

Spatial variability in distribution and prevalence of Caribbean scleractinian coral and octocoral diseases. II. Genera-level analysis

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ABSTRACT: Geographic assessments of coral/octocoral diseases affecting major reef-building genera and abundant reef species are important to understand their local and geographic spatial-temporal variability and their impact. The status and spatial variability of major Caribbean coral/octocoral diseases affecting important reef-building coral (*Montastraea*, *Diploria*, *Siderastrea*, *Stephanocoenia*, *Porites*, and *Agaricia*) and common, widespread octocoral genera (*Gorgonia* and *Pseudopterogorgia*) was assessed along 4 permanent 10 × 2 m band-transects in each of 3 depth habitats (<4, 5–12 and >15 m) on 2 reefs in 6 countries across the wider Caribbean during the summer and fall of 2005. A permutational multivariate analysis of variance was used to test the spatial variability (countries, reef sites and depth habitats) in prevalence of major diseases in these genera. We found a significant interaction of disease prevalence in the different coral and octocoral genera between reef sites and habitats (depth intervals). *Montastraea* was primarily affected by both white plague (WP-II) and yellow band disease in deep ($16.9 \pm \text{SE } 16\%$ and $16.9 \pm \text{SE } 2.3\%$) and intermediate ($8.1 \pm \text{SE } 1.6\%$ and $15.5 \pm \text{SE } 2.3\%$) depth habitats of Culebrita (Puerto Rico) and Chub Cut (Bermuda), respectively. Prevalence of multiple diseases simultaneously and other compromised-health problems affecting *Montastraea* colonies varied between 0.2 to 2% and 0.2 to 1.8%, respectively. *Agaricia* and *Diploria* were mostly affected by WP-II (0.5 to 16%), black band disease (0.4 to 5%) and Caribbean ciliate infections (0.2 to 12%). *Siderastrea* and *Stephanocoenia* were mainly affected by dark spots disease in Curaçao, with higher prevalence in intermediate ($40.5 \pm \text{SE } 6.2\%$) and deep ($26.6 \pm \text{SE } 4.2\%$) habitats. Aspergillosis and other compromised-health conditions affected *Gorgonia ventalina* (0.2 to 8%) and other common and widespread octocoral genera (1 to 14%), respectively.

KEY WORDS: Coral diseases · Caribbean corals · Octocorals · Wider Caribbean · Distribution

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INTRODUCTION

Coral reefs around the world are experiencing severe deterioration due to the combination of anthropogenic and natural factors (Hughes et al. 2003). Although the role of each factor might vary across localities, regions and time, diseases of coral reef organisms seem to have become a major player in the deterioration dynamics of these communities (Weil 2004, Weil et al. 2006). Coral and octocoral diseases seem to be rapidly spreading across the wider Caribbean, the Indo-Pacific and the Red Sea, affecting

the major reef-building coral species and other important coral reef organisms (Harvell et al. 1999, 2007, Green & Bruckner 2000, Smith & Weil 2004, Sutherland et al. 2004, Weil 2004, Willis et al. 2004, Winkler et al. 2004, Bourne 2005, Bruckner & Bruckner 2006, Dalton & Smith 2006, Weil et al. 2006, Bruno et al. 2007).

During the last 35 yr, Caribbean-wide and local epizootics of white band disease (WBD), white plague (WP-II), aspergillosis (ASP), and unidentified syndromes have impacted populations of important scleractinians (i.e. Dustan 1977, Gladfelter 1982, Aronson & Precht 2001, Aronson et al. 2003, Borger 2003,

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Richardson & Voss 2005), octocorals (Guzmán & Cortés 1984, Garzón-Ferreira & Zea 1992, Nagelkerken et al. 1997a,b), sea urchins (Lessios et al. 1984) and other reef organisms at local and regional scales. More recently, species of the most important Caribbean reef-building genus (*Montastraea annularis*, *M. faveolata* and *M. franksi*) have lost significant amounts of live tissues and/or colonies due to recurrent yellow band disease (YBD) and WP-II epizootic events, and a recent intense bleaching event in many localities (Santavy et al. 1999, Miller et al. 2003, 2006, Weil et al. 2003, Bruckner & Bruckner 2006). Temperature stress affects the physiology of many benthic organisms, including reproduction of major reef-building species (Szmant & Gassman 1990). Increasing seawater temperature seems to facilitate the emergence of new diseases and increase frequency and intensity of epizootic events (Harvell et al. 2002, 2007, Bruno et al. 2007) that could challenge coral reef resilience by promoting the continuous reduction of reef-building corals and other reef groups (Hughes et al. 2003, Bellwood et al. 2004, Weil et al. 2006). There is still limited information on the severity of most of these, usually localized, mortality events and the potential for recovery of populations impacted by diseases, but trends seem to indicate that increasing frequency and intensity of bleaching events might accelerate coral reef decline in the near future.

Even though most Caribbean coral species have been reported to be susceptible to at least one disease (Sutherland et al. 2004, Weil 2004), only a few of the many reported coral diseases/syndromes are actually affecting a few species and genera in particular reef localities. However, these are the most abundant and important reef-building species. Prevalence at the coral community level is widely used to characterize levels of coral diseases in reef communities; however, assessments of disease at the population/species/genera level provide a better indicator of disease impacts on coral reefs than assessments at the community level (Weil & Cróquer 2009, this issue), and might serve as a better tool for management efforts, especially for diseases with narrow host ranges. We tested the null hypothesis that the prevalence of diseases within populations of 6 prominent, disease susceptible, reef-building genera (*Montastraea*, *Diploria*, *Agaricia*, *Porites*, *Siderastrea* and *Stephanocoenia*), and 2 octocoral genera (*Gorgonia* and *Pseudopterogorgia*) was similar at different spatial scales using a multivariate, non-parametric approach. Here, we present results of the current status and the spatial variability at different scales of diseases affecting major scleractinian coral and octocoral genera in 12 reefs from 6 geographically distant localities across the wider Caribbean. We also discuss the benefits and problems of using community-level or species/genera-level approaches.

