

Geographic variability in the incidence of coral and octocoral diseases in the wider Caribbean

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ABSTRACT

Lack of base-line information on the epizootiology and the spatial and temporal variability of most coral diseases/syndromes prevents accurate interpretations of their potential effects on coral reefs. Here, we present quantitative results on the incidence of all diseases/syndromes found in 19 reef sites from six geographic areas across the wider Caribbean. We compare the pathogenesis of the common diseases/syndromes and their variability at geographic scales. Data were collected between August and December of 1999 to avoid seasonal variability. The CARICOMP coral disease protocol was used. All coral and octocoral colonies were counted and checked for diseases/syndromes in up to twelve, 40 m² (20 x 2) band-transects laid over the bottom of at least two reef sites in each geographic locality. Overall, the average incidence of diseases was low at the coral community level (3.02%) and varied significantly (0.40-0.78%) across sites. White Plague-II (WP-II), Yellow Blotch Disease (YBD), Black Band Disease (BBD), and Aspergillosis (ASP) were present in all geographic areas sampled. Aspergillosis showed the highest incidence at both the community (0.60-5.94%) and population (*Gorgonia ventalina*) level (5.56-30.56%). Thirty eight reef-building coral species were susceptible to at least one disease/syndrome. WP-II affected the highest number of species (32), followed by BBD (16), Dark Spots Disease (DSD) (12), YBD (6) and White Band Disease (WBD) (3). All four *Montastraea* spp and *Colpophyllia natans* were each affected by five syndromes. Aspergillosis infected ten species from six genera of octocorals, a significant increase from the 2 susceptible sea fan species reported until now. These results show that even though the incidence rates were low at the community level, the high number of important reef-building species affected, the widespread distribution of most diseases/syndromes, and their wide host breadth present a potential problem for coral reef communities throughout the Caribbean. More frequent epizootic events coupled with current trends in reef degradation might be a lethal combination for the future of these communities. However, before we speculate what the outcome of the current events might be, we need more information and epidemiological models developed with sound quantitative data.

Keywords Corals, Diseases, Geographic variability, Caribbean

Introduction

Over the past decades coral reef communities around the world have been experiencing increasingly stressful conditions due to a combination of natural and anthropogenic detrimental factors (Epstein et al. 1998). The Caribbean in particular is viewed as a disease "hot spot" due to the increase in frequency of epizootic events and fast emergence of "new" diseases associated with corals, octocorals, and other reef organisms. A relationship between these events with the deterioration of marine environmental conditions and higher incidence of African dust clouds moving into the Caribbean in recent times have been suggested (Peters 1997, Goreau et al. 1998, Antonius and Ballesteros 1998, Geiser et al. 1998, Harvell et al. 1999).

Widespread and/or virulent epizootics can play important roles in the deterioration and/or changes in community composition, structure, and dynamics at local and geographic scales. The mass mortality events of the long-spined sea urchin *Diadema antillarum* (Lessios et al. 1984) and corals (Gladfelter 1982, Bythell and Sheppard 1993) brought about substantial changes in coral reef communities throughout the Caribbean (Lessios 1988, Hughes 1994, Aronson and Precht 1997).

The inability to explain the source and sudden emergence of the majority of the coral/octocoral diseases/syndromes (but Hayes and Goreau 1998 and Harvell et al. 1999) is just one of the problems in this field. Most diseases have been named according to their ecological characteristics (not pathology) creating confusion in the number of diseases/syndromes present. Eventhough reef-related diseases have been identified and described for some time (i.e. Antonius 1981a,b, Garret and Ducklow 1975, Mitchell and Chet 1975, Gladfelter 1982, Peters et al. 1983, Taylor 1983, Goldberg et al. 1984), only recently have a number of cnidarian diseases been studied in some detail. Only four of the seventeen coral/octocoral diseases/syndromes put forward by researchers have their causative agents identified. These are: Black Band Disease (Antonius 1981b, Garret and Ducklow 1975, Ducklow and Mitchell 1979, Rützler and Santavy 1983, Richardson et al. 1997), White Plague type II (Richardson et al. 1998a), Aspergillosis (Smith et al. 1996, 1998), and White Band Disease type II (Ritchie and Smith 1998). The mechanism causing the host tissue mortality is only known for BBD (Richardson et al. 1997). General aspects of coral diseases have been reviewed by Peters (1997), Santavy and Peters (1997), Goreau et al. (1998) and Hayes and Goreau (1998). Coral disease etiology was reviewed by Richardson (1998). Most recently, Green and Bruckner (2000) summarized all the information available on the epizootiology of coral and octocoral diseases.

