ANNUAL REVIEWS

Annual Review of Marine Science

Microbial Interactions with Dissolved Organic Matter Are Central to Coral Reef Ecosystem Function and Resilience

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Annu. Rev. Mar. Sci. 2023. 15:431–60

First published as a Review in Advance on September 13, 2022

The *Annual Review of Marine Science* is online at marine.annualreviews.org

https://doi.org/10.1146/annurev-marine-042121-080917

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Keywords

coral reefs, deoxygenation, dissolved organic matter, ecosystem function, microbiomes, nutrient cycling

Abstract

To thrive in nutrient-poor waters, coral reefs must retain and recycle materials efficiently. This review centers microbial processes in facilitating the persistence and stability of coral reefs, specifically the role of these processes in transforming and recycling the dissolved organic matter (DOM) that acts as an invisible currency in reef production, nutrient exchange, and organismal interactions. The defining characteristics of coral reefs, including high productivity, balanced metabolism, high biodiversity, nutrient retention, and structural complexity, are inextricably linked to microbial processing of DOM. The composition of microbes and DOM in reefs is summarized, and the spatial and temporal dynamics of biogeochemical processes carried out by microorganisms in diverse reef habitats are explored in a variety of key reef processes, including decomposition, accretion, trophic transfer, and macronutrient recycling. Finally, we examine how widespread habitat degradation of reefs is altering these important microbe–DOM interactions, creating feedbacks that reduce reef resilience to global change.

1. THE CENTRAL ROLE OF MICROBE–DISSOLVED ORGANIC MATTER INTERACTIONS IN CORAL REEF ECOSYSTEM PROCESSES

The widespread analogy of coral reefs as the rain forests of the sea is based largely on the high biomass, three-dimensional structural complexity, successional dynamics, and biodiversity common to these two ecosystem types (Connell 1978). Reefs are often described as teeming with visible animal life and notably have minimal evidence of accumulated litter or soil; they are vibrant, conveying dynamism with no visible evidence of the languorous decay so prominent in the first impression of a rain forest. Perhaps because of this contrast, with forests perceived as hotbeds of microbial decomposition, there is a misconception that reefs have only a thin veneer of microbial life. On the one hand, reefs do not accumulate litter, because their denizens are so voracious for resources that everything is recycled as rapidly as it is discarded: Both rain forests and coral reefs exhibit relatively high gross primary production (the rate of ecosystem carbon fixation), but whereas rainforests accumulate a significant percentage of the carbon they fix as detritus, the net metabolic balance of reefs is very near zero (Crossland et al. 1991). Coral reefs are bathed in the invisible so-called soil of the sea: the dissolved organic matter (DOM) ubiquitous throughout the world oceans that rivals the biomass of land plants (Carlson & Hansell 2015). Because these dissolved organic resources are bioavailable primarily to unicellular organisms (Azam et al. 1983), reefs may be viewed as secretly teeming with the invisible bustle of microbes interacting with DOM as it is rapidly produced and consumed by all the flora and fauna that together make up the visible beauty of the reef.

Yet coral reefs are changing: Centuries of increasing proximal impacts of human exploitation, such as overharvesting (Jackson et al. 2001), nutrient enrichment (Lapointe 1997), terrigenous pollutant inputs, and increased sediment loading (Dubinsky & Stambler 1996), are coupled with the growing impacts of increasing temperature and decreasing pH throughout the global oceans (Hoegh-Guldberg et al. 2007). Reefs worldwide have measurably shifted the composition of their benthic producers, decreasing the cover of hermatypic corals and calcifying algae and increasing the cover of fleshy macroalgae and mixed algal turfs that do not accrete reef framework (Hughes et al. 2007). These impacts and responses are fundamentally altering the ecosystem processes that allow coral reefs to thrive in the waters of tropical oceans around the globe, where they have adapted to maximize performance in the stable light and nutrient-poor waters of the subtropical gyres (Hatcher 1988). Therefore, in the final section of this review, we summarize how these changes in reefs alter interactions between microbes and DOM and the role of these interactions in the response of reef ecosystems to global change.

Dissolved organic matter (DOM): a heterogeneous mixture of hundreds to thousands of largely unknown water-soluble reduced organic compounds found in all aquatic ecosystems

Ecosystem processes: processes that integrate abiotic (physical and chemical) factors with interactions of assemblages of organisms (e.g., community production and biogeochemical cycling)

Among ecosystem types globally, coral reefs are characterized by relatively high rates of production with balanced net metabolism (Crossland et al. 1991, Kinsey 1985) and relatively low rates of detrital accumulation (Alongi 1988) attributable to high rates of detritivory (Mumby & Steneck 2018), decomposition (Cebrian 2002), or offshore export of detritus (Gruber et al. 2018, Wyatt et al. 2013). In addition, coral reefs are defined by high rates of accretion of calcium carbonate (Andersson & Gledhill 2013) and high biodiversity (Knowlton 2001), particularly in terms of animal and algal species richness. Central to reef persistence is the idea of nutrient recycling (Atkinson 2011, Crossland & Barnes 1983): Darwin's paradox, the puzzling observation of a productive ecosystem emerging from some of the most nutrient-poor waters on Earth (Darwin 1889, Rougerie 1998), is one guiding principle underlying the long-standing idea that coral reefs exhibit intense biogeochemical cycling to support nutrient recycling and retention (Duarte & Cebrián 1996, Odum & Odum 1955).

The maintenance of five core ecosystem processes sustains the unique success of coral reefs in the marine environment: high productivity, high decomposition, high biodiversity, high accretion, and both rapid and diverse biogeochemical cycling (Hatcher 1997). Microbial interactions with DOM play central roles in the characteristics of each of these processes (outlined below), and these interactions are critical for maintaining reef ecosystem functions (**Figure 1**):

1. Recycling dissolved primary production: Coral reefs sustain some of the highest rates of gross primary production of any ecosystem globally, and photosynthate released into the water as DOM by benthic producers constitutes a significant flux of carbon to coastal food webs. Fixed carbon substrates exuded from both algae and corals are highly labile, and the rapid utilization and transformation by reef microbial assemblages influence microbial community structure and constitute a significant link in transferring reef carbon to higher trophic levels.
2. Enhancing nutrient availability and retention: DOM released by reef benthic organisms is enriched in nitrogen and phosphorus resources, and microbes are the primary route for the transformation and metabolism of these nutrient sources. Microbial remineralization of dissolved organic nutrients is a critical nutrient source that allows primary producers in reef ecosystems to persist in oligotrophic tropical waters. Robust microbial production is a significant fuel for corals and other heterotrophic suspension feeders to subsidize oceanic particulate nutrient inputs. Microbial transformation of DOM released as waste by these suspension-feeding processes completes the recycling loop.
3. Rapid decomposition of detrital accumulation: Despite their relatively high gross photosynthetic production, coral reefs exhibit remarkably low detrital accumulation and net ecosystem production near zero, with accordingly high measured and derived rates of decomposition. Although rapid remineralization of photosynthetic exudates is a well-established principle, the broader trophic interplay among benthic suspension feeders, microbes, and DOM represents an underappreciated route for maintaining energetic efficiency on coral reefs, ultimately playing a key role in net metabolic balance and minimal detrital accumulation.
4. Facilitating net accretion: Net positive accretion is essential for maintaining the structural integrity and biodiversity of coral reefs. Microbial growth and metabolism influence net ecosystem calcification through both direct and indirect processes, including fueling coral growth through heterotrophic feeding, supporting microbial precipitation of calcite calcification, and driving microbial remineralization of compounds that influence local alkalinity and concentrations of carbonate ions for reef-building macroorganisms.
5. Maintaining high biodiversity: Highly productive ecosystems inherently exhibit increased richness, but it is the complexity and dynamism of scarce resource recycling that further enrich biodiversity in these ecosystems. The tightly coupled species mutualisms and metabolic exchange of organic resources are fundamental to this diversity enrichment and position microbial interactions with DOM as a central driver in maintaining the diversity of reefs.

Figure 1 illustrates conceptually how these five coral reef processes are influenced by microbial interactions with DOM. A significant fraction of the remarkably high primary production of reefs is consumed by microbial communities, and this process is central to the intense recycling of elements that define reefs. The anabolic incorporation of photosynthate into microbial biomass

Productivity: the biomass accrual rate of an organism or ecosystem, separated into gross production and net production, with the latter accounting for waste

Remineralization: the transformation of organic molecules into inorganic forms, typically as metabolic waste products released into the environment

Oligotrophic: having relatively low productivity, typically characterized by nutrient limitation and an ample supply of oxidants

Exudates: organic compounds steadily discharged into the environment by organisms

