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Coral disease prevalence and host susceptibility on mid-depth and deep reefs in the United States Virgin Islands

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Abstract: Both the number of coral diseases and the intensity of their outbreaks have increased in recent years. Little is known however why certain species are more susceptible to disease. This study examines coral disease prevalence and species susceptibility to disease using data collected over a four year period at 25 sites in the U.S. Virgin Islands. Twelve species of scleractinian coral were found to be affected by disease. Yellow band disease (YBD) and dark spots disease (DSD) were the most common diseases found on USVI reefs. Four diseases, YBD, DSD, white syndrome, and black band disease (BBD) were observed in three species; *Montastraea annularis*, *Montastraea franksi* and *Siderestrea siderea*. *Siderestrea siderea* was most frequently affected by disease with a total prevalence of 23%, largely due to the high number of incidences of DSD. YBD was the second most common disease and had the highest prevalence in *Montastraea annularis* (5.1%). BBD was most common in *Colpophyllia natans* (1.2%) while white syndrome was most often seen in the *Montastraea annularis* complex (2.9%). Four of the 12 species affected by disease had above average susceptibility to disease, and included species in the *Montastraea* genus as well as *Siderastrea siderea*. Of the 12 species with signs of disease, *Diploria strigosa* was afflicted least, showing only slight susceptibility to YBD. Two species of scleractinian coral, *Porites porites* and *Diploria labrynthiformis*, and two species of hydrocoral, *Millepora alcicornis* and *M. complanata*, were healthy, suggesting low disease susceptibility. Rev. Biol. Trop. 56 (Suppl. 1): 223-234. Epub 2008 May 30.

Key words: coral reefs, monitoring, disease, susceptibility, USVI.

The growing intensity and frequency of coral disease outbreaks and subsequent coral reef degradation have become cause for major concern among scientists and managers (Harvell *et al.* 1999). Disease outbreaks are beginning to have profound effects on the structure of modern coral reefs, yet little is known about the etiology and modes of transmission of many of these diseases (Richardson 1998, Nugues 2002). This is troubling since there has been an emergence of new diseases since the 1990's and many of the known diseases, such as black band, white plague, white band and white pox, have apparently become even more widespread (Goreau *et al*. 1998, Richardson *et al.* 1998). At least one disease, white band, is now recognized as a major driver in the alteration of coral reef ecosystems in the Caribbean (Aronson and Precht 2001). The outbreak of the white band disease in the 1980s dramatically reduced coral cover by decimating two major frame-building corals, *Acropora palmata* and *A. cervicornis*, thus changing the structure and composition of reefs to this day (Gladfelter 1982, Aronson and Precht 2001). Corals in the genus *Montastraea*, some of the most abundant reef builders in the region (Miller *et al*. 2003), appear to be becoming more vulnerable to stress and disturbance than in the past (Bruckner and Bruckner 2006a). This, along with their slow growth rate (Gladfelter *et al.* 1978), and low number of recruits (Rogers *et al.* 1984) could result in the extirpation of these species on many Caribbean reefs if current conditions continue (Edmunds and Elahi 2007).

Causes behind the increase in the incidences and severity of disease outbreaks have been attributed to a variety of factors including the elevation of ocean temperatures and proximity to anthropogenic influences (Harvell *et al.* 1999, 2002, Kaczmarsky *et al.* 2005). These factors may induce stress on a coral and reduce its resistance to pathogens. For example, coral bleaching prevalence was greater than 90% on a majority of reefs monitored in the USVI from September to November 2005, and was attributed to unprecedented regional sea surface temperatures (Donner *et al.* 2007, Manzello *et al.* 2007). High temperature stress preceded high levels of coral mortality in the months following the bleaching, largely due to outbreaks of disease (Miller *et al.* 2006, Authors unpub. data). Some studies are beginning to show linkages between disease and external factors; however, the exact causes of many diseases are still unknown. Kaczmarsky *et al.* (2005) found that on St. Croix, USVI, closer proximity to sewage discharge was associated with greater incidences of black band disease and white plague type II. Conversely, Page and Willis (2006) found that on the Great Barrier Reef, the prevalence of black band disease was not related to distance from anthropogenic pressures and suggested that black band disease is part of the natural ecology of coral assemblages on the GBR. Aronson and Precht (2001) also concluded that there was no relationship between white band disease outbreaks and proximity to human influences.

