The future of coral reefs in the US Virgin Islands: Is *Acropora palmata* more likely to recover than *Montastraea annularis* complex?

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Abstract. Coral diseases have played a major role in the degradation of coral reefs in the Caribbean, including those in the US Virgin Islands (USVI). In 2005, bleaching affected reefs throughout the Caribbean, and was especially severe on USVI reefs. Some corals began to regain their color as water temperatures cooled, but an outbreak of disease (primarily white plague) led to losses of over 60% of the total live coral cover. *Montastraea annularis*, the most abundant coral, was disproportionately affected, and decreased in relative abundance. The threatened species *Acropora palmata* bleached for the first time on record in the USVI but suffered less bleaching and less mortality from disease than *M. annularis*. *Acropora palmata* and *M. annularis* are the two most significant species in the USVI because of their structural role in the architecture of the reefs, the large size of their colonies, and their complex morphology. The future of the USVI reefs depends largely on their fate. *Acropora palmata* is more likely to recover than *M. annularis* for many reasons, including its faster growth rate, and its lower vulnerability to bleaching and disease.

Key words: disease*, Acropora palmata, Montastraea annularis*

Introduction

Coral diseases have played a major role in the degradation of coral reefs in the Caribbean, including those in the US Virgin Islands (USVI) (Weil et al. 2006, Rogers et al. 2008a). White band disease, first described from St. Croix, USVI (Gladfelter 1982), decimated *Acropora palmata* in the late 1970s and 1980s (Gladfelter 1982, Aronson and Precht 2001). Now there are many more coral diseases, and they are affecting virtually all coral species (Weil 2004). White plague has been the primary disease affecting *Montastraea annularis* and other massive corals. Although white band disease is less common now in the USVI, white pox disease and other un-described diseases are affecting *A. palmata*. In this paper we use the terms white pox and white plague based on the similarity of the gross signs observed in the field to descriptions in the scientific literature. These diseases have been associated with the pathogens *Serratia marcescens* (Patterson et al. 2002) and *Aurantimonas coralicida (*Denner et al. 2003), respectively, but these bacteria have not consistently been isolated from diseased corals at USVI (or other) study sites (Polson 2007). As Work et al. (2008) and others have noted, coral disease investigations are at a very early stage.

Although the coral reefs in the USVI have deteriorated from overfishing, runoff, hurricanes, and

a number of other causes (Rogers and Beets 2001, Rogers et al. 2008a, Rothenberger et al. 2008), the greatest losses since studies began over 40 years ago have been from the combination of bleaching and disease from 2005 to 2006 (Miller et al. 2006, Muller et al. 2008, Rogers et al. 2008b). Conclusions that 18% of the world's coral reefs will likely be "lost" by 2030 (IPCC 2007) are appearing in the scientific literature. Although there is no clarification of just what is meant by the word "lost", many reefs have certainly deteriorated severely. Specifically, in the Caribbean, live coral cover has declined significantly, and primary reef-building species such as *Acropora palmata* and *Montastraea annularis* have decreased in abundance.

Here we briefly describe the recent declines in the USVI and discuss the potential for recovery of the two most significant species, *A. palmata* and *M. annularis*. *Montastraea annularis* is the most abundant coral on deeper (5 to 20 m) reefs, outside the *A. palmata* zones. These species are the main reef builders, with colonies that can reach several meters across, and with a complex morphology that provides shelter and habitat for a diversity of fish and other

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organisms (Goreau 1959, Shinn 1963, Ogden and Ehrlich 1977, Lirman 1999).

Effects of bleaching and disease on deeper (5 to 20 m) reefs in the USVI

The Caribbean-wide bleaching event in 2005 and subsequent disease outbreak led to an average loss of over 50% of the living coral cover at long-term study sites in the USVI in one year and an average loss of over 60% in two years (Rogers et al. 2008b). Four of the five sites are within Marine Protected Areas [Virgin Islands National Park (St. John) and Buck Island Reef National Monument (St. Croix)]. These are being monitored by National Park Service (NPS) biologists with the South Florida Caribbean Inventory & Monitoring Network. An average of c. 96% of the total coral cover bleached, including over 90% of the *Montastraea annularis* complex. [*Montastraea annularis* complex, abbreviated as *Ma*cx, refers to *M. annularis*, *M. franksi*, and *M. faveolata* (Weil and Knowlton 1994)]. Over 90% of the disease lesions and the area killed by disease occurred on *Ma*cx, and the relative abundance of *Ma*cx went from 79.2% to 58.6%. *Montastraea annularis* initially made up 55.6% of the coral cover but declined to 40.9% by 2007. The total coral cover on these reefs fell from an average of 21.4% to 10.3% after 1 yr and then to 8.3% after 2 yrs. Because National Park Service and US Geological Survey scientists increased the frequency of monitoring to every few months during the bleaching event and subsequent disease outbreak, it was clear that the significant coral mortality was from disease, not directly from bleaching.