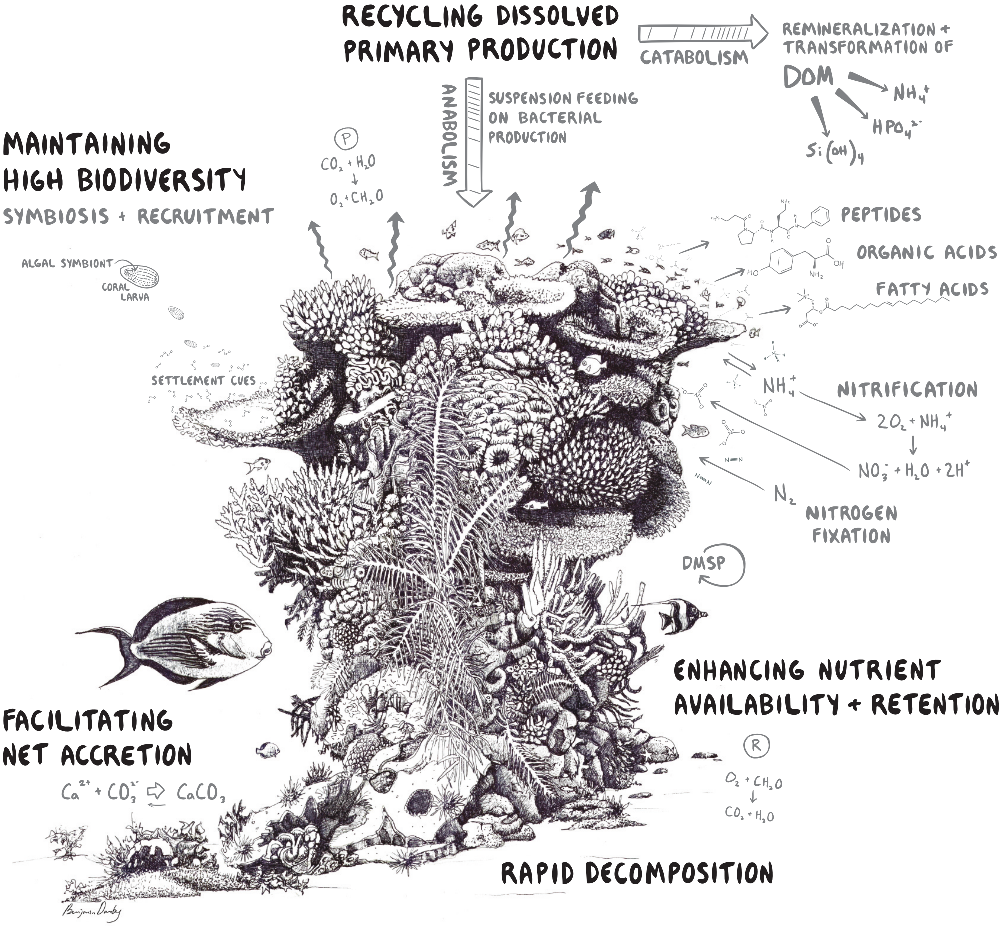


Figure 1

The role of microbe–DOM interactions in central coral reef processes. Primary production by the reef benthic community leads to exudation of fixed carbon into the reef water column. These newly synthesized organic substrates contribute to the local DOM pool, supporting anabolic bacterial production and selecting for distinct microbial taxa. The enrichment of microbial growth promotes nutrient availability on the reef through catabolic microbial mineralization of nutrient-rich organic matter. Microbial communities play key roles in nitrogen fixation, transformation of ammonium into nitrite and nitrate, transformation of DMSP into amino and nucleic acids, iron scavenging, and synthesis of B vitamins, contributing widely to the exchange of mineral nutrients and cofactors essential for reef fauna. Coral reef production and consumption processes are balanced, with a ratio of production to respiration of approximately 1:1, and rapid decomposition of reef-derived organic matter supports this metabolic balance by transferring energy primarily through detrital pathways. Detrital food webs are more efficient at sequestering energy and chelating nutrients into biomass, minimizing wasteful respiratory processes that promote erosion and dissolution. The tightly coupled recycling of energetic resources by benthic primary producers, microbes, suspension feeders, and detritivores sustains the biodiverse myriad of life on coral reefs that extends from single-cell algae to top predators. Abbreviations: DMSP, dimethylsulfoniopropionate; DOM, dissolved organic matter. Coral reef drawing by Ben Darby; graphic design by Shayle Matsuda.

becomes a source of particulate matter for suspension feeding by corals and other invertebrates, while catabolism remineralizes nutrients that influence biogeochemical cycles and fuel primary production locally. The efficiency of microbial processing of this organic material thus determines the energy transfer and nutrient retention on coral reefs, as it is dictated by both the structure of the microbial community and the types and amounts of DOM released by benthic assemblages. These processes also work to regulate the overall decomposition rates and net metabolic balance of the system, contributing to the lack of detrital accumulation in intact reefs that is so unique among productive ecosystem types worldwide. The rapid accretion, structural complexity, and resulting biodiversity all derive from these fundamental drivers of production–decomposition dynamics. The diverse ways in which microorganisms interact symbiotically with other denizens of the reef—from mutualism to competition and from facilitation to pathogenesis—all reinforce the central role of microbial ecology in reef ecosystem function.

2. DISSOLVED ORGANIC MATTER TROPHIC DYNAMICS ON CORAL REEFS

The production and consumption dynamics of DOM in part determine the degree to which nutrients are retained and recycled within the reef ecosystem. Essential processes specific to reefs are the rapid production of DOM by the highly productive reef benthos, the factors governing how allochthonous and autochthonous DOM is transformed into microbial biomass, the fate of that biomass (particularly the potential for trophic transfer), and the role of these trophic processes in regulating both decomposition and accretion processes in reefs. The quantity and quality of DOM interact with the metabolic potential and biomass of microbial osmotrophs that are the primary transformers of the material to determine the rates of these processes and ultimately the potential for DOM to contribute to reef nutrient recycling.

2.1. Exudation of Primary Production as Dissolved Organic Matter Is a Common Feature of Coral Reef Ecosystems

Primary producers in all ecosystems release a significant fraction of their fixed carbon as organic exudates (photosynthates) into the surrounding environment (Aluwihare & Repeta 1999, Bertilsson & Jones 2003, Hütsch et al. 2002). In terrestrial ecosystems, these exudates are released via the roots, where they contribute to labile carbon fertilization of soil microbial communities and facilitate symbiotic interactions between plants and microbial associates to acquire the mineral nutrients required to sustain growth (Hütsch et al. 2002). In aquatic ecosystems, these exudates are released by planktonic and benthic autotrophs as DOM and typically range from 10% to 40% of photosynthetic production (Haas et al. 2011), though nutrient limitation, flow dynamics, and other physiological aspects regulate the proportion of production exuded (Mueller et al. 2014, 2016; Quinlan et al. 2018).

Coral reefs sustain some of the highest rates of gross primary production of any ecosystem globally (Crossland et al. 1991, Gounand et al. 2018), and photosynthates released into the water by benthic producers are thus a significant flux of carbon to coastal food webs. Coral reef benthic primary production is dominated by calcifying producers—particularly hermatypic coral holobionts (via photosynthesis by their endosymbiotic Symbiodiniaceae dinoflagellates, known as zooxanthellae) and coralline algae (both crustose and macroalgae)—and noncalcifying producers such as fleshy macroalgae and turfing microalgae, with additionally significant production from the microphytobenthos. A reanalysis of compiled data across multiple reef ecosystems (Brocke et al. 2015, Haas et al. 2010) quantifies that algae exhibit higher mean areal DOM exudation rates than corals ($p = 0.012$): Mean DOM exudation rates (mmol C m^{-2} h^{-1}) are highest in turfing algae (1.86) followed by Rhodophyta (1.24), Chlorophyta (0.61), Phaeophyta (0.51), and corals (0.36). Microphytobenthos production ranges from 0.29 to 1.00 (Suzumura et al. 2002), indicating that benthic carbon production in coral reef sands and sediments may rival those of macroalgae and corals. As such, changes in the benthic cover of reefs can translate to significant shifts in the rate of

UNTARGETED METABOLOMICS OF DISSOLVED ORGANIC MATTER IN CORAL REEFS

The extraordinary diversity of small organic molecules released and transformed by organisms in the aquatic environment has long been a barrier to understanding organismal interactions and ecosystem processes. A combination of emerging technologies, including methods to concentrate, extract, and measure a larger and less biased diversity of small molecules, is facilitating an explosion of research on molecular interactions and organismal communications. Untargeted metabolomics, which couples a diversity of analytical tools (including mass spectrometry and nuclear magnetic resonance spectroscopy) with advanced computational bioinformatics to characterize unknown molecules, is an emerging field with great potential to characterize DOM. In addition to being used to identify the compounds involved in microbe–DOM metabolisms highlighted in this review, untargeted metabolomics has the potential for discovering compounds involved in mutualism, competition, reproduction, and settlement among all domains of life in coral reefs. As microbial transformation of signaling compounds and nutrient-rich molecules is widespread, there is no doubt that microbial interactions will remain central to understanding this vibrant molecular commerce underpinning reef ecosystem functions.

autochthonous DOM production and differential responses to factors that may have repercussions for recycling and trophic transfer of DOM, such as eutrophication, fishing, or warming.

Corals and algae produce compositionally distinct DOM that is processed differently by reef microbial communities. Primary examinations of exudate composition showed that a significant fraction of macroalgae DOM was composed of polysaccharides (Haas & Wild 2010). Further characterization of the dissolved combined neutral sugar component of exudates (oligosaccharide derivates of larger polysaccharides) indicated a significant difference between algae and reef-building corals but also clear species-specific differences among algae (Nelson et al. 2013). New research has employed targeted and untargeted metabolomics (see the sidebar titled Untargeted Metabolomics of Dissolved Organic Matter in Coral Reefs) to characterize the specific molecules and compound classes that make up the DOM in coral reefs (Kido Soule et al. 2015, Petras et al. 2017). Studies published to date include surveys of ambient DOM across Caribbean reefs (Weber et al. 2020a), characterization of DOM exhalent from sponges in Caribbean waters (Fiore et al. 2017), and untargeted metabolomic characterization of hundreds of compounds exuded by various species of coral and algae (Wegley Kelly et al. 2022). The study by Wegley Kelly et al. (2022) relied on untargeted metabolomics to organize hundreds of exuded compounds into distinct networks of compound classes differentiating corals and algae, further demonstrating bulk differences in the nutrient and energetic content of the metabolite pools. These early interrogations of the diversity of molecules in reefs illustrate previously invisible pathways of microbial recycling of nutrients through DOM as well as mechanisms by which shifts in benthic producers may translate to fundamental shifts in energy flow through microbes into higher trophic levels.