Not only are the processes causing outbreaks of disease varied, but corals also show different responses and susceptibilities to disease and other disturbances (Bythell *et al.* 1993). While white band disease is known for its devastating effects on only two species of Acroporids (Gladfelter 1982), white plague symptoms, which are similar to white band disease, have been shown to affect up to 32 species (Richardson 1998). In the Florida Keys, *Dichocoenia stokesi* was found to be the most prone coral species to infection by white plague type II in 1995 (Richardson *et al*. 1998). White plague was observed on St. John in 1997, where it affected 14 different coral species including *Montastraea cavernosa*, *Colpophyllia natans*, *Siderastrea siderea*, and *Diploria* species (Miller *et al*. 2003). The most extensive mortality however was seen in the major reef building species of the *Montastraea annularis* complex (Miller *et al*. 2003). Previously, Weil (2004) had observed eight different diseases affecting the *Montastraea annularis* species complex. A study by Miller and Williams (2007) found that disease prevalence was higher in large coral colonies, most specifically large colonies of *Montastraea* spp. These findings are further supported by a study by Bruckner and Bruckner (2006a) which found that outbreaks of yellow blotch disease resulted in the loss of over 90% of living tissue on *M. annularis* and *M. faveolata* colonies in Curaçao. In Dominica, the most common disease is dark spots disease, which primarily affects *Siderastrea siderea*, yet black band disease and white plague were responsible for the largest amount of tissue death (Borger 2005).

In order to understand if the large apparent differences in disease susceptibility found in other regions of the Caribbean apply to the U.S. Virgin Islands, we examined the prevalence of diseases among scleractinian coral and hydrocoral species over four years. We concentrated our sampling on medium and deep depth coral reefs (10 – 42 m) that are often underrepresented in disease surveys in the USVI and Caribbean. We developed an index to compare susceptibility to disease across species, and discuss the relevance of these rankings of susceptibility with respect to previous research on Caribbean coral diseases. Increased understanding of species susceptibility to a disease will help mangers and policy makers in developing effective management strategies, such as applying closer monitoring and protection to areas with the most vulnerable species composition (Bythell *et al.* 1993, Downs *et al*. 2005).

MATERIALS AND METHODS

A total of 25 reef sites were surveyed annually or semi-annually over four years (with the exception of South Water and Perseverance Bay which were only sampled once) on all three major islands of the USVI (Figure 1, Table 1). Nearshore sites monitored in this study differ from USVI sites monitored in previous studies (e.g., Gladfelter 1982, Rogers *et al.* 1984) in that they tend to be deeper and/or are not dominated by the genus *Acropora*. Community composition of every site, with the exception of Great Pond, is dominated by species in the *Montastraea annularis* species complex (authors unpub. data). Sites were established between 2002 and 2005 by the University of the Virgin Islands as part of a long term monitoring program. At each location, transects were deployed at sites that characterized the reef location (e.g. similar topography, cover, and species composition). Locations were chosen in areas underrepresented in previous federal and territorial monitoring programs. At each site, six 10 m transects (either permanent or random, Table 1) were surveyed using SCUBA, with the exception of 2003 when ten transects were completed at College Shoal, Seahorse Cottage Shoal, South Capella, Grammanik Bank, Red Hind Bank, and South