MATERIALS AND METHODS

Sampling design. Distribution and prevalence of diseases affecting major Caribbean reef-building scleractinian coral genera and 2 widespread and abundant octocoral genera were estimated within 3 depth intervals in each of 12 reef localities from 6 countries of the wider Caribbean (see Fig. 1, Table 1 in Weil & Cróquer 2009). Six major reef-building, disease-susceptible scleractinian genera that are abundant and widely geographically distributed were selected for the analyses (*Montastraea*, *Diploria*, *Agaricia*, *Siderastrea*, *Stephanocoenia* and *Porites*) and colonies of all species in the same genus were pooled. The genus *Montastraea* included the 3 main reef-building species (*M. faveolata*, *M. annularis* and *M. franksi*). *M. cavernosa* was not affected by diseases during our surveys. The genus *Porites* included *P. astreoides*, *P. porites* and *P. furcata*, the most common species at our survey sites, whereas *Agaricia* comprised all species of this genus found in the depth range surveyed. The octocorals *Gorgonia ventalina*, *Pseudopterogorgia americana* and *P. acerosa* were tested independently and all other octocoral genera were pooled in a single group because the latter were seldom found with aspergillo-sis; but frequently affected by other undescribed and putative compromised-health problems (OTH).

Surveys were performed in Grenada, Curaçao, Panamá, Puerto Rico, Cayman Islands, and Bermuda, the northern-most coral reef distribution in the Caribbean-Atlantic. Reefs in each country were at least 5 km apart and surveys were conducted as described in Weil & Cróquer (2009). For each spatial level (habitat, reef, country), the average prevalence of each disease/syndrome affecting the major coral and octocoral genera was estimated as the number of diseased colonies over the total number of colonies in each species/genus. Surveys were conducted between the end of August and first week in December of 2005 (ca. 3.5 mo) to include the season of highest water temperature and usually, highest disease prevalence, and to reduce, as much as possible, temporal variability in the prevalence of coral and octocoral diseases. Because of the wide geographical scope of this study, it was impossible to replicate sampling periods within each site, and therefore our design cannot detect the natural within-seasonal variability (i.e. spatial and temporal patterns are confounded by the sampling period). Previous surveys that were replicated over the summer in Puerto Rico and observations of the last several years indicate that once summer temperatures are reached (our surveys took place well into summer temperatures) and if there are no major warm water intrusions (such as those triggering bleaching), no significant changes in the levels of prevalence of major diseases occur (E. Weil unpubl. data).

Data analysis. Because of failure to fulfill parametric model conditions (homogeneity of variances and normality) (Underwood 1999), disease prevalence data for each coral and octocoral genera was analyzed using a multivariate permutational analysis of variance (PERMANOVA) based on Bray-Curtis similarities (Anderson 2001). The model included 3 different spatial scales: 4 belt transects (each 20 m²) (replicates) in each of 3 depth intervals (i.e. habitats: shallow, <4 m; intermediate, 5–12 m; deep, >15 m) (Factor 3: fixed and crossed) at each reef site; 2 reef sites (Factor 2: random and nested within countries) in each country, and 6 countries (Factor 1: fixed and crossed) (N = 144). Pairwise post hoc comparisons based on permutations were performed among statistically significant factors. Non metric multidimensional scaling (NMDS) was used to detect spatial patterns of prevalence of each particular disease affecting each particular genera and their contribution to average dissimilarity (SIMPER) wherever statistical differences were found. For this, data was log(x + 1)-transformed to prevent weighting of the more prevalent diseases in the ordination (Clarke & Warwick 2001).

RESULTS

Prevalence of diseases in major reef builders across different spatial scales

Overall, high variability in disease prevalence was found at all spatial scales for each of the 6 major reef-building genera considered, with significant interaction between sites (nested in country) and habitat (depth interval) ($F = 1.4$, $df = 12$, $p = 0.004$) (Table 1). On average, 4.2% of all colonies surveyed of these genera were affected by the most common and widespread diseases across the wider Caribbean (i.e. black band disease [BBD], white plague type II [WP-II], yellow band disease [YBD], dark spot disease [DSD] and

Caribbean ciliate infection [CCI; Rodríguez et al. 2009]) which explained the spatial patterns (Table 2).

BBD mainly affected colonies of *Diploria* (*D. strigosa* and *D. labyrinthiformis*) in shallow habitats of Guánica (16 ± SE 3.1%) in Puerto Rico, Sea Aquarium (4.4 ± SE 3.1%) and Habitat Hotel (4.3 ± SE 3.1%) in Curaçao; and Rita's (2.7 ± SE 3.1%) in Bermuda (Fig. 1a). *Diploria* colonies were only affected by BBD in deep transects (>15 m) of Habitat Hotel (11.3 ± SE 3.1%) (Curaçao) and Valleys (8.6 ± SE 3.1%) (Grenada) (Fig. 1a). Other genera such as *Siderastrea* and *Montastraea* showed lower BBD prevalence in shallow habitats of Valleys (3.3 ± SE 0.7%) in Grenada and South Point (1.3 ± SE 0.2%) in Grand Cayman (Fig. 1b,c). BBD was never observed on *Porites*, *Agaricia* or *Stephanocoenia*.

