



Reefs under Siege—the Rise, Putative Drivers, and Consequences of Benthic Cyanobacterial Mats

Amanda K. Ford^{1,2*}, Sonia Bejarano¹, Maggy M. Nugues^{3,4}, Petra M. Visser⁵, Simon Albert⁶ and Sebastian C. A. Ferse^{1,2}

¹ Ecology Department, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany, ² Faculty of Biology and Chemistry (FB2), University of Bremen, Bremen, Germany, ³ EPHE, PSL Research University, UPVD-Centre National de la Recherche Scientifique, USR3278 CRIOBE, Perpignan, France, ⁴ Labex Corail, CRIOBE, Moorea, French Polynesia, ⁵ Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands, ⁶ School of Civil Engineering, University of Queensland, Brisbane, QLD, Australia

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*Correspondence:

Amanda K. Ford
amanda.ford@leibniz-zmt.de

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Benthic cyanobacteria have commonly been a small but integral component of coral reef ecosystems, fulfilling the critical function of introducing bioavailable nitrogen to an inherently oligotrophic environment. Though surveys may have previously neglected benthic cyanobacteria, or grouped them with more conspicuous benthic groups, emerging evidence strongly indicates that they are becoming increasingly prevalent on reefs worldwide. Some species can form mats comprised by a diverse microbial consortium which allows them to exist across a wide range of environmental conditions. This review evaluates the putative driving factors of increasing benthic cyanobacterial mats, including climate change, declining coastal water quality, iron input, and overexploitation of key consumer and ecosystem engineer species. Ongoing global environmental change can increase growth rates and toxin production of physiologically plastic benthic cyanobacterial mats, placing them at a considerable competitive advantage against reef-building corals. Once established, strong ecological feedbacks [e.g., inhibition of coral recruitment, release of dissolved organic carbon (DOC)] reinforce reef degradation. The review also highlights previously overlooked implications of mat proliferation, which can extend beyond reef health and affect human health and welfare. Though identifying (opportunistic) consumers of mats remains a priority, their perceived low palatability implies that herbivore management alone may be insufficient to control their proliferation and must be accompanied by local measures to improve water quality and watershed management.

Keywords: coral reefs, ecosystem degradation, alternative states, ecological feedbacks, global environmental change, social-ecological traps, local management

INTRODUCTION

Without the earliest cyanobacteria that evolved around three billion years ago introducing oxygen to the atmosphere (Brocks et al., 1999), life as we know it would not exist. Today marine cyanobacteria remain an integral component of healthy ecosystems, offering critical functions such as nitrogen fixation and primary production (Charpy et al., 2007). Such roles are particularly important within oligotrophic systems such as coral reefs, where cyanobacteria are profusely

embedded in algal turfs and microbial biofilms (Barott et al., 2011; Fricke et al., 2011; Charpy et al., 2012a; Cardini et al., 2014). Under certain environmental conditions, some benthic marine cyanobacteria, which may have previously been a benign component of the benthos, can form dense mats (hereon referred to as benthic cyanobacterial mats) comprising species from a single genus (Paul et al., 2005) or diverse microbial consortia (Echenique-Subiabre et al., 2015). While receiving relatively little attention in benthic reef ecology studies to date, these mats should be considered as major players on degraded or degrading reefs where they are increasingly reported to cover extensive areas (**Figure 1**; **Table 1**). Rectifying this oversight is critical because reefs dominated by benthic cyanobacterial mats are likely to produce significantly less of the ecosystem services associated with healthy, coral-dominated reefs. For example, coastal protection and fisheries decline as structural complexity is reduced on degraded reefs (Sheppard et al., 2005; Pratchett et al., 2014). Considering rapid reef degradation worldwide, it is thus important to better understand the biology and ecology of tropical benthic cyanobacterial mats.

Modern (phylo)genetic approaches have revealed that species richness in tropical cyanobacterial mats is very high and includes many unknown species otherwise overlooked by traditional morphology-based taxonomic approaches (Engene et al., 2013a; Echenique-Subiabre et al., 2015). For example, though filamentous mat-forming cyanobacteria have regularly been grouped within the genus *Lyngbya* (C. Aghard ex Gomont 1892), recent analyses have separated many species from this group into newly-described genera such as *Moorea* (Engene et al., 2012) and *Okeania* (Engene et al., 2013b). Within mats, tropical cyanobacteria probably also associate with a consortium of heterotrophic bacteria, as shown for mats in other regions (Stal, 2012). Microbial consortia are likely to enhance production, growth rates, and nutrient cycling over what a single population alone can achieve under similar environmental settings (Paerl et al., 2000). Indeed, mats can exhibit high plasticity in their ability to modify the diversity and composition of their constituting microbial assemblages in response to their local environment (Echenique-Subiabre et al., 2015).

Benthic cyanobacterial mats usually inhabit a very small proportion of reef space (e.g., <1%; Bednarz et al., 2015), but can exhibit higher nitrogen fixation rates (8–110 mg nitrogen $m^{-2} day^{-1}$) compared to (cyano)bacteria associated with other benthic groups such as algal turfs and fleshy algae (0.44–22.69 mg nitrogen $m^{-2} day^{-1}$) or scleractinian corals (0–9.75 mg nitrogen $m^{-2} day^{-1}$, Cardini et al., 2014). Furthermore, nitrogen fixation of (seasonal) mats is up to one order of magnitude higher than surrounding sediments and/or rubble (Casareto et al., 2008; Bednarz et al., 2015), and even when they are uncommon (<2% benthic coverage) they have been found to contribute up to 27–64% of benthic nitrogen fixation (Cardini et al., 2016). Heterocystous species that can simultaneously fix nitrogen and photosynthesize are not advantageous in oligotrophic tropical waters, and indeed non-heterocystous planktonic *Trichodesmium* are the dominant nitrogen fixers in tropical oceans (Staal et al., 2003; Stal, 2012). Mats have been shown to comprise heterocystous and/or non-heterocystous

cyanobacteria, with both strategists in some instances fixing nitrogen at similar rates (Charpy et al., 2010, 2012b). There is however a high variation in the ability to fix nitrogen within benthic cyanobacteria (Zehr, 2011), with some common mat-forming types including *Moorea* in fact lacking the genes involved in nitrogen fixation (Engene et al., 2012). Depending on local environmental conditions, cyanobacterial mats are able to modulate their nitrogen fixation activity (increasing when nitrogen is limiting, decreasing when nitrogen is high) via changes in overall taxonomic composition or the activity of individual nitrogen-fixing species (Paerl, 2008; Charpy et al., 2012b).

A recent surge of reports of benthic cyanobacterial mats occurring or proliferating on coral reefs (**Table 1**), as well as concern for the detrimental effects of these mats on ecosystem processes, stimulated this scientific review. Surveys conducted over decadal scales (40 years) provide robust evidence that cyanobacterial mats are increasing on some southern Caribbean reefs alongside a decline in organisms such as scleractinian corals (de Bakker et al., 2017). Also in subtropical areas, blooms of benthic cyanobacterial mats which were first restricted to the summer months have become significantly more persistent (Albert et al., 2005; Paul et al., 2005). Increased awareness of the presence of cyanobacteria may account at least partially for the rise of reports (e.g., Duarte et al., 2015). Nonetheless it is clear that mats have received much less attention than other reef organisms (**Figure 2A**), with the first reef-focused scientific article mentioning cyanobacterial mats only published in 1991 compared to 1930 and 1959 for algae and sponges, respectively according to Web of Science® (**Figure 2B**). Underreporting may be due to cyanobacteria remaining undistinguished from (i) more conspicuous reef benthic groups such as algal turfs (Kuffner and Paul, 2001; Fong and Paul, 2011) within which they are often dominant (Fricke et al., 2011), (ii) the organisms that they grow over (e.g., fleshy algae—Puyana and Prato, 2013), or (iii) abiotic substrate such as dead coral pavement, sand or rubble which is realistically never bare (Harris, 2015). Arguably, temporary blooms of cyanobacterial mats might have historically been a natural phenomenon on reefs, exhibiting a pulsing nature (Puyana et al., 2015) that may not be prolonged or stable enough to be considered regime shifts themselves. These blooms may however catalyze long-lasting shifts from coral-dominated reefs to other alternative states (Kelly et al., 2012). Even such conspicuous phenomena as mass spawning of corals have only been reported relatively recently (Harrison et al., 1984), underlining the dearth of scientific knowledge on basic ecological phenomena in reefs.

