Infectious diseases of reef corals

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ABSTRACT

The continuing degradation of coral reefs throughout the world is accompanied by increasing observations of infectious diseases and disease outbreaks of corals and other coral reef benthic organisms.   Microbial pathogens of both stony corals and gorgonians have been isolated and in some cases characterized. Underlying mechanisms of the pathogenesis of several diseases are being studied at the microbiological, physiological, and molecular levels. The short- and long-term ecological effects of disease outbreaks on reefs in different geographic regions are being documented as they occur.   In one paleoecological study a coral disease was revealed to have caused an unprecedented alteration in community structure. Here we review recent progress in the field of coral diseases.

Keywords Coral disease, Reef degradation, Coral health

Introduction

The first coral disease was reported in 1973 by A. Antonius. In the following three decades, coral diseases have come to be recognized as important contributors to reef degradation on a global scale (Epstein et al. 1998, Harvell et al. 1999).   While the effects of individual diseases and disease outbreaks vary, in at least one case a disease outbreak restructured an entire reef community for the first time in more than 3,000 years (Aronson and Precht, in press).   Here we provide an overview of the status of knowledge of coral diseases and of uncharacterized syndromes that may be emerging diseases. Our emphasis is on microbial coral pathogens as well as on the ecological role of diseases on coral reefs. While much progress has been made since the last comprehensive review (Richardson 1998), many questions remain to be answered.

Coral Diseases

Research focused on characterizing coral diseases, including bacterial bleaching, has revealed an impressive diversity of microbial pathogens.   The microbial pathogens of corals that have been isolated, identified, and studied in the laboratory include single fungal or bacterial species as well as microbial consortia, the latter ranging from highly structured to loosely organized populations. Microbial pathogens include phototrophic as well as heterotrophic species, with a wide range of metabolic modes exhibited.   Accompanying this microbiological diversity, coral diseases have equally diverse etiologies.

Despite 30 yr of work in this field, however, which includes an increased focus on microbiology over the past decade, we still have a limited understanding of the microbial pathogens of corals. Only four coral diseases have been characterized in terms of microbial pathogens and, to a lesser extent, pathogenesis: black band disease, white band disease type II, plague type II, and aspergillosis.   Bacterial bleaching is a fifth well-characterized pathogenic microbial/coral interaction. One previously postulated coral disease, termed "rapid wasting disease," has now been shown to be caused by extensive parrotfish biting rather than by a pathogen (Bruckner and Bruckner in press).   Research efforts have resulted in partial characterization of several coral syndromes that include white pox, dark spots, and red band diseases. There is an additional suite of postulated diseases for which no pathogen has been isolated despite efforts by several research groups. These include white band type I and yellow blotch. Each is discussed below.

Black band disease

Black band disease, the first coral disease to be reported (Antonius 1973), is also one of the best-characterized (reviewed in Richardson 1998).   It is caused by a pathogenic microbial consortium that includes the oxygenic photosynthetic cyanobacterium *Phormidium corallyticum*, sulfate-reducing bacteria dominated by *Desulfovibrio* spp., and the sulfide-oxidizing bacterium *Beggiatoa*.   An assortment of uncharacterized gram-negative, heterotrophic bacteria are also present.   The consortium consists of a highly structured microbial assemblage that generates and maintains its own sulfuretum (biogeochemical sulfur cycle) and closely resembles the well-studied, laminated microbial mat communities found in many sulfide-rich, illuminated aquatic environments.   High levels of toxic sulfide produced within the consortium, in conjunction with the microbially generated and maintained microenvironment of anoxia present at the base of the black band community, combine to produce a lethal effect on the underlying coral tissue. The active degradation and complete mineralization of coral tissue, which occurs as the disease moves across coral colonies, is believed to sustain the dynamic microbial community. Black band disease is one of only two coral diseases (the other being aspergillosis) for which the reservoir is known; non-pathogenic biofilms of the black band community have been found in sediment patches on the surface of healthy, black band disease-susceptible corals.

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On an ecological level, studies in Florida and the Caribbean have shown that black band disease, although not as prevalent as aspergillosis or white band disease (discussed below), has a deleterious effect on reef communities by killing framework-building corals in the genera *Montastraea*, *Diploria* and *Colpophyllia*. Although Edmunds (1991) originally postulated that newly-exposed coral skeletons could be beneficial to the reef by providing fresh substrate for the recruitment of scleractinian corals, long-term monitoring studies in the Caribbean (St. John, USVI) and the Florida Keys have shown that the coral skeleton exposed by black band disease is colonized primarily by gorgonians (Edmunds 1991, 2000, Kuta and Richardson 1997). Only after a period of 5-11 yr following black band-induced mortality has the recruitment of scleractinian corals become evident (Kuta and Richardson 1997, Edmunds 2000). In each study area only one framework-building coral colony (one each of *Diploria strigosa* and *Colpophyllia natans*) was observed to recruit onto a total of 27 coral colonies monitored. In both studies non-framework corals of the genera *Agaricia*, *Porites* and *Favia* colonized the dead coral substrate rather than the original, framework-building species.

