5	19.9	21.8	21.8
corals w/ BBD		115	91	129	4	0
no. species		8	9	9	17	13
Density (#corals/m ²)		5.8	2.7	3.4	13.9	2.5
Diversity						
H'		1.24	1.41	1.57	1.9	1.75
H' c		0.28	0.26	0.55	0.35	0.56
Evenness (J')						
H'/H_{max}		0.59	0.64	0.71	0.79	0.68
H'_c/H_{max}		0.14	0.12	0.24	0.15	0.22

DISCUSSION

Over the last sixteen years a steadily increasing number of disturbance events have been documented in Jamaica; these include storm damage, urchin mass mortality, depletion of fish populations, rampant increases in algal biomass and coral bleaching events. These perturbations have resulted in considerable loss of live coral (Goreau 1992; Hughes 1994). Between 1992 and 1995 (3.5 years) the population of massive corals was reduced by an additional 15% on four reefs near St. Ann's Bay. We provide evidence that BBD is a significant factor in the recent decline of live coral on these reefs.

Black-band disease was infrequently reported from Jamaica prior to 1992. Liddell and Ohlhorst (1992) observed BBD on the north coast of Jamaica and noted that infections were sporadic and occurred at low frequencies. Since 1992, we have documented a high incidence of BBD on widely separated, shallow (<5m) reefs located between Ocho Rios and Runaway Bay, Jamaica, suggesting that BBD has greatly increased during the 1990's. In addition, permanent monitoring has demonstrated that BBD, once it invades a reef, will persist for several years, slowly spreading throughout the population (Bruckner et al. in press).

The localized intercolonial and intracolonial spread of BBD observed in this study suggest that BBD is readily transmissible from one individual to another. Single infection events resulted in the death of small colonies in 1-8 months. After the initial appearance of BBD on one reef, the disease was dispersed to neighboring corals, especially those colonies attached by contiguous skeleton, but unconnected by live tissue (Bruckner et al. in press). Dispersal analysis (T-square index of spatial pattern and distance index of dispersion) revealed that the spread of BBD resulted in a clumped distribution of BBD infections, with clusters of BBD corals uniformly distributed throughout the reef.

On large corals, black-band disease often did not cause immediate colony death. The loss of tissue may affect growth, resistance to injuries and other diseases, reproductive capacity and the ability to compete with other organisms, however. During initial infections, BBD removed small areas of tissue, and often divided individual corals into several isolated remnant colonies. This resulted in an increase in the abundance of small colonies of *M. cavernosa* and *S. siderea* on some reefs. Tissue regeneration after termination of BBD has never been observed in this study. Photographs of BBD corals taken over several years indicate that smaller colonies resulting from BBD continue to decrease in size and eventually die after repeat infection events.

Damage from BBD appeared to render colonies vulnerable to competitors, predators and other pathogens. Coral skeleton exposed by BBD was initially colonized by filamentous algae. In the back reef, bare substrata was later colonized by turf algae and crustose *Ralfsia*. This alga initially invaded the eastern end of the back reef

(SAER), and has progressively spread throughout the back reef and shallow fore reef. Some sites (TI, FT and UC, <7 m) have exhibited reduced macroalgal abundance, which may be attributed to an increase in *D. antillarum* populations noted between 1992 and 1995 (pers. obs.); urchins were conspicuously absent from the back reef during all surveys. Sponges (especially *Cliona* and *Anthosigmella*), tunicates (*Trididemnum*) and other cnidarians (*Millepora*) have colonized tissue-stripped corals on the fore reef. Continued replacement of live coral by encrusting and bioeroding invertebrates and macroalgae may lead to an eventual breakdown of the coral reef structure. Furthermore, Chornesky and Peters (1987) noted that a coral's reproductive status and reproductive output is size dependent, with colonies becoming sexually productive upon reaching a threshold size. Disease events, like those observed in Jamaica, may push a reproductively active colony below the minimum size necessary for it to reproduce. No sexual recruits of the dominant massive corals were identified in our study sites.