2.2. Conversion of Exudates to Microbial Biomass Is a Significant Trophic Pathway in Reefs

Exudation of DOM fuels a rapid and constant production of microbial cells in the vicinity of primary producers (Azam & Ammerman 1984, Cole et al. 1988). Consequently, variation in DOM release and composition from reef benthic producers has a major effect on reef bacterioplankton growth (Haas et al. 2011) that drives selection for different microbial communities (Nelson et al. 2013). In addition, the microbial metabolism of dissolved primary production is one determinant of trophic efficiency in reefs. The conversion of exudates to bacterial production and the direct consumption of this biomass by reef suspension feeders promotes recycling of autochthonous carbon sources and may be one mechanism that supports the inverted biomass ecosystem structure (greater biomass of consumers than producers) widely reported for coral reefs (DeMartini et al. 2008, McCauley et al. 2018, Sandin et al. 2008, Woodson et al. 2018). In this context, key controls on the microbial loop are central to reef persistence, including the dynamics of DOM lability, bacterial biomass, bacterial production, bacterial growth efficiency, and rates of bacterivory. Understanding the composition of these exudates and how it drives variation in microbial growth, biomass growth efficiency, and subsequent grazing by higher trophic levels is critical for understanding how reef ecosystems process energy.

Microbial loop: the conversion of DOM to particles that can be consumed by higher trophic levels, driven by single-celled heterotrophs

Lability: the bioavailability of organic compounds for use in anabolic or catabolic transformation pathways, ranging from labile to recalcitrant to refractory

Bacterial growth efficiency: the proportion of reduced carbon consumed that is anabolically incorporated into microbial biomass

Co-metabolism: the microbial transformation of a compound with limited resource value facilitated by the obligate addition of a substrate that can support growth

2.2.1. Dissolved organic matter quantity and lability are fundamental controls on organic matter recycling in reefs.

Measured concentrations of DOM and nutrients in aquatic ecosystems reflect the allochthonous inputs and autochthonous production left over after community consumption processes. However, the lability of specific sources must be considered to understand fluxes rather than stocks of DOM. The absolute quantity of DOM on reefs varies widely (Tanaka & Nakajima 2018), but global surveys have demonstrated that dissolved organic carbon (DOC) stocks decline as algal cover increases (Haas et al. 2016). Reefs with residence times on the order of days are consistently depleted in DOC but enriched in inorganic nitrate and phosphate relative to offshore waters, suggesting either that consumption is outpacing production and inputs or that there are significant dilution effects (Nelson et al. 2011, Suzuki et al. 2001). Reefs with shorter residence times (minutes to hours) are often slightly enriched in DOM relative to oceanic waters, but some that have significantly longer residence times (days to weeks) can also have elevated concentrations—as much as fourfold higher than those of the adjacent oceanic waters. The enriched DOM is attributed to elevated autochthonous production that exceeds consumption (Tanaka & Nakajima 2018). It is likely that the quantity of DOC found on reefs varies widely even on diel timescales (e.g., Tanaka et al. 2011) and reflects complex source–sink dynamics that couple rapid autochthonous production with the microbial metabolism of both allochthonous and autochthonous sources.

Autochthonous DOM on reefs, such as exudates from both algae and corals, is highly labile and rapidly consumed by ambient assemblages of reef bacterioplankton (Gast et al. 1998, Moriarty et al. 1985, Torréton & Dufour 1996), fueling rapid increases in microbial abundance. Coral mucus also fosters very high growth rates of bacterioplankton (Allers et al. 2008, Nakajima et al. 2008, Wild et al. 2004b), implying that it is an additional source of labile organic matter on reefs. By contrast, observations of consistent depletion of DOC in reefs relative to the adjacent ocean (Nelson et al. 2011) are remarkable both because of the high productivity of reefs and because a significant fraction of the open ocean DOM is consistently recalcitrant to microbial degradation (Carlson & Hansell 2015). These conflicted observations suggest that not only are local (labile) DOM exudates being metabolized, but reef ecosystems are co-metabolizing some of the recalcitrant DOM in the surface subtropical gyres (Dalton & Stirling 1982). Work on sponge-dominated reefs in the Caribbean and the Red Sea has shown that, in reefs where sponge biomass and pumping rates are high, there is potential for sponge-driven depletion of DOC (de Goeij et al. 2013, Rix et al. 2018). However, more work needs to be done in Pacific reefs, where sponges are primarily encrusting and cryptic (Freeman & Easson 2016). Taken together, the evidence indicates that reefs have multiple allochthonous and autochthonous sources of labile DOM that are converted to biomass within the system.

2.2.2. Bacterial production and growth efficiency ultimately regulate trophic transfer.

The production rates of microbes grown on the exudates of aquatic organisms can be highly variable. Consistent with work in diverse aquatic systems, the variability in production rates is dictated primarily by differences in the chemical composition of the exudates rather than being solely a function of DOM quantity (Azam & Ammerman 1984, Cole et al. 1988). The high benthic primary production rates of reefs should favor higher bacterial production than open ocean waters because primary productivity and heterotrophic microbial production are often coupled (Cole 1982). Consistent with this idea, bacteria-specific growth rates on reefs (averaging 0.58 d^{-1}; Tanaka & Nakajima 2018) are up to three times higher (Torréton & Dufour 1996) than those in the adjacent ocean waters (less than 0.2 d^{-1}; Kirchman 2016) and tend to be highest in the afternoon, when organic exudates released by benthic primary producers are potentially highest (Moriarty et al. 1985). The degree to which bacterial production supported by exudates is a trophic link or an energetic sink for carbon transfer to higher trophic levels in reefs is determined by the bacterial growth efficiency and the subsequent consumption rates of grazers and benthic invertebrate suspension feeders (including corals, sponges, and a diversity of benthic infauna). Bacterial growth efficiency is typically low in the ambient tropical surface waters, with medians of 8% and 16% in oceanic and coastal waters, respectively (Robinson 2008). However, measurements of bacterial growth efficiency on exudates of coral and algae show that algal exudates reduced this efficiency to as low as 6%, while coral exudates may in fact be more efficiently metabolized, at efficiencies exceeding 18% (Nelson et al. 2013). Because bacterial growth efficiency is such an important control over trophic transfer potential of DOM (del Giorgio & Cole 1998), developing a clearer understanding of how different DOM sources and reef microbial communities interact to regulate this parameter is a priority for understanding food webs in reefs.

2.2.3. Biomass and grazing rates of bacterioplankton are a key link in reef recycling. The amount of microbial biomass is a fundamental control on microbe–DOM interaction rates. Atoll lagoon systems tend to exhibit some of the highest microbial biomass of coral reef ecosystems worldwide, and this is likely due to longer residence times and concomitant accumulation of organic matter (Tanaka & Nakajima 2018, Torréton & Dufour 1996). By contrast, observations have demonstrated that rapidly flushing reefs have lower microbial biomass, sometimes even lower than that of the open ocean (Gast et al. 1998, Moriarty 1979, Nelson et al. 2011, Tanaka & Nakajima 2018), which is consistent with rapid grazing by benthic suspension feeders (such as coral; e.g., McNally et al. 2017) or planktonic micrograzers (i.e., the picoplankton loop; Legendre et al. 1988). Reefs are hotbeds of suspension and filter feeders, from annelids to arthropods, from ciliates to coelenterates, and from cnidarians to nematocerans (Nicol 1979), all of which likely graze on planktonic and/or biofilm-associated microbial communities (Bak et al. 1998). Organic subsidies, in the form of small particles (<5 µm), represent a significant contribution to nutrient budgets on reefs (Wyatt et al. 2010, 2013). The relationships among these organic particulates, the benthic community, and microbes govern the enhanced nutrient availability measured on coral reef platforms compared with that of the surrounding ocean water. Corals and other suspension- and filter-feeding organisms withdraw significant concentrations of plankton and DOM from the surrounding water that bathes them (Ayukai 1995, Bak et al. 1998, Ferrier-Pagès & Gattuso 1998, Gast et al. 1998, Houlbrèque & Ferrier-Pagès 2009, Sorokin 1995). The degree to which grazing is targeted or selective may place benthic organismal grazing as a significant factor structuring reef bacterial communities and turnover of microbial biomass. Observations globally have demonstrated increased bacterial concentrations (Haas et al. 2016) and biomass (McDole et al. 2012) on degraded and algae-dominated reefs, further suggesting that reduced benthic suspension feeding plays a role in controlling bacterial abundance. The grazing rates of microbes in coral reef habitats require further exploration, and although there is considerable evidence that corals actively consume bacteria (e.g., McNally et al. 2017), these grazing rates need to be further resolved in other benthic organisms to develop more holistic reef ecosystem energetic budgets.

2.3. Microbe–Dissolved Organic Matter Interactions Facilitate Reef Metabolic Balance and Low Detrital Accumulation

Despite their relatively high gross photosynthetic production, coral reefs exhibit remarkably low detrital accumulation and a net ecosystem production near zero, with accordingly high measured and derived rates of decomposition (Cebrian 2002). Trophic structure in coral reefs varies widely (Heenan et al. 2020) but can support inverted trophic pyramids at remote islands devoid of human exploitation (DeMartini et al. 2008, Sandin et al. 2008). This large biomass of primary and secondary consumers generates significant quantities of organic-rich waste as DOM. While much attention has been paid to the direct fertilization of corals and algae by inorganic nutrients released as waste (Shantz et al. 2015), microbial remineralization or microbial loop recycling of organic matter may have just as much impact on overall reef nutrient budgets. In support of this idea, there is isotopic evidence that detrital material, potentially cycled through microbes, supports significant consumer biomass in reefs (Zgliczynski et al. 2019). As bacterial growth efficiency is thought to be inversely related to nutrient limitation (del Giorgio & Cole 1998), the microbial metabolism of photosynthates and animal waste products is likely a highly efficient trophic transfer via the microbial loop that deserves significant research attention as a mechanism for nutrient retention in higher trophic levels in reefs. These dissolved consumer waste products do not aggregate and accumulate as litter in part due to rapid microbial decomposition and internal recycling processes, representing an underappreciated source of energy and nutrients on coral reefs.