In light of the indications that the geographic extent and prevalence of benthic cyanobacterial mats are progressively increasing, this review first summarises the factors that may be facilitating this phenomenon. We subsequently evaluate the associated ecological and social implications, and finally identify potential management strategies and future research priorities. An improved understanding of the dynamics behind the proliferation of benthic cyanobacterial mats is critical to shed some light on the factors influencing the probability of recovery toward coral dominance vs. degradation toward

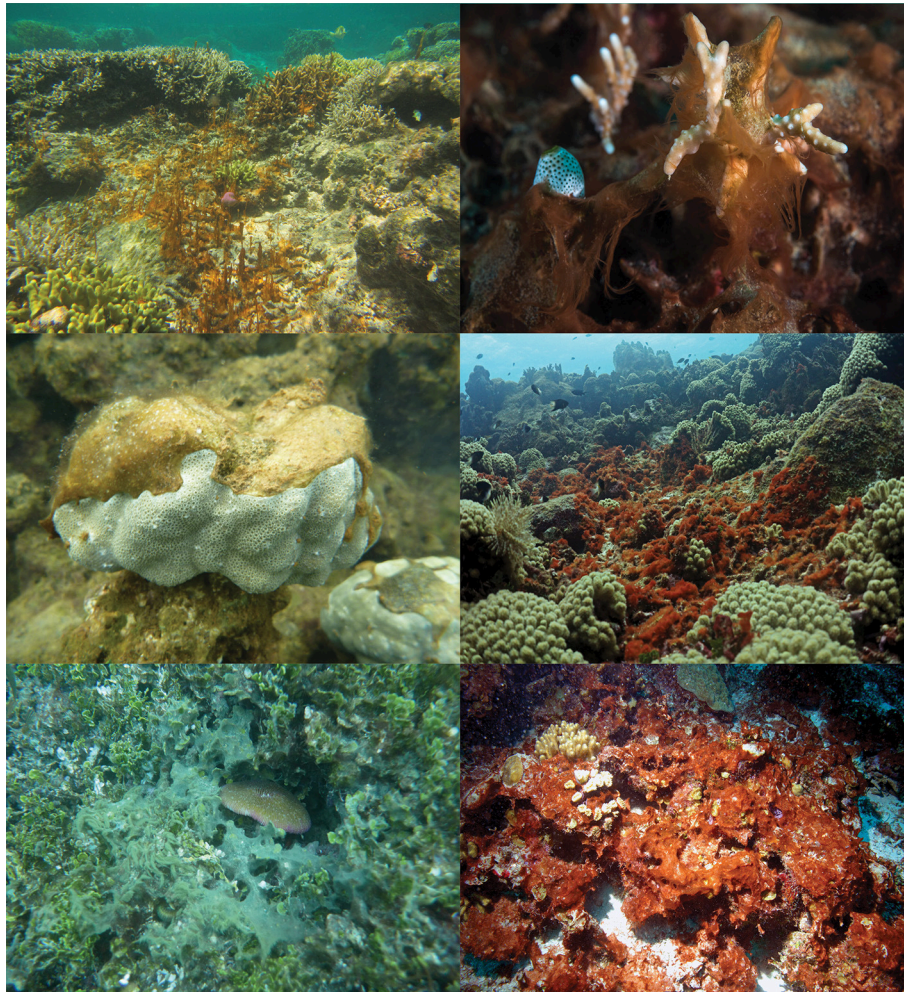


FIGURE 1 | Photographs of benthic cyanobacterial mats on coral reefs. From top-left clockwise: cyanobacterial mat at Coral Coast, Fiji (credits: Victor Bonito); cyanobacterial mat overgrowing coral at Menjangan Island, Bali (credits: Tom Vierus); *Oscillatoria*-dominated mat at Curaçao (credits: Benjamin Mueller); *Oscillatoria*-dominated mat at Curaçao (credits: Maggy Nugues); cyanobacterial mat overgrowing *Halimeda* algae at Ahus Island, Papua New Guinea (credits: Amanda Ford); cyanobacteria mat overgrowing coral at Marovo Lagoon, Solomon Islands (credits: Simon Albert).

alternative states. Though important research gaps remain, this review provides tangible evidence that this emerging benthic phenomenon requires more attention from researchers, managers, and policy-makers.

FACTORS PROMOTING CYANOBACTERIAL MAT PROLIFERATION ON REEFS

Microorganisms are becoming increasingly abundant on reefs, with a global analysis showing a positive correlation of cell abundances with algal cover (i.e., with reef degradation), stimulated by increased labile dissolved organic carbon (DOC) production (Haas et al., 2016). Mat-forming cyanobacteria likely benefit from a variety of additional inherent properties. Whilst growth rates of most organisms are constrained within

a given and often narrow range of conditions, cyanobacterial mats display characteristics that allow them to thrive under a multitude of environmental settings. For example, cyanobacteria species themselves have versatile metabolic capabilities, switching between auto-, hetero-, and mixotrophy (Rippka, 1972). Not only does the physiological and trophic plasticity of mats (Echenique-Subiabre et al., 2015) provide them with a distinct advantage over most benthic organisms, but environmental changes associated with anthropogenic impacts often further favour their proliferation.

Cyanobacteria can dominate algal turf assemblages (Fricke et al., 2011), and are commonly found as epiphytes seeking refuge among complex fleshy algae such as *Halimeda* which are robust to, and may in fact benefit from, their presence (Barott et al., 2011; Hensley et al., 2013). Consequently, as the integrity of reefs worldwide is compromised by global environmental change, increasing prevalence of algal turfs and other hosts of

TABLE 1 | Reports of benthic cyanobacterial mats from tropical coasts worldwide, with genus/species identification and implicated drivers given where possible.