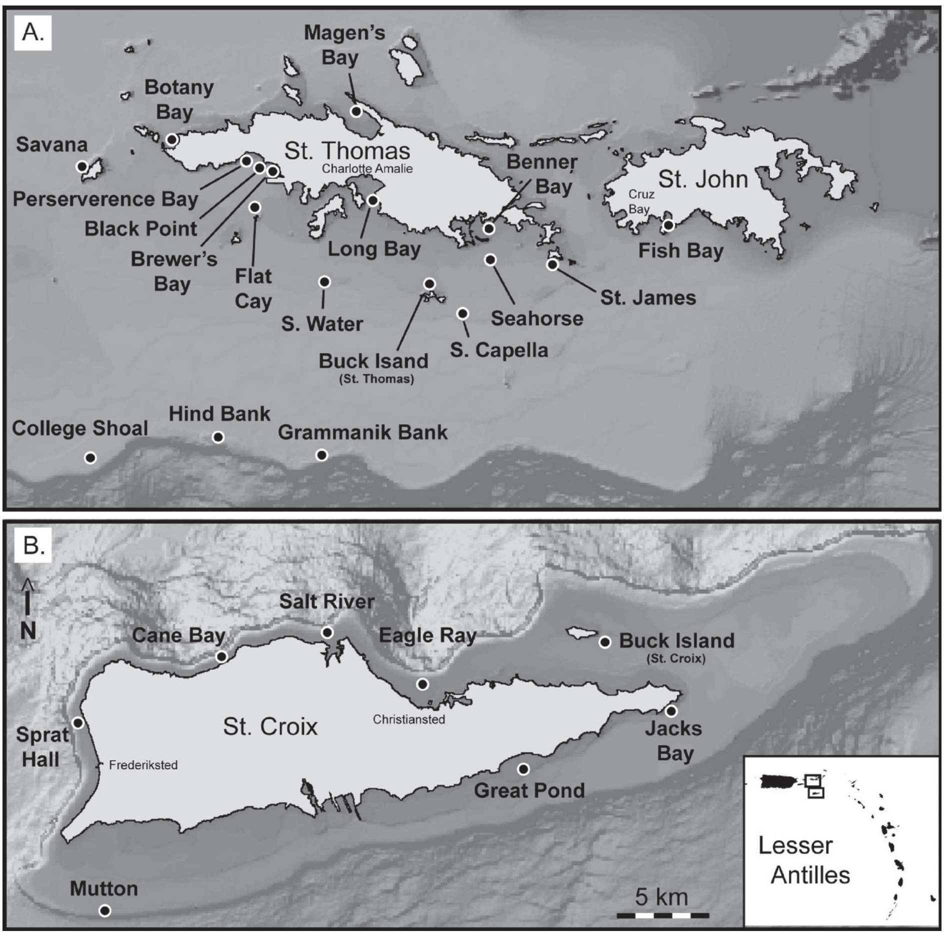

Fig. 1. U.S. Virgin Islands: the 25 study locations in (A) St. Thomas – St. John and (B) St. Croix. Scale bar and orientation the same for both panels.

TABLE 1

Sites assessed around St. Thomas – St. John and St. Croix and their characteristics.
Sampling design refers to method of transect placement

Site	Orientation	Depth (m)	Dates Sampled	Sampling Design
St. Thomas – St. John				
Benner Bay	Nearshore	7	12/12/2002 5/20/2003 12/4/2003 12/7/2004 6/14/2005	Permanent
Black Point	Nearshore	13	9/9/2003 5/20/2005	Random
Botany Bay	Nearshore	8	10/21/2002 1/29/2003 5/30/2003 12/16/2003 12/16/2004 6/19/2005	Permanent
Brewer's Bay	Nearshore	8	12/20/2002 6/25/2003	Permanent
Fish Bay	Nearshore	5	2/6/2003 5/5/2003 12/9/2004 12/15/2004	Permanent
Long Bay	Nearshore	6	3/3/2003 5/23/2003 1/16/2004	Permanent
Magen's Bay	Nearshore	8	5/30/2003 11/21/2003 12/23/2003 12/16/2004 6/19/2005	Permanent
Perseverance Bay	Nearshore	8	10/21/2003	Random
Buck Island	Midshelf - Island	15	2/11/2005 6/12/2005	Random
Flat Cay	Midshelf - Island	15	6/4/2003 11/20/2003 7/16/2004 12/7/2004 5/12/2005	Random
Savanna	Midshelf - Island	10	9/29/2003 12/13/2004 5/11/2005	Random
St. James	Midshelf - Island	18	2/11/2005 6/1/2005	Random

TABLE 1 (Continued)

Sites assessed around St. Thomas – St. John and St. Croix and their characteristics. Sampling design refers to method of transect placement