Decomposition of litter by benthic filter- and suspension-feeding invertebrates is another key process whereby microbial interactions with DOM may play a key role in facilitating reduced litter accumulation rates and net metabolic balance in reefs. One of the reef habitats with the highest areal productivity is sand flats (Suzumura et al. 2002), a ubiquitous feature of coral reefs that would be promptly covered were any litter accumulation to occur. The high production rates in sands are driven by high surface areas colonized by microbial biofilms (Wild et al. 2006), growing primarily on DOM released by microphytobenthos. But diatom and biofilm production is associated with high concentrations of interstitial DOM, and reef sands tend to have high redox gradients with anoxic sediments within millimeters where organic remineralization slows (Alongi et al. 2007). Bioturbation and digestion by various invertebrate scavengers ensure that the sand does not accumulate decomposing organic matter, limiting the successional stagnation of the biofilms (Williamson et al. 2021). Biofilm structure and function in reefs are driven largely by the composition of benthic exudates released locally (Remple et al. 2021) and in this way may link the benthic producers and invertebrate consumers through the structure and function of sand biofilm communities.

2.4. Reef Accretion Is Influenced by Microbial Interactions with Dissolved Organic Matter

The three-dimensional complexity of reefs is important for maintaining niche diversity and species richness (Newman et al. 2015) and is structured largely by accretion processes. Calcification rates on reefs are influenced by rates of primary production, coral heterotrophy, and local environmental conditions, including alkalinity, pH, and aragonite saturation (Andersson & Gledhill 2013, Courtney et al. 2017). However, microbial interactions with DOM can influence net ecosystem calcification through both direct and indirect processes. These processes include fueling direct

Resilience: the potential for an ecosystem to maintain nutrient cycling and biomass production after a disturbance, through either resistance or recovery

microbial calcification, driving remineralization of compounds that influence local alkalinity and concentrations of carbonate ions for calcifiers, and fueling coral growth.

The most obvious positive influence of microbe–DOM interactions on calcification is indirect stimulation of coral holobiont calcification by heterotrophic feeding on reef-produced microbes (Ferrier-Pagès et al. 2003). There are also two significant mechanisms for direct microbial calcification driven by organic matter metabolism. The first, known as microbially induced calcite precipitation, is facilitated by extracellular polymeric matrices and occurs widely through heterotrophic metabolism but can also be carried out by cyanobacteria (Seifan & Berenjian 2019). The second, perhaps more relevant to coral reefs, is the symbiolite formations produced by associations between free-living Symbiodiniaceae dinoflagellates and various biofilm-producing bacterial taxa (Nitschke et al. 2020).

Processes that dampen net accretion, induced by the effects of aerobic microbial respiration on the reef carbonate system, include metabolic dissolution (Eyre et al. 2014). Ecosystem-scale metabolic dissolution requires a negative net ecosystem production driven by an imbalance in organic matter supply. While this process is a fundamental control on the long-term accretion of reefs and net ecosystem calcification, the efficiency of microbial remineralization of DOM regulates rates of carbon dioxide release and oxygen consumption, both of which control dissolution. For example, increased algal and coral DOM production stimulated by one month of chronic low-level inorganic nutrient enrichment (Quinlan et al. 2018) was associated with precipitous declines in net community calcification (Silbiger et al. 2018), posited to be driven in part by increased metabolic dissolution (Andersson 2015, Eyre et al. 2014). Thus, microbial remineralization of DOM plays a central role in the fate of reefs, as coastal eutrophication and ocean acidification enhance these dissolution processes (Andersson 2015).

3. MICROBIAL COMMUNITY SEASCAPES ON CORAL REEFS

Most coral reefs occupy shallow habitats, in many cases rising from depths along the flanks of subsiding islands. This results in stark spatial transitions between oceanic and coastal ecosystems. The rapid change in nutrient and DOM sources from the relatively homogeneous tropical surface ocean to a complex habitat comprising benthic primary producers, terrestrial runoff, and groundwater sources causes reef waters to exhibit a unique biogeochemical signature. These biogeochemical influences enrich distinct microbial taxa in reefs relative to the ocean, a pattern demonstrated in reefs across the globe (Frade et al. 2020, McCliment et al. 2012, Nelson et al. 2011, Weber et al. 2020b). Additionally, inputs of microbes from land sources (e.g., streams, runoff, and groundwater) and from the microbiomes of the diverse fauna that make up the benthic community further influence microbial signatures in reef environments (Quinlan et al. 2019, Remple et al. 2021, Wilkins et al. 2019).

Characterizing the microbial ecology and biogeochemistry of different reef habitats is important for understanding the role of microbe–DOM interactions in coral reef ecosystem function and ecosystem resilience to stressors. There are many different coral reef types and subhabitats, often defined largely by flow dynamics, terrigenous inputs, and the lithology of the benthos on which they accrete, and indeed, residence time and flow dynamics further structure coral reef habitats (Lowe & Falter 2015). The spatial complexity of reefs at various scales enhances microbial gamma diversity in reefs relative to that of the oceanic waters that bathe them (Frade et al. 2020, Glasl et al. 2019, McCliment et al. 2012); possible mechanisms include complex microscale boundary dynamics, reef matrix and sand habitats with large surface areas, local habitat patchiness, and regional habitat differentiation among reef types. In this section, we explore the dynamics and differentiation of microbes and DOM in coral reefs and discuss what is known about the factors that support the unique microbiology of these ecosystems.

Several studies have clearly shown that microbial communities in coastal waters are distinct from those in the open ocean, particularly with respect to the dramatic shift in the dominant picocyanobacterial taxon, from *Prochlorococcus* offshore to *Synechococcus* nearshore (James et al. 2020, McCliment et al. 2012, Nelson et al. 2011, Wear et al. 2018). Broad surveys have defined some microbial groups that are enriched on reefs relative to the ocean. **Table 1** links paired coral reef benthos–water column survey data from 54 coral reef sites throughout 22 islands across the insular North Pacific to compiled literature data comparing reef-associated microbial taxa with those of the associated oceanic regime, resolving broad taxonomic groupings that are consistently enriched on reefs in the Great Barrier Reef (Frade et al. 2020, Tout et al. 2014), the Caribbean (Weber & Apprill 2020; Weber et al. 2019, 2020b), and the Pacific (Apprill et al. 2021, Nelson et al. 2013, Wegley Kelly et al. 2014). Offshore oceanic communities are dominated by Cyanobiaceae (*Prochlorococcus* and *Synechococcus*), the Gammaproteobacteria SAR86, Actinomarinaceae, and the Alphaproteobacteria families Pelagibacteraceae (SAR11) and Puniceispirillaceae (SAR116), while nearshore communities are enriched with Rhodobacteraceae, Sphingomonadaceae, Flavobacteriaceae, and Alteromonadaceae; these groups and others highlighted in **Table 1** are candidates for further exploration of the types of organisms that may play central roles in the function of reef ecosystems.

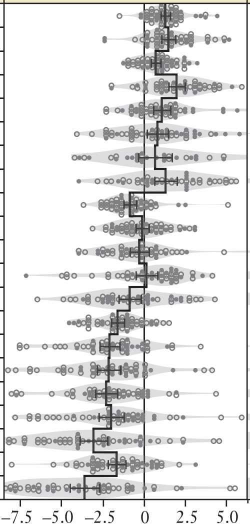
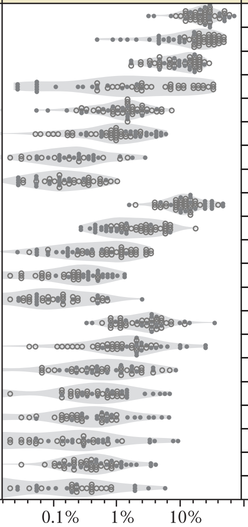
Coral reefs appear to further partition distinct microbial communities, with evidence of strong gradients in overall community structure and specific taxa within and among reef habitats (Frade et al. 2020, Glasl et al. 2019, McCliment et al. 2012, Nelson et al. 2011, Weber et al. 2020b). Because reefs reduce wave energy and shear while increasing rugosity and boundary turbulence, their physical complexity can significantly extend residence time and thus the magnitude and duration of interactions between water and benthos. Preliminary evidence suggests that the degree of differentiation between reef and ocean microbiomes is a function of reef flushing rate. Reefs also vastly increase the surface area of the benthos (Richter et al. 2001) and with that the potential for interactions.

Benthic community composition clearly plays a role in the taxonomic structure of reef-associated bacterial communities (Dinsdale et al. 2008; Haas et al. 2016; Wegley Kelly et al. 2012, 2014), with differences between coral-dominated and algal-dominated reefs equal to or greater than the differences between reef and offshore communities. Recent work on the "coral ecosphere" (Weber et al. 2019) and organismal "aurabiomes" (Walsh et al. 2017) in reef ecosystems indicates a significant organismal influence on microbial communities immediately surrounding different reef taxa (Tout et al. 2014, Wegley Kelly et al. 2014). Other recent studies have demonstrated the highly specific microbiomes of different coral reef taxa and microhabitats (e.g., Glasl et al. 2019), and these are likely a significant influence on the characteristic microbial denizens of reef waters. Coral reef biofilm communities are consistently distinct from the surrounding plankton even when both shift in response to changes in dominant benthic organisms (Remple et al. 2021), but both are dominated by the same reef-associated taxa identified in **Table 1**. Finally, recent work demonstrates the potential for significant and predictable diel shifts in community structure that may be tied to the diel dynamism of the benthic habitat (Weber & Apprill 2020, Wegley Kelly et al. 2019). Taken together, the evidence is clear that reefs embody considerable small-scale spatial and temporal heterogeneity in microbial community composition that is tied at least in part to the structure and function of the benthos.