Current microbiological research efforts on black band disease include investigations into the metabolism of the microbial members of the black band community and its relation to pathogenesis, and nucleic acid sequence analyses and comparisons to determine if the consortial members are the same species in different infections and geographic regions. Recently-published results include demonstration that the black band cyanobacterium has a very low light requirement for optimal photosynthesis, which may be the physiological basis of observed motility patterns that are important in the formation of the band matrix (Kuta 2000, Viehman and Richardson in press). Current ecological research includes several ongoing studies aimed at linking black band disease with elevated nutrients. Although some data suggest that there is a correlation (Antonius 1988, Bruckner and Bruckner 1997, Kuta 2000), a causal connection has not been established.

White band disease

White band disease of the Caribbean framework-building species *Acropora palmata* and *A. cervicornis* continues to be one of the most intriguing and ecologically significant of all the coral diseases. White band disease was one of the first coral diseases to be described (Gladfelter et al. 1977) and was the subject of some of the earliest efforts aimed at isolating and identifying microbial pathogens (Peters et al. 1983). Microbiological studies that focused on bacterial aggregates present in white band-diseased coral tissue, first observed in the 1980s (Peters et al. 1983), have yielded no bacterial isolates despite repeated attempts at laboratory culturing; however, during these investigations similar aggregates have also been observed in healthy coral tissue (Santavy and Peters 1997), suggesting that the aggregates may not be involved in pathogenesis.

More promising results have been obtained using a different approach: characterizing microbial populations of white band-diseased tissue in comparison with non-diseased tissue of the same coral species. Ritchie and Smith (1995) utilized a combination of molecular methods (rDNA sequence analysis and comparison) and metabolic profiling (carbon source utilization patterns) to investigate the microorganisms associated with white band disease. They found that, as the disease progressed, there was an apparent shift in composition of the normal bacterial population associated with the surface mucopolysaccharide layer of coral colonies (Ritchie and Smith 1995). Diseased tissue consistently contained relatively high concentrations of the gram-negative bacterium *Vibrio carchariae* within a diverse bacterial community.

Ritchie and Smith (1998) also discerned two distinctive patterns in the progression of white band disease, which they termed white band types I and II. White band type I is characterized by tissue necrosis and degradation in which there is always a distinctive line between the exposed coral skeleton and the healthy tissue. In contrast, type II, when active, exhibits a transient zone between tissue necrosis and exposed skeleton that consists of bleached but intact coral tissue. Studies are ongoing to compare these diseases. In the following discussion we refer to white band disease in the singular for linguistic convenience.

Aronson and Precht (in press) compiled published and anecdotal reports of the effects of white band disease on populations of *A. palmata* and *A. cervicornis* throughout the Caribbean. They concluded that white band disease has been the leading cause of coral mortality on shallow Caribbean reefs over the past two to three decades. White band disease caused extensive mortality of *A. palmata* and removed *A. cervicornis* almost entirely from reefs around the region in the 1980s and 1990s. Since the two species of *Acropora* had been the dominant space occupants (as well as important framework-builders) in reef-crest and fore-reef spur-and-groove habitats, respectively, from at least as far back as the 1950s until the late 1970s or early 1980s, their loss was the leading cause of declining coral cover. A coring study, carried out over a large spatial scale (hundreds of km^2) in the central sector of the shelf lagoon of the Belizean barrier reef system, revealed that mass mortalities of *A. cervicornis* from white band disease (or from any other causes) had not occurred before in at least the past 3,000-4,000 yr (Aronson et al. in press).

Plague

Plague, also called white plague, was first observed by Dustan (1977) on reefs of the Florida Keys. At that time no efforts were made to culture any associated microorganisms, although rod-shaped and flexi-bacteria were observed microscopically in infected tissue (Dustan 1977). A pathogen was isolated from a subsequent, much more virulent plague outbreak (designated plague type II) that occurred on the same reefs in 1995 (Richardson et al. 1998). The pathogen, a gram-negative

bacterium, was characterized by metabolic profiling as well as molecular sequence data, and was determined to be most closely related to the genus *Sphingomonas* (Richardson et al. 1998). It may be a new bacterial genus. The same pathogen has been reisolated from recurring outbreaks of plague type II on reefs of the Florida Keys and elsewhere in the Caribbean region (Polson, Smith, Ritchie and Richardson in prep.) and also from an even more virulent form of the disease designated plague type III (see below). The reservoir of this pathogen has not been determined.