Site	Orientation	Depth (m)	Dates Sampled	Sampling Design
Seahorse	Midshelf - No Island	18	6/12/2003 5/25/2004 5/9/2005	Random
South Capella	Midshelf - No Island	20	12/4/2003 6/8/2004 5/3/2005	Random
South Water	Midshelf - No Island	20	5/10/2005	Random
College Shoal	Shelf Edge	34	10/28/2003 4/28/2005	Random
Grammanik Bank	Shelf Edge	39	7/29/2003 7/15/2004 4/27/2005	Random
Hind Bank	Shelf Edge	42	8/6/2003 8/13/2003 6/18/2004 4/29/2005	Random
St. Croix				
Buck Island	Midshelf - Island	11	7/30/2002 5/2/2003 5/5/2004	Permanent
Cane Bay	Nearshore	9	5/28/2002 4/21/2003 5/25/2004 3/16/2005	Permanent
Eagle Ray	Nearshore	9	5/30/2002 3/28/2003 5/3/2004 2/4/2005	Permanent
Jacks Bay	Nearshore	11	6/11/2002 9/5/2003 5/28/2004	Permanent
Salt River	Nearshore	6	5/23/2002 4/8/2003 5/12/2004	Permanent
Sprat Hole	Nearshore	12	6/14/2002 5/14/2003 5/10/2004	Permanent
Mutton	Shelf Edge	27	1/17/2003 5/19/2003 10/20/2004	Permanent

Water Island. All coral colonies 10 cm or greater in diameter or height, that were located directly under the transect lines, were assessed by the diver for signs of disease, bleaching, and mortality following a modified Atlantic Gulf Rapid Reef Assessment protocol (Kramer *et al*. 2005). Although excluding corals below 10 cm may bias disease prevalence if size is correlated with different susceptibilities (e.g, Kaczmarsky *et al.* 2005), in order to facilitate the completion of transects in deep reef locations, we chose to only sample adult corals. Diseases identified were recognized Caribbean scleractinian diseases and syndromes that included black band disease, dark spots disease, white syndrome, and yellow blotch disease. "White" syndromes are a complex of diseases (Bythell *et al.* 2004) and programmed cell death reactions (Ainsworth *et al.* 2007) that are variably characterized. With the exception of white band disease, which is found only on *Acroporid* corals that were rare in our sampling, we grouped all obvious white disease lesions into the white syndrome category. A certain number of unidentified disease lesions were classified as "unknown" and assessed in the same manner. The unknown disease lesion category was used to represent any recent mortality (within the last 30 days) or lesion not attributable to predation or other signs of tissue abrasion, and that could not be placed into a known disease category. We followed a conservative approach in disease assessment and only placed disease into a known category if they presented standard signs, as described by Bruckner (2007).

In order to calculate disease prevalence, the number of affected colonies of a particular species was divided by the total number of colonies sampled for that species. In order to guard against false zero prevalence (i.e., failure to detect disease because of a low sample size) species were only included in the analysis if they were sampled at least 50 times. This criterion provided a 50% detection probability for 1% prevalence of disease. Caution should be used in interpreting lack of disease in species that were only sampled between 50 and 100 times (50 to >99% detection probability for 1% prevalence of disease); however, a high incidence of disease for many species suggests a sufficient sampling effort. The susceptibility index of a species to a disease was determined by calculating the percent deviation of a species' prevalence from the average prevalence of the disease among all species, divided by the average prevalence of the disease among all species. Species with values greater than the average prevalence were positive and indicated increased susceptibility relative to the total coral fauna, and vice versa.

RESULTS

A total of 5,036 individual coral colonies were sampled over the four-year study period. Eleven species of scleractinian corals sampled more than 50 times were found to have been affected by some form of disease. Within a total of 4,361 colonies sampled for these 11 species, 218 diseased colonies were recorded (Table 2). Yellow blotch disease and dark spots disease were the most common diseases affecting 83 and 77 colonies, respectively. White syndrome was responsible for 29 instances of disease, while black band disease was responsible for 17. Disease lesions that could not be identified into a recognized category (unknown) made up the remaining 12 instances of disease.

Of the 11 species that were afflicted with a disease (Fig. 2), four had above average total disease susceptibility, and included *Siderastrea siderea* and species in the *Montastraea annularis* complex. *S. siderea* was the species most frequently affected by disease with a total prevalence of 23% (Table 2). This was largely accounted for by a high prevalence of dark spots disease, as indicated by the largest susceptibility index score for any coral species or disease (Fig. 2). *S. siderea* was also the coral most affected by unknown disease lesions. The high prevalence of dark spots disease and unknown disease lesions in *S. siderea* gave this species the highest total disease susceptibility relative to the remainder of the coral fauna. The massive corals *Montastraea faveolata* and *M. annularis* were the species most commonly

TABLE 2

Percent prevalence of disease and the number of colonies sampled is presented for those species which were sampled over 50 times