Region	Location	Cyanobacterial mat extent	Species/genera encountered	Implicated drivers	References
Atlantic	Broward County, Florida (2002-2004)		<i>Lyngbya</i>		Paul et al., 2005
Caribbean Sea	Barbados		Unknown	Domestic sewage	DeGeorges et al., 2010
Caribbean Sea	Curaçao and Bonaire, Netherland Antilles	Mean cover 22.2% in 2013 (only 0.1% in 1973)	<i>Hydrocoleum</i> , <i>Lyngbya</i> , <i>Phormidium</i> , <i>Symploca</i> , <i>Oscillatoria</i> , <i>Tychonema</i> , <i>Schizothrix</i> , <i>Pseudanabaena</i> , <i>Dichothrix</i>	Degraded reef with low coral cover—eutrophied, high OM input (e.g., sewage)	Brocke, 2013; Brocke et al., 2015a; de Bakker et al., 2017
Caribbean Sea	Old Providence Island, Colombian Caribbean (2009-2010)	18–72%	<i>Okeania</i> , <i>Lyngbya</i> , <i>Symploca</i> , <i>Phormidium</i> , <i>Oscillatoria</i> , <i>Spirulina</i>	Warm waters, anthropogenic input (e.g., sewage)	Puyana et al., 2015
Indian Ocean	Nosy Hara, Madagascar	Extensive mats from 3 m and deeper	<i>Lyngbya</i>	Terrestrial freshwater and nutrient input	Obura, 2009
Pacific	Moreton Bay, Australia	Periodic dominance of shallow habitats since 1996	<i>Lyngbya majuscula</i>	High organic matter input (flooding), bioavailable phosphorous and iron, warm water, high light	Albert et al., 2005; Watkinson et al., 2005
Pacific	Guam (1994)	Periodically dominate hundreds of meters of reef flat	<i>Schizothrix</i> , <i>Lyngbya</i> , <i>Hormothamnion</i>		Pennings et al., 1997; Nagle and Paul, 1998
Pacific	Manus Province, Papua New Guinea (2014)	Up to 66% at 3 m depth		Untreated sewage in overfished system	Ford et al., 2017
Pacific	Marovo Lagoon, Solomon Islands (2011)	Up to 100% at 6 m		Eutrophication following toxic diatom and dinoflagellate bloom	Albert et al., 2012
Pacific	Millennium atoll, Line Islands	Up to 71% (turf-cyanobacteria mixed assemblage)		Iron enrichment from shipwrecks	Kelly et al., 2012
Pacific	Okinawa, Japan	26% <i>Annela reticulata</i> colonies affected at 20 m depth	<i>Moorea bouillonii</i>		Yamashiro et al., 2014
Pacific	Oundjo, New Caledonia (2004)	24% cover within lagoon			SPC unpublished data
Pacific	Rose Atoll, American Samoa	Initially up to 90% cover, then remained at ~40% (<i>Jania</i> —cyanobacteria mixed assemblage)	<i>Lyngbya</i> and <i>Oscillatoria</i>	Ship grounding in 1995 and associated contaminant spill	Green et al., 1997; Schroeder et al., 2008
Pacific	Sideia, Papua New Guinea (2006)	15% cover on back reef			SPC unpublished data
Pacific	Tsoilaunung, Papua New Guinea (2006)	15% on outer reef			SPC unpublished data

Sections are left blank when no information is available. Species/genera identified as *Lyngbya* may have been reclassified since the study took place (morphologically similar but genetically different, see Introduction section).

cyanobacterial epiphytes may provide an important source of, and substrate for, cyanobacteria from which mats can develop. Reef degradation also generates newly available substrate that is easily colonisable by fast-growing cyanobacterial mats (e.g., mats can cover up to 30 km² within 2–3 months; Albert et al.,

2005). Even on a reef where space is highly limited, cyanobacterial mats can overcome this constraint by growing directly over living organisms such as scleractinian corals and fleshy algae (Ritson-Williams et al., 2005; Puyana and Prato, 2013; de Bakker et al., 2016, 2017). Besides benefitting from newly available space and

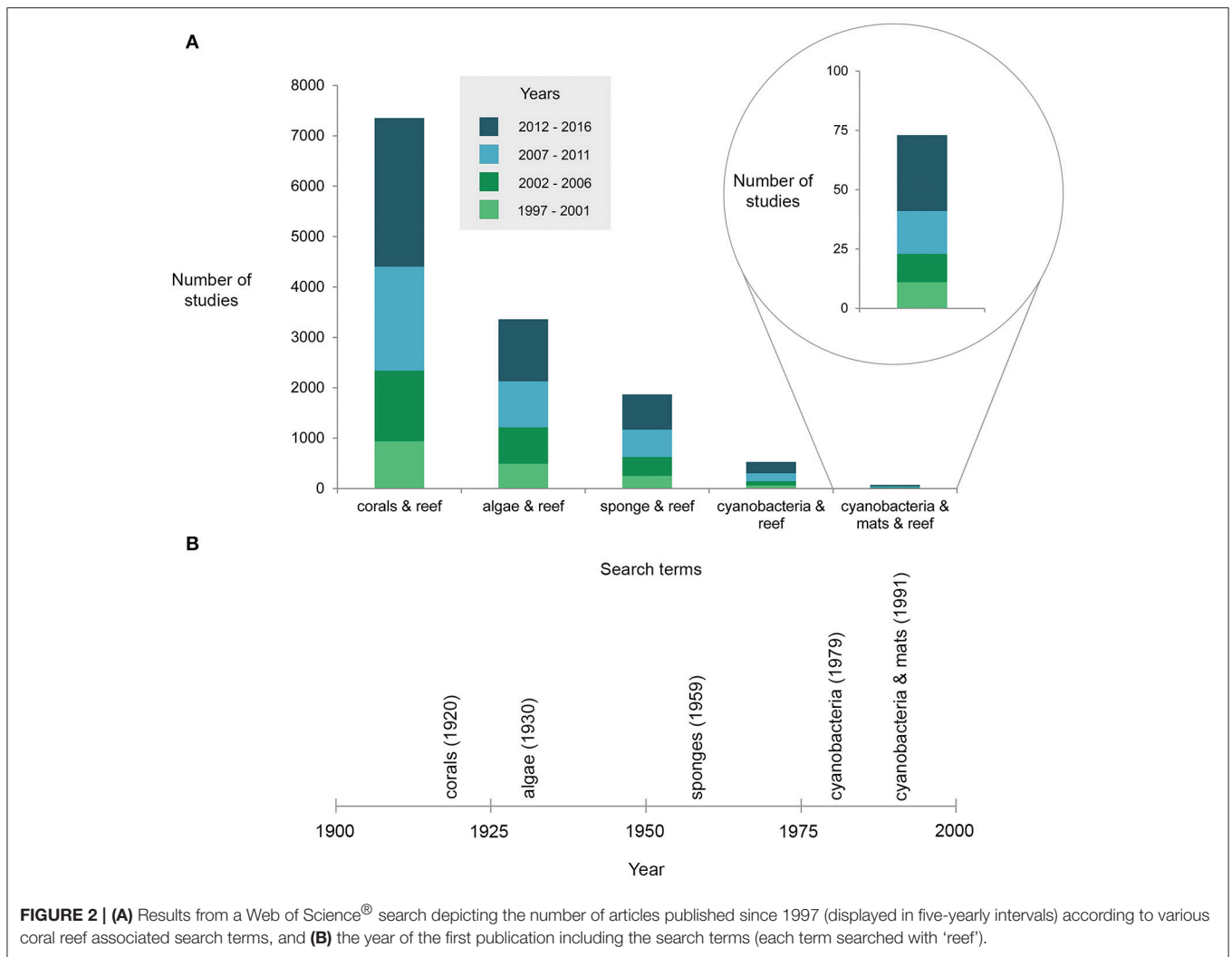
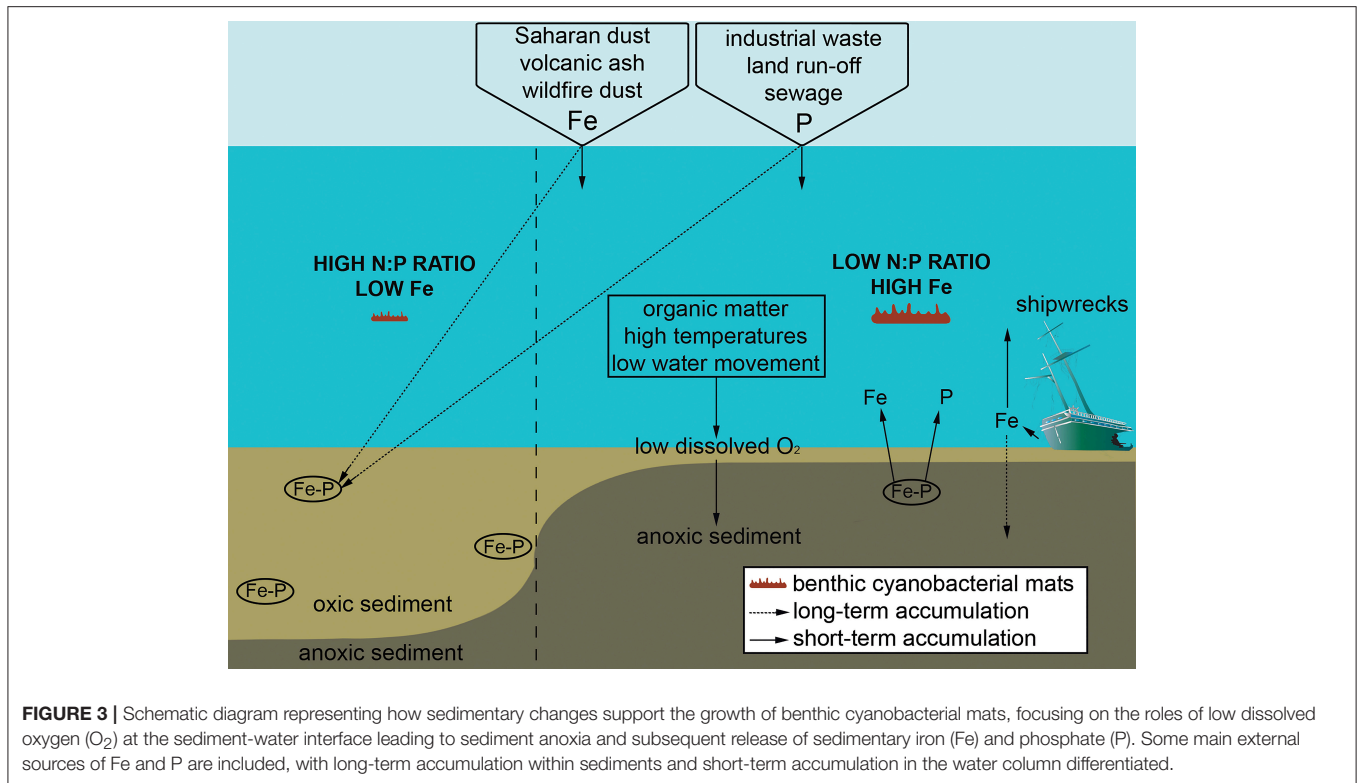