WP-II affected a wider range of hosts showing high variability in prevalence across all combinations of genera, habitats and reef sites (Fig. 2). The genus *Montastraea* showed the highest prevalence in the deep (17 ± SE 1.4%) and intermediate (8.1 ± SE 3.4%) habitats of Culebrita (Puerto Rico); and lower but similar prevalence at intermediate (3.8 ± SE 1.4%) and shallow (3.3 ± SE 3.4%) depth intervals at Habitat Hotel (Curaçao). WP-II prevalence levels on *Montastraea* were significantly lower in the other localities (Fig. 2a). Populations of *Diploria* had higher WP-II prevalence at the intermediate habitats of Culebrita (8.3 ± SE 1.7%) (Puerto Rico), and lower but similar prevalence in shallow habitats of Flamingo Bay (4.6 ± SE 1.7%) (Grenada) and deep habitats of South Point (4 ± SE 1.7%) (Grand Cayman) (Fig. 2b). Similarly to *Montastraea*, the genus *Agaricia* was severely affected by WP-II across all habitats of Culebrita (Puerto Rico) with epizootic levels of prevalence in shallow habitats (33.3 ± SE 3.8%), and lower prevalence at intermediate (7.1 ± SE 3.8%) and deep (8.3 ± SE 3.8%) habitats (Fig. 2c). *Siderastrea* populations were more affected by WP-II at the intermediate (7.7 ± SE 1.9%) and shallow (7.5 ± SE 1.9%) habitats of South Point (Grand Cayman) (Fig. 2d), and showed significantly lower WP-II prevalence in the other reef localities. The highest WP-II prevalence in *Stephanocoenia intersepta* were found at the intermediate (13.3 ± SE 2%) and deep habitats (8.3 ± SE 2%) of Sea Aquarium (Curaçao) and Culebrita (Puerto Rico) (Fig. 2e). The prevalence of WP-II in *Porites* was significantly higher in shallow (27.1 ± SE 3.9%) and intermediate (16.6 ± SE 3.4%) habitats of Roldán (Panamá), and at the deeper (8.3 ± SE 3.9%) habitat of Culebrita (2.2 ± SE 2.8%) (Puerto Rico) (Fig. 2f).

Table 1. Three factorial multivariate PERMANOVA based on Bray Curtis similarity for the prevalence of 11 coral diseases affecting 6 coral genera at N = 144 belt-transects. Factor 1 (Country, crossed and fixed), Factor 2 (Reef site, nested within Factor 1 and random), Factor 3 (Depth habitat, crossed and fixed). Bold indicates significant source of variation

Source	df	SS	MS	F	p
Country	5	96811.11	19362.22	1.919	0.01
Site (Country)	6	60529.96	10088.33	3.129	0.001
Depth	2	14997.97	7498.99	1.619	0.064
Country × Depth	10	54109.14	5410.91	1.168	0.198
Site (Country) × Depth	12	55550.58	4629.22	1.435	0.004
Residual	108	348193.28	3224.01		
Total	143	630192.03			

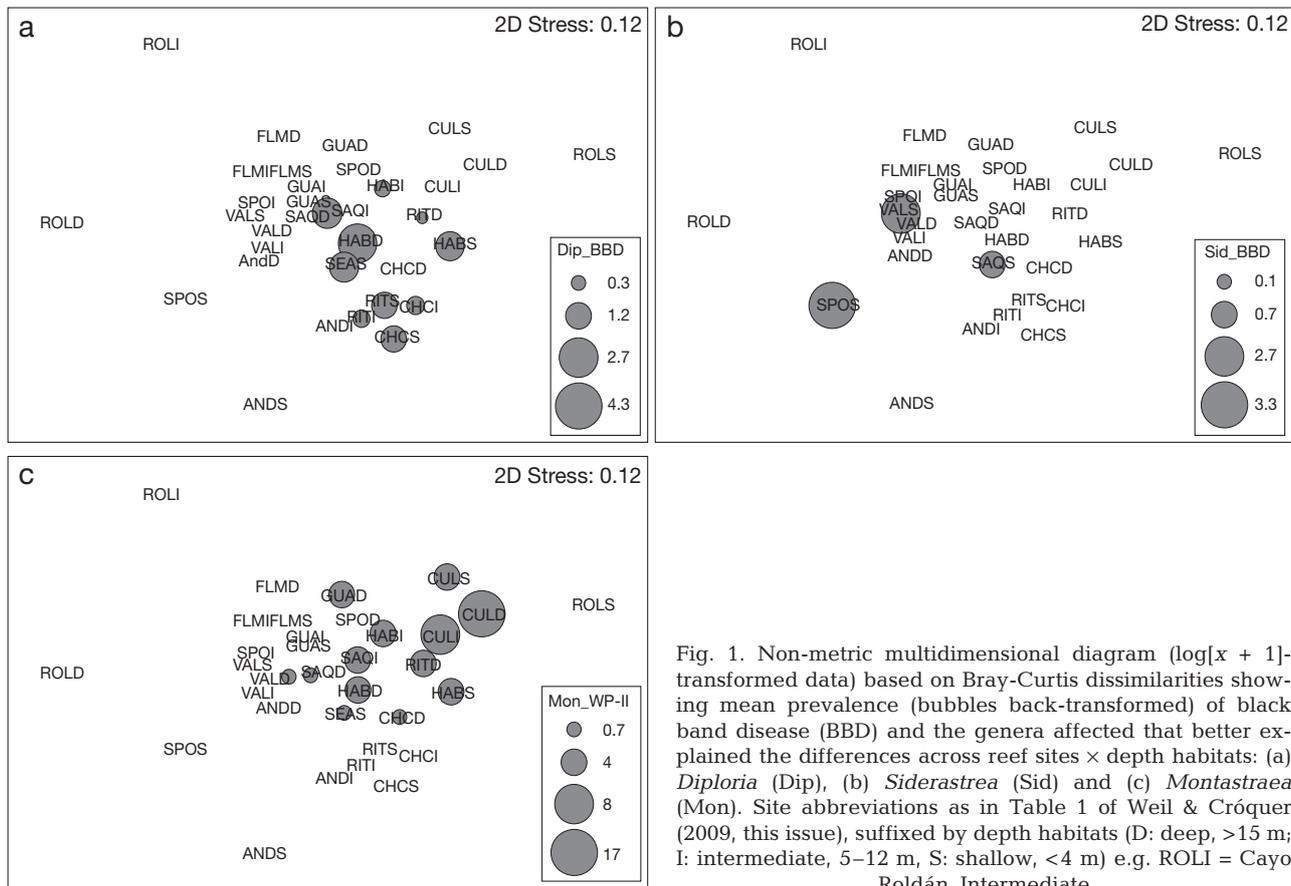


Fig. 1. Non-metric multidimensional diagram ($\log[x + 1]$ -transformed data) based on Bray-Curtis dissimilarities showing mean prevalence (bubbles back-transformed) of black band disease (BBD) and the genera affected that better explained the differences across reef sites \times depth habitats: (a) *Diploria* (Dip), (b) *Siderastrea* (Sid) and (c) *Montastraea* (Mon). Site abbreviations as in Table 1 of Weil & Cróquer (2009, this issue), suffixed by depth habitats (D: deep, >15 m; I: intermediate, 5–12 m, S: shallow, <4 m) e.g. ROLI = Cayo Roldán, Intermediate