Species	**N**	**BBD**	**UNK**	**DSD**	**SYN**	**YBD**	**Total**
Siderastrea siderea (Ellis and Solander, 1976)	338	0.3	0.9	21	0.3	0.3	22.8
Montastraea faveolata (Ellis and Solander, 1976)	207	0.00	1.0	0.00	0.00	6.8	7.7
Montastraea annularis (Ellis and Solander, 1976)	627	0.3	0.3	0.2	1.0	5.1	6.9
Montastraea annularis species complex	242	0.4	0.4	0.00	2.9	2.1	5.8
Montastraea franksi (Gregory, 1895)	1337	0.6	0.2	0.1	0.6	1.9	3.5
Meandrina meandrites (Linnaeus, 1767)	57	0.00	0.00	1.8	0.00	0.00	1.8
Montastraea caveronosa (Linnaeus, 1767)	501	0.6	0.2	0.4	0.00	0.2	1.4
Porites astreoides (Lamarck, 1816)	543	0.00	0.00	0.00	0.9	0.4	1.3
Colpophyllia natans (Houttuyn, 1772)	83	1.2	0.00	0.00	0.00	0.00	1.2
Agaricia agaricites (Linnaeus, 1758)	267	0.4	0.00	0.00	0.7	0.00	1.1
Diploria strigosa (Dana, 1846)	137	0.00	0.00	0.00	0.00	0.7	0.7

Diseases are black band disease (BBD), dark spots disease (DSD), white syndrome (SYN), yellow band disease (YBD), unknown disease lesions (UNK), and the total of all diseases (Total). The *Montastraea annularis* species complex grouping signifies corals within the *M. annularis* species complex that could not be identified to species in the field due to high phenotypic plasticity within the genus.

affected by yellow blotch disease (the most common disease), while indistinguishable corals within the *Montastraea annularis* species complex had a much higher prevalence of white syndrome. *Colpophyllia natans* was the species most affected by black band disease, followed by *Montastraea cavernosa* and *M. franksi*. All four categories of recognized coral diseases were observed in three species: *M. annularis, M. franksi* and *S. siderea.* Of the 11 species that showed susceptibility to disease, *Diploria strigosa* was the species that was affected by the fewest diseases, with a minor prevalence of yellow blotch disease. *Madracis decactis* also showed incidence of yellow blotch disease; however, the accuracy of the prevalence estimate (4.5%) may be low due to a small sample size (22 colonies).