FIGURE 2 | (A) Results from a Web of Science® search depicting the number of articles published since 1997 (displayed in five-yearly intervals) according to various coral reef associated search terms, and **(B)** the year of the first publication including the search terms (each term searched with 'reef').

reduced health of other benthic organisms with ongoing reef degradation, benthic cyanobacterial mats can profit directly from increased temperatures and unusual rainfall patterns (Paul, 2008; O'Neil et al., 2012). Additionally, increasingly acidic oceans may stimulate marine cyanobacteria which have high photosynthetic demands (Levitan et al., 2007). Some cyanobacteria exhibit high genetic adaptability to changes in carbon availability, and are able to utilise bicarbonate ions (which increase with ocean acidification) as a carbon source (Badger and Price, 2003; Paerl and Paul, 2012; Sandrini et al., 2016; Visser et al., 2016). Recent experimental evidence found ocean warming in isolation, and when combined with low pH, facilitates proliferation of benthic cyanobacteria relative to algal turfs (Ullah et al., 2018). Similarly, a relative increase of mat-forming cyanobacteria within algal turfs under a low pH and high temperature treatment provides further experimental evidence that future ocean conditions may favour benthic cyanobacterial mat expansion (Bender et al., 2014, but see Hassenrück et al., 2016). On the other hand storms, which will also increase in intensity in the coming decades, may dislodge and remove benthic cyanobacterial mats (Becerro et al., 2006).

Rapidly growing human populations on tropical coastlines are also having a profound effect on coastal marine environments locally through increased sewage input and nutrient runoff driven by land-use change and agricultural development (Burke et al., 2012). Benthic cyanobacterial mats are able to compete for nitrogen when it is available but can also circumvent nitrogen limitation in nitrogen-deficient waters (Paerl, 2008). Although the ability of marine cyanobacteria to fix nitrogen can indeed vary across species (Zehr, 2011), growth of common mat-forming types is not promoted by nitrogen input to the same extent as by iron or phosphorous (Ahern et al., 2007). This implies that the concentrations of other nutrients are relatively more important in controlling cyanobacterial growth.

Because of the ability of many mat-forming cyanobacteria to fix nitrogen when it is limiting, phosphorous enrichment that shifts a system from phosphorous to nitrogen limitation (i.e., transitions from high to low N:P ratio) likely favours growth of cyanobacteria over other primary producers (Figure 3; Schindler, 1977; Kuffner and Paul, 2001). Whilst reefs are often phosphorous limited (Lapointe, 1997; Rosset et al., 2017),



this nutrient can enter tropical reef systems via wastewater discharge, aquaculture, and terrestrial runoff from urbanised and agricultural land (Figure 3). Sewage input for instance can strongly shift the canonical Redfield ratio from 16:1 (N:P) to <10 (Lapointe et al., 2005), and has been linked to proliferation of benthic cyanobacterial mats (Ford et al., 2017). Furthermore, occurrence of mats during the rainy season at a site in Curaçao coincided with N:P ratios dropping from 50 to 16 (Brocke et al., 2015a; den Haan et al., 2016). Alongside direct input from terrestrial sources, one pathway recognised to increase levels of phosphorous is release from surface sediments of the marine benthos, where phosphorous is usually bound with stable insoluble iron oxyhydroxides within the oxidised layer (Sundby et al., 1992; Rose and Waite, 2005). Following high organic matter (OM) input (e.g., from sewage) and/or low dissolved oxygen levels at the water-sediment interface, surface sediments become anoxic, leading to iron (III) reduction to bioavailable iron (II), and in turn releasing reactive phosphate and iron (Figure 3; Jensen et al., 1995; Brocke et al., 2015a; Hanington et al., 2016). A similar mechanism likely applies following phytoplankton blooms (caused by eutrophication) which decay and produce particulate OM which settles onto the reef floor. This potentially explains a prolonged shift toward cyanobacterial mats alongside mortality of reef-associated organisms following an extensive phytoplankton bloom (>20 km²) observed within a Solomon Islands lagoon (Albert et al., 2012).

In addition to reactive phosphate, the associated sedimentary release of bioavailable iron (Figure 3) is likely important for mat development. Iron concentrations differ regionally with the degree of exposure to Aeolian dust, ash from volcanic eruptions,

emergent basaltic rock associated with past volcanic activity, shipwrecks, dust from wildfires and terrestrial run-off (Abram et al., 2003; Kelly et al., 2012; Roff and Mumby, 2012; Schils, 2012). At areas not naturally exposed to iron from Aeolian dust such as the Pacific, benthic cyanobacterial mats establish quickly following supply of iron to the water column, for instance, through volcanic ash (Schils, 2012). Furthermore, ship groundings on strongly iron-limited reefs in the central Pacific have facilitated long-lasting shifts toward “black reefs” dominated by mixed benthic assemblages of cyanobacteria, turf and fleshy algae, and corallimorphs (Schroeder et al., 2008; Kelly et al., 2012). Where sediments contain iron, growth of cyanobacterial mats can be stimulated following the reduction and release of iron when sediments become anoxic following flooding and/or phytoplankton blooms, as observed at Moreton Bay, Australia (Ahern et al., 2006, 2007, 2008; Hanington et al., 2016). As well as controlling cyanobacterial growth, iron is critical for the nitrogenase enzyme which controls nitrogen fixation (Berman-Frank et al., 2001; Mills et al., 2004; Ahern et al., 2008). Given that cyanobacterial mats grow rapidly following the addition of iron in areas that are naturally iron-limited, and that iron binds readily to phosphate in sediments (thus linked to another key nutrient), iron availability is likely a key factor determining the proliferation of cyanobacterial mats.