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There is limited (or lack of) quantitative data and information on the pathology and etiology of most diseases, as well as on their spatial and temporal variability in incidence, pathogenesis, and their local and geographic distribution. Without this information, it is difficult to assess changes in the disease/syndromes' temporal and spatial distribution, epidemiology, and potential detrimental effects at population and community levels at local and regional geographic scales. This study is part of an effort to increase the information available for some of these aspects. Here, we present quantitative results of the number and incidence of different diseases/syndromes from 19 reef sites in 6 geographic localities across the wider Caribbean, and compare the pathogenesis of the different diseases/syndromes and their variability across geographic localities.

Methods

Geographic locations

Nineteen reef sites were sampled in six geographic locations (Table 1, Fig. 1) between August and December of 1999. The geographic distribution covers a latitudinal gradient from Bermuda to Venezuela and Colombia; and from the north-eastern (Puerto Rico) and south-central Caribbean (Venezuela and Bonaire) to the north- (Jamaica) and south-western Caribbean (San Andres, Santa Marta and Rosario islands in Colombia). In each of the six geographic localities, at least two reefs or coral communities were quantitatively sampled. In most sites, one of the reefs selected was a CARICOMP (1998) reef site.

Survey methods

A preliminary qualitative, visual assessment for the presence of diseases and their depth distribution was conducted in the different sites. Then, a modified version of the disease-survey-protocol developed by CARICOMP was used to quantify: (1) presence of the different coral and octocoral diseases/syndromes, and (2) the average proportion of colonies of each coral/octocoral species infected by each particular disease. Between six and fourteen belt-transects ($20 \times 2 \text{ m} = 40 \text{ m}^2$ each) were laid out haphazardly over the reef. For those reefs with a vertical profile, 3 depth intervals were selected (0-5 m; 5.1-12 m and 12.1-18 m) to include major reef habitats/zones. In most sites, rebars were hammered into the substrate and tagged with flagging tape to mark the positions of the belt-transects for future monitoring. At least three belt transects were surveyed at each depth interval.

A set of bilingual underwater-laminated cards with descriptions and photographs of the diseases (published by Bruckner, Bruckner and Weil) was used as a guide to standardize identification of the different diseases and other causes of coral mortality. The sample unit was one colony (ramet). All scleractinian corals, hydrocorals and octocorals were included in the survey in which each

colony was checked for the presence of any of the described diseases/syndromes and/or injuries. All scleractinian and hydrocoral species were identified to species, but only the sea fans (*Gorgonia* spp.) and *Pseudopterogorgia americana* were distinguished amongst the octocorals.

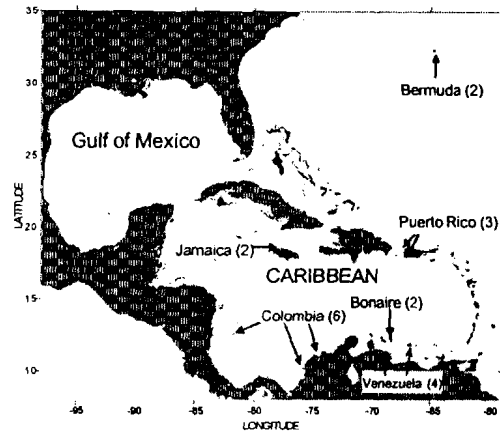


Fig. 1 Map of the Caribbean showing geographic locations where the surveys were conducted. Numbers in parentheses represent the number of reef sites sampled in each location.