Four coral species sampled more than 50 times showed no incidence of disease. Of

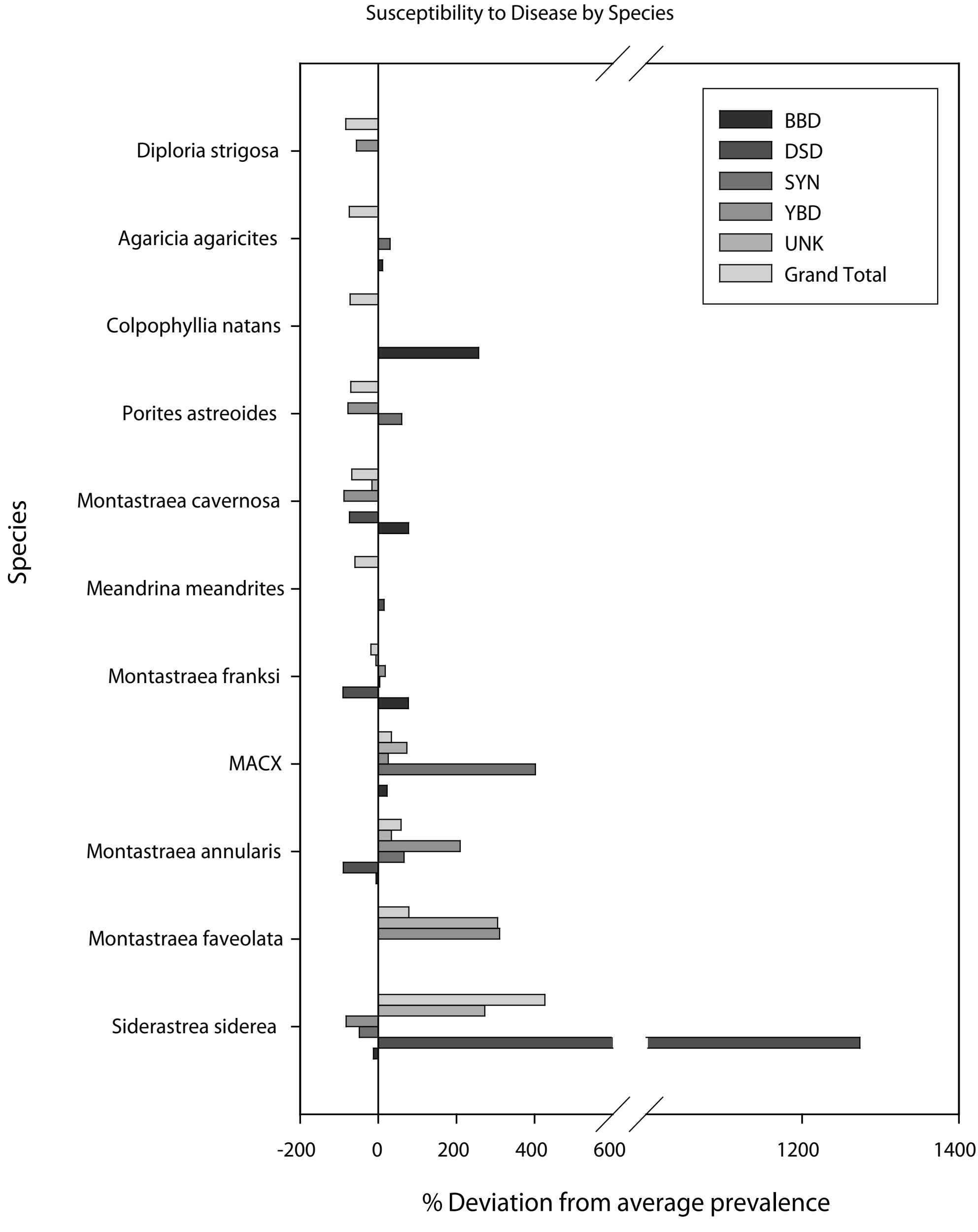

Fig. 2. The susceptibility index of disease (normalized percent deviation from average prevalence) for black band disease (BBD), unknown (UNK), dark spots disease (DSD), white syndrome (SYN), yellow blotch disease (YBD), and all diseases combined (Total). Results are shown only for species that presented signs of disease. The *Montastraea annularis* species complex grouping (MACX) signifies corals within the *M. annularis* species complex that could not be identified to species in the field due to high phenotypic plasticity within the genus.

corals sampled over 100 times (>99% detection probability for 1% disease prevalence), only *Porites porites* (n = 265) was not susceptible to disease. Of corals with sample sizes between 50 and 100 (50-99% detection probability for 1% disease prevalence) only *Diploria labyrinthiformis* (n = 90), *Millepora alcicornis* (n = 72), and *Millepora complanata* (n = 56) showed no disease incidence. These results suggest a low susceptibility to disease within these species; however, greater sample sizes may be necessary.

DISCUSSION

Diseases are affecting massive and important reef structure building corals in the USVI. Our results showed that species in the *Montastraea annularis* complex and *Siderastrea siderea* were the most susceptible to disease. Overall, the *Montastraea annularis* species complex (including corals that were identified to species in the field and those only identified to genus) was the most susceptible to yellow blotch disease, the most prevalent disease on mid-deep reefs in the USVI. Among species in the *M. annularis* complex, yellow blotch disease was found to primarily affect *M. faveolata* and *M. annularis* which is consistent with previous studies of this disease (Cervino *et al.* 2001, Bruckner and Bruckner 2006a and b, Foley *et al*. 2005). Species in the *M. annularis* complex also showed susceptibility to white syndromes, including white plague, which supports other studies in the USVI where WPII has been shown to cause significant declines in coral cover on St. John reefs (Miller *et al*. 2003). The high disease susceptibility found for the *Montastraea annularis* species complex is another troubling indication of continued degradation within these important reef building corals in the USVI and the Caribbean (Weil and Knowlton 1994, Cervino *et al.* 2001, Miller *et al.* 2003, Bruckner and Bruckner 2006a and b, Miller and Williams 2007). Also troubling is that disease states were seen across sites and depths (authors unpub. data) and not necessarily associated with proximity to anthropogenic influences. The presence of diseases on deeper reefs is also similar to observations of WPII made on deep reefs surrounding St. John (Miller *et al*. 2003).