Effects of bleaching and disease on *Acropora palmata* colonies

USGS biologists were monitoring individual *A. palmata* colonies during this event and observed bleaching of this species for the first time on record in the USVI. About 48% (of a subset of 467 colonies that were being monitored) bleached, 13% died partially, and only 8% died completely. Muller et al. (2008) found a positive relationship between temperature and disease in 2005, the year of the bleaching event. In addition, the average area of disease-associated mortality was significantly higher on bleached colonies, suggesting that disease severity was related to bleaching susceptibility. Although some colonies died partly or totally from bleaching and disease, this species did not suffer such extensive losses as *M. annularis* and many other species. The bleached *A. palmata* colonies around St. John had regained their normal color by January 2006. In contrast, *M. annularis* colonies at the long-term study reefs remained pale until at least October 2006.

Potential for recovery of *Acropora palmata* and *Montastraea annularis*

For a variety of reasons, *A. palmata* has a greater chance of recovering than *M. annularis*. What exactly is meant by recovery? In the strictest sense, full recovery would entail a return to the same number of colonies, overall amount of living coral cover, and genotypic diversity present at a specified time. Currently *M. annularis* is found to depths over 40 m (Armstrong et al. 2006) and in several reef zones, and is far more abundant than *Acropora palmata* which occurs typically in less than 8 m and in fewer zones. Even before the 2005/2006 bleaching and disease event, Edmunds and Elahi (2007) predicted possible extirpation of *M. annularis* at one site in St. John, based on a demographic model using data from three 10-m long transects dominated by this species.

More information is needed on the levels of sexual recruitment in both species. Both species are broadcast spawners and both spawn in late summer, a time of higher vulnerability because of hurricanes and generally warmer water. Several studies show low levels of recruitment for both species (Bak and Engel 1979, Rogers et al. 1984, Edmunds 2000). However, the genotypic diversity of *A. palmata* around St. John is quite high and is evidence that sexual recruitment is occurring here as well as elsewhere in the Caribbean (Baums et al. 2006, Rogers et al. 2008b; but see Williams et al. 2008). For example, in Haulover Bay, 43 of 48 colonies were different genotypes. Sexual recruits of *A. palmata* on dead portions of *A. palmata* colonies cannot be distinguished from surviving remnants, but around St. John many small colonies growing directly on rock substrate are further evidence of sexual recruitment. Genotypic diversity of *Ma*cx is unknown in this area and certainly a confounding factor when evaluating the potential for recovery.

Although both *A. palmata* and *M. annularis* are able to reproduce asexually (Highsmith 1982, Foster et al. 2007), *A. palmata* as a branching species probably has a greater potential for dispersal through fragmentation. This species typically has more damage from storms than massive colonies (Woodley et al. 1981, Hubbard et al. 1991). The columnar or lobar morphology of *M. annularis* begins to develop when the colony is still relatively small, in some cases less than 30 cm across. Although the separate lobes can be dislodged and dispersed, fragmentation is not as likely as in *A. palmata* and the separate "fragments" are heavier and probably not often transported far from the donor colony. (Unlike *A. palmata* fragments, the lobes often separate from the colony at the base where there is coral skeleton, not

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living coral.) Of course, not all *A. palmata* fragments attach and survive (Lirman 2000a, Williams et al. 2008). At Saltpond Bay, on the south side of St. John, 60% of the (naturally-generated) fragments survived for three or more months (USGS, unpublished data).

A few recent studies use analysis of genotypes to document dispersal of clones. Baums et al. (2006) showed that *A. palmata* fragments from one genet had dispersed over a distance of more than 70 m on one Florida reef. Foster et al. (2007) reported dispersal of *M. annularis* lobes (columns) up to 9 m away on Honduras reefs affected by storms, but the clonality was lower than reported for many *A. palmata* populations (Baums et al. 2006).

The scientific literature has few studies of growth rates of corals from different locations. However, in the USVI *A. palmata* has much higher growth rates (about 5 to 10 cm per year, Gladfelter et al. 1978) than *M. annularis* (less than 1 cm per year, Gladfelter et al. 1978, Hubbard and Scaturo 1985).

Healing rates of *A. palmata* after physical damage, for example from storms, and regeneration of disease lesions can be quite rapid (Rogers et al. 1982, Lirman 2000b, Muller 2007). Less is known about the ability for lesions on *M. annularis* to regenerate, and the nature of the damage to this species differs in that colonies are often abraded by sand or dislodged from their bases rather than fractured. The cause of the lesions can make a difference in the coral's ability to regenerate tissue or tissue and skeleton. Meesters et al. (1994) noted that experimentally-created lesions on *M. annularis* usually did not completely close, leaving bare space for colonization by algae and other organisms. Bak et al. (1977) showed repair of small, experimentally-created lesions on *M. annularis* over several days. Bak (1983) showed that regeneration of small, artificially-created lesions was more rapid in *A. palmata* than in *M. annularis*.