Top-down control of benthic cyanobacterial mats is often restricted due to their chemical defences which reduce palatability and deter grazing even where herbivorous fish are abundant (Thacker et al., 1997; Capper et al., 2006a,b, 2016), though it must be noted that data are limited to well-studied species in few locations. Lyngbyatoxin-A is the most

extensively researched secondary metabolite in marine benthic cyanobacteria, and although its production varies across different locations, it can have community-wide consequences (Paul et al., 2007). The cover of cyanobacterial mats does not increase, and can even decrease, in the absence of herbivorous fish (i.e., inside herbivore exclusion cages—Wanders, 1977; Thacker et al., 2001). A 3-year experiment in Florida observed distinct summer blooms of benthic cyanobacteria under nutrient enrichment in the presence of herbivores, weaker blooms when nutrient enrichment was combined with herbivore exclusion, and no blooms under herbivore exclusion alone where fleshy algae such as *Turbinaria*, *Sargassum*, and *Hypnea* were relatively more dominant (Zaneveld et al., 2016). These findings suggest that nominally herbivorous fish cannot control the development of cyanobacterial mats, or that high levels of herbivory are in fact necessary for cyanobacteria to maintain dominance over fleshy algae. Some mesograzers and a few reef fish species have been documented to graze on mats directly or on foods experimentally coated in their secondary metabolite extracts (Table 2). In contrast to most studies, a recent review by Clements et al. (2016) proposed that parrotfishes actually target endo- and epilithic cyanobacteria, and provides evidence of direct consumption of mats by *Bolbometopon muricatum*. The degree to which fishes feed selectively on cyanobacteria may depend on their life stage (Paul et al., 1990), exposure time, and access to alternative food (Thacker et al., 1997). Interestingly, growth rates of benthic cyanobacterial mats on soft sediments are significantly reduced in the presence of sea cucumbers both in aquaria (Uthicke, 1999; Michio et al., 2003) and *in situ* (Moriarty et al., 1985). Within enclosures containing sea cucumbers in Madagascar, abundance of bacteria and concentration of photosynthetic microorganisms within surface sediments were 50 and 22% lower compared with controls (Plotieau et al., 2013). The expansion of cyanobacterial mats may be limited in the presence of sea cucumbers because of direct consumption (e.g., Sournia, 1976), and bioturbation of benthic sediments. Bioturbation of sediments by sea cucumbers can increase the thickness of the oxic sediment layers under increased temperatures, nutrients, and OM loads (Mactavish et al., 2012; Lee et al., 2017), thus contributing to the continued persistence of healthy sediment-associated microbial communities and sediment integrity. Overexploitation of sea cucumbers across the Indo-Pacific (Anderson et al., 2011) and associated changes in the sediment might thus contribute at least partially to the increasing prevalence of cyanobacterial mats in coastal (sandy) habitats.

LINKING CYANOBACTERIAL MATS TO REEF DEGRADATION

Recent research on coral reef ecosystem dynamics has primarily focused on the factors driving benthic community shifts whereby reef-building corals are replaced by alternative organisms. Most commonly, coral-dominated reefs shift to systems where fleshy algae establish and become dominant (e.g., Hughes, 1994), but shifts to soft corals, sponges, and algal turfs may also occur

(Norström et al., 2009; Jouffray et al., 2015; Smith et al., 2016). As mentioned previously, under scenarios where reefs become dominated by algae, increased labile DOC production stimulates growth of microorganisms (Haas et al., 2016). However, instances in which coral- or algal-dominated reefs shift to systems dominated by benthic cyanobacterial mats have received comparatively little attention. Mats can be ephemeral symptoms of recent reef degradation events resulting in freed space (Schroeder et al., 2008), but can also push stressed systems toward alternative stable states (Albert et al., 2012). For example, elevated nitrogen fixation rates on recently bleached corals or dead coral skeletons imply that cyanobacteria are important colonisers of available substrate and that their nitrogen fixation activity may be sufficient to direct a stressed system toward algal dominance (Davey et al., 2008; Holmes and Johnstone, 2010). The proliferation of benthic cyanobacterial mats on coral reefs has serious direct and indirect effects on numerous reef organisms and ecological processes. Some mats overgrow and smother benthic organisms, including scleractinian corals and fleshy algae (Ritson-Williams et al., 2005; Puyana and Prato, 2013; de Bakker et al., 2016, 2017). Subsequent tissue necrosis of overgrown organisms can occur as a result of oxygen deficiency, contact with allelopathic chemicals, tissue abrasion, or light reduction (Puyana and Prato, 2013). The impact of cyanobacterial mats on localised bleaching and mortality of coral colonies can indeed exceed that of other competitors such as fleshy algae (Titlyanov et al., 2007).

The presence of cyanobacterial mats also directly impairs coral recruitment which is an essential ecological process for reef recovery following disturbances (McClanahan et al., 2012). Recruitment success may be reduced by (i) coral larvae avoiding settling near to cyanobacteria due to negative settlement cues, or (ii) cyanobacteria killing newly settled corals (Kuffner and Paul, 2004; Ritson-Williams et al., 2016). Benthic cyanobacterial mats have been implicated in reducing the recruitment success of both broadcast spawning and brooding corals (Kuffner and Paul, 2004; Kuffner et al., 2006). Importantly, mats can bloom at the same time of year when corals spawn. For instance, in Fiji, both broadcast spawning and cyanobacterial mats occur simultaneously during the warmest mid-summer months (Quinn and Kojis, 2008; Victor Bonito, pers. comm., 2016). Similarly, in Curaçao, spawning takes place in September/October (Van Veghel, 1994), and mats are particularly prevalent in October/November (Brocke et al., 2015a) when the coral spat would be settling on the substrate. At this critical time, the effects of cyanotoxins on coral recruits are also strongly exacerbated by warmer temperatures (Ritson-Williams et al., 2016). Further studies into the temporal prevalence of mats together with information on coral spawning times are needed to assess the extent of this potential threat, as large-scale inhibition of coral recruitment by cyanobacterial mats could have severe implications for the replenishment of coral populations.

The health of adult coral colonies can also be indirectly affected by the development of benthic cyanobacterial mats, for example from increasing levels of bioavailable nitrogen (see introduction—Cardini et al., 2014). Stress may also result from increasing DOC, as mats not only profit from DOC

TABLE 2 | Documented reports of cyanobacterial mat consumption by coral reef-associated fauna.