habitats ($F = 1.9$, $df = 12$, $p = 0.002$) (Table 3). Differences among reef-habitats were better explained by other syndromes affecting other octocoral species (i.e. *Pseudoterogorgia americana*, *Briareum asbestinum*, *Erythropodium caribaeorum*, *Pseudoplexaura porosa*, *Eunicea* spp. and *Plexaurella nutans*) and ASP affecting *Gorgonia ventalina* (Table 4). Higher levels of compromised-health problems (other syndromes = OTH) affecting other gorgonians were found at the shallow habitats of Rita (Bermuda) ($34.2 \pm SE 4.9\%$) and the deep transects of Habitat (Curaçao) ($20 \pm SE 4.9\%$). Other reefs with relatively high OTH prevalence were the shallow habitat of Flamingo bay (Grenada) ($12.8 \pm SE 4.9\%$) and the shallow habitat of South Point ($8.8 \pm SE 4.9\%$) (Grand Cayman) (Fig. 4a). Aspergillosis was found through all the surveyed reefs. Populations of *Gorgonia ventalina* were more affected by ASP in the shallow habitats of Valleys ($22.7 \pm SE 1.4\%$) (Grenada) and Sea Aquarium ($6.7 \pm SE 1.4\%$) in Curaçao. *G. ventalina* populations had significantly lower ASP prevalence in most of the other reef sites (i.e. Flamingo in Grenada with $2.3 \pm SE 1.4\%$) (Fig. 4b). Prevalence of growth anomalies or tumors was low (<1%).

DISCUSSION

Loss of resilience has been linked with the recent decline of coral reef ecosystems. (Hughes et al. 2003, Jackson et al. 2001, Gardner et al. 2003, Pandolfi et al. 2003, 2005, Bellwood et al. 2004, Micheli & Halpern 2005). This trend is in part driven by significant reductions in coral cover and population sizes of major reef-building genera worldwide, but particularly, in the Caribbean region where coral diseases play an important role in producing coral mortality (Weil 2004). However, the actual role of coral diseases as primary cause of reef decline is controversial because for many scientists coral diseases are the secondary (i.e. the secondary consequence of a myriad of stress factors) and not the primary cause of coral reef decline (Lesser et al. 2007).

Only a limited number of the 27 scleractinian (68 zooxanthellate species) genera recognized for the Caribbean (Wells & Lang 1973, Veron 2000, Weil 2003) are considered major reef-builders in the region (i.e. *Montastraea*, *Diploria*, *Porites*, *Siderastrea*, *Agaricia*, *Stephanocoenia*, *Colpophyllia* and *Madracis*, among others). Results from this and other studies show these

