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# Cyanobacterial mats as benthic reservoirs and vectors for coral black band disease pathogens

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**Abstract**

The concurrent rise in the prevalence of conspicuous benthic cyanobacterial mats and the incidence of coral diseases independently mark major axes of degradation of coral reefs globally. Recent advances have uncovered the potential for the existence of interactions between the expanding cover of cyanobacterial mats and coral disease, especially black band disease (BBD), and this intersection represents both an urgent conservation concern and a critical challenge for future research. Here, we propose links between the transmission of BBD and benthic cyanobacterial mats. We provide molecular and ecophysiological evidence suggesting that cyanobacterial mats may create and maintain physically favorable benthic refugia for BBD pathogens while directly harboring BBD precursor assemblages, and discuss how mats may serve as direct (mediated via contact) and indirect (mediated via predator–prey–pathogen relationships) vectors for BBD pathogens. Finally, we identify and outline future priority research directions that are aligned with actionable management practices and priorities to support evidence-based coral conservation practices.

**KEYWORDS**

coral reef, cyanobacteria, management, pathogenesis, transmission, water quality

## INTRODUCTION

The increasing prevalence of coral diseases is an urgent conservation concern and management priority (Muller et al., 2020; Porter & Meier, 1992). Generally, preventive strategies that include both top-down and bottom-up approaches spanning multiple spatial scales are required for coral reef management (Lapointe et al., 2019). Managing fisheries, regulating coastal development, controlling run-off, and wastewater treatment are all local management strategies actively pursued to combat and control disease drivers. An understanding of reservoirs and vectors for coral disease pathogens is integral to explaining disease transmission, yet our knowledge of these factors remains alarmingly inadequate for many coral diseases. Alongside the continued study of pathogenicity and virulence, a better understanding of coral disease transmission is critical for tailoring specific and effective coral monitoring, management, and restoration strategies, and creating evidence-based policies governing sustainable coastal development (Fraser et al., 2004).

Loss of biodiversity and overall trophic simplification are thought to accelerate the rate of emergence and transmission of disease across diverse ecosystems (Keesing et al., 2006, 2010). On coral reefs, rising coral disease prevalence has coincided with widespread trophic downgrading and an increased predominance of macroalgae and benthic cyanobacterial mats (de Bakker et al., 2017; Estes et al., 2011; Puyana et al., 2014; Stokes et al., 2010). Increasing cover of algae and cyanobacteria increases their contact rate with corals. Macroalgae alter the community composition of coral microbiomes via direct contact-mediated effects (Nugues et al., 2004), and indirectly via water-mediated effects (Haas et al., 2011; Morrow et al., 2013; Smith et al., 2006), although holobiont stability and effect size may be strongly species and context dependent (Clements et al., 2020; Sweet et al., 2013). For example, contact with the alga *Halimeda opuntia*, although itself not directly tied to the etiology of any known coral disease, induces microbiome changes and triggers white plague type II in the coral *Montastraea faveolata* (Nugues et al., 2004).

Benthic cyanobacterial mats are also often observed in close association with corals (Figure 1; Ritson-Williams et al., 2005), where direct contact can slow coral growth rates and lead to localized coral tissue mortality (Puyana et al., 2019), as well as facilitate antagonistic allelopathic impacts on the growth and photochemical efficiency of coral zooxanthellae (Titlyanov et al., 2007). Indeed, many of the environmental drivers implicated in the higher prevalence of coral diseases are proposed to spur cyanobacterial mat growth, including elevated temperatures and nutrient loading (Brocke, Polerecky, et al., 2015; Ford et al., 2018; Howells et al., 2020; Huisman et al., 2018; Miller & Richardson, 2015; Ruiz-Moreno et al., 2012; Wang et al., 2018). Increased cover of cyanobacterial mats has been documented to be synchronous with massive disease outbreaks on important reef-building corals, including *Montastraea cavernosa* and *Colpophyllia natans* (de Bakker et al., 2017; Stokes et al., 2010). Cyanobacteria are known associates of numerous coral diseases, including BBD (Carlton & Richardson, 1995), and inoculation experiments suggest that cyanobacterial taxa play dominant roles in the creation of BBD mats (Myers et al., 2007; Richardson et al., 2014). Through release of dissolved organic carbon (Brocke, Wenzhoefer, et al., 2015) and bioavailable nitrogen (Brocke et al., 2018), benthic cyanobacterial mats may promote pathogenic bacterial expansion and generate feedbacks that enhance coral