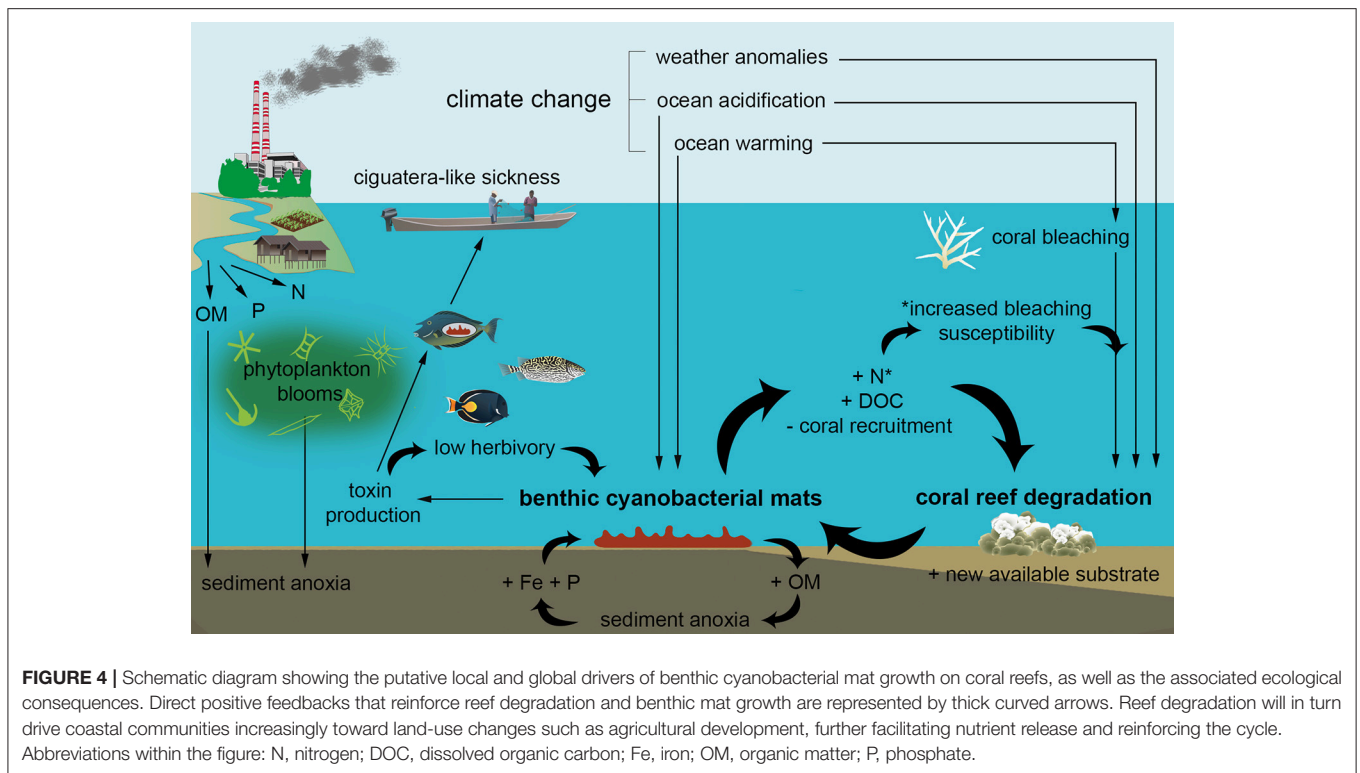
Group	Species	Feeding material	Type of study	References
Bivalve	<i>Tridacna maxima</i>	<i>Hydrocoleum kützing</i>	Tissue analysis	French Polynesia, New Caledonia, Vanuatu—Laurent et al., 2008, 2012
Crustaceans	<i>Cymadusa imbroglio</i> , <i>Menaethius monoceros</i> , <i>Parhyale hawaiiensis</i>	<i>Lyngbya</i> , <i>Tolypothrix</i>	Laboratory	Cruz-Rivera and Paul, 2006
Damselfish	<i>Pomacentrus amboinensis</i>	<i>Lyngbya</i>	Gut investigations	Marnane and Bellwood, 1997
Damselfish	<i>Stegastes apicalis</i>	<i>Lyngbya</i>	Field observations	Klumpp and Polunin, 1989
Emperorfish	<i>Lethrinus</i>	Mixed blooms—e.g., <i>Oscillatoria</i> , <i>Hydrocoleum</i> , <i>Anabaena</i>	Tissue analysis	New Caledonia—Laurent et al., 2012
Gastropods	<i>Haminoea cymbalum</i>	<i>Tolypothrix</i>	Laboratory	Cruz-Rivera and Paul, 2006
Gastropods	<i>Stylocheilus striatus</i>	<i>Lyngbya</i>	Laboratory	Cruz-Rivera and Paul, 2002, 2006
Gastropods	<i>Haminoea ovalis</i>	<i>Lyngbya</i> , <i>Tolypothrix</i>	Laboratory	Cruz-Rivera and Paul, 2006
Gastropods	<i>Trochus</i>	Mixed blooms—e.g., <i>Oscillatoria</i> , <i>Hydrocoleum</i> , <i>Anabaena</i>	Tissue analysis	French Polynesia, New Caledonia, Vanuatu—Laurent et al., 2012
Holothurians	<i>Holothuria (Halodeima) atra</i>	<i>Oscillatoria limosa</i>	Field observations	Moorea—Sournia, 1976
Holothurians	<i>H. atra</i> , <i>Stichopus chloronotus</i>	Unidentified mat	Laboratory	Uthicke, 1994
Parrotfish	<i>Scarus schlegeli</i> , <i>Scarus rivulatus</i>	Mixed blooms—e.g., <i>Oscillatoria</i> , <i>Hydrocoleum</i> , <i>Anabaena</i>	Tissue analysis	New Caledonia—Laurent et al., 2012
Parrotfish	<i>Chlorurus sordidus</i> , <i>Scarus altipinnis</i>	Mixed blooms—e.g., <i>Oscillatoria</i> , <i>Hydrocoleum</i> , <i>Anabaena</i>	Tissue analysis	French Polynesia, Vanuatu—Laurent et al., 2012
Parrotfish	<i>Bolbometopon muricatum</i>	Unknown	Field observations	Great Barrier Reef—Clements et al., 2016
Rabbitfish	<i>Siganus fuscescens</i>	<i>Lyngbya</i> (only in absence of lyngbyatoxin-A)	Laboratory	Moreton Bay—Capper et al., 2006b
Rabbitfish	<i>Siganus argenteus</i> juveniles—medium preference (21–60% eaten)	<i>Microcoleus lyngbyaceus</i>	Laboratory	Guam—Paul et al., 1990
Surgeonfish	<i>Ctenochaetus striatus</i>	Mixed blooms—e.g., <i>Oscillatoria</i> , <i>Hydrocoleum</i> , <i>Anabaena</i>	Tissue analysis	Vanuatu—Laurent et al., 2012
Unicornfish	<i>Naso unicornis</i>	Mixed blooms—e.g., <i>Oscillatoria</i> , <i>Hydrocoleum</i> , <i>Anabaena</i>	Tissue analysis	French Polynesia, New Caledonia—Laurent et al., 2012

Species/genera identified as *Lyngbya* may have been reclassified since the study took place (morphologically similar but genetically different, see Introduction section).