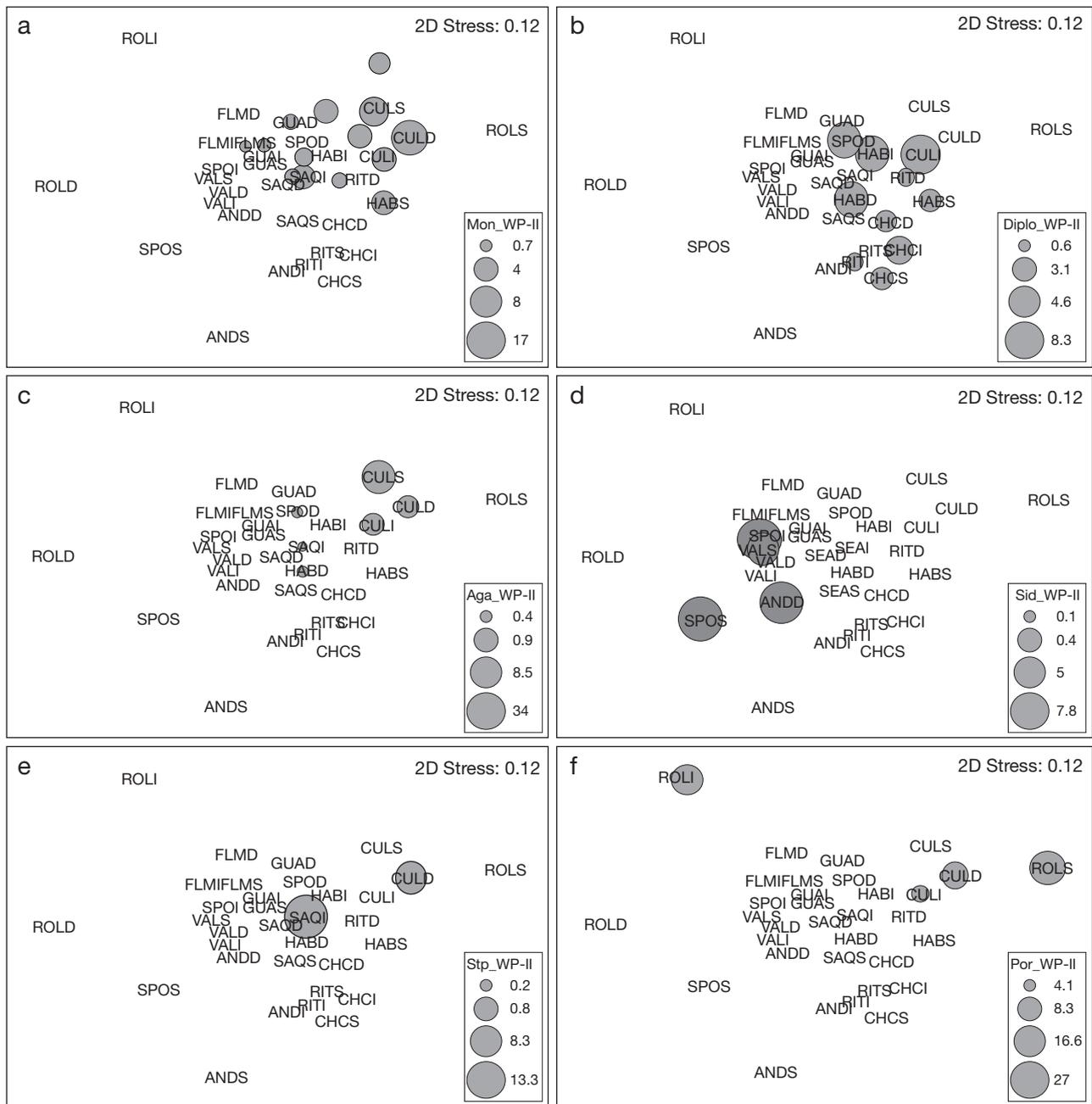


Fig. 2. Non-metric multidimensional diagram ($\log[x + 1]$ -transformed data) based on Bray-Curtis dissimilarities showing mean prevalence (bubbles back-transformed) of white plague disease (WP-II) and the genera affected that better explained the differences across sites \times depth habitats: (a) *Montastraea* (Mon), (b) *Diploria* (Dip), (c) *Agaricia* (Aga), (d) *Siderastrea* (Sid), (e) *Stephanocoenia intersepta* (Stp) and (f) *Porites* (Por). Site abbreviations as in Table 1 of Weil & Croquer (2009, this issue)

genera to be particularly susceptible to coral diseases (for review see Sutherland et al. 2004). The potential of disease outbreaks to change coral reefs was evidenced in the early 1980s, after the wider-Caribbean disease-induced massive mortalities of one Caribbean keystone species, the black sea urchin *Diadema antillarum* (Lessios et al. 1984, Carpenter 1990a,b) and 2 structurally

important coral species, *Acropora palmata* and *A. cervicornis* (Gladfelter 1982). These mortalities brought about a cascade of significant ecological changes in the dynamics, function and structure of coral reefs at local and geographic scales (Hughes 1994, Harvell et al. 1999, Aronson & Precht 2001, Bruckner et al. 2002, Lirman et al. 2002, Weil et al. 2003, 2006, Weil 2004).

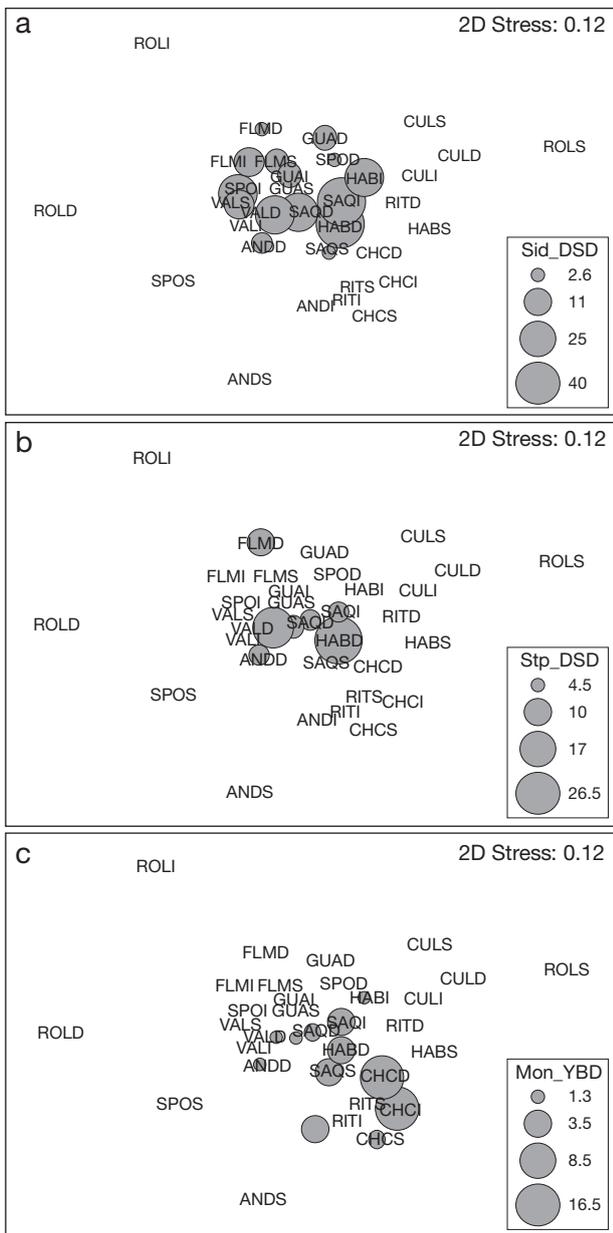


Fig. 3. Non-metric multidimensional diagram ($\log[x + 1]$ -transformed data) based on Bray-Curtis dissimilarities showing mean prevalence (bubbles back-transformed) of diseases and genera that better explained the differences across sites \times depth habitats: dark spots disease (DSD) affecting (a) *Siderastrea* (Sid) and (b) *Stephanocoenia intersepta* (Stp) and (c) yellow band disease (YBD) affecting *Montastraea* (Mon) species complex. Site abbreviations as in Table 1 of Weil & Cróquer (2009, this issue)

Our surveys indicate that with only few exceptions (WP-II in Culebrita, CCI in Habitat Hotel and YBD in the deeper and intermediate habitats of Chub Cut), the overall prevalence of coral diseases seldom exceeded 5 to 6% at the community level (Weil & Cróquer 2009)

