Fish or Germs? Microbial Dynamics Associated with Changing Trophic Structures on Coral Reefs

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1 Introduction

Overfishing major predators has dramatically changed the trophic structures of coral reefs. Here, we argue that the photosynthate, which would normally support the large predators via trophic transfers, is being used by microbes (Bacteria and Archaea) on degraded reefs. The supply of higher concentrations of photosynthate to the microbes increases their population size and enables heterotrophic microbes to dominate the community. In turn, the heterotrophic microbes detrimentally affect the corals causing disease outbreaks and death, which causes the phase shift from coral to fleshy algae (including macroalgae and turf algae) dominated reefs. To succeed, conservation and restoration efforts need to understand and consider the influence of microbes.

2 Trophic Structure on Coral Reefs

Most coral reefs exist today with few top-level predators: a trophic structure that is very different from historical coral reefs (Jackson et al. 2001; Pandolfi et al. 2005; Essington et al. 2006; Hughes et al. 2007; Jackson 2008). Friedlander and DeMartini (2002) showed that the fish biomass on nearly pristine coral reefs in the Northwest Hawaiian Islands have a trophic structure resembling an inverted pyramid, where more than 54% of the fish biomass is apex predators. In comparison, in the Main Hawaiian Islands apex predators make up less than 3% of the trophic structure (Friedlander and DeMartini 2002). Similarly, on the remote and completely protected Kingman Reef in the Northern Line Islands (Halpern et al. 2008; Knowlton and Jackson. 2008), an inverted trophic biomass pyramid also exists, where 85% of the total fish biomass are sharks and large piscivores. On the most heavily fished reefs of Kiritimati, which has the highest levels of human activity in the same island chain, top predators are essentially nonexistent (DeMartini et al. 2008; Sandin et al. 2008). Calculations based on the number of monk seals, a major predator in the Caribbean, prior to fishing also support the idea that the trophic structure in the Caribbean would have been an inverted biomass pyramid (McClenachan and Cooper 2008).

Coupled with the removal of apex predators on coral reefs is an increase in fleshy algae cover (Done 1992; Hughes 1994; Mumby et al. 2006; Hughes et al. 2007). These phase shifts on coral reefs have occurred from the Caribbean to the Pacific (Done 1992; Hughes 1994). The phase shifts often coincide with an increase in nutrient inputs from industrialized agriculture, including dissolved forms of inorganic nitrogen and phosphate. Whether the removal of fish or increase in dissolved inorganic nitrogen and phosphate compounds is the major factor leading to the death of corals has received much debate in the literature (Littler et al. 1991; Hughes 1994; Lapointe 1997; McCook et al. 2001; Smith et al. 2001; Thacker et al. 2001; Boyer et al. 2004; Albert et al. 2008).

3 Herbivores

On most occasions, phase shifts are associated with overfishing (Munro 1983; Hughes 1994). However, the trajectory of a coral reef from high-coral-covered to fleshy-algae-dominated does not always occur immediately after the removal of herbivorous fish (Bellwood et al. 2004; Ledlie et al. 2007). The time lag can occur because of the presence of other herbivorous groups, such as sea urchins, on the reef. It is likely that the large numbers of sea urchins help maintain the high cover of corals in the Caribbean until a disease killed most of them (Lessios 1988; Forocucci 1994; Lessios 2005). Sea urchins do not appear to be able to protect Pacific coral reefs,

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possibly because these sea urchins do not feed on fleshy algae with high tannin and phenol content (Coppard and Campbell 2007; Nordemar et al. 2007). The types and size of herbivores present affects their efficiency in removing fleshy algae and therefore the rate of the phase shift (Bellwood et al. 2006; Fox and Bellwood 2008; Lokrantz et al. 2008).

Predators exert various pressures on the trophic structure of the ecosystem (Connell 1998; Carpenter et al. 2008). One expected outcome of removing predators is an increase in prey biomass, which are mostly herbivores. On coral reefs with high and low predator biomass, the biomass of the prey species remains relatively constant (DeMartini et al. 2008; Sandin et al. 2008) and in protected coral reefs where there are higher predator biomass there are more herbivores (Mumby et al. 2006; Kramer and Heck 2007; Mumby et al. 2007). Therefore, even when the herbivores are not removed by fishing, without predators they are not effective at removing fleshy algae.