Although the 1995 outbreak of plague type II on reefs of the Florida Keys was one of the most severe disease events recorded in terms of the diversity of coral species affected, the mortality rate, and the rapidity of spread along the reef tract (Richardson et al. 1998), it has had a minimal long-term impact on these reefs. The most susceptible coral species, *Dichocoenia stokesi*, began recolonizing these reefs within the first year after the 1995 disease event. Additionally, individual colonies that were partially killed continued to grow. One of the most intriguing aspects of this disease is the fact that it has not recurred as an outbreak in Florida, although ~3% of *D. stokesi* can exhibit initial disease signs that do not progress. While the same microbial pathogen has been reisolated from such colonies, healthy colonies collected and tested in the laboratory are not susceptible to either the original or newly isolated strains of the pathogen. It is still unclear whether this is due to an immunity acquired during the original disease event or to a natural resistance in some colonies, which then remained to constitute the post-outbreak coral population. The first hypothesis is supported by the observation of L.L.R. that corals which survived the 1995 outbreak, but which were infected and partially killed, are no longer susceptible to the pathogen.

In 1999 a third plague outbreak (type III) occurred on the same Floridian reefs (Richardson 2000, Richardson et al. in press). Plague type III exhibits the typical distinctive line between healthy tissue and exposed skeleton, but this form of plague is characterized by the fact that it infects only the largest (2-3 m) colonies of *Colpophyllia natans* and *Montastraea annularis*. Tissue degradation is much faster than either types I or II. This form of plague was also newly observed in the Caribbean in 2000 and 2001.

Aspergillosis

Aspergillosis is a lesion-inducing fungal disease that infects sea fans (*Gorgonia ventalina* and *G. flabellum*) and sea whips, including *Pseudo-pterogorgia americana*, *P. acerosa,* and other species (Weil et al. in press). The pathogen, *Aspergillus sydowii,* was isolated and proved to be the causative agent by fulfillment of Koch's postulates (Smith et al. 1996, Geiser et al. 1998). This species has recently been characterized (Alker et al. in press). Aspergillosis is of particular interest because it is caused by a fungal species of terrestrial origin, yet other strains of *A. sydowii* isolated from the terrestrial environment are not pathogenic to corals (Smith et al. 1998). There is some evidence to support the intriguing hypothesis that *A.*

sydowii was transported to Caribbean reefs in clouds of dust from western Africa (Shinn et al. 2000). Viable spores have been isolated from recent dust events (J. Weir, pers. comm.); thus the reservoir of this coral disease includes atmospheric transport from the source in Africa. An ongoing regional outbreak of aspergillosis, which began in 1995-96, appears to be considerably more severe than an earlier episode in the western Caribbean during the 1980s (Nagelkerken et al. 1997a, b).

Aspergillosis is the only coral disease to date for which researchers have determined that corals can respond to, and counteract, infection (Kim et al. 2000). Upon exposure, sea fans have been observed to produce purple-pigmented galls that encapsulate the pathogenic fungal hyphae and prevent the infection from spreading.

Bacterial bleaching of *Oculina patagonica*

Coral bleaching can be induced by a number of environmental factors (Brown 1997), and there is one well-documented case in which coral bleaching is caused by a bacterium. E. Rosenberg and colleagues have characterized bleaching of the coral *Oculina patagonica* by the gram-negative bacterium *Vibrio shiloi* (Banin et al. in press). They have fullfilled Koch's postulates to demonstrate that the bleaching mechanism is directly caused by the bacterium, and they have demonstrated mechanistic pathogenic properties that include adhesion of the pathogen to a specific surface receptor on the coral surface, bacterial penetration of coral cells in an infection process, and production of an associated toxin (Banin et al. 2000, in press). The virulence of *V. shiloi* is strongly temperature-dependent, leading these authors to the suggestion that the widely recognized positive association between sustained, elevated water temperature and coral bleaching may have a bacterial component in other corals as well (Banin et al. in press).