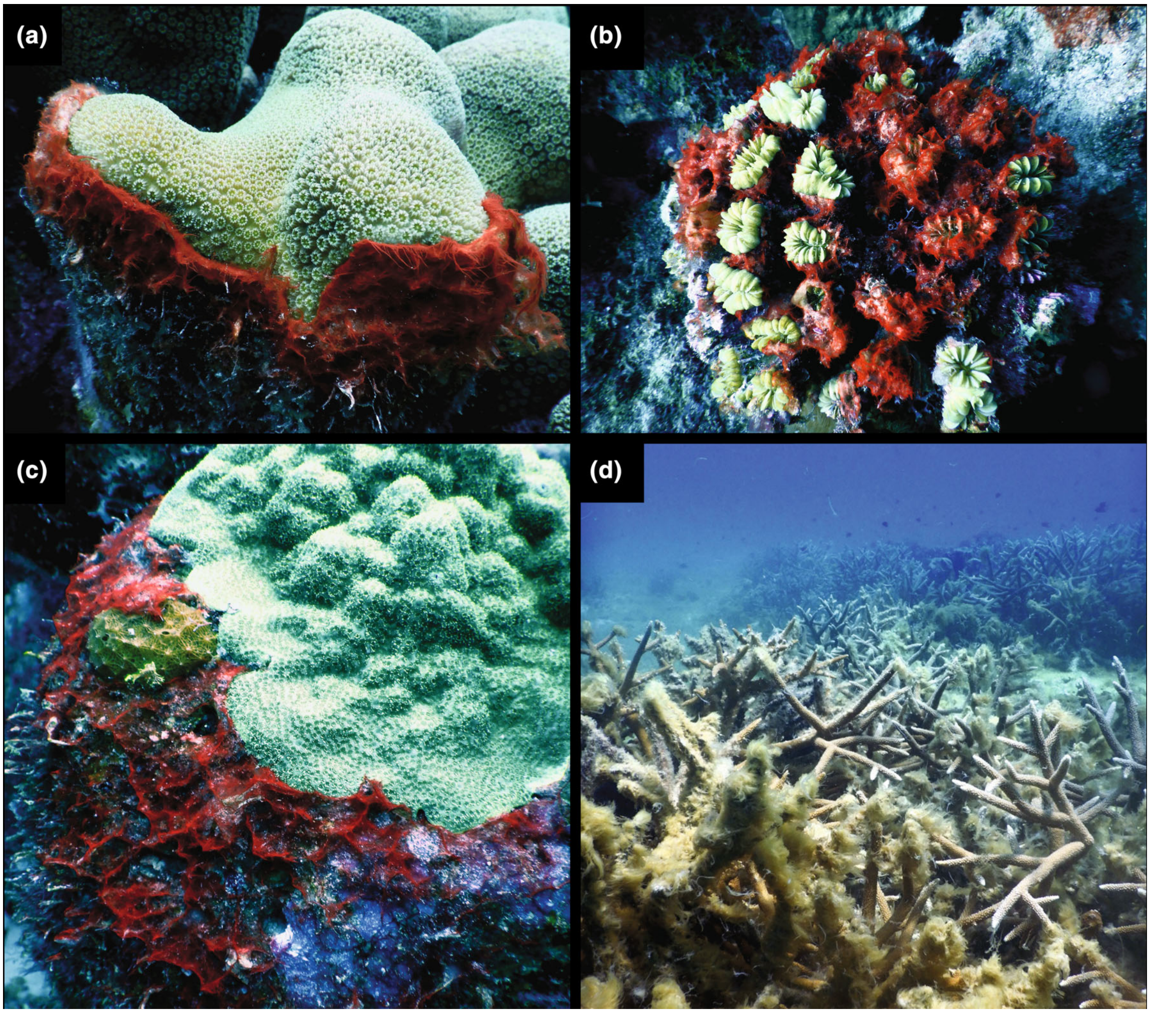


**FIGURE 1** Marginal and direct overgrowth of coral colonies by cyanobacterial mats. Examples of cyanobacterial mats growing along the margins or directly over colonies of (a) *Orbicella annularis*, (b) *Eusmilia fastigiata*, (c) *Porites astreoides*, and (d) *Acropora cervicornis*. All photographs are by E. C. Cissell and were taken in Bonaire, Caribbean Netherlands.

disease incidence and sustain degraded states via the maintenance of altered abiotic environments (Haas et al., 2016). However, mechanistic links among cyanobacterial mat–coral competition, microbiome structure, and overall disease prevalence, to our knowledge, have never been tested.