input, but are themselves responsible for releasing high amounts of DOC. For example mats, fleshy algae and algal turfs in Curaçao released 0.59, 0.04, and 0.11 mmol C m⁻² h⁻¹, respectively, while corals and bare sediments did not exhibit net DOC production over 24 h (Brocke et al., 2015b). Such amounts may be regarded insignificant when considering the coverage of benthic cyanobacterial mats on healthy reefs (e.g., around 1% of the benthos—Charpy et al., 2010; Bednarz et al., 2015), but are substantial when mats become dominant (e.g., over 50% of the benthos - Thacker and Paul, 2001). Both DOC and bioavailable nitrogen can shift the balance of the benthic community by favouring fast-growing primary producers (e.g., fleshy algae) over scleractinian corals. Island-wide benthic surveys in Curaçao indicated that the abundance of benthic cyanobacterial mats was indeed positively correlated with fleshy algae and negatively correlated with scleractinian corals (Brocke et al., 2015a). At the organism-scale, increased DOC stimulates the activity of coral-associated microbes within the coral mucus, potentially leading to coral tissue

hypoxia and subsequent mortality (Kline et al., 2006; Smith et al., 2006). Bacteria within the coral mucus exhibiting the strongest growth responses to DOC are often pathogenic (Morrow et al., 2011). Moreover, during night-time fermentation, certain cyanobacteria (e.g., *Oscillatoria*, Heyer and Krumbein, 1991) release easily degradable compounds including lactate, ethanol and acetate, which could further enhance heterotrophic metabolism and pathogenic microbes (Haas et al., 2013). Coral (massive *Porites*) margins in contact with benthic cyanobacteria are characterised by a thick diffusive boundary layer and hypoxia at night, which may in turn facilitate cyanobacterial overgrowth of live corals (Jorissen et al., 2016). Lastly, increased levels of bioavailable nitrogen on reefs may lead to increased bleaching (susceptibility) in corals (Wiedenmann et al., 2013; Rådecker et al., 2015; Pogoreutz et al., 2017), resulting in reinforcing feedbacks that continue to favour reef degradation (Figure 4).

Recent evidence from the Caribbean suggests that benthic cyanobacterial mats may not be limited to shallow reef



environments and can occur at depths of up to 40 m (de Bakker et al., 2017). Though the ability of marine benthic cyanobacteria to grow under reduced light remains relatively unknown, cyanobacteria (e.g., *Planktothrix*) have been identified as the group within phytoplankton communities which can grow best under low light conditions (Mur et al., 1999). Such findings could challenge the potential for the “deep reef refugia hypothesis” (Bongaerts et al., 2010), which proposes that deeper corals that are less affected by heat and light stress could restock degraded shallow areas in the future through vertical genetic connectivity, underlining the importance of further information on the ecology of mesophotic benthic cyanobacteria.

Cyanobacterial mats can also affect reef fish communities. Recent experimental data indicated that climate change-driven shifts toward benthic cyanobacteria could ultimately lead to food web collapse due to reduced energy flow to higher trophic levels (Ullah et al., 2018). A major die-off of juvenile rabbitfish *Siganus argenteus* and *Siganus spinus* occurred as mats became dominant on coral reefs around Guam, which was attributed to starvation (Nagle and Paul, 1998). Furthermore, aquaria experiments revealed that the rabbitfish *Siganus fuscescens* chose to starve rather than to consume *Moorea producens* containing lyngbyatoxin-A (Capper et al., 2006b). Contrastingly, proliferation of benthic cyanobacterial mats following a ship grounding at Rose Atoll, American Samoa, led to long-term increases in the local abundance and biomass of herbivorous fish (Green et al., 1997; Schroeder et al., 2008). These observations may be due to the cyanobacteria being mixed with algal turfs and/or the additional shelter offered by the wreckage.

“SOCIAL-ECOLOGICAL TRAPS” ASSOCIATED WITH CYANOBACTERIAL MATS

Benthic marine cyanobacteria may pose direct threats to human health, similar to their freshwater counterparts (e.g., Bell and Codd, 1994). Summertime blooms of benthic cyanobacterial mats on some New Caledonian inshore reefs have been identified as the causative agents of ciguatera-like disease outbreaks in coastal human populations (Laurent et al., 2008). Symptoms included (clinically similar to ciguatera) gastrointestinal disorders, fatigue, limb and joint pain, reversal of hot and cold sensations, and some cardiovascular symptoms. In fact the sickness seemed to manifest in more severe symptoms than ciguatera, with one third of sufferers being hospitalised which was far higher than usual in the area. Instead of containing the common ciguatera causative agent (i.e., the dinoflagellate *Gambierdiscus*), these mats were dominated by *Hydrocoleum*, a common cyanobacterium within tropical mats (Abed et al., 2006; Echenique-Subiabre et al., 2015). *Hydrocoleum* was subsequently found to produce cyanotoxins with very similar characteristics to cigua- and paralyzing-toxins (Laurent et al., 2008). Several fish species, some of which are prime targets of fisheries, carried the cyanotoxins, and giant clams were also intoxicated (see Méjean et al., 2010, **Table 2**). A subsequent study encompassing New Caledonia, French Polynesia and Vanuatu confirmed that the link between benthic cyanobacterial mats and ciguatera-like sickness is rather widespread in the Pacific (Laurent et al., 2012). An estimated 500,000 Pacific islanders have suffered from ciguatera

symptoms between 1973 and 2008, with a 60% increase in documented cases between 1973-1983 and 1998-2008 (Skinner et al., 2011), underlining the urgency of identifying management practices that can control the causal organisms. Bathers and fishers exposed to coastal waters where benthic cyanobacterial mats are common have also often reported severe dermatitis and asthma-like symptoms (Osborne et al., 2001).

Rapidly growing coastal populations will continue to drive increased nutrient and OM input into coastal waters over the coming decades. In the absence of wastewater treatment and land-use management, poor water quality could facilitate benthic cyanobacterial mat growth which will likely be magnified under future climate change. Combined, the stressful environmental conditions and development of benthic cyanobacterial mats can negatively impact the health of coral-dominated systems. Together with the inhibition of coral recruitment, ecological feedbacks favouring cyanobacterial growth and reef degradation could be further strengthened by increasing bioavailable nitrogen and DOC (Figure 4). Degraded reefs have reduced structural complexity, impairing their capacity to protect shorelines from wave energy (Sheppard et al., 2005) and to sustain productive fisheries (Graham and Nash, 2013; Pratchett et al., 2014). The accumulation of ciguatera-like toxins in fishes in connection with cyanobacterial mats may also pose limits to the utilisation of fishery resources. As human communities are faced with progressively degraded coastal resources, they may increasingly resort to terrestrial resources such as agriculture, facilitating further reductions in coastal water quality from increased nutrient run-off. These practices can promote a social-ecological trap with self-reinforcing feedbacks as has been similarly described for reefs that become dominated by fleshy algae (Cinner, 2011). Escape routes to shift algal-dominated systems back toward a more desirable state include adaptive fisheries management (Mumby et al., 2006; Hughes et al., 2007; Cinner, 2011), and where positive feedbacks are particularly strong additional “shock” events (e.g., storms) can be necessary to reset the system by clearing space for coral recruits to settle (Edmunds and Carpenter, 2001; Graham et al., 2013). However, where mechanisms that facilitate mat proliferation are in place, fast-growing cyanobacteria could rapidly pre-empt space even where herbivorous fishes are abundant, thus truncating coral recruitment. As local fishing regulations alone may be insufficient to counteract cyanobacterial proliferation, escaping a social-ecological trap whereby cyanobacterial mats have developed extensively may be very challenging. These feedbacks may call for integrated efforts to regulate appropriate fisheries and manage watersheds.