Black-band disease is a major factor responsible for the continued reduction of live coral on reefs near St. Ann's Bay, Jamaica during the 1990's. This study demonstrates that a substantial (abnormally high) mortality of corals was observed over a short duration (3.5 years) on four shallow reefs; loss of coral was greatest in the back reef. These reefs have been exposed to physiological and environmental stresses (Goreau 1992; Hughes 1994), and many of the corals which died were greatly reduced in size prior to this study. In addition, living corals here are subject to a slow, progressive overgrowth by macroalgae. Black-band disease has been observed on 6.1% of the massive corals; nearly one half have since died. The disease abundance presented in this study is most likely an underestimate, as census data was not collected between Sept 1993 and Aug 1995. Thus, the effects of BBD may be more severe than documented.

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REFERENCES

- Antonius A (1973) New observations on coral destruction in reefs. 10th Meeting Assoc Isl Mar Lab Carib 10:3
- Antonius A (1985a) Coral diseases in the Indo Pacific: a first record. PSZNI (Mar Ecol) 6:197-218
- Antonius A (1985b) Black band disease infection experiments on hexacorals and octocorals. Proc Fifth Int Coral Reef Symp 6:155-160
- Antonius A (1988) Black band disease behavior on Red Sea reef corals. Proc Sixth Coral Reef Symp 3:145-150
- Antonius A (1995) Incidence and prevalence of coral diseases on coral reefs-what progress in research? Coral Reefs 14:224
- Bruckner AW, Bruckner RJ, Williams EH (in press) Spread of a black-band disease epizootic through the coral reef system in St. Ann's Bay, Jamaica. Bull Mar Sci
- Carlton RG, Richardson LL (1995) Oxygen and sulfide dynamics in a horizontally migrating cyanobacterial mat: Black band disease of corals. FEMS Microbiol Ecol 18:155-162
- Chornesky EA, Peters EC (1987) Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol Bull 172:161-177
- Edmunds PJ (1991) Extent and effect of black band disease on a Caribbean reef. Coral Reefs 10:161-165
- Feingold JS (1988) Ecological studies of a cyanobacterial infection on the Caribbean sea plume *Pseudopterigorgia acerosa* (Coelenterata: Octocorallia). Proc Sixth Int Coral Reef Symp 3:157-162
- Garrett P, Ducklow H (1975) Coral Diseases in Bermuda. Nature 253:349-350
- Goreau TF (1959) The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology 40:67-89
- Goreau TJ (1992) Bleaching and reef community change in Jamaica: 1951-1991. Amer Zool 32:683-695
- Hughes TP (1994) Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef. Science 265:1547-1549
- Liddell WD, Ohlhorst SL (1992) Ten years of disturbance and change on a Jamaican fringing reef. Proc Seventh Int Coral Reef Symp 1:144-150
- Ludwig JA, Reynolds JF (1988) Statistical Ecology. John Wiley & Sons, New York pp 55-63
- Miller I (1996) Black band disease on the Great Barrier Reef. Coral Reefs 15:58
- Peters EC (1993) Diseases of other invertebrate phyla: Porifera, cnidaria, actinophora, annelida, echinodermata. In: Fournie CA (ed) Adv Fish Science, Pathology of Marine and Estuarine Organisms. CRC Press, pp 393-449
- Porter JW, Meier GW (1992) Quantification of loss and change in Floridian reef coral populations. Amer Zool 32:625-640
- Rützler K, Santavy DL (1983) The black band disease of Atlantic reef corals. I. Description of the cyanophyte pathogen. PSZNI (Mar Ecol) 4:301-319
- Rützler K, Santavy DL, Antonius A (1983) The black band disease of Atlantic reef corals. III. Distribution, ecology and development. PSZNI (Mar Ecol) 4:329-358
- Sokal RR, Rohlf FJ (1981) Biometry. W.H. Freeman, New York pp 691-778.
- Weil E, Knowlton N (1994) A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). Bull Mar Sci 55:151-175.
- Williams EH, Bunkley-Williams L (1990) The world-wide coral reef bleaching cycle and related sources of coral mortality. Atoll Res Bull (Smithsonian) 335:1-71