4 Dissolved Inorganic Nitrogen and Soluble Reactive Phosphorus

Increases in dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) are implicated in the death of corals and have received much research attention (Littler et al. 1991; Lapointe 1997; Boyer et al. 1999; Haynes 2001; Koop et al. 2001; McClanahan et al. 2003; D'Croz et al. 2005; Schaffelke et al. 2005; Littler et al. 2006; Bell et al. 2007). A threshold value for both of these nutrients has been proposed, above which a reef is considered eutrophic and the coral cover is expected to decline (Lapointe 1997). Proving the effect of increased concentrations of DIN and SRP on coral health has been difficult. A large field experiment that increased concentration of these nutrients by approximately 10 times found that DIN and SRP did not kill corals (Koop et al. 2001). In the highest concentration phase of the same experiment, where concentrations of DIN and SRP were increased by 30 times, one coral species showed increased mortality levels compared to the control sites (Koop et al. 2001). Similarly, large-scale treatments of nubbins from several Caribbean corals did not find any adverse effects of either DIN or SRP (acting singly or in combination) (Kuntz et al. 2005; Kline et al. 2006), suggesting that nutrients on coral reefs are not the direct cause of coral mortality.

Many nutrient studies have been conducted on the Great Barrier Reef, because it is situated adjacent to an area of high levels of industrial agriculture runoff. In a review of these studies, Furnas et al. (2005) showed that nutrient concentrations were low given the high levels of inputs (except during floods). It was proposed that the low levels were maintained by pelagic phytoplankton communities. Most of the nutrients delivered to the benthic community are delivered as organic matter from the phytoplankton (Furnas et al. 2005; Atkinson 2010).

5 Dissolved Organic Carbon and Coral Reef Microbes

In contrast to DIN and SRP, an increased organic carbon load (by approximately twofold to threefold) causes coral bleaching and mortality (Hodgson 1990; Fabricius et al. 2003; Kuntz et al. 2005; Kline et al. 2006). These deleterious effects increase exponentially with time. Some species-level differences have been observed: *Montastraea annularis* (Kline et al. 2006) and *Agaricia tenuifolia* (Kuntz et al. 2005) showed high levels of mortality associated with organic carbon load, while *Porites furcata* was less susceptible (Kuntz et al. 2005). Similarly, *Oxypora glabra*, *Porites lobata*, and *Pocillopora meandrina* experienced high levels of mortality when they were exposed to organic loaded sediment, whereas *Montipora verrucosa* was less susceptible (Hodgson 1990). Organic-carbon-killing of corals, whether in the form of simple sugars, polysaccharides, or complex compounds associated with sediment, is negated by antibiotics (Hodgson 1990; Kuntz et al. 2005; Kline et al. 2006), which suggests microbes are playing a role.

The standing stock of dissolved organic carbon (DOC) is determined by a combination of carbon fixation via photosynthesis, consumption via heterotrophic bacterial growth, and import/export from exogenous sources (Carlson 2002). In general, the standing stock of DOC in the ocean is 70–80 µM and grossly consists of two pools. Labile DOC (mostly fresh photosynthate) (Carlson 2002; Carlson et al. 2002), which is rapidly turned over within minutes to days, and represents a major dynamical component of the marine carbon cycle (Opsahl and Benner 1997). Most of the measured standing stock is actually refractory DOC, which can exist for thousands of years (Carlson 2002). The DOC pool consists of thousands, and possibly millions, of different compounds. Together, these attributes (i.e., the rapid turnover of some DOC components and the complex structure) make it difficult to measure DOC and many of the earlier measurements on coral reefs were unreliable (UNESCO 1994).

Much of the DOC on coral reefs is produced by *in situ* photosynthesis (i.e., is not transported onto the reef) (Sakka et al. 2002). Different forms of DOC are produced by the actions of microbes, plankton (both phytoplankton and zooplankton), and other larger organisms, including corals and sponges (Ducklow and Mitchell 1979b; Crossland et al. 1980; Crossland 1987). Mucus and coral spawn have been shown to be broken down such that they contribute to the

DOC pool (Ducklow and Mitchell 1979b; Crossland 1987; van Duyl and Gast 2001; Wild et al. 2004a, b, 2005; Allers et al. 2008; Patten et al. 2008b; Wild et al. 2008). Mean DOC measurements (including both the liable and refractory fractions) associated with coral reefs range from 34 to 160 µM (Pages et al. 1997; Torreton et al. 1997; van Duyl and Gast 2001; Dinsdale et al. 2008), suggesting there is variable production and use of DOC on each individual reef. DOC flux is higher above the coral reef structure than surrounding "oceanic" water (Hata et al. 2002). DOC levels are highest in the water above the surface of the corals and decrease within the crevices between coral colonies and the reef structure (van Duyl and Gast 2001; van Duyl et al. 2006). The labile component of the DOC is difficult to measure, but has been estimated to be approximately 20% in some coral reef waters (Sakka et al. 2002).