The white and yellow syndromes (WBD, WP-II and YBD) were carefully checked to avoid confusion with bleaching signs. If the colony did not have any of the disease/syndrome signs, it was considered to be healthy. If the colony had old injuries (over many months) or dead areas (partial mortality) already colonized by algae or other benthic organism but without any signs of being stressed or of degenerating tissue, it was considered to be healthy. If a colony had a disease plus any of the other afflictions (bleaching or injuries) it was included in the disease category. Notes about the other signs were taken. Those syndromes that did not fit the current descriptions were included in a category termed "Other". Few, well-trained individuals participated in the data collection to reduce errors. Data were frequently checked by surveying transects twice.

The proportion of colonies in each category (healthy, injured, and affected by each of the diseases) was calculated for each transect as the pooled occurrence of each condition in all coral (or octocoral) colonies affected, normalized against the total number of coral colonies (or octocoral colonies) for each transect. Then, the average proportion (standard deviation and standard error) of colonies affected by each syndrome for each geographic locality was calculated from the pooled transects in each geographic locality. With the exception of Aspergillois in *Gorgonia ventalina*, in this report we compare average disease incidences and their variability across geographic localities at the community level only. Significant differences were tested with parametric and non-parametric (if data did not fulfill conditions) ANOVAS (Kruskal-Wallis and Dunn's test). Percentage data were transformed with the arcsine function.

Table 1 Summary of relative proportions of corals and octocorals affected by diseases at all reef sites (ordered from north to south) surveyed. IROS1 and IROS2 = Islas del Rosario. N/A= category not included in survey. Missing values refer to sites where disease was not observed or susceptible species not present. Values for physically injured and bleached colonies not included. BBD= Black Band Disease; WBD= White Band Disease; WP-II= White Plague type II; DSD= Dark Spots Disease; Other= other unidentified syndromes.

Country	Locality	Latitude	Longitude	Depth M	Corals								Octocorals	
					Healthy col	Disease col	% YBD col	% WP col	% DSD col	% WBD col	% BBD col	% Other col	Healthy col	% ASP col
Bermuda	HBreakers	32°27.55	64°49.89	8-10	97.13	1.04	0.06	0.26			0.48	0.24	99.32	0.68
	Cathedral	32°20.45	64°39.50	8-10	96.53	0.48	0.02	0.11			0.17	0.19	99.4	0.60
Prico	Desecheo	18°22.69	67°29.04	2-22	89.04	3.25	1.98	0.81	0.22	0.00	6.79	0.08	94.06	5.94
	Laurel	17°58.19	67°03.59	0.8-6	82.75	0.74	0.19	0.19	0.32	0.00	0.03	0.00	95.62	4.38
	Turumote	17°56.06	67°01.07	0.8-17	89.94	0.71	0.20	0.16	0.29	0.07	0.00	0.00	97.87	2.13
Jamaica	DBay	18°28.41	77°24.94	5-18	66.63	5.31	1.11	3.20	0.00	0.42	1.11	13.68	N/A	N/A
	StAnn	18°26.90	77°12.63	5-18	93.59	0.07	0.14	0.00	0.00	0.00	0.00	3.90	N/A	N/A
Bonaire	CARIC	12°11.76	68°18.13	2-18	95.36	0.90	0.40	0.03	0.33	0.13	0.00	0.70	96.39	3.61
	MargateB	12°03.08	68°16.30	3-17	92.09	5.94	4.66	0.37	0.66	0.09	0.17	0.40	97.92	2.08
Colombia	SAndres1	12°30.78	81°43.46	1.5-5	73.17	9.78	0.35	1.67	7.61	0.00	0.16	N/A	N/A	N/A
	SAndres2	12°30.05	81°44.03	1.5-5	84.50	7.52	0.27	2.03	5.23	0.00	0.05	N/A	N/A	N/A
	SMarta1	11°19.48	74°07.41	1.5-5	93.85	3.11	0.00	0.18	0.16	0.07	0.00	N/A	N/A	N/A
	SMarta2	11°19.32	74°07.40	1.5-5	94.39	1.77	0.07	1.12	0.70	0.16	0.00	N/A	N/A	N/A
	Iros1	10°14.03	75°44.47	1.5-5	82.66	0.27	0.00	0.11	0.23	0.07	0.05	N/A	N/A	N/A
	Iros2	10°10.24	75°46.14	1.5-5	81.54	2.10	0.23	1.06	0.81	0.00	0.00	N/A	N/A	N/A
Venezuela	LRoques1	11°47.54	66°53.64	3-17	94.96	2.67	0.18	0.31	1.66	0.00	0.09	0.43	94.55	5.45
	LRoques2	11°47.58	66°53.83	1-18	91.60	2.78	0.00	0.27	1.41	0.27	0.18	0.64	100	0.00
	Sombrero	10°52.16	68°12.90	3-17	85.56	4.06	2.25	0.76	1.05		0.00	0.00	98.52	1.48
	CNorte	10°46.09	68°12.30	2-10	83.74	4.78	1.99	1.99	0.80		0.00	0.00	100	0.00
Average					87.84	3.02	0.74	0.77	1.26	0.08	0.49	0.79	90.45	2.40
SE					1.88	0.61	0.28	0.20	0.49	0.03	0.36	0.38	2.61	0.65
SD					7.98	2.60	1.17	0.86	1.98	0.12	1.51	1.30	8.24	0.65