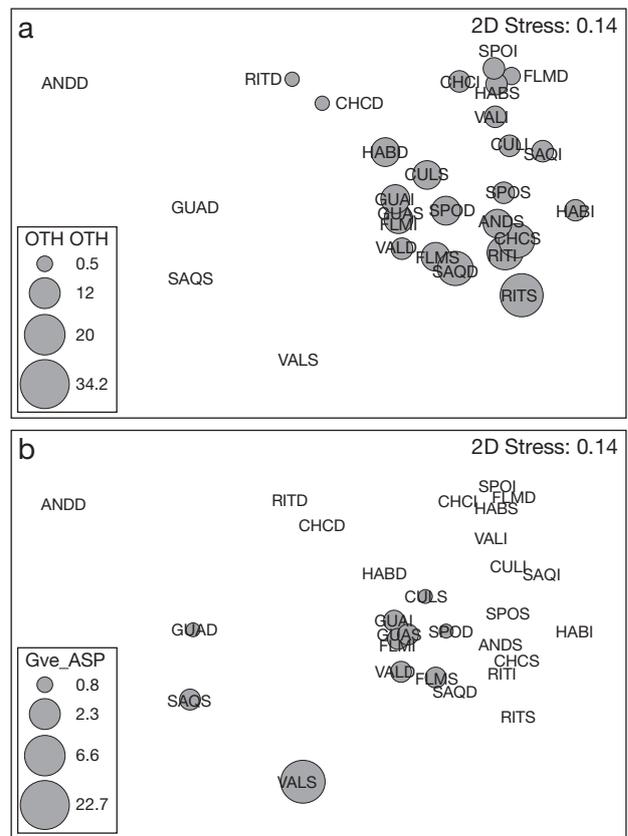


Fig. 4. Non-metric multidimensional diagram ($\log[x + 1]$ -transformed data) based on Bray-Curtis dissimilarities showing mean prevalence (bubbles back-transformed) of (a) other syndromes affecting other species of octocorals (OTH) and (b) aspergillois (ASP) affecting *Gorgonia ventalina* (Gve). Site abbreviations as in Table 1 of Weil & Cróquer (2009, this issue)

and in populations of major reef builders (Table 5). Nonetheless, all 6 major Caribbean reef-building coral genera were affected by diseases in most localities in 2005, some of which with epizootic levels of prevalence, confirming the persistence and importance of this problem. Furthermore, diseases like white band disease (WBD) and white pox (WPX) were rarely seen in our sites (<1%) because they mostly affect species of *Acropora*, and this genus had low densities or was absent in the localities surveyed (data not shown). The genus *Montastraea*, the most important reef-building group in the wider Caribbean, was affected by all the common and most virulent diseases, and some colonies had more than one disease at the same time, a recent trend in many localities throughout the region (authors' pers. obs.). Overall, WP-II, YBD and DSD were the most common diseases affecting the major reef-building genera, all of which had local populations with high abundance of colonies in most of the reefs surveyed.

Table 5. Overall mean and standard error of total disease and black band disease (BBD), white plague type II (WP-II), yellow band disease (YBD), dark spots disease (DSD), Caribbean ciliate infection (CCI), multiple-diseases (MULTI), tumors (TUM) and other syndromes (OTH) for 6 important reef-building genera across the 12 reef sites studied

Disease	<i>Agaricia</i>	<i>Montastraea</i>	<i>Diploria</i>	<i>Porites</i>	<i>Siderastrea</i>	<i>Stephanocoenia</i>
Total	1.4 ± 0.68	4.8 ± 0.7	4.0 ± 0.8	2.7 ± 0.8	7.7 ± 1.2	4.8 ± 1.2
BBD		0.06 ± 0.04	1.5 ± 0.5		0.2 ± 0.1	
WP-II	1.2 ± 0.6	1.3 ± 0.3	0.7 ± 0.3	1.5 ± 0.6	0.6 ± 0.3	0.6 ± 0.4
YBD		1.7 ± 0.5				
DSD		0.3 ± 0.2			6.3 ± 1.2	2.5 ± 0.8
CCI	0.2 ± 0.09	0.3 ± 0.1	1.0 ± 0.5	0.02 ± 0.02		
MULTI	0.06 ± 0.06	0.2 ± 0.1	0.2 ± 0.09			1.5 ± 0.2
TUM			0.05 ± 0.05			
OTH		0.4 ± 0.1	0.2 ± 0.09	1.0 ± 0.2	0.14 ± 0.08	0.13 ± 0.1
Total colonies	8964	6271	6461	8309	5461	2812

2003) compared to other diseases. Ongoing monitoring of reefs in La Parguera, Puerto Rico showed that 3 WP-II epizootic events (affecting mostly *Montastraea*, *Diploria*, *Colpophyllia*, *Meandrina*, *Mycetophyllia* and *Siderastrea*) occurred in this area during the last 5 yr (E. Weil unpubl. data). These observations are consistent with those from St. John (Miller et al. 2003, 2006).

Even though WP-II has been reported Caribbean-wide affecting more than 40 coral species (Weil et al. 2002, Sutherland et al. 2004, Weil 2004), there is high spatial variability in genera infected across habitats and localities. Recurrent outbreaks have produced significant reductions in abundance and live cover of the important reef-building coral species in the Florida Keys (Richardson 1998, Richardson et al. 1998a, Richardson & Voss 2005), loss in live coral cover in Dominica (Borger 2003, Borger & Steiner 2005), Saint Lucia (Nugues 2002), Puerto Rico (Weil 2004) and Venezuela (Cróquer et al. 2005). The WP-II pathogen (*Aurantimonas corallida*) advances fast (2 to 3 cm d⁻¹) killing small colonies in a few days (Richardson 1998, Richardson et al. 1998a,b, Nugues 2002, Denner et al. 2003, Miller et al. 2003, Borger & Steiner 2005). Large colonies have been shown to be more affected by WP-II than small colonies; however, the former have better chances of survival if the infection stops before killing the whole colony (Nugues 2002). Two other conspicuous scleractinian genera, *Agaricia* (in the deeper and shallower habitats of Culebrita and Roldán) and *Diploria* (in Culebrita) were also affected by WP-II.