Whether the water column-associated microbes or benthic community are driving variations in the DOC pool is a major outstanding question. In the open ocean (where more research has been conducted), microbes consume most of the liable DOC and have been shown to be carbon limited (Carlson et al. 1996; Carlson et al. 2002; Carlson et al. 2004). On coral reefs, complex interactions between DOC, microbial growth, and filter feeders (e.g., sponges) exist (de Goeij and van Duyl 2007; de Goeij et al. 2008a,b). Using labeled carbon, it was shown that both the sponge cells and the associated microbes assimilated DOC (de Goeij et al. 2008a), which may account for much of the consumption of the DOC pool on coral reefs. DOC can also be assimilated into the sediments (Wild et al. 2008) but this has been estimated to be low (Charpy and Charpy-Roubaud 1990). Despite this complexity, one take-home message from the numerous studies conducted in other marine environments is that higher production of labile DOC will support more heterotrophic microbes (Fuhrman et al. 1989; Carlson et al. 1996; Carlson et al. 2002; Carlson et al. 2004) and this may occur on coral reef ecosystems (Charpy and Charpy-Roubaud 1990).

6 Microbes and the Coral Holobiont

Microbes are an integral part of the coral holobiont (Ducklow and Mitchell 1979a; Rohwer et al. 2002; Rohwer and Kelley 2004; Rosenberg and Loya 2004) and provide important nutrients and other resources to the coral host (Reshef et al. 2006). In addition to zooxanthellae, Bacteria, Archaea, Fungi, and viruses are all found in association with corals and many form species-specific associations (Rohwer et al. 2001; Bourne and Munn 2005; Beman et al. 2007; Marhaver et al. 2008; Patten et al. 2008a; Littman et al. 2009). Functional roles of coral-associated microbes include

ammonia, nitrate, sulfur, and carbon metabolism (Lessar et al. 2004; Beman et al. 2007; Lesser et al. 2007; Wegley et al. 2007; Siboni et al. 2008). Symbiotic cyanobacteria produce nitrogen that is taken up by the zooxanthellae (Lesser et al. 2004; Lesser et al. 2007). Together, these studies demonstrate the fundamental roles that the microbes play in the growth and survival of the coral holobiont.

Much of the energy in the coral holobiont is provided via photosynthesis by the zooxanthellae (Falkowski et al. 1993; Yellowlees et al. 2008). The amount of DIN and SRP in the water column affects the rate of production and translocation of products by the zooxanthellae (Muscatine and D'elia 1978; Tanaka et al. 2006; Yellowlees et al. 2008). Simple sugars are converted by the animal into complex carbohydrates, lipids, and released as coral mucus or DOC (Wild et al. 2004b). The exact composition of coral mucus is unknown and varies from species to species (Ducklow and Mitchell 1979b). The mucus forms a layer between the animal and surrounding seawater and is colonized by hundreds of millions of microbes per square centimeter (Wegley et al. 2004; Koren and Rosenberg 2006; Johnston and Rohwer 2007; Klaus et al. 2007; Lampert et al. 2008). Metagenomic analysis of these coral-associated microbes shows that they encode enzymes to metabolize the coral mucus and transport the resulting sugars into their cells for energy (Wegley et al. 2007). The species-specific nature of microbial association with corals (Rohwer et al. 2002; Bourne and Munn 2005; Littman et al. 2009) may be based on a mutualistic relationship of mucus composition and enzymes to metabolize the mucus, as first suggested by Ducklow and Mitchell (1979a). Disruption of this relationship by addition of exogenous DOC leads to uncontrolled microbial growth and coral death (Hodgson 1990; Kuntz et al. 2005; Kline et al. 2006).