3.1. Microbial Communities Transform and Recycle Benthic Production in Reefs

Exudates from reef benthic primary producers that are bioavailable selectively enrich different reef microbial taxa (McNally et al. 2017, Nelson et al. 2013, Quinlan et al. 2019). Benthic

Table 1 Bacterial families associated with coral reef habitats

Phylum/class	Family	log$_2$(benthos:water)	Benthos relative abundance	Mean relative abundance		Benthos: water	Habitat localization	Experimental enrichment	Regions and references
				Benthos	Water				
Alphaproteobacteria	Rhodobacteraceae			15.58%	6.60%	**2.36**	Mixed boundary	Algae exudates	GBR, CRB, PAC
Alphaproteobacteria	Sphingomonadaceae			9.42%	3.42%	**2.75**	Coral boundary	Coral exudates	CRB, PAC
Bacteroidetes	Flavobacteriaceae			6.76%	4.28%	**1.58**	Algae boundary	Algae exudates	GBR, PAC
Gammaproteobacteria	Moraxellaceae			1.08%	0.30%	**3.58**	Mixed boundary		CRB, PAC
Alphaproteobacteria	Hyphomonadaceae			0.85%	0.35%	**2.47**	Coral boundary	Coral exudates	PAC
Gammaproteobacteria	Methylophagaceae			0.71%	0.42%	**1.70**	Mixed boundary		
Gammaproteobacteria	Vibrionaceae			0.19%	0.12%	**1.59**	Algae boundary	Algae exudates	GBR, CRB, PAC
Alphaproteobacteria	Rhizobiaceae			0.13%	0.05%	**2.67**	Coral boundary		CRB, PAC
Gammaproteobacteria	Alteromonadaceae			9.08%	15.08%	0.60	Algae boundary	Algae exudates	GBR, CRB, PAC
Gammaproteobacteria	Halomonadaceae			1.46%	1.65%	0.89	Mixed boundary		GBR, PAC
Gammaproteobacteria	Marinobacteraceae			0.33%	0.38%	0.86	Unclassified		
Bacteroidetes	Cyclobacteriaceae			0.14%	0.12%	1.19	Unclassified		
Bacteroidetes	Cryomorphaceae			0.09%	0.14%	0.59	Mixed boundary	Algae exudates	GBR, CRB, PAC
Cyanobacteria	Cyanobiaceae			2.20%	7.47%	**0.29**	Reef water	Reef water	GBR, CRB, PAC
Alphaproteobacteria	SAR11 clade I			1.27%	5.40%	**0.24**	Reef water	Reef water	GBR, CRB, PAC
Gammaproteobacteria	Pseudoalteromonadaceae			0.50%	1.53%	**0.33**	Reef water	Algae exudates	GBR,CRB, PAC
Alphaproteobacteria	Rhodospirillaceae			0.29%	1.43%	**0.20**	Reef water		
Alphaproteobacteria	SAR11 clade II			0.29%	1.14%	**0.26**	Reef water	Reef water	PAC
Gammaproteobacteria	SAR86			0.15%	1.17%	**0.13**	Reef water		
Actinobacteria	Actinomarinaceae			0.33%	1.09%	**0.30**	Reef water	Reef water	PAC
Alphaproteobacteria	SAR116 clade			0.09%	1.03%	**0.09**	Reef water	Reef water	PAC

This list of families comprises those found in more than 95% of paired coincident reef benthic and water column samples in a survey of 54 sites on 22 islands throughout the North Pacific during two cruises, one in the Hawaiian Archipelago in 2016 (*open circles*) and one in the eastern and central Pacific in 2017 (*closed circles*). The mean relative abundances of each family are listed for the reef benthos and reef water column, along with the mean log$_2$ ratio of benthos:water for each family; benthos:water ratios for families that were statistically enriched ($p < 0.05$) in either habitat are in boldface. The black line passes through the mean, with whiskers showing the 95% confidence intervals. The three right-hand columns review studies that have reported reef benthic and water measurements for each family in different regions, where applicable: GBR, Great Barrier Reef (Frade et al. 2020, Tout et al. 2014); CRB, Caribbean (Weber & Apprill 2020; Weber et al. 2019, 2020b); PAC, Pacific (Apprill et al. 2021, Nelson et al. 2013, Wegley Kelly et al. 2014).

producers in reefs exude a significant fraction of photosynthate as DOM, and the rates of release have been the subject of several recent reviews (Brocke et al. 2015, Silveira et al. 2017, Tanaka & Nakajima 2018). Planktonic primary producers in reefs, including the abundant tropical coastal cyanobacterial clade *Synechococcus* and larger eukaryotic photosynthetic picoplankton, produce a significant quantity of DOM, of which a portion is labile (Nelson & Carlson 2012) and may be largely recycled within the planktonic ecosystem (Haas et al. 2013). The lability of all of these different sources of DOM is dictated primarily by the interactions among DOM composition, the metabolic potential of the microbial community, and the availability of macro- and micronutrient resources necessary for microbial metabolism. Experimental measurements have shown that coral exudates foster the growth of more oligotrophic taxa generally associated with slower growth rates, higher growth efficiencies, and more diverse cell and genome sizes (Nelson et al. 2013), while algal exudates are associated with copiotrophic lifestyles, including rapid growth rates, low growth efficiencies, and generally larger cell and genome sizes (Lauro et al. 2009, Machado et al. 2021, Yooseph et al. 2010). There is some evidence that coral exudates select for more efficient bacterial community production (Nelson et al. 2013), possibly through higher nutrient content and/or more oxidized compounds (Wegley Kelly et al. 2022). Chronic nutrient enrichment significantly alters reef biofilm and planktonic community structure but is a secondary factor relative to benthic community composition in both experimental (Remple et al. 2021) and field settings (Wegley Kelly et al. 2012). There is a need for more work to explore how nutrient enrichment and DOM composition interact to influence DOM remineralization and metabolism by microbes in reefs.

3.2. Reef Microbial Diversity Maintains Nutrient Recycling Pathways Critical for Persistence

For two centuries, scientists have sought to explain how coral reef communities achieve such high productivity in nutrient-poor water. Early biogeochemical studies of reef ecosystems observed that the uptake of nutrients was lower across the reef flat than anticipated and that many reef communities actually exhibited a net release of nitrogen (D'Elia & Wiebe 1990) and/or phosphorus (Andrews & Müller 1983, D'Elia 1977). The explanation of this paradox is the basis for the widely accepted conceptualization of tight nutrient recycling and trophic efficiency on reefs (Odum & Odum 1955). Further studies explored the importance of external nutrient inputs such as terrestrial runoff and groundwater, internal waves, and upwelling, but investigations of uptake rates and nutrient fluxes were still lacking. In addition, none of the external sources listed above could adequately balance the high productivity or sustain the large food webs observed on reefs (Furnas et al. 1995). Moreover, reefs have extraordinarily low levels of litter accumulation and median net primary productivities approaching zero (Crossland et al. 1991), implying that all nutrient requirements must be supported by nutrient scavenging from seawater fluxes, nitrogen fixation, and internal recycling of organic matter (Tribble et al. 1994). This section summarizes evidence that the nutrient composition of exudates and the dynamics of remineralization are central to the persistence of coral reefs in oligotrophic waters and help explain Darwin's paradox.

3.2.1. Nutrient (re)cycling on coral reefs is facilitated by diverse microbe–dissolved organic matter interactions. Recent research has shown that organic exudates released from reef producers are enriched in nitrogen and phosphorus macronutrients, suggesting that a key component of reef food webs would be microbial transformation and remineralization of these large DOM pools (Wegley Kelly et al. 2022). DOM released by coral reef benthic primary producers can be high in limiting macronutrients such as nitrogen (C:N ratios of 10–15:1 in corals and 20–40:1 in algae); corals in particular exhibit high nitrogen and phosphorus content in DOM (D'Elia 1977,

Coral bleaching: the predictable dissociation of hermatypic corals and their dinoflagellate endosymbionts triggered by stress, particularly elevated temperatures

Wegley Kelly et al. 2022), which is consistent with previous findings from coral mucus (Nakajima et al. 2015, Wild et al. 2004a) and suggests that this may be a common feature of corals. The rates of nitrogen and phosphorus remineralization by microbial metabolism of this DOM released by primary producers couple the production and nutrient recycling processes. Local uptake of microbially remineralized nitrogen and phosphorus by primary producers can be rapid and important for the growth of both corals and algae in reefs, as evidenced by work showing enhancement of both growth and nitrogen content of corals housing fish relative to those without fish (Shantz et al. 2015) and by recent evidence that DOM released from coral bleaching fueled local algal nitrogen uptake (Vaughan et al. 2021). The strong diel dynamics of coral reefs, with corals and coralline algae carrying out both calcification and photosynthesis during the day (Smith et al. 2013) but DOM exudation occurring both during the day and at night (Mueller et al. 2014, 2016; Wegley Kelly et al. 2022), suggests that there may be a diel component to nutrient availability from exudate remineralization that further synchronizes and tightens interaction networks on reefs.

The metabolic potential for specific nutrient transformation pathways varies among microbial taxa such that the interaction between DOM composition and microbial community structure drives both DOM metabolism and selective enrichment of microbial taxa (Nelson & Wear 2014). Microbial community structure in open ocean waters changes significantly as it moves onto the reef platform (Leichter et al. 2013, McCliment et al. 2012, Nelson et al. 2011). Benthic community cover sets the taxonomic structure template of the reef microbial community, at least partially through influence on DOM composition, and these microbial populations tune their metabolic range by adapting to local nutrient conditions (Wegley Kelly et al. 2014). Following this logic, DOM stoichiometry and molecular structure can influence the prevalence of many metabolic processes, such as nitrogen fixation and denitrification, by influencing when and where nutrient limitation or low-oxygen conditions occur and whether the community genetic potential is present to execute specific nutrient pathways (e.g., Babbin et al. 2021). In sum, there is strong evidence supporting the idea that benthic organisms control microbial transformations of nutrients through selective adaptations that dictate the composition and lability of their organic exudates (Nelson et al. 2013, Wegley Kelly et al. 2019). Thus, the timing, magnitude, and composition of exudates released by coral reef producers select for microbial populations that contribute to nutrient recycling and availability in reef systems.