Spatial variability of YBD across sites and depth habitats

YBD mainly affects the genus *Montastraea* (Gil-Agudelo et al. 2004, Weil 2004, Bruckner & Bruckner 2006). In the present study YBD had low prevalence in most reefs surveyed, with the exception of the deeper

habitats of Chub Cut (~17%), in Bermuda, and Sea Aquarium (~3.5%) in Curaçao. High prevalence of YBD in Chub Cut was not observed in 1999 and 2000 (Weil et al. 2002). During these years, YBD was more prevalent in Bonaire (12.5%), Colombia (12.58%), Venezuela (8.8%) and Puerto Rico (5.45%) (Weil 2004). Outbreaks of this syndrome have also been reported for Panamá (Santavy et al. 1999), Colombia (Garzón-Ferreira et al. 2001) and Venezuela (Cróquer et al. 2003).

In La Parguera, southwest coast of Puerto Rico, YBD has been significantly affecting populations of mostly *Montastraea faveolata* since 1997 (A. W. Bruckner pers. comm.), with low numbers of *M. franksi* and *M. annularis* colonies showing any signs of this syndrome until recently (Bruckner & Bruckner 2006, E. Weil unpubl. data). Outbreaks of WP-II and YBD affected large numbers of colonies of *M. faveolata* at intermediate depths while populations of *M. franksi* were more affected in deep habitats right after the bleaching event of 2005 (authors' unpubl. data). Bruckner & Bruckner (2006) reported YBD prevalence of up to 52% for the *M. annularis* species complex in Mona Island, west of Puerto Rico, the highest level reported in this country. YBD affects other important favids throughout the Caribbean (Garzón-Ferreira et al. 2001, Weil et al. 2002, Weil 2004) but with very low prevalence; in the present study, only colonies of *M. annularis*, *M. faveolata* and *M. franksi* were observed with signs of YBD. The rate of tissue mortality produced by this disease is variable, ranging from several millimeters to several centimeters per month depending on water temperature (Cervino et al. 2004) and nutrient concentration (Bruno et al. 2003). Persistent outbreaks in Puerto Rico produced significant tissue loss with rates ranging from 5 to 15 cm yr⁻¹ in *Montastraea* populations (Bruckner & Bruckner 2006). Rates of growth of this species complex are at least an order of magnitude lower (0.7 to 1.2 cm yr⁻¹) (Knowlton et al. 1992), which means that if the

disease/syndrome is persistent over time, infected colonies would not survive. Tissue regeneration rates reported in controlled experiments ranged from 0.7 to 160 mm² d⁻¹ for *M. annularis* (see review by Henry & Hart 2005) which suggest that if infection stops, the coral has the capacity to regenerate part of the lost tissue. However, this might not happen if the substrate is already colonized by other fast growing organisms.

YBD and WP-II have different patterns of infection; while YBD tends to be persistent (i.e. colonies remain infected for longer periods and nowadays, throughout the year with relatively slow rates of tissue loss, WP-II usually appears as outbreaks during the summer and fall months, affecting a wider range of hosts (high prevalence at the community level, 25 to 40%), with faster rates of tissue loss (up to 30 cm mo⁻¹), and signs of arresting quickly after water temperatures drop during winter. These 2 diseases continue to be the most widespread and virulent coral diseases in the wider Caribbean (Nugues 2002, Weil et al. 2002, 2006, Borger & Steiner 2005, Richardson & Voss 2005, Bruckner & Bruckner 2006).

The widespread mortality of acroporids due to white band disease in the early 1980s produced a cascade of ecological changes in a relative short time in many reef communities. Similar problems are being produced at local and geographic scales by the high frequency of WP-II outbreaks and the persistent and widespread epizootics of YBD. These diseases showed higher prevalence (>20%) and wider geographical distributions compared to the other common diseases (BBD, WBD, WPX, DSD, CCI) and other widespread compromised-health problems with low prevalence levels (<1%), narrower geographic distributions and narrower host ranges, and continue to significantly reduce areas of live coral cover, opening more space for algal colonization and reducing coral populations of the major reef-building genera across the Caribbean.

Spatial variability of DSD across sites and depth habitats

DSD also varied in space, as reported by Gil-Agudelo & Garzón-Ferreira (2001), and showed narrow host range and spatial distribution compared to WP-II. *Siderastrea siderea* and *Stephanocoenia intersepta* were the main species affected (Table 5) with highest prevalence in deeper habitats of Curaçao and Grenada. Few colonies of *Montastraea faveolata* and *M. annularis* were observed with the typical DSD signs (small, dark depressed areas) in shallow to intermediate habitats in Puerto Rico, and the wide darker depressions in *M. cavernosa* in deeper habitats off Grand Cayman. Besides changes in the patterns of

pigmentation and depression of the skeletal structure, recent tissue mortality associated with DSD was rarely observed and most colonies did not have any tissue-devoid areas close to the disease signs as reported by Borger (2005).

Spatial variability of octocoral diseases across sites and depth habitats

Similarly to coral diseases, prevalence of ASP and other diseases/syndromes on octocoral populations were highly variable at the different spatial scales. ASP mainly affected *Gorgonia ventalina* populations in reefs in the southern and northern Caribbean but prevalence levels were significantly lower (0 to 8.1%) compared to previous estimates (5.5 to 30%) for the same localities in 1999–2000 (Weil et al. 2002). This reduction in prevalence has been reported for other areas of the Caribbean (Kim & Harvell 2004, Ward et al. 2006) and might result from changes in environmental conditions, a decline in the pathogen's virulence, an increase in the host's resistance (diverse immune mechanisms) or a combination of these. Other compromised-health problems affecting a wide range of octocorals were more prevalent than ASP. Increasing numbers of colonies of encrusting octocorals such as *Briareum asbestinum* and *Erythropodium caribaeorum* had signs of unhealthy-looking tissue and showed extensive tissue mortality in many of the surveyed reefs, mostly after the onset of the bleaching of 2005 (Weil et al. 2006). Branching octocorals such as *Pseudoplexaura porosa*, *Eunicea* spp. and *Plexaurella nutans* showed similar problems with unhealthy-looking tissue and tissue loss along the branches and at the tips. Similar observations were reported for surveys performed in 1999–2001 (Weil et al. 2002) which emphasize the persistence and increase of disease in octocorals and the importance of not overlooking epizootics in other important reef organisms (Weil et al. 2006). Only ASP has been well documented and is by far the best understood of all the diseases and there is little information on the etiology and pathology of all the other octocoral diseases. Octocorals may be more prone to water-borne infections and express disease signs faster than scleractinians and other benthic organisms and could become good environmental indicators.