7 Local Connections Between Coral Disease, Fishing, and Fleshy Algae

There has been an increase in the types and incidence of coral disease over the last 30 years (Green and Bruckner 2000; Aronson and Precht 2001; Harvell et al. 2002; Harvell et al. 2007). While the number of described disease morphologies has increased, specific pathogen for each morphology has not been identified to date (Harvell et al. 1999; Rosenberg and Loya 2004; Willis et al. 2004; Rosenberg et al. 2007; Toledo-Hernandez et al. 2008; Rosenberg and Kurshmaro 2010). This suggests that the increased level of disease may be associated with a change in the relationship between microbes and corals, rather than the introduction of new specific pathogenic microbial strains. The relationship between specific and opportunistic pathogens and the influence of host response, infective dose, and environmental

conditions is visualized in Fig. 1. Specific pathogens, such as those associated with black band disease, white band disease, etc., described in Rosenberg and Kurshmaro (2010), would cause disease when the host response is strong, even in pristine environments. Diseases, such as bacterial bleaching, would occur when the microbes are present and there is an environmental trigger, such as, increased temperature, which reduces host response or increasing microbial virulence allowing the microbe to cause disease. If part of the normal microbial flora increases in abundance it may lead to disease, as was shown in the dosing experiment by Kline et al. (2006). Where environmental influences increase, such as higher temperatures, more dissolved organic carbon, etc., the microbial dose rate increases and the host response is weakened, microbes that are normally present within the environment may opportunistically cause disease. We believe that most of the world's coral reefs are approaching the right-hand side of the continuum and overfishing and/or nutrient additions are the drivers of increased coral diseases leading to increased mortality and the mechanism of phase shifts.

One of the most straightforward ways that fishing changes coral reefs is by increasing the number and length of coral – fleshy algal interaction zones. Smith et al. (2006) showed that when corals are placed immediately next to fleshy algae, the corals die. Death occurs even when there is an intervening filter that prevents the passage of microbes and viruses to

Fig. 1 The proposed interactions between host response, microbe type, infective dose, and environmental conditions, and how they lead to an increase in the prevalence of disease in the coral populations are provided in a stylized diagram. The red hatched area is the condition that most of the world's coral reefs are approaching. BBD=black band disease, WBD=white band disease, and bacterial bleaching are defined in Rosenberg and Kurshmaro (2010)

the corals but allows the flow of dissolved compounds like DOC. Addition of antibiotics into the experimental setup prevented coral death, implying the involvement of microbes. The pattern occurred across a range of corals and fleshy algae, with some species-level variation. Oxygen microprobe readings showed that the coral – fleshy algal interface was hypoxic. The hypoxia was relieved by antibiotic addition. Together with the previously mentioned DOC experiments, these results suggest that DOC released by the fleshy algae enhances growth of microbes on the coral surface. These microbes then grow so fast that they use up all the oxygen and smother the coral.

In the Smith et al. (2006) experiment, coral death was associated with change in the microbial community already present within the water column or associated with the corals. Nugues et al. (2004) showed that fleshy algae harbor coral pathogens, which would enhance the negative effects of fleshy algae on corals via microbial activity. Vermeij et al. (2008) showed that algal exudates kill coral recruits and the addition of antibiotics alleviates this mortality.