3.2.2. Microbial nutrient transformations are a fundamental reef function. Microbes are master manipulators of nutrient availability in the sea, promoting release through mineralization of organic matter (Azam et al. 1983), hydrolytic ectoenzyme activity (Arnosti 2011), and viral lysis (Breitbart 2012). Microbes also facilitate the exchange of nutrients among different community members through chemical transformations as part of their diverse metabolic repertoire (Atkinson 2011, Falkowski et al. 2008). The role of DOM in controlling the composition of microbial communities may be a key part of nutrient retention and recycling, ultimately controlling the persistence of reefs. Consistent patterns of reef-associated microbial taxa have emerged, including a set that are significantly enriched in reef habitats across the Pacific (Rhodobacteraceae, Sphingomonadaceae, Flavobacteriaceae, Moraxellaceae, Hyphomonadaceae, Methylophagaceae, Vibrionaceae, and Rhizobiaceae; **Table 1**) and additional taxa that are consistently associated with reefs worldwide (Alteromonadaceae, Halomonadaceae, and Cryomorphaceae; e.g., Apprill et al. 2021, Frade et al. 2020, Weber et al. 2019, Wegley Kelly et al. 2014; **Table 1**). Many of these taxa likely play key roles in microbially mediated nutrient transformations.

Transformations of nitrogen in reefs are driven largely by microbial processes, and many of the abundant reef-associated bacteria listed above have been associated with nitrogen cycling. Rhodobacteraceae, including *Roseobacter* lineages, have a wide metabolic repertoire (Buchan et al.

2005, Wagner-Döbler & Biebl 2006) and are capable of both nitrogen fixation and denitrification. Members of the family Rhizobiaceae are well known in terrestrial environments for their symbiotic roles in nitrogen fixation, but this function is not well established in marine habitats. Nitrogen fixation is a key microbial process that elevates reef nitrogen concentrations and promotes reef primary production (Cardini et al. 2014, 2015; Charpy-Roubaud et al. 1990; Wiebe et al. 1975), and the availability of labile organic matter influences the rate and timing of nitrogen fixation (Pogoreutz et al. 2017). Corals and other marine animals excrete ammonium as waste, which can serve as mineral nutrient enrichment for algae and microbes or fuel microbial nitrification (Rädecker et al. 2015), a chemoautotrophic process on reefs that has had limited investigation but likely represents an underappreciated source of nitrate (Webb & Wiebe 2011). Nitrogen loss is facilitated by suboxic denitrification, where microbial taxa use oxidized nitrogen (nitrite and nitrate) as an alternate electron acceptor in organic matter oxidative decomposition. On reefs, this process occurs when and where reduced oxygen concentrations coincide with DOM availability, such as the nighttime boundaries of corals and algae (Shashar et al. 1993). The waters transiting across reef communities show little to no change in phosphate (D'Elia 1977, Falter et al. 2004), and there is ample evidence to suggest that this nutrient is rapidly cycled and retained by most microorganisms (Atkinson 2011, Falter et al. 2004, Nakajima et al. 2015, Suzumura et al. 2002).

The cycling of sulfur compounds is driven by microbes, transforming inorganic sulfur into organic compounds such as the sulfur-containing amino acids cysteine and methionine, coenzymes, and bridging ligands (Sievert et al. 2007). Coral holobionts elicit active and diverse microbial sulfur cycling driven fundamentally by the production of dimethylsulfoniopropionate (DMSP) (Raina et al. 2009) by the cnidarians and their endosymbiotic Symbiodiniaceae dinoflagellates. Other coral reef organisms, such as corals and clams, produce organic sulfur analogs by similar mechanisms (Guibert et al. 2020). Several of the consistently enriched reef water column taxa are known to be capable of breaking down DMSP or the breakdown products dimethyl sulfide (DMS) and acrylic acid (*Roseobacter*, *Vibrio*, *Alteromonas*, and *Halomonas*) (Raina et al. 2009, Seymour et al. 2010). Transformation of these organic sulfur exudates by reef microbial communities may have significant impacts on a variety of biogeochemical processes in reefs, including oxidative stress and chemoattraction (Garren et al. 2014, Seymour et al. 2010, Tout et al. 2015).

Beyond inorganic nutrients, *Halomonas* and *Roseobacter* are also known synthesizers of B vitamins, which play significant roles in syntrophy with marine autotrophs (Sañudo-Wilhelmy et al. 2014). Specific metabolic functions, such as motility, cell signaling, and chemotaxis, are also more prevalent in microbial metagenomes from reef water (Tout et al. 2015). Diel dynamics of community genomic potential in reefs synchronized across hundreds of miles demonstrated nighttime enrichment in motility, carbohydrate and aromatic metabolisms, and daytime enrichment of nucleic acid and enzyme cofactor metabolisms (Wegley Kelly et al. 2019). To achieve a mechanistic understanding of these complex habitats, it is paramount that biologists appreciate the diverse linkages among organisms that influence different aspects of reef ecology, from symbiosis to signaling to gross productivity.

3.3. Microbe Interactions Promote Biodiversity in Coral Reefs

Coral reefs are perhaps most appreciated for their high biodiversity (Knowlton 2001), and the dynamism of reefs at short and long scales of time and space is arguably one intrinsic driver of this diversity (Connell 1978). Hatcher (1997) declared the maintenance of biodiversity in reefs to be a fundamental ecosystem process, one that is attributable to the established complex interactions between carbon storage and nutrient recycling that ultimately influence species diversity and ecosystem function (Worm et al. 2002). In coral reef habitats, we predict that species mutualisms and metabolic exchange of resources are paramount to this maintenance, and both are tied to the

Microbialization: an increase in the proportion of biomass and energy use in an ecosystem allocated to single-celled microbial organisms

Deoxygenation: the depletion of oxygen in aquatic habitats through a variety of mechanisms both directly and indirectly related to human activities

interactions between microbes and DOM that facilitate connectivity among coral reef organisms. There are several excellent reviews of organismal interactions that describe how metabolic exchanges can enhance or stabilize diversity in marine systems (Apprill 2020, Cavalcanti et al. 2020, Lesser et al. 2018, Vanwonterghem & Webster 2020, Wegley Kelly et al. 2021). The physical complexity of reefs influences these processes as well; for example, cell signaling and chemotaxis are important mechanisms for the recruitment and colonization of symbionts. Concentration gradients and boundary hydrodynamics (Davis et al. 2021) can regulate niche heterogeneity and facilitate species diversity. Moreover, many interactions are directly microbially mediated through metabolite transformations or signaled by microbial metabolism, including localized hypoxia or detection of microbial waste products (Garren et al. 2014, Tout et al. 2015). The ubiquitous utilization of benthic-derived exudates in both negative (competition, disease toxins, and allelopathy) and positive (settlement cues, signaling pheromones, and symbiotic metabolite exchange) interactions among macroorganisms ensures that microbial processes play an active role in reef community ecology (Barott & Rohwer 2012). There is substantial evidence suggesting that microbes mediate the settlement and metamorphosis of coral larvae. Both the spatial variability and species composition of microbial biofilms influence the induction of larval settlement (Webster et al. 2004) via the detection of diffusible signal metabolites produced by microbes. Put simply, microbes dictate the communication and signaling among myriad reef denizens, and though invisible to the human eye, they are instrumental to maintaining diverse life cycles in the visible world.

4. MICROBIALIZATION OF CORAL REEFS DESTABILIZES MICROBE–DISSOLVED ORGANIC MATTER INTERACTIONS

The global occurrence of coral reef degradation manifests in the reduction or complete loss of ecosystem attributes (Hatcher 1997) such as high productivity and biodiversity, rapid decomposition and accretion, and highly diverse and synchronized nutrient recycling—all processes in which microbe–DOM interactions play a key role. The dismantling of ecosystem functions provided by microbe–DOM interactions is a concept we term microbialization (Haas et al. 2016, Jackson et al. 2001, McDole et al. 2012) (**Figure 2**). In this section, we outline how changes in microbe–DOM interactions during microbialization are associated with the breakdown of core ecosystem processes in reefs.

4.1. Microbialization Changes the Source and Fate of Primary Production

The decline of reef builders such as hermatypic coral and coralline algae is typically associated with an increase in fleshy macroalgae and turfing algae (Smith et al. 2016). Fleshy algae have higher DOM release rates per unit surface area, and these substrates tend to select for copiotrophic microbes with higher growth rates and lower metabolic efficiencies (Haas et al. 2011, Nelson et al. 2013) via altered metabolic pathways (Haas et al. 2016). The selective pressure of algal exudation additionally facilitates a transition to larger and more numerous microbes in algae-dominated ecosystems (Dinsdale et al. 2008, Haas et al. 2016, Wegley Kelly et al. 2012), altering community structure (e.g., species diversity and evenness) and shunting energy and organic nutrients away from higher trophic levels. Recent data suggest that fleshy algae release DOM with reduced organic nutrient content and reduced nominal carbon oxidation states, yielding greater free energy (Wegley Kelly et al. 2022), which could contribute to the elevated microbial biomass observed in algae-dominated systems. The increased shunting of remineralized carbon by more abundant and larger microbes fueled by algal DOM also corresponds to greater biological oxygen demand contributing to local microbially driven deoxygenation (Jorissen et al. 2016, Smith et al. 2006).