Montastraea annularis currently appears more vulnerable to diseases than *A. palmata*. Although almost 90% of the *A. palmata* colonies in studies around St. John had disease (primarily white pox) when observed in monthly surveys, many of these lesions healed. In contrast, growth of original colony tissue over white plague lesions has never been seen on *M. annularis* colonies.

It is possible that regeneration rates in *M. annularis* are slower than in the past. Also, the lesions associated with white plague are usually larger than those from white pox. White plague and Caribbean yellow band disease which disproportionately affect *M. annularis* and *M. faveolata* are especially virulent diseases (Bruckner and Bruckner 2006). Also, lesions (artificial or natural) surrounded by living tissue, such as those from white pox, may heal faster than those

that border on bare or algal covered skeleton such as those from white plague.
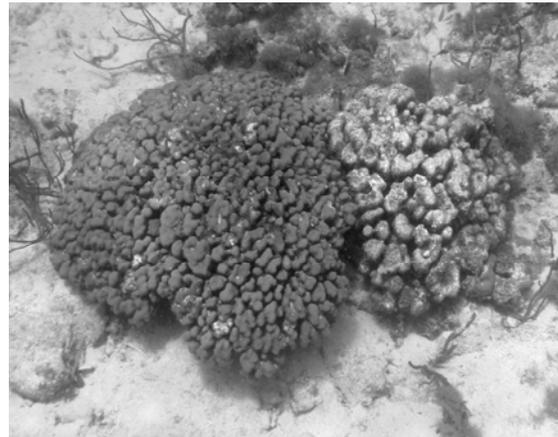

Figure 1. Adjacent colonies of *M. annularis*, with the one on the left apparently healthy and the one on the right entirely dead.

Some colonies of both of these species seem to have more resistance to bleaching and disease than adjacent or nearby colonies (Fig. 1). Future research on different types of zooxanthellae and on the characteristics of different host coral genotypes may shed some light on this interesting phenomenon.

Evidence of recovery in the USVI and elsewhere
Acropora palmata is showing signs of limited recovery in the USVI, including in areas devastated by white band disease about 30 years ago (Gladfelter 1982, Rogers et al. 2003). Few people have followed *A. palmata* populations in precisely the same reef areas over time. Some signs of recovery have been noted at Buck Island Reef National Monument (Mayor et al. 2006), however these observations were before the major 2005 bleaching event that led to at least partial mortality of many colonies there (NPS, unpublished data). Our studies in St. John do not show clear evidence of an increase in number of colonies and in the overall amount of living coral tissue from 2003 through 2007 (Rogers et al. 2008a).

Recent observations indicate presence of new colonies of *A. palmata* in many areas (e.g., Macintyre and Toscano 2007, Zubillaga et al. 2008), but no clear signs of complete recovery back to the numbers (and overall colony condition) from two to three decades ago. One-time observations of the presence of this species are not irrefutable evidence of recovery. Macintyre et al. (2007) found no living *A. palmata* colonies on a bank-barrier reef off Barbados that was formerly dominated by this species.

Conclusions
The 2005 bleaching event and subsequent outbreak of disease caused the biggest decline ever recorded for

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USVI coral reefs. No other stressors have caused so much loss, over such a large geographical area, in such a short time. Similar losses were observed in nearby Puerto Rico (Ballantine et al. 2008).

The fate of the coral reefs in the USVI is uncertain, largely because the fate of the major reef-building species, *Acropora palmata* and *Montastraea annularis*, is not known. Global climate change is expected to bring more intense hurricanes, warmer sea temperatures, more bleaching episodes, and ocean acidification, all of which are great concerns. How will these two species deal with these and other stressors in the future? Which of the stressors are amenable to local management and which must be managed on a global basis? What is the human component of global climate change? Extensive bleaching has not been seen on USVI reefs since 2005, but active white plague disease was seen in August 2008 at one of the St. John long-term study sites.

We are certainly not able to predict the future of the USVI seascape. We need to understand the links between human activities and diseases. Although *A. palmata* seems to have a better chance of recovery than *M. annularis*, based on its higher growth rate, greater potential for dispersal via fragmentation, and its greater resistance to bleaching and disease, there is no evidence of significant increases in the number and size of *A. palmata* colonies around the islands in the last five years. We also need to know more about water circulation patterns and connectivity between USVI reefs and upstream sources which have the potential to supply coral and fish larvae to replenish these degraded ecosystems.

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