8 Large-Scale Connections Between Coral Disease, Fishing, Fleshy Algae, and Eutrophication

In addition to the microbial activity associated with fleshy algae – coral interaction zones, the microbe–coral–fleshy algae DOC model could also work at larger scales. Figure 2 outlines how DOC loading might work at a reef scale. On a "Healthy Coral Reef," primary production is nutrient limited (DIN and SRP are represented by *green* arrows). The limited nutrients are used by the fleshy algae and the zooxanthallae for photosynthesis. Most of the organic carbon produced from photosynthesis is assimilated (via trophic transfer) by the complex macroorganism-dominated food web, which includes the fish and corals. As organic carbon (represented by the *black* arrows) moves through the food web, it is respired and lost as carbon dioxide (~90% from trophic level to trophic level). The inverted trophic biomass pyramid described for reefs with minimal fishing (Friedlander and DeMartini 2002; Mora et al. 2006; DeMartini et al. 2008; Sandin et al. 2008) suggests there is a movement of carbon through the food web until it is stored in the apex predators. There are relatively low numbers of sponges on the healthy coral reef (Aerts 1998), because DOC and the associated microbial food web is small. Coral growth is successful in the minimal nutrient conditions, because the coral animal is able catch plankton and their associated microbes fix nitrogen (Lesser et al. 2007; Wegley et al. 2007). DOC released into the water column is used by the water column microbes, directly by some filter feeders (link not shown in diagram),
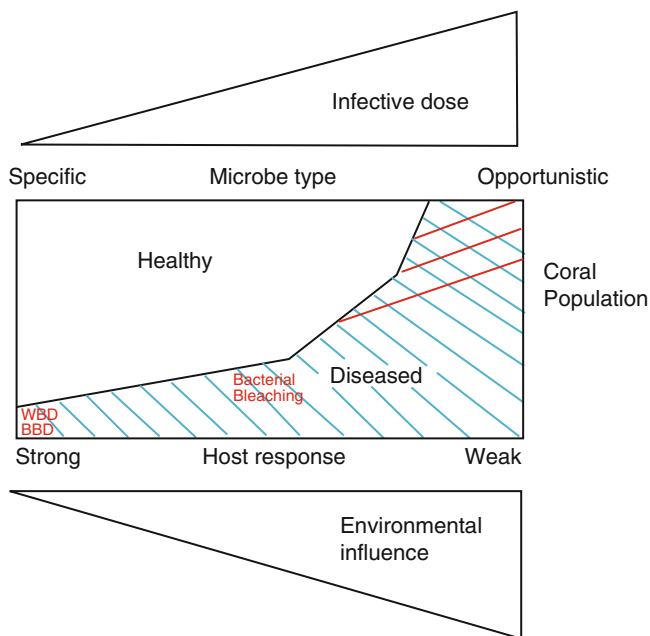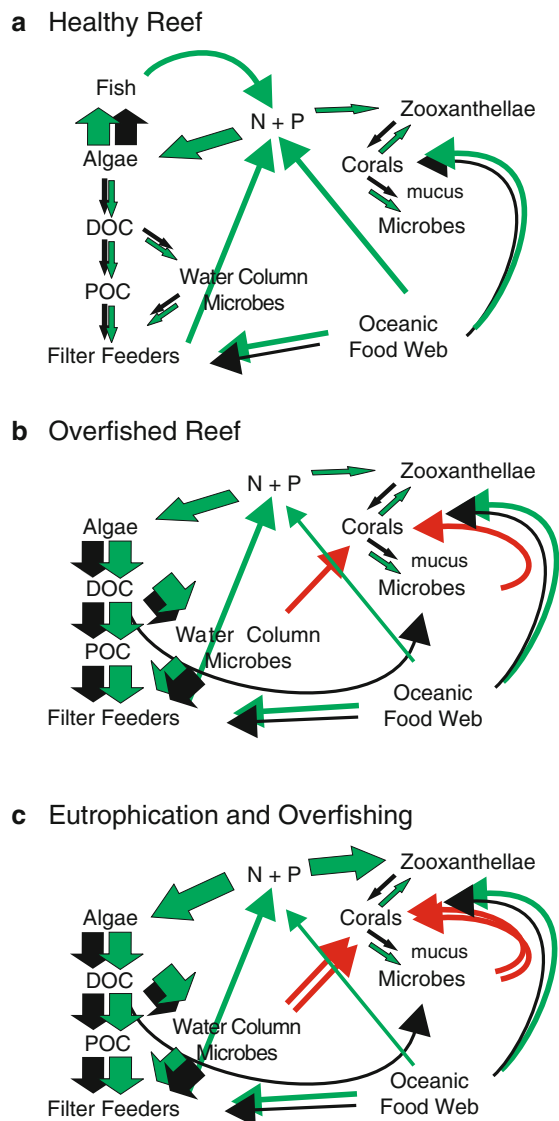
a Healthy Reef

b Overfished Reef

c Eutrophication and Overfishing

Fig. 2 A model of the proposed response of the microbes within a coral reef ecosystem under three different conditions: (**a**) healthy, (**b**) overfished, and (**c**) overfished with eutrophication. The model is stylized and only shows major interactions. The green arrows represent the flow of nutrients (dissolved inorganic nitrogen and soluble reactive phosphate), the black arrows represent the flow of organic carbon and the red arrows suggest a negative impact of one organism on the next. Note: healthy is being used to denote a coral reef prior to industrialized fishing

and can spontaneously form into particulate organic matter (Chin et al. 1998; Verdugo et al. 2004). The particulate matter is used by benthic filter feeders and pelagic planktivores. The carbon assimilated by the microbes passes to the macroorganism food web via the microbial loop (Azam et al. 1983; Azam and Smith 1991; Azam 1998) (but for simplification this link is not shown either).