Results

Overall, White Plague-II (WP-II), Yellow Blotch Disease (YBD), Black Band Disease (BBD), and Aspergillosis (ASP) were present in all geographic areas sampled (Table 1, Figs. 2B and 3). Although observed in Jamaica and Colombia, ASP was not included in the quantitative surveys in these localities. Dark Spots Disease (DSD) was observed in 79% of all sites sampled (with susceptible species present in all localities). WBD was observed in 42% of the sites. The average incidence of diseases at the community level was generally low (3.02% of all coral colonies affected) and varied (0.07-9.78%) significantly across reef sites (Table 1). San Andres had a significantly higher average incidence of coral diseases compared to the other geographic locations (Table 1), mostly due to a high DSD incidence. The average disease incidence increased significantly from north to south in the wider Caribbean (Fig. 2A). The average incidence of individual diseases was low overall for the Caribbean and varied significantly across

geographic areas. Aspergillosis showed the highest average incidence with 2.40% (0.60-5.94%) infected colonies of all octocorals surveyed. DSD had the highest average incidence amongst scleractinian diseases with 1.26% (0.16-7.61%) of all coral colonies surveyed, followed by WP-II with 0.77% (0.11-3.20%), and WBD with 0.08% (0.07-0.41%) (Table 1).

Puerto Rico had a significantly higher average incidence of ASP at the community level (Fig. 2B), however, populations of *G. ventalina* were more affected in Bonaire, Venezuela, and Bermuda (Table 2). Significant differences in average incidence between the geographic areas were found for each disease/syndrome (Fig. 3). WP-II had the highest average incidence in Jamaica ($1.46 \pm 1.69\%$) and Colombia ($1.24 \pm 1.78\%$). DSD had the highest incidence in Colombia ($2.67 \pm 5.38\%$) and Venezuela ($1.15 \pm 1.67\%$) *Siderastrea siderea* and *Stephanocoenia intersepta* were the two species most affected. YBD was higher in Bonaire ($2.82 \pm 4.38\%$) and Venezuela ($1.65 \pm 4.16\%$). WBD had the lowest

incidence at the community level with the highest average incidence in Jamaica ($0.4 \pm 1.14\%$). Results also show that disease incidences at the community level were generally low and highly variable geographically indicating patchy distributions of the affected colonies.

Observations of several reef sites within a geographic location showed that one or two reef sites had a high incidence of one or several diseases, while other sites were healthy. Also, for particular diseases (YBD), high incidences were observed in restricted depth intervals, while the rest of the community was not affected.