A surging cover of cyanobacterial mats concurrent with coral disease incidence across reefs globally suggests an important relationship between benthic cyanobacterial mats and coral disease. Here, we discuss the mechanisms by which cyanobacterial mats may act as reservoirs and vectors for coral pathogens on reefs, with a focus on BBD, and propose priority research areas for furthering global conservation and management goals.

Since its discovery as the first reported disease affecting stony corals (Antonius, 1973), BBD has spread globally. BBD is a polymicrobial disease with an etiology linked to darkly pigmented microbial mats dominated by cyanobacteria, sulfate-reducing bacteria (SRB), and diverse heterotrophs (Miller & Richardson, 2011; Sato et al., 2016, 2017). Although cyanobacteria build the mat framework and dominate BBD mat biomass and carbon production, the production of sulfide from the activity of SRB is integral to the pathology of BBD (Sato et al., 2016, 2017). Sulfide production relies on coupled microbial interactions creating anoxic (reducing) microenvironments within the mat, which are similar to diel distributions of oxygen and sulfide found in archetypical microbial mats (Brocke, Polerecky, et al., 2015; Carlton & Richardson, 1995). In this way, a cooperative cyanobacteria–SRB–heterotroph consortium is a BBD hallmark, and a fingerprint for its detection (Sato et al., 2017).

Reservoirs and vectors of BBD pathogens remain unclear (Sato et al., 2016). Benthic cyanobacterial mats are strikingly similar to BBD cyanobacterial patches and advanced-stage BBD mat consortia in composition and support diverse taxa, including SRB taxa from Gammaproteobacteria and Bacteroidota, as well as other pathogenic taxa (Cytophagales; Biessy et al., 2021; Cissell & McCoy, 2021). Like typical microbial mats (Revsbech et al., 1983; Stal, 1995), reef cyanobacterial mat community physiology creates and maintains steep physiochemical gradients that facilitate extensive intramat metabolic niche diversification to include taxa utilizing anoxic and oxygenic energy metabolism (Brocke, Polerecky, et al., 2015; Cissell & McCoy, 2021). Additionally, reef mats, although generally dominated by a single cyanobacterial population, are built by multiple cyanobacterial taxa (Cissell & McCoy, 2021; Echenique-Subiabre et al., 2015), which may confer plasticity in cyanobacterial sulfide tolerance (Sato et al., 2017).

Given these similarities, cyanobacterial mats may serve as benthic reservoirs and refugia for BBD pathogens by harboring precursor BBD assemblages and via persistent maintenance of requisite microenvironmental conditions on non-coral benthic substrata (especially sediment), facilitating prolonged pathogen persistence, despite suboptimal ambient conditions (Brocke, Polerecky, et al., 2015). In addition to serving as benthic reservoirs, benthic cyanobacterial mats may enhance coral susceptibility to secondary infection via localized tissue necrosis (Puyana et al., 2019; Titlyanov et al., 2007), or alter coral microbiomes via overgrowth, either by modifying the physiochemical microenvironment on the host tissue to promote pathogenic conversion of the resident microbiome, as benthic cyanobacterial mats are known to promote underlying hypoxia (Brocke, Polerecky, et al., 2015), or by serving as direct vectors of BBD pathogens through contact-mediated inoculation (Miller et al., 2011).

Predator–prey–pathogen relationships have a rich literary history, including those in coral diseases (Aeby & Santavy, 2006; Nugues & Bak, 2009; Renzi et al., 2022; Wolf & Nugues, 2013). Facultative and obligate corallivores are known to alter coral microbiomes both directly through predation and indirectly through farming behavior, increasing alpha diversity and inducing compositional shifts (Ezzat et al., 2019) toward more potentially pathogenic communities (Casey et al., 2014), and may promote secondary infection via direct mechanical injury, as documented in other predator–prey–pathogen systems (García-Guzmán & Dirzo, 2001). Reef fish also facilitate disease transmission by direct pathogen inoculation following feeding on diseased lesions (Chong-Seng et al., 2011).

Cyanobacterial mats may also inoculate facultative corallivores (acting as mobile direct vectors) during opportunistic feeding on cyanobacterial mats (Cissell et al., 2019), followed by the introduction of pathogens to coral colonies during subsequent coral predation events, or via fecal dispersal (Grupstra et al., 2021; Smriga et al., 2010). Transmission via feces is an especially intriguing link, considering that nutrient subsidies during cyanobacterial passage through the fish gut are thought to increase cyanobacterial growth (Kolmakov & Gladyshev, 2003). Fish management strategies are likely to need to carefully integrate both positive (top-down control on mat abundance) and negative (vectoring) effects of mat consumption when prioritizing protections.