Overfishing disrupts the system by removing the macroorganisms, such as sharks, that are main consumers of primary production via trophic transfers (Hairston and Hairston

1993; Hairston and Hairston 1997). The removal of the apex predators does not appear to cause a predation release that allows lower trophic levels to increase and consume more fleshy algae (Mumby et al. 2006; Newman et al. 2006; Mumby et al. 2007; Sandin et al. 2008). In fact, it appears that the remaining herbivores are less effective in consuming fleshy algae and there is a reduction in the amount of carbon that is drawn up the macroorganismal food web. This excess carbon (released by the fleshy algae and not drawn up the macrobial food web) is available for the microbial food web, causing them to become more abundant. Increased microbial activity directly threatens corals (*red* arrows), increasing the level of coral disease. Both the water column microbes and those associated with the coral may be involved in the death of the corals. The extra microbes support more filter feeders (Aerts 1998; Bak et al. 1998; Yahel et al. 2003) and their bioeroding activity may help explain the rapid loss of rugosity on declining reefs.

Eutrophication, by providing greater amounts of DIN and SRP to the fleshy algae, increases fleshy algae growth and thus increases DOC production further (Schaffelke and Klumpp 1998). Zooxanthellae are also released from their nutrient limitation (Hoegh-Guldberg and Smith 1989; Falkowski et al. 1993; Dubinsky and Stambler 1996; Grover et al. 2003; Hoegh-Guldberg et al. 2004; Grover et al. 2006). Increased zooxanthellae production may increase the number of coral-associated microbes (Ducklow and Mitchell 1979c; Pascal and Vacelet 1981) and encourages microbes that have more pathogenic characteristics (i.e., ones that grow more rapidly and consume oxygen). Nutrient additions may also increase the severity of an existing coral disease lesion (Voss and Richardson 2006).

In this model, overfishing and eutrophication are synergistic. Note that eutrophication by itself can also lead to phytoplankton blooms that kill coral reefs (Abram et al. 2003) and fleshy algae that directly overgrows the coral (McCook et al. 2001). In the model, a positive feedback occurs because coral death, due to microbial activity, creates more free space for fleshy algal growth, which in turn leads to more DOC release into the water. The proposed positive feedback is not at odds with the alternative stable state hypotheses (Done 1992; Knowlton 1992; Hughes 1994; Tanner et al. 1994; Bellwood et al. 2004; Pandolfi et al. 2005; Hughes et al. 2007; Knowlton and Jackson. 2008), rather it is a mechanism for the system bifurcation. As stated by Mora (2006; 2008), "the drivers of coral degradation have been challenging" to identify – we suggest that microbialization of the reef may be the driver.

To directly investigate this model in the field, the microbial communities on coral reefs with varying fish and benthic communities were studied in the Northern Line Islands. As mentioned above, this archipelago lies in a remote area of the Pacific Ocean, with a gradient of human and fishing activities,

from preindustrial to those experienced on most coral reefs today (DeMartini et al. 2008; Dinsdale et al. 2008; Halpern et al. 2008; Knowlton and Jackson. 2008; Sandin et al. 2008). Consistent with the proposed model, there was a positive correlation between microbial number and fishing activity across the four islands. There were 10 times more microbes per ml of seawater on Kiritimati (which had essentially no apex fish predators, extremely low coral cover, and high fishing levels) than there were on Kingman (the relatively pristine coral reef) (Dinsdale et al. 2008). A more extensive survey conducted on the coral reefs, the entire way around the island of Kiritimati, which provides a fishing gradient without the latitudinal gradient of the Northern Line Islands expedition, showed that microbial number were positively correlated with the area of the reef that received the most fishing pressure (McDole et al. 2008).

There were also dramatic changes in microbial trophic interactions in the Northern Line Islands. On Kingman, there were approximately equal numbers of microbial heterotrophs and autotrophs. As the amount of human activity increased and the fish biomass declined, the microbes were dominated by heterotrophs. On Kiritimati approximately 30% of the microbes were classified as "super-heterotrophs," Bacteria that live in extremely energy-rich environments. These microbes are classically thought of as opportunistic pathogens, and include representatives that most people have heard of including, *Escherichia coli*, *Staphylococcus*, *Streptococcus*, *Enterobacteria*, etc. (Dinsdale et al. 2008).