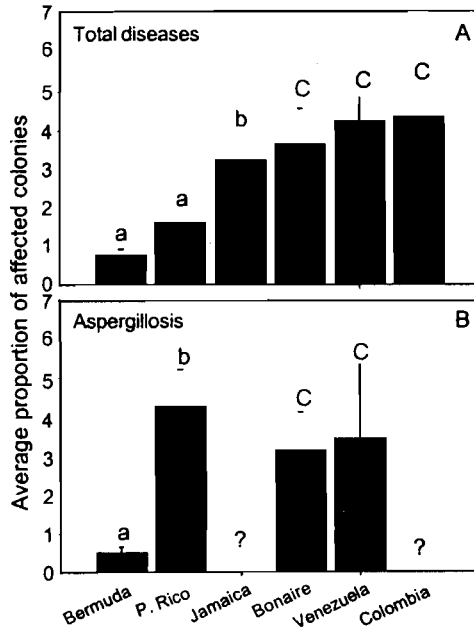


Fig. 2 Average proportion of affected colonies in each geographic locality. (A) is the average for the pooled diseases for the coral community, and (B) is the incidence of Aspergillosis in the octocoral community in the different geographic areas. Different letters between bars represent significantly different incidence rates (K-W, $P < 0.01$).

A total of thirty eight scleractinian species and ten octocoral species were observed to be affected by at least one disease/syndrome in the areas surveyed (Fig. 4A). WP-II affected the highest number of coral species (32) and two hydrocorals, followed by BBD (16), DSD (12), ASP (10+), YBD (6) and WBD (3). The number and taxonomic compositions of species affected varied at local and geographic scales. Most of the important reef building species in the Caribbean were affected by at least one disease.

Five important, reef building coral species (all members of the genus *Montastraea*, plus *Colpophyllia natans*) were each affected by five diseases/syndromes. Of the four species of *Montastraea*, *M. annularis* showed the highest incidences (5.45-12.58%) across geographic locations followed by *M. faveolata* (4.65-10.37%), *M. franksi* (1.1-5.6%), and *M. cavernosa* (0.15-5.99%). *Colpophyllia amaranthus* and *Diploria labyrinthiformis*

were affected by 4 diseases each, *D. strigosa*, *Mycetophyllia ferox* and *Stephanocoenia intersepta* were affected by three different syndromes, ten other species were affected by two, and nineteen by one disease only (Fig. 4B). Puerto Rico had the highest number of major reef building species affected, but some of these species had their highest disease incidences in Colombian reefs in the southwestern Caribbean.

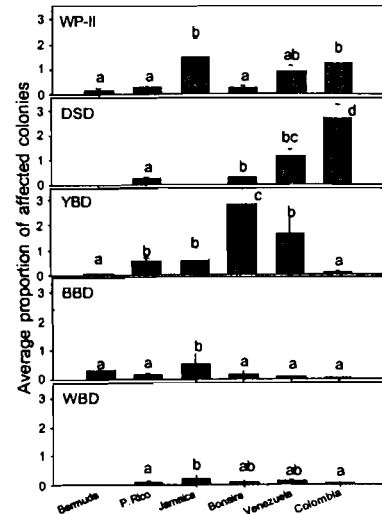


Fig. 3 Average proportion of affected colonies (incidence) for each disease within the coral community present at the different geographic locations depicted. Different letters represent significantly different incidence rates (K-W, $P < 0.01$). WP-II= White Plague-II, DSD= Dark Spots Disease, YBD= Yellow Blotch Disease, BBD= Black Band Disease, WBD= White Band Disease

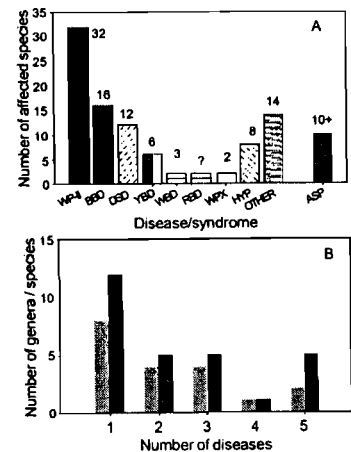


Fig. 4 (A) Number of scleractinian corals and octocoral species affected by each of the major diseases/syndromes. WP-II= White Plague-II, BBD= Black Band Disease, DSD= Dark Spots Disease, YBD= Yellow Blotch Disease, WBD= White Band Disease, RBD= Red Band Disease, WPX= White Pox, HYP = Hyperplasias, ASP= Aspergillosis, OTHER= includes all corals with signs that could not be classified as any of the diseases or syndromes. (B) Number of coral genera (gray) and species (black) affected by one or more diseases.