In consideration of the potential links outlined above, we have identified five priority research areas that are aligned with current actionable management approaches. An overview of these research directions is presented in Figure 2, and each is discussed in turn below.

# FIVE PRIORITY RESEARCH AREAS

## Assess influence of abiotic condition on mat communities

Although previous research has assessed the relationship between broad nutrient loading and cyanobacterial

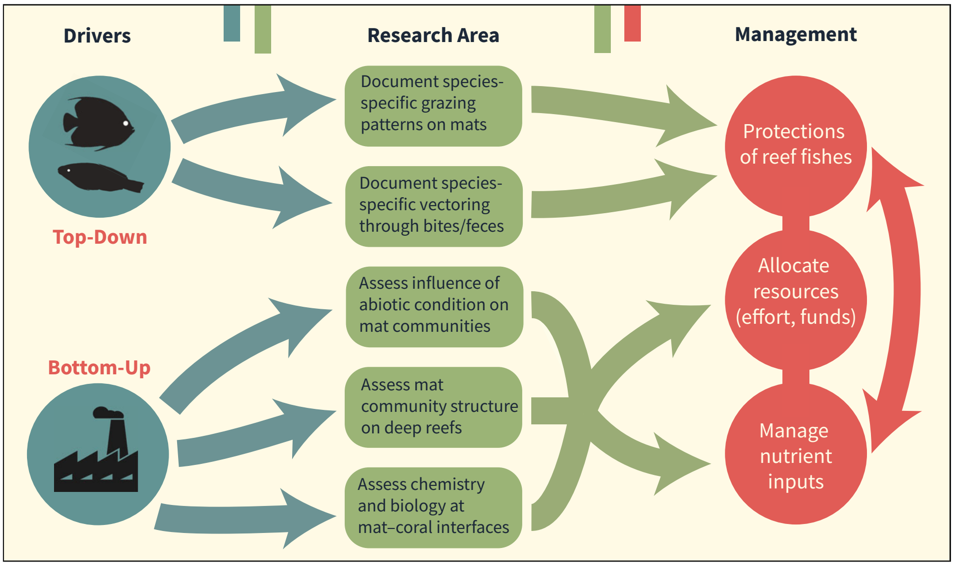


**FIGURE 2** Priority research areas aligned with actionable management strategies. Flow chart diagram depicting where each identified research area connects to broad trophic drivers (top-down versus bottom-up) and informs active management strategies that are pursued to mitigate the transmission and effects of coral black band disease. Management approaches are depicted as interconnected in acknowledgment of both intrinsic and emergent interactions among strategies.

composition and growth rate in mats (Ahern et al., 2007; Arthur et al., 2009; Charpy et al., 2012; Echenique-Subiabre et al., 2015; Kuffner & Paul, 2001), to our knowledge no study has experimentally assessed the influence of specific nutrient loadings on whole mat composition from reefs. Spatial heterogeneity in water quality (Slijkerman et al., 2014) may deterministically interact with cyanobacterial mat community structure and be coupled to the relative abundances of different BBD precursor community members. Furthermore, the effects of wave energy, potentially important in controlling mat abundance (Thacker & Paul, 2001), may additionally create successional mosaics in composition both within and among mats. These patterns may also differ among unique macroscopic mat morphotypes that are often built by taxonomically distinct cyanobacterial populations (Brocke et al., 2018), especially considering species specificity in cyanobacterial response to different nutrient regimes (Kuffner & Paul, 2001). Assessing whole mat community structure in multiple mat morphotypes using next-generation sequencing approaches across gradients of physical wave disturbance, gradients of natural water quality conditions (e.g., in areas with and without run-off), and experimentally with controlled single nutrient pulses will be critical towards a better understanding of the interaction of physical disturbance and different stoichiometries from variable nutrient regimes with mat community structure and, consequently, the ability of mats to serve as reservoirs for BBD pathogens. This will allow for more informed prioritization of nutrient regime regulations for both mitigation of cyanobacterial mat proliferation and BBD reservoir capacity, contextualize preferred locations for coral restoration to minimize BBD transmission, and overall inform evidence-based policy and regulations for wastewater treatment and sustainable coastal development.