Uncharacterized coral diseases and syndromes: white pox, dark spots, red band and yellow blotch diseases

There are a number of other potential pathologies that have not yet been completely characterized, although they are all currently being investigated. Of these, white pox of Caribbean acroporids is the only one for which a possible (bacterial) pathogen has been isolated (Smith pers. comm.). This syndrome is characterized by white, circular lesions on the surface of infected colonies (Porter in press). Dark spots syndrome (first described by J. Garzón-Ferreira, manuscript in preparation) is increasingly common on Caribbean scleractinians. While it primarily affects the species *Siderastrea siderea*, it also has been noted on *Montastraea annularis* and *Stephanocoenia intersepta* in the southern Caribbean (Weil et al. in press).

Microbiological studies of dark spots syndrome have not yet yielded a pathogen although attempts are ongoing (Smith pers. comm.). This pathology is associated with only minor tissue degradation and is primarily manifested as a pigmentation anomaly in which purple spots and patches are present in the tissue. 'Yellow blotch'

syndrome, which primarily affects *Montastraea annularis* (Porter in press), is also increasingly common. Like dark spots, no pathogen has been isolated after continuing attempts (Smith, pers. comm.), and associated tissue mortality, while present to some extent, is much slower than the characterized diseases. 'Red band' has been reported on both scleractinians and gorgonians (reviewed in Richardson 1998), but the only conclusive evidence to date is the recognition of two unidentified species of the cyanobacterial genus *Oscillatoria* in the band community. There is much disagreement as to the occurrence of this syndrome. Reports range from widespread to not present in the Florida Keys, and very different photographs of "red band" have been published on coral disease identification cards.

Conclusions

Disease has played a crucial role in the ecology of Caribbean reefs over the past few decades. Coral disease has clearly been a major cause of coral mortality. Other, more localized sources of mortality have included hurricane damage, ship groundings, and massive nutrient input. At the same time, herbivory on reefs has declined, due to the near-extirpation of the sea urchin *Diadema antillarum* in 1983-83 (presumed to have been caused by a water-borne pathogen, Lessios 1988), and overfishing of herbivorous parrotfish (Scaridae) and surgeonfish (Acanthuridae). The combination of coral mortality and declining herbivory has precipitated a regional-scale phase shift from coral to macroalgal dominance on these reefs (Done 1992, Ginsburg 1994).

Acropora spp., which were primary space occupants and framework builders in shallow reefs throughout the Caribbean, have largely succumbed to white band disease. The decline of massive, reef-framework corals due to black band disease and plague, during disease events which have occurred simultaneously and which have become more frequent in recent years, has further decreased the cover of live corals on Caribbean reefs. Aspergillosis continues to kill gorgonians around the region. The uncharacterized syndromes "dark spots," "yellow blotch," and "white pox" are rapidly increasing in terms of the numbers of coral colonies affected and the numbers of lesions or pigmentation anomalies present on individual colonies (Weil et al. in press). While these three potential pathologies have not as yet resulted in a mass coral mortality, the dramatic increase in prevalence suggests that they may begin to severely affect coral health. This is discussed in detail by Weil et al. (in press), who documented, for example, dark spots syndrome on 79% of study reefs in a survey encompassing six geographic areas throughout the Caribbean.

Although most of the research on diseases of corals has been conducted throughout the greater Caribbean region, reports of coral disease on Indo-Pacific reefs (Antonius 1988) have also dramatically increased during the past few years. Much of this information is currently unpublished. Dinsdale (in press) documented black band

disease at Heron Island on the Great Barrier Reef. One of us (R.B.A.) observed the characteristic signs of white band disease on *Acropora* spp. during dives at Nusa Lambongan (off Bali) and around Komodo Island in conjunction with the Ninth International Coral Reef Symposium (9ICRS) held in October 2000. Presentations at the 9ICRS raised our concern that coral diseases may soon severely affect reefs in the Indo-Pacific region. Of additional concern are new reports that diseases of other reef organisms besides corals are increasing, both in the Caribbean and the Indo-Pacific (Littler and Littler 1995, Diaz-Pulido in press).

It has become apparent that research on coral disease pathogenesis requires an interdisciplinary approach that includes, and combines, both laboratory and field methods. In particular, an integrated approach is necessary to study the etiologies of coral diseases. To date the extreme variability of the characterized diseases has required different combinations of many methodologies (Richardson et al. in press). The techniques of microbiology, chemical microsensors, advanced microscopy, microbial physiology, and molecular genetics, as well as ecology and paleoecology, are already in use. New, as yet unapplied methods in coral immunology and coral tissue culture will also be needed. Continuing efforts in all of these areas are required to gain the understanding of coral diseases necessary to contribute to the effective management of coral reefs.

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