These super-heterotrophs would be expected to: (a) act as opportunistic pathogens, and (b) consume large amounts of DOC. The benthic observations from the Northern Line Islands support both of these points. First, the presence of the super-heterotrophic Bacteria was directly correlated with a known historical decline in coral cover, as well as an increase in the prevalence of unhealthy surviving corals (Dinsdale et al. 2008; Knowlton and Jackson. 2008; Sandin et al. 2008). Second, the standing stock of DOC was much lower on the severely degraded coral reef because the super-heterotrophic microbes were eating it (Dinsdale et al. 2008).

9 The DDAMed Model

The ways DOC, Disease, fleshy Algae, and Microbes (DDAM) work together to kill corals is summarized in Fig. 3. The feedback loop is driven by overfishing and/or eutrophication, which encourage algal growth. It can also be driven by other factors like bleaching or heavy metal poisoning, which will compromise the coral's ability to mount an immune response to the super-heterotrophic microbes. Increasing sea surface temperatures may be particularly problematic because it will: (a) cause bleaching, (b) increase
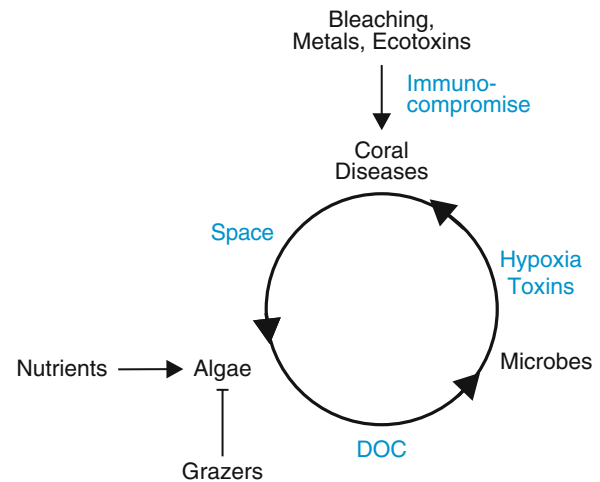

Fig. 3 The proposed feedback loop created by the elements dissolved organic carbon (DOC), Disease, fleshy Algae, and Microbes (DDAMed), which work together to undermine coral health. The removal of grazers and/or increase in nutrients allows higher cover of fleshy algae, releasing more DOC, which enhances microbial growth leading to low oxygen levels that cause disease in corals. Coral disease may be exacerbated by other environmental variables that compromise the immune response by the corals, all of which leads creates more bare space for fleshy algae recruitment

microbial activity, and (c) enhance photosynthesis and DOC release. Recent studies suggest that increased temperature is also related to reduction in herbivores, which will further increase fleshy algae (Smith 2008).

10 The Future

To further understand the relationship between microbes, DOC, and coral reef decline, there are many research questions that need to be answered. The production rate of microbes on coral reefs associated with varying levels of human activity needs to be estimated. The consumption rate of DOC and production by fleshy algae needs to be measured. In particular, the amount of labile DOC produced by different types of fleshy algae needs to be quantified (e.g., do turf algae produce more labile DOC than *Halimedia* spp.?). A major unanswered question is why removal of predators does not lead to a dramatic increase in the biomass of lower trophic levels (Mumby et al. 2006; Newman et al. 2006; Sandin et al. 2008). It is this inability of the macroorganisms to assimilate the organic carbon on disturbed reefs that appears to favor the microbes. Corals can adapt and respond to microbial changes, but this area of research is in its infancy (Mullen et al. 2004; Rosenberg et al. 2007). The movement of microbes onto and off the reef also needs to be considered in the future. The viral shunt, which cycles DOC within the microbial loop (Suttle 2007), will play a role in the proposed

DDAMed model, but to date there is not enough research to include these organisms in the model. And for restoration, experiments that increase fish on overfished reefs and assess the response of the microbial community need to be performed.

It currently appears that human activities on coral reefs are doing everything to give microbes the upper hand. To conserve these remarkable ecosystems understanding how to prevent microbial heterotrophic dominance or how to reestablish a balanced microbial community on coral reefs is required.

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