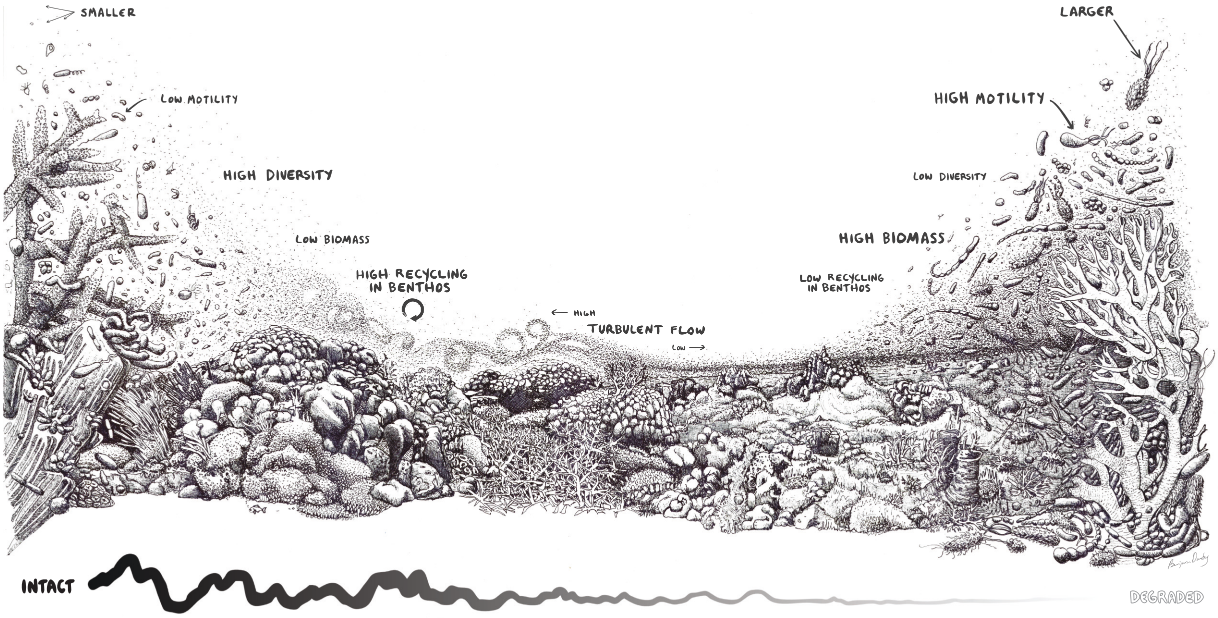


Figure 2

Microbialization processes on coral reefs. Degradation of coral reef habitats is associated with a decline in calcifying corals and coralline algae and a concomitant increase in fleshy algae. Microbial community structure and dynamics shift in concert with changes to DOM dynamics as nutrient-poor and energy-rich algal exudates foster a reduced diversity of larger, motile copiotrophic taxa with increased potential for opportunistic pathogenesis. The reductions in habitat complexity, surface area, and boundary-layer turbulence limit interaction between the benthos and water column, increasing water column microbial concentrations and reducing recycling of microbial biomass by benthic suspension feeders, ultimately limiting the ability of the reef to recycle valuable nutrients from the dissolved pool into higher trophic levels. Abbreviation: DOM, dissolved organic matter. Coral reef drawing by Ben Darby; graphic design by Shayle Matsuda.

The enrichment of copiotrophic microbes at fleshy algae–dominated reef sites is exacerbated by the reduced cover of suspension-feeding invertebrates, which can result in elevated microbial biomass by an order of magnitude compared with coral-dominated reefs (Brainard et al. 2019, Haas et al. 2016). Reefs undergoing microbialization exhibit a shift in the rates of decomposition, characterized by increased detrital accumulation and elevated phytoplankton biomass that decreases light penetration to the benthic community (Mumby & Steneck 2018). These indirect, microbially mediated effects, including selection for microbial taxa with increased virulence genes (Wegley Kelly et al. 2012, Nelson et al. 2013) and more widespread hypoxia, are thought to act as feedback loops working against recolonization by corals and ultimately maintaining reefs in an algae-dominated state (Barott & Rohwer 2012).

Phase shift: the reconfiguration of ecosystem composition and dynamics following disturbance; a shift from coral to algal dominance is widespread in tropical reefs

4.2. Microbialization Disrupts Highly Synchronized Nutrient Biogeochemical Cycles

The majority of bioavailable macronutrients are organically bound in coral reef systems; therefore, the efficient transfer of organic macronutrients through trophic food webs is thought to be crucial to maintaining reef productivity and biodiversity (Atkinson 2011, Tribble et al. 1994). During phase shifts, a more homogeneous DOM pool sourced from a lower diversity of benthic producers may facilitate reduced diversity in the microbial community, as has already been observed in experimental comparisons of microbial diversity on coral versus algal exudates (Nelson et al. 2013).

The community dominance by copiotrophs with larger genomes and less auxotrophic lifestyles diminishes syntrophy between organisms and fundamentally reduces macronutrient transformation pathways (Machado et al. 2021). Once reef builders and suspension feeders are reduced below some theoretical threshold, the benthic–pelagic coupling processes that govern syntrophic interactions, diel synchronization between organisms, diverse nutrient transformations, and the immense biomineralization essential to sustain these ecosystems are lost. Ultimately, the inefficient trophic transfer of abundant DOM fluxes from reef organisms translates to a breakdown in the transfer of nutrients to higher trophic levels, reducing the ability of the reef to support consumer-rich or top-heavy ecosystems (McDole et al. 2012, Sandin et al. 2008).

4.3. Microbialization Reduces the Diversity of Coral Reefs

Reef degradation reinforces biological interactions that cause further mortality of reef-building corals, particularly enhancing coral mortality and decreasing settlement and recruitment. Coral disease prevalence is higher in algae-dominated states, even though coral densities are lower (Sandin et al. 2008, Sweet et al. 2013). This likely can be attributed to the higher standing stocks of microbial cells and a community structure dominated by clades of Gammaproteobacteria and Bacteroidetes that are known opportunistic pathogens (Haas et al. 2016, Nelson et al. 2013). The increased prevalence of disease on degraded reefs may be as simple as surpassing the infectious dose required to cause infection; as water masses become stratified, corals may be subjected to a higher concentration of cells within their diffusive boundaries, providing more opportunity for attachment, invasion, and infection. Regardless, any additional loss of hermatypic corals only feeds back into further microbialization through loss of key coral reef functions (Nyström et al. 2012). These missing functions include suppression of microbial activity through direct consumption, selection for diverse communities of resource-facilitating microbes through exudation, and the creation of habitat complexity that governs water movement and material exchange.

Microbialization reduces processes maintaining macroorganismal diversity on reefs, including settlement opportunities and recruitment cues necessary for invertebrates and vertebrates alike. Algal holobionts preempt space by preventing the settlement of coral larvae and instigating recruitment failure of corals and herbivorous fishes (McCook et al. 2001). Soluble chemicals such as toxic secondary metabolites produced by benthic cyanobacteria are known to deter coral settlement (Kuffner et al. 2006). Loss in rugosity due to degradation of hard substrates is the most influential attribute driving fish richness in Caribbean reefs, where shelter and refuge space are essential for maintaining local fish biodiversity (Alvarez-Filip et al. 2009, Gratwicke & Speight 2005). The abundances of corallivores and planktivores decline as a direct effect of their preferred corals dying. Additionally, coral mortality causes significant declines in herbivorous fishes attributed to habitat degradation, which leads to greater competition, predation, and ultimately recruitment failure (Graham et al. 2007). Reductions in herbivory foster algal competition, facilitating a feedback that enhances microbialization and ecosystem degradation, termed the rise of slime (Jackson 2008, Pandolfi et al. 2005).

4.4. Reef Transitions, Deoxygenation, and the Rise of Slime

In this section, we illustrate one way in which the degradation of reef habitats erodes ecosystem functions by disrupting microbial interactions with benthic organic matter sources. One key aspect of the loss of coral and calcifying algal cover in coral reef degradation is a reduction in reef rugosity, which directly impacts turbulent flow dynamics and the extent and duration of hypoxia, a phenomenon known as reef deoxygenation (**Figure 3**). Despite its global prevalence, reduced availability of oxygen (hypoxia or anoxia and the associated phenomenon of dead zones) has only

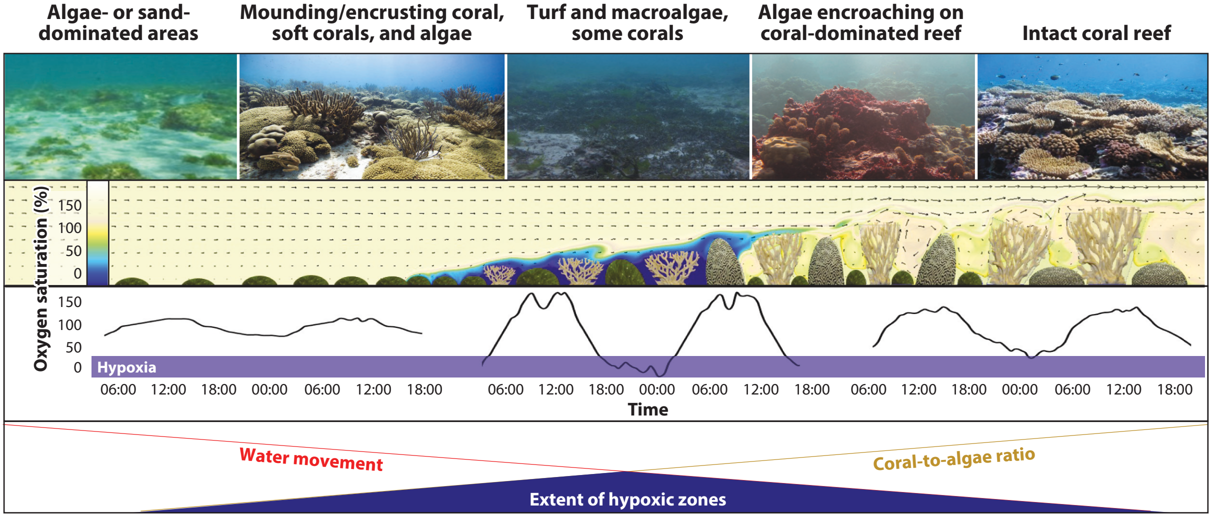


Figure 3

Conceptualized effects of shifts in benthic cover, rugosity, and flow on the distribution and temporal extent of hypoxic zones. In the central part of the figure, local oxygen minimum zones are shown in blue, and arrows indicate the water movement. Biogenic local hypoxic zones have severe impacts on corals and promote a feedback loop during phase shifts toward algae-dominated systems. Algae-derived organic matter fosters a higher microbial oxygen consumption rate. When combined with the direct effects of algal metabolism on oxygen availability, this higher oxygen consumption enhances the diurnal variability of oxygen concentrations with steeper gradients. The extended durations of nighttime hypoxia ultimately suffocate corals, which are rapidly overgrown by more algae. This algae-induced, microbially mediated local hypoxia in coral–algae interactions is one of the main causes of coral death. The severity of its impacts is determined by fluid dynamics and propagates more effectively across reef regions subject to weak ocean flows. Decreased rugosity due to loss of reef framework may decrease water residence time in boundary layers and dampen the effect of local hypoxia and microbialization.

recently been recognized as an imminent threat to coral reefs (Altieri et al. 2017, Hughes et al. 2020, Johnson et al. 2021). Deoxygenation events represent one type of microbial feedback system where localized hypoxia extends across reef surfaces, and these conditions favor noncalcifying organisms that are more tolerant of prolonged oxygen depletion (Haas et al. 2014). This shift is aided by positive feedbacks whereby increased algal biomass releases more labile organic carbon that fosters a copiotrophic microbial community with high biological oxygen demand, resulting in suffocation of corals and thus paving the way for further increases in algal cover.