Spatial variability of diseases and host distribution across sites and habitats

Most pathogens are usually species-specific and susceptibility to different pathogens could vary within and

across taxa (McCallum et al. 2004). Since the distribution and disease susceptibility of different host species vary across habitats within and across reefs, it is therefore expected that the distribution and prevalence of different coral and octocoral diseases would vary accordingly. Even though most pathogens affecting corals seem to have wide host ranges (Sutherland et al. 2004, Weil 2004), observations over the years and results of this study indicate that (1) only a few of the host species are commonly affected by the most detrimental and common diseases; (2) these hosts are found over wide depth intervals; and (3) there was significant variability in the distribution and prevalence of the different diseases at different spatial scales, from reef habitats to geographic regions. The high spatial variability observed could be interpreted as evidence of the patchy distribution of diseases and their hosts. This hypothesis was tested by Ward et al. (2006) who found a weak correlation between disease prevalence and host abundance, indicating that other factors such as host resistance may be also important in determining levels of prevalence. Observations and data from several reef localities in La Parguera (Puerto Rico) showed that reefs with similar species composition but significantly lower densities of *Montastraea* (e.g. San Cristobal and Romero) had significantly lower prevalence levels of both WP-II and YBD compared to nearby sites with higher densities and larger colonies of *Montastraea* (e.g. Turrumote and Media Luna). This seems to indicate that host densities might influence the spread of these diseases within particular reefs, that pathogens did not spread similarly over wide areas or that they have not spread effectively from highly infected reefs to other nearby reefs. Furthermore, populations of the same species in different reefs may have different susceptibilities to the different diseases, local environmental conditions (e.g. temperature, water chemistry, light) could vary slightly from reef to reef, and/or the physiological and biological characteristics of local populations might be different, all of which, independently or combined, might affect disease prevalence and incidence in particular populations.

Community- versus genera-level analysis: 2 important levels of information

A review of the literature published on coral diseases showed that several approaches have been used to evaluate the significance of coral diseases in coral reef decline. While the prevalence in the community and/or in targeted populations prone to be affected by particular diseases is often used (Weil et al. 2002, Cróquer et al. 2003, García et al. 2003, Santavy et al. 2005, Ward et al. 2006), other epidemiological parameters such as the

incidence, recovery and recurrence have received less attention. Community level analysis may be useful to characterize epizootic events of diseases that affect a wide range of hosts (e.g. WP-II). In such cases, prevalence in the community will be high, indicating that the whole community was impacted by the epizootic event (e.g. Cróquer et al. 2003). When there are no widespread or intensive disease outbreaks, estimates of average disease prevalence at the community level generally produce low values, between 2 and 6% (range 0.5 to 9.8%) for corals and 2.4% (range 0.6 to 6%) for octocorals (Weil & Cróquer 2009). These values represent the proportion of diseased colonies in the whole coral community, which includes hundreds of colonies of species that are not usually affected by disease. Therefore, prevalence at the community level could mask the potential impact of particular diseases affecting those few important and more susceptible species. Nonetheless, knowing the background levels of disease in the coral community is helpful to characterize this problem at the community level and epizootic events affecting a large number of species in the community. Nevertheless, the use of 'prevalence' in the coral community has a conceptual pitfall; as prevalence (by definition) is one out of several epizootiological parameters used to describe the dynamic of diseases within populations.

Average prevalence at the genus/species level is more informative than estimates at the community level when only a few diseases with a narrow range of hosts are present in a particular site and when major reef-building species are being affected by few, highly infectious diseases. Population- or genera-level analysis represents the proportion of colonies of each population/species/genus affected by the particular disease providing a more accurate assessment of the status and potential impact of the disease and better information for epidemiological and management actions. This is clearly the case for the genus *Montastraea* which has been mostly affected by outbreaks of WP-II and YBD, producing significant losses of live coral tissue (partial and total colony mortality) at local and geographic scales. In the present study, prevalence of YBD in Chub Cut (Bermuda) at the community level was 5%, whereas the genera analysis shows a prevalence of 16.5% at the genus level, providing a better estimate of the disease impact on this important genus.

Overall, all major reef-building genera were affected by at least one important disease in the 12 reefs surveyed. *Siderastrea*, *Montastraea* and *Diploria* had the highest overall disease prevalence, but this trend significantly depended on habitats and reef sites. The most important genus, *Montastraea*, was mostly affected by the 2 most widespread and virulent diseases in the region, WP-II and YBD. Other reef build-

ders such as *Diploria*, *Siderastrea* and *Stephanocoenia* were mostly affected by WP-II and DSD. Although CCI was observed in several localities, the highest prevalence was observed in Curaçao, where *Diploria* was more affected than other species. The frequency of colonies of these species with multiple affections seems to be increasing with time; this will be corroborated in future surveys. *Porites* and *Agaricia*, although highly abundant, were significantly less susceptible to observable diseases compared to the other genera. The fungal infection ASP showed drastic reductions in prevalence compared to previous years possibly indicating a change in the dynamics of the disease, a decline in virulence, an increase in resistance or a combination of these. Diseases affecting octocorals and other important components of the coral reef community are becoming more prevalent and should be included in future surveys.

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