## Document species-specific grazing patterns on mats

Strong species- and region-dependent patterns have recently been observed in the consumption of cyanobacterial mats by reef fish (Cissell et al., 2019; Ford et al., 2021). If cyanobacterial mats do act as benthic reservoirs or as direct vectors of coral pathogens, then the control of standing mat abundance must be combined with common bottom-up approaches that address abiotic mat drivers (e.g., remediation of run-off) to manage hotspot locations of coral pathogen persistence. Therefore, to control mat abundance, management plans will need to leverage mat consumption (including consideration of regional and temporal variability in consumption across mat morphotypes) by maximizing protections on important consumers, while respecting local fisheries. A more detailed understanding of species-specific consumption patterns from a broader regional and temporal (e.g., seasonal) context is needed to support a well informed and balanced protection (stock maximization) versus take (permissible mortality) strategies.

## Document species-specific vectoring through bites and feces

Vectoring of coral pathogens are likely to occur through coral predation (opportunistic corallivores) and fecal transmission (not necessarily corallivores) by reef fish that also consume cyanobacterial mats. These processes may reduce, counterbalance, or even outweigh any top-down control that reef fish can exert on disease incidence from moderating cyanobacterial mat abundance. The net effects are likely to display strong taxon- and context-dependent relationships, similar to the effects synthesized in a recent meta-analysis between coral disease incidence and predator presence for the family Scaridae (Renzi et al., 2022), which may be unequally driven by differences in environmental context or feeding mode (Nicolet et al., 2018). Furthermore, we hypothesized that strong context dependence may emerge between different complex biotic and abiotic axes, driving variability in the consumption of cyanobacterial mats (Cissell & McCoy, 2022), and differential contributions from unique mat morphotypes to total foraging. The systematic assessment of vectoring capabilities through *in situ* and *ex situ* experimentation is needed to understand the trade-offs between the top-down control of mat abundance versus mats as secondary vectors. This will aid managers to effectively tailor fish protection strategies to maximize BBD goals, especially in areas of poor water quality.

## Assess mat community structure on deep reefs

Previous work has documented extensive mat coverage on mesophotic reefs (>30 m depth) and compositional differences among deep and shallow cyanobacterial mats on reefs surrounding Bonaire (van Heuzen, 2015). The environmental context and stressors can differ wildly between shallow and deep reefs (Bak et al., 2005). However, few quantitative assessments of BBD or cyanobacterial mat dynamics on mesophotic reefs exist, therefore it is impossible to assess whether cyanobacterial mats on deep reefs are important contributors to general mat proliferation, or to previously described shallow-water BBD dynamics. Understanding the disease dynamics on mesophotic reefs, as well as linkages among deep and shallow reefs, is critical to allocating limited monitoring resources, designing sustainable water treatment infrastructure, and to a better understanding of the vulnerability and resilience of ecologically important reef corals to BBD (Bridge et al., 2013).

## Assess chemistry and biology at mat–coral interface

Although microenvironmental physiochemistry at mat–coral interfaces has received some research attention (Titlyanov et al., 2007), contact-mediated destabilizing effects on the coral or cyanobacterial mat microbiome have not been explored previously. Stoichiometric changes at this interface may mediate the shifts among dominant cyanobacterial populations within mats (Tee et al., 2021) toward sulfide-tolerant clones and overall cause comparatively benign cyanobacterial mats to become virulent. Microenvironment changes or direct microbial transfer (mat-to-coral inoculation) at the interaction interfaces may also alter the resident coral microbiome, inducing dysbiosis similar to macroalgal contact-mediated effects (Nugues et al., 2004). Paired microelectrode and sequencing studies followed by macroscopic coral colony monitoring will be integral to the development of this research front to understand cyanobacterial mats as possible direct vectors of BBD pathogens mediated through cyanobacterial mat–coral competition.

Additionally, we echo the call made in Ford et al. (2018) that conspicuous cyanobacterial mats must be explicitly included in common benthic monitoring protocols moving forward (i.e., distinctly reported from broader functional groupings such as *Epilithic Algal Matrix* or *Algae*). This is vital to improving a baseline understanding of global mat distribution and to facilitating a generalizable assessment of correlative associations between mat density and BBD prevalence across diverse environmental contexts. Finally, global (climactic) drivers of coral disease and mat expansion should not be ignored, and active global efforts to combat these underlying drivers should continue to expand and not rely solely on local management actions.

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## CONFLICT OF INTEREST

The authors declare they have no known competing financial interests or personal relationships that could have appeared to influence the work in this paper.

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