AVOIDING REEFS SLIPPING TO SLIME

Coral reefs and their associated ecosystem services would be better conserved if environmental conditions facilitating development and prevalence of benthic cyanobacterial mats can be prevented. In concert with global actions, an assortment of relatively cost-effective local management practices (e.g., Richmond et al., 2007; Klein et al., 2010) may reduce the

likelihood and temporal duration of mats. In particular, mat development seems to be facilitated when systems enter a low N:P ratio and when iron concentrations increase, implying that managers should reduce the level of phosphate and iron of terrestrial origin entering reefs. This could be achieved by limiting the use of certain fertilisers, reducing soil erosion, and protecting mangroves. Furthermore, studies have shown that nutrient and OM input can trigger the release of iron and phosphate following oxygen depletion within sediments (Brocke et al., 2015a; Hanington et al., 2016). Where iron is already present in sediments (e.g., in volcanic areas, reefs exposed to Aeolian dust), targeted management of nutrient and OM input may thus be particularly important. Sewage is a major source of both nutrients and OM, and just as benthic cyanobacterial mats can increase significantly close to a point of sewage input, improved sewage treatment can reverse mats to grazable algal turfs, as shown in Barbados (DeGeorges et al., 2010). In addition to limiting growth of cyanobacterial mats (and unfavourable algae), improvements in water quality could reduce the otherwise stimulating effects of increasing carbon dioxide and temperature on cyanobacterial growth (Visser et al., 2016), thus indirectly reducing the effects of climate change which cannot be tackled at the local level. Furthermore, managing reefs with an integrated approach to build resilience to climate change impacts (e.g., McClanahan et al., 2012) may be beneficial in promoting resilience against the initiation and establishment of cyanobacterial mats after disturbances.

Current knowledge implies that management of reef fish communities alone could be futile in counteracting benthic cyanobacterial mats. However, following a shift toward a cyanobacteria-algal turf mixed assemblage following a ship grounding at Rose Atoll, biomass of some surgeonfish and parrotfish species showed a counterintuitive increase (Green et al., 1997; Schroeder et al., 2008). *In situ* video observations aimed at quantifying herbivory on mats may identify novel opportunistic species, similar to the unexpected finding that batfish act as key herbivores following blooms of fleshy *Sargassum* algae (Bellwood et al., 2006). Such knowledge could support protective measures aimed at regulating the fishery of important consumers of cyanobacteria where mats are becoming increasingly prevalent. For example, *B. muricatum* has been observed directly feeding on mats (Clements et al., 2016), adding to the body of evidence that this heavily targeted species warrants special protection where it is threatened (e.g., Bellwood et al., 2003). Herbivorous fish species may vary greatly in their sensitivity to cyanotoxins, and prior or repeated exposure may even allow for some adaptation (Thacker et al., 1997; Capper et al., 2006a). Trade-offs between growth and defence drive differential anti-herbivore toxin production in fleshy algae across areas with different water qualities (Van Alstyne and Pelletreau, 2000). Although specific studies are currently scarce, cyanotoxin production usually increases with conditions that favour cyanobacterial growth, such as increased temperatures (Kaebernick and Neilan, 2001). A combined approach incorporating toxin production and functional genes could investigate how toxin production varies across

environmental gradients and whether this results from changes in mat composition or functional gene expression (Golubic et al., 2010; Echenique-Subiabre et al., 2015). Such patterns would suggest predictable differences in cyanobacteria palatability with water quality management or over environmental gradients.

Considering the potentially limited control of benthic cyanobacterial mats by reef fishes, management policies may have to pertain to more than herbivorous fishes and explicitly address other organisms capable of hindering mat proliferation. One example of such an organism in sandy environments (e.g., reef flats, lagoons, patch reefs) is sea cucumbers. Their bioturbation activity may moderate the development of anoxic sediment conditions (particularly under additional heat stress—Lee et al., 2017) that could otherwise facilitate the release of iron and phosphate (Brocke et al., 2015a). Experimental manipulations should quantify densities of sea cucumbers that are necessary to maintain sediment integrity under declining water quality and ocean warming scenarios. Whilst many mesograzers (e.g., sea hares) recognised to directly consume cyanobacteria likely have a relatively small impact on large-spread mats, their potential to regulate mat growth should be further explored alongside other larger grazing species. For example, the generalist sea urchin *Diadema* seems undeterred by cyanobacterial secondary metabolites (Capper et al., 2016), and perhaps the loss of this species throughout the Caribbean has helped facilitate the proliferation of mats across the region.

Research attention should be directed to clarifying the role of benthic cyanobacterial mats as symptoms vs. drivers of reef degradation. Benthic monitoring surveys need to improve their capacity to distinguish benthic cyanobacterial mats from other benthic groups, and whenever possible different cyanobacterial morphotypes should be recorded separately. Samples should be collected for subsequent genetic analyses to better clarify the taxonomic diversity within mats. This increased level of detail in benthic surveys will allow for the detection of changes in benthic cyanobacterial communities, in turn providing critical information on their potential as a bioindicator of coral reef degradation. A study on Southern Caribbean reefs in Colombia, for instance, suggested that >15% benthic cover of cyanobacteria indicates degradation (Puyana et al., 2015). As overgrowth does not always lead to the death of the underlying organism, studies should identify the characteristics of coral-cyanobacteria contacts. Detailed chemical characterisation of cyanobacterial mats is also important to predict future outbreaks of ciguatera-like sickness (Laurent et al., 2008, 2012). Concurrently, to improve the understanding of the link between human health and cyanobacterial mats, samples of mats and seafood should be collected for identification to assess human pathogenicity where significant cyanobacteria cover is observed.

FUTURE RESEARCH

We identify four key research areas that present tangible opportunities for novel future research. First, to prioritise local actions that minimise development and persistence of

cyanobacterial mats, the relative contributions of different components of global environmental change on cyanobacterial mat prevalence and toxicity require further experimental testing, as well as improved information on the occurrence and extent of marine benthic cyanobacteria. Secondly, opportunistic consumption of cyanobacterial mats by key functional groups of herbivores such as reef fishes and echinoderms needs to be explored, and species warranting special conservation policies should be identified where mats are prevalent. Thirdly, experiments can determine which densities of sea cucumbers can effectively decrease the formation of cyanobacterial mats to inform managers of minimum stock sizes and harvest quotas. Lastly, the relative importance of benthic cyanobacterial mats as a driver or symptom of coral reef degradation needs to be better understood. To achieve these four goals, mats need to be reliably and consistently identified by monitoring programmes and researchers, and no longer grouped together with algal types or abiotic substrate. New developments in the use of molecular tools, such as DNA barcoding, may provide important tools in this regard. Once this is achieved, the temporal and spatial scale of such surveys can be expanded to better understand the ephemeral or stable nature of mats at different areas, to verify putative drivers and controls, and to better link the occurrence of benthic cyanobacterial mats to the biology and ecology of other reef organisms, such as stony corals.

CONCLUDING REMARKS

While an increase in awareness of the presence of benthic cyanobacterial mats may account partially for the recent increase of reports, they appear to be important players in coral reef degradation. The proliferation and establishment of these mats carries important implications for both ecosystem and human health. A wealth of factors are facilitating mat development and persistence, including increasing availability of space on degrading reefs and declining water quality. Projected climate change conditions will likely favour growth of cyanobacterial mats while being detrimental to other benthic reef organisms. Systems where human populations and reefs are closely linked and that experience cyanobacterial blooms may be particularly prone to enter social-ecological traps with strong positive feedbacks. Not only can these traps threaten ecosystem services and human wellbeing, but they can be very challenging to escape from. Considering the serious risk that benthic cyanobacterial blooms pose directly to the future of reefs and their associated ecosystem services as well as human health, further focused research and resources for this topic are important.

AUTHOR CONTRIBUTIONS

AF proposed the original idea of this review. AF, MN, PV, SB, SA, and SF each then contributed to developing the concept of the review. AF developed the initial draft, and MN, PV, SB, SA, and SF critically revised the draft. Following AF's inclusion of revisions, MN, PV, SB, SA, and SF approved the final version

for submission. AF, MN, PV, SB, SA, and SF all agree to be accountable for all aspects of the work.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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