Discussion

The Caribbean is viewed as a disease "hot spot" because of both the emergence of a relatively high number of new diseases/syndromes associated with reef organisms, and the increase in the frequency of known disease epizootics (Harvell et al. 1999). The causes and consequences of the emergence and higher frequencies of epizootic events remain obscure (but see Antonius and Ballesteros 1998, Hayes and Goreau 1998, Harvell et al. 1999). However, there are several recent examples that indicate that wide-spread, virulent epizootics can play important roles in the deterioration of, and/or change in, coral reef community composition, structure, and dynamics at local, geographic, and temporal scales. These include the *Acropora* (WBD-I) and *Diadema antillarum* mass mortality events of the 1980s, and the *Gorgonia* mortality event of the 1990s (Gladfelter 1982, Lessios 1988, Garzon-Ferreira and Zea 1992, Hughes 1994, Aronson and Precht 1997).

The possibility that an increase in the number of new syndromes, and in the frequency of events of known epizootics, could eventually bring about the demise of some coral reef communities in the Caribbean has been suggested (Porter and Meier 1992, Porter et al. 1999). Current trends in the deterioration of reef communities (Epstein et al. 1998, Goreau et al. 1998), and the high rate of emergence of new syndromes/diseases (Harvell et al. 1999), leads to speculation about a potential scenario in which some of these syndromes may become epidemic and significantly reduce populations of many of the major reef building species at local and geographic scales, accelerating the degradation of these communities. However, more information on the epizootiology of all diseases/syndromes supplemented by quantitative monitoring programs are needed to support such speculation.

All major diseases/syndromes described today are widespread throughout the Caribbean and are affecting populations of the most important reef-building species in the region. Our observations expand the geographic distribution of YBD, WP-II, and ASP to include Bermuda (the northern-most zone of coral reefs of the Western Atlantic), and several localities in the south and western Caribbean. The absence of some syndromes in some sites could be related to the pathogen's dispersion capabilities, or the result of limiting or more extreme environmental conditions (DSD for example, was not observed in Bermuda even though several of the species susceptible to this syndrome were present). There may also be resistance to the pathogen by a local host population, or the particular host(s) might not be present (for example WBD has only been reported to infect acroporids, which are not found in Bermuda). Alternatively, host populations may have been significantly reduced as was the case for the southern Caribbean where the WBD epidemic of the 1980s decimated most of the acroporid populations.

Local patchiness of diseases within a single coral community is probably related to the local distribution of the host species in the depth gradient, the sensitivity of the pathogen to changing conditions, by a particular

clonal population or group of host colonies, and/or water current patterns present. Distribution patterns for BBD were reported to be random in the Virgin Islands (Edmunds 1991), but clumped in the Florida Keys (Kuta and Richardson 1997), and Jamaica (Bruckner and Bruckner 1997). With the exception of Desecheo island, to the west of Puerto Rico, which had the highest BBD incidence (6.79%) of all the sites surveyed, levels of incidence of this disease were very low throughout the geographic localities sampled. Incidence levels reported in other areas (1-10%) for BBD (Green and Bruckner 2000) were higher than the ones found in this study. In 1996, 8-10% of *Diploria* corals were infected with BBD, YBD was rare, and WP-II was not observed in the back reef area of Mona Island, Puerto Rico. In 1999 however, the distribution and incidence of these diseases increased in the fore reef. In the early 1990s, St. Ann's Bay in Jamaica had high incidences of BBD (Bruckner and Bruckner 1997), however, a repeat survey showed no colonies affected in late 1999 (Bruckner and Bruckner 1999). Either the colonies were dead, the disease was in remission, or the same areas were not sampled. In Bermuda, surveys conducted in 1998 by McKinney showed low levels of disease (0.1-0.365%) in all localities sampled with BBD the most common disease affecting 0.8% of the susceptible species, compared to 0.17 %-0.48% in this study.