The community structure of marine benthic assemblages is strongly driven by dissolved oxygen concentrations (Nelson & Altieri 2019). In scleractinian corals, moderate levels of microspatial oxygen fluctuations can enhance structural complexity and reef rugosity: Short-term oxygen depletions induce anaerobic metabolisms within the coral holobiont that stimulate rates of skeletal extension, accelerating upward growth (Wooldridge 2013). Different organisms within the reef system exhibit a variable range of sensitivity to deoxygenation, which can be attributed to the selection of divergent life strategies and the extensive niche space. This habitat diversity is what allows branching coral morphologies to accelerate vertical growth in calmer waters with more pronounced stratification. Beyond the growth patterns of individual species, the concentration of dissolved oxygen can control the appearance of entire ecosystems. For instance, within coral lagoons, faster and more vertically growing colonies thrive at the edges, whereas within the center of lagoons, water is rapidly depleted of oxygen, hindering new coral growth and further reinforcing morphotype divisions (Altieri et al. 2017).

Boundary layer: a zone of variable thickness formed where drag forces reduce flow velocity as a liquid passes across a solid surface

The biggest factor in determining the extent of hypoxic zones is the physical supply of oxygenated water. This supply is determined by fluid dynamics and affects multiple ecological parameters in every marine ecosystem at any spatial scale. Sessile coral reef organisms with limited or no mobility depend on water motion for their basic functions, such as food supply and waste removal (Reidenbach et al. 2006). Large-scale circulation patterns determine rates of dispersal across the reef (Hamner & Wolanski 1988), while microscale turbulence influences the mass transfer of materials on the scale of individual coral polyps (Price 1999). Complex reef topologies enhance turbulent boundary conditions, exhibiting microscale oxygen heterogeneity temporally and spatially, and prevent long-term reef-scale anoxia (Jorissen et al. 2016, Nelson & Altieri 2019, Werner et al. 2006): As reefs flatten during microbialization, pockets of extended anoxia may increase in spatial and temporal extent, decreasing rates of nighttime calcification (Wijgerde et al. 2014).

Flow conditions become increasingly more complicated when water approaches a boundary (e.g., a reef framework or coral surface). Water molecules directly next to a boundary stick to the surface rather than slip by it, creating a velocity gradient known as the boundary layer. The extent of these boundary layers determines the transfer of molecules between the water column and benthic organisms and influences the residence time of solutes in the system. The organisms themselves also have significant influences on the flow field surrounding them that differ among species and morphologies (Brown 2012, Jorissen et al. 2016, Shashar et al. 1996). Shifts toward algal dominance, particularly as dense assemblages, may lead to thicker diffusive boundary layers (increasing the magnitude and duration of hypoxia) and higher concentrations of metabolic waste metabolites that can be detrimental. The density of microbes also increases, enriching the abundance of pathogens along coral borders and leading to coral mortality, further exacerbating the positive feedback loops and eventually dissolving reefs into a slimy seafloor (**Figure 2**). In other locations, altered fluid dynamics might provide a second chance for coral reefs to recover. A decrease in benthic rugosity due to reduced calcification and dissolution of the three-dimensional framework may increase the exchange of water in the boundary layers, diminishing the potential for small-scale low-oxygen zones (**Figure 3**). This implies that at a certain point during the loss of three-dimensional structure, more resilient species can—on the brink of dying from hypoxic conditions—survive and may even start growing again, replacing less resilient species.

4.5. Considerations for Managing Microbialization of Coral Reefs

While declining coral and calcifier cover in reefs is an increasingly widespread phenomenon globally associated with human impacts, phase shifts to algal dominance are not a foregone conclusion. Restoration efforts can acknowledge and address the degradation of ecosystem processes associated with microbialization, and approaches such as ecosystem-based management (Harvey et al. 2018; McLeod & Leslie 2012; Weijerman et al. 2016, 2018) and resilience-based management (Mcleod et al. 2019) are advocated to minimize the negative outcomes associated with these trajectories. Advancements in molecular approaches to characterize complex DOM pools (Moran et al. 2016, Petras et al. 2017) and annotate whole genomes assembled from uncultured microbial populations provide new analytical windows to link substrate production and consumption to specific taxa (Vorobev et al. 2018). Deeper knowledge about how organisms interact to exchange metabolites or signal a physiochemical event will be essential to successfully manipulate complex environments for the sake of conservation. Restoration efforts should focus on facilitating processes such as production, accretion, decomposition, and biogeochemical cycling in the service of maintaining biodiversity. Because these are systems-level agendas, restoration efforts that prioritize critical mass manipulations of reef communities, rather than solely fostering the growth of one or more focal species, are likely to have the greatest success. Microbial communities can serve as indicators of reef ecosystem state (Glasl et al. 2019), requiring assessment of baselines to contextualize future dynamics (Glasl et al. 2017), and restoration strategies that specifically consider microbial dynamics will be critical components of a successful management program (Vanwonterghem & Webster 2020). A clearer understanding of the microbial taxa critical to each of the central processes of coral reefs (**Figure 1**; **Table 1**) is a broad research priority for the coming decades in reef ecosystem microbiology (Wegley Kelly et al. 2018) to minimize microbialization (**Figure 2**) and deoxygenation (**Figure 3**) of one of Earth's most treasured ecosystems.

SUMMARY POINTS

1. Benthic primary producers exude diverse types of dissolved organic matter (DOM) that differentially influence the structure and metabolism of reef microbial communities, such that changes in benthic composition are associated with shifts in the sources and microbial processing of DOM.
2. Nutrient recycling by microbe–DOM interactions is crucial for reef persistence, providing a tight remineralization circuit by which nutrients are retained in coral reef food webs.
3. Coral reef microbial communities are a link between DOM and higher trophic levels, recycling DOM exuded by primary producers and consumers, entraining terrestrial and marine allochthonous DOM, and directly transferring carbon into filter- and suspension-feeding benthic and planktonic consumers.
4. Microbe–DOM interactions play a key role in the basic ecology of reef organisms, including chemical communication, interspecific competition, settlement, disease, and spatial structuring.
5. Many of the key system features that allow coral reefs to persist in the oligotrophic ocean are facilitated in part by microbe–DOM interactions (**Figure 1**), including metabolism and transformation of primary production, trophic transfer of DOM back into benthic suspension-feeder communities, nutrient remineralization and transformation, diverse biogeochemical cycles, regulation of metabolic dissolution, and interactions that foster the highly networked niche structure that is the core of high biodiversity in reefs.
6. Relative to the surrounding tropical oceans, coral reefs are biogeochemically and microbiologically distinct (**Table 1**), with characteristic DOM pools, microbial taxa, and microbial community functional potential.
7. Microbialization (**Figure 2**) is associated with a breakdown in the efficiency of trophic transfer of DOM through the microbial loop, a decline in suspension-feeding recycling of microbial organic matter into the benthos, a breakdown of nutrient transformation and recycling mechanisms driven by microbe–DOM interactions, microbially mediated dissolution, an increased duration and extent of microscale hypoxia, and a suite of shifts in crucial positive and negative organismal interactions in which microbial dynamics and the production, transformation, and remineralization of DOM are involved.
8. Microbially mediated local deoxygenation (**Figure 3**) is a key mechanism in coral reef decline that is influenced by the interactions between microbial community types and DOM sources, including differential bacterial growth efficiency on DOM with different redox, nutrient, and energy compositions; flow dynamics and three-dimensional structure; and shifts in the metagenomic potential of microbes driven by local benthic community structure.

FUTURE ISSUES

1. Detailed inventory: What is the natural spatial and temporal variability in healthy reef environments—the chemical and microbial baseline?
2. Host–water integration: How do the ecosystem engineers establish the system microbiome and react toward disturbances?
3. Resistance/resilience: Which molecular and microbial mechanisms stabilize healthy systems and reduce hysteresis effects?
4. Molecular control: Which compounds elicit which microbiome reactions?
5. Global threats: What is the microbial component in the biggest threats to coral reefs (deoxygenation, coral bleaching, and dissolution)?
6. Co-metabolism: How and to what extent do reef organisms metabolize oceanic DOM?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank our mentors—Jennifer Smith, Craig Carlson, Forest Rohwer, and Christian Wild—for introducing us to these remarkable marine ecosystems and enabling us to visit amazing coral reefs during our early career stages. We are grateful to artist Ben Darby for his stunning coral reef illustrations, to Shayle Matsuda for his masterful graphic design skills, and to Heather Maughan for her writing expertise and encouragement. We also thank two anonymous reviewers and Production Editor Jim Duncan for helping us improve the article. This work was supported by US National Science Foundation awards OCE-1949033 and OCE-2023298 to C.E.N. and OCE-2118617 and OCE-2118618 to L.W.K. in collaboration with the Moorea Coral Reef Long-Term Ecological Research project (MCR-LTER; OCE-1637396). Finally, we wish to thank Rusty Brainard and his NOAA Coral Reef Ecosystem Division (CRED) team for including us microbe hunters on the Pacific Reef Assessment and Monitoring Program (RAMP) cruises to survey microbial dynamics at more than 100 reef sites (summarized in **Table 1**).

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Annual Review of
Marine Science

Volume 15, 2023

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Errata

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