Siderastrea siderea showed the highest prevalence of disease due to its high susceptibility to dark spots disease. This susceptibility pattern was similar to findings by Borger (2005) in Dominica, where *S. siderea* was the only species affected by dark spots disease, and by Gochfeld *et al*. (2006) who also found that dark spots most frequently affects *S. siderea*. Although these results suggest the potential for degradation within *S. siderea*, another study by Borger (2003) found that the effects of dark spots disease on the coral community were low compared to the more virulent tissue eroding diseases white plague and black band disease.

White plague and black band disease are two widespread and serious Caribbean diseases that cause rapid tissue destruction and high mortality rates in corals (Goreau *et al*. 1998, Richardson *et al*. 1998, Nugues *et al*. 2004, Aeby and Santavy 2006). Such rapid tissue loss and partial and whole colony mortality could have lead to lower detection of white syndrome and black band disease in our annual and semi-annual reef monitoring relative to dark spots and yellow blotch disease. For example, white plague has been shown to spread up to 20 mm a day (Richardson 1998) and black band disease up to 3.1 mm a day (Rützler *et al.* 1983). On the other hand, dark spots disease (0.12 mm a day, Borger 2005; 1.3 mm a day, Cervino *et al.* 2001) and yellow blotch disease (0.2 mm a day, Cervino *et al.* 2001; 0.14 mm a day, Bruckner and Bruckner 2006b) tend to spread relatively slowly and persist as more chronic conditions. Thus, because signs are more persistent in slower progressing diseases, they should be more detectable during annual or semi-annual monitoring.

Although the mechanisms behind differential susceptibility of coral species to various diseases are not well established, disease is undoubtedly continuing to change the structure and composition of coral reefs. As shown in this study, the high susceptibility to disease in the dominant mid-depth reef builders, *Montastraea* spp., may be leading to changes in mid-depth coral reef species composition similar to those that occurred after the white band epizootics killed off most of the shallow water Caribbean Acroporids (Gladfelter *et al*. 1982, Bruckner and Bruckner 2006a). Furthermore, from another study in The US Virgin Islands, WPII often resulted in no evidence of recovery (Miller *et al*. 2003).

Whether disease is being caused by global or local factors, continued increases in global and local stresses are likely to cause the number of future diseases and outbreaks to rise (McClanahan *et al.* 2002). Coral reef monitoring programs in the USVI, the Caribbean, and around the globe are critical to providing the information necessary to understand the changes that are occurring on coral reefs over time and providing evidence for the processes behind degradation and recovery.

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RESUMEN

La cantidad e intensidad de las enfermedades de coral han aumentado en los últimos años. Sin embargo, poco se sabe de porqué algunas especies son más susceptibles. El presente estudio examina la prevalencia de estas enfermedades y la susceptibilidad de las especies, utilizando los datos recolectados durante cuatro años, en 25 sitios en las Islas Vírgenes de los Estados Unidos. Doce especies de corales escleractinios estaban enfermas. Las más comunes fueron la enfermedad de la banda amarilla (YBD: yellow band disease) y la enfermedad de las manchas oscuras (DSD: dark spot disease). En tres especies (*Montastraea annularis*, *Montastraea franksi* y *Siderestrea siderea*) observamos cuatro enfermedades, las dos mencionadas anteriormente, el síndrome blanco y la enfermedad de la banda negra. La especie *S. siderea* fue la más frecuentemente afectada, con una prevalencia de 23%, debido, en gran parte, al alto número de casos de DSD. La YBD fue la segunda enfermedad más común, y mostró la más alta prevalencia en *M. annularis* (5.1%). La BBD fue más común en *Colpophyllia natans* (1.2%), mientras que el síndrome blanco se observó con más frecuencia en el complejo de *M. annularis* (2.9%). Cuatro de las 12 especies afectadas por una enfermedad tenían una susceptibilidad a la enfermedad mayor que el promedio, entre ellas las especies del género *Montastraea*, así como *S. siderea*. De las 12 especies con señales de enfermedad, *Diploria strigosa* fue la menos afectada, con solamente una leve susceptibilidad a la YBD. Dos especies de corales escleractinios, *Porites porites* y *Diploria labrynthiformis*, y dos especies de hidrocoral, *Millepora alcicornis* y *Millepora complanata*, no mostraron indicios de enfermedad, lo que sugiere una baja susceptibilidad a las enfermedades.

Palabras clave: arrecifes coralinos, monitoreo, enfermedad, susceptibilidad, USVI.

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