Yellow Blotch Disease showed higher incidences in Bonaire and Venezuela where we also observed a high proportion of recently dead ramets of *M. annularis* that most probably died from the disease. High incidences of YBD have been reported mainly for the *Montastraea* spp. complex in Panama, the Florida Keys, Curacao, and Mona Island (Bruckner and Bruckner 1999). Between 1996 and 1999, YBD incidence levels in Mona island increased from less than 1% to 50%. This island is far away from any major, direct anthropogenic perturbation.

White Plague type II had the highest average incidence in Jamaica and Colombia. Lack of quantitative information about average incidences in other areas limit the interpretation of our results. However, Richardson et al. (1998a) indicated that between 9 and 38% of all colonies of *Dichocoenia stockesii* were infected by WP-II on reefs surveyed in the northern Florida Keys. White Band Disease showed, in general, the lowest incidences at the community level. The highest average incidence was found in Jamaica ($0.4 \pm 1.14\%$). Some sites with reduced populations of acroporids showed a few colonies infected which translated into high incidences at the population level for *A. cervicornis* (39.58% in Colombia) and *A. palmata* (14.9 and 28.13% in Colombia and Venezuela respectively). These values are similar to those reported in the 1980s (Gladfelter 1982). In Puerto Rico and Bonaire for example, populations of these two species were found to be in good shape with large numbers of colonies, and the average incidence of WBD was significantly lower for both species (data will be published elsewhere).

Previous reports stated that most coral diseases affect only a few species (Goreau et al. 1998), however, results from this study and other reports (Richardson et al. 1998a,

Green and Bruckner 2000), show that the total number of species affected is increasing and varies geographically, and that host breadth of most diseases is wider than previously thought. We found 38 important reef-building scleractinian species affected by at least one disease/syndrome. WP-II had the widest host range with 32 scleractinian species from 21 genera and two hydrocoral species, up from 17 species reported previously (Richardson et al. 1998b). Host ranges for BBD and DSD were also greater with 16 and 12 coral species respectively, also up from previous reports. While ASP was previously thought to affect only two octocoral species in the genus *Gorgonia* (Garzón-Ferreira and Zea 1992, Nagelkerken et al. 1997), our observations and preliminary lab tests indicate that at least 6 other species from five genera (*Pseudopterogorgia*, *Gorgonia*, *Plexaura*, *Pseudoplexaura*, and *Plexaurella*) are infected on reefs of Bermuda, the Bahamas, and the northern Caribbean. These findings represent a significant increase in the number of coral and octocoral species affected on a local and regional scale, and in the host range for most diseases; not good news for the future of reefs.

Whatever the causes put forward by researchers to explain the emergence and higher frequency of epizootics in coral reef environments, it is very difficult to predict what the potential effects of these events will be without epidemiological models developed and supported by quantitative data. More sites within each geographic locality must be surveyed since diseases tend to have patchy distributions. The increased frequency of epizootic events and the emergence of new diseases may be correlated with the deterioration of environmental conditions (Harvell et al. 1999), and with the decline in the integrity of the marine environment (Green and Bruckner 2000). However, our results and observations show that diseases seem to be more abundant further away from human impacted areas. Mona Island in Puerto Rico and Los Roques in Venezuela, are 75 and 115 km away respectively from the mainland and human development, yet they showed higher disease incidences than reef areas near the highly populated mainland coasts.

Signs of climate-mediated physiological stress (i.e. the correlation of the highest temperatures of the century and the global increase in coral bleaching) are likely to compromise host resistance and to increase the frequency of opportunistic diseases (Harvell et al. 1999) in symbiotic organisms. Another factor that may play an important role might be new pathogens associated with African dust. The frequency of dust events reaching the Caribbean has increased in the last decades, which may improve the chances of pathogens crossing the Atlantic associated with dust clouds. The high number of reports of reef deterioration around the Caribbean coupled with the emergence of new diseases and increased frequency of epizootic events and mass mortalities of the last decades is a clear signal that something is changing, and seems to be changing for the worst. There is an urgent need for baseline data and monitoring programs to support development and analysis of models with predictive

power that can then be used to define potential effects and consequences of disease outbreaks on coral reefs.

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