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The Coral Holobiont: A Brief Overview of Corals and Their Microbiome[1]

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Coral reefs support 25% of the world's known marine species and create billions of dollars in economic value from fisheries, storm protection, and tourism (Blackall, Wilson, and van Oppen 2015; Velázquez-Ochoa and & Enríquez 2023; Prideaux and Pabel 2018). However, reefs have declined drastically since the 1970s, including the loss of branching corals, by almost 98% in areas like the Florida Keys (Miller, Bourque, and Bohnsack 2002). These declines are caused by repeated stresses such as high ocean temperatures and coral disease (Cramer et al. 2021; Dubinsky and Stambler 2011; AGRRA 2022). Current efforts to restore reefs have low long-term success rates. Researchers strive to improve the growth of stony corals to overcome heat stress and disease (Arias-González et al. 2022; Silliman et al. 2023). The coral microbiome is an important component of stony coral health, nutrition, and disease defense (van Oppen and Blackall 2019; Peixoto, Sweet, et al. 2021; Peixoto, Rosado, et al. 2017). This publication was created to highlight some of the important contributions that microbes make to supporting a healthy coral reef. These microscopic creatures can transform the way scientists and restoration practitioners study corals to improve restoration outcomes.

This publication is intended for coral reef managers, reef restoration practitioners, and other natural resource professionals who are searching for concise information about corals, microbiomes, and how coral microbiology research is advancing our understanding of coral health and restoration.

What are corals?

Corals are marine animals that belong to the phylum **Cnidaria** and share many characteristics with jellyfish and sea anemones (Montano 2020; Henry et al. 2018; Vanwonterghem and Webster 2020). Scleractinian corals, also called stony corals, create a hard calcium carbonate skeleton that grows and contributes to the formation of tropical coral reefs (Montano 2020; Henry et al. 2018). Coral reefs are formed very slowly by the buildup of stony corals over time and are among the most ecologically significant and biologically diverse ecosystems on Earth (Blackall, Wilson, and van Oppen 2015; Sheppard 2017). This is because stony corals are an important **foundational species** and **ecosystem engineer** that supports marine biodiversity by providing habitat and shelter for many other marine animals (Carlson et al. 2024). Corals are typically found in warm, clear, and shallow waters, and they are highly

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vulnerable to environmental stress (Montano 2020; Henry et al. 2018). Stress factors such as ocean warming, eutrophication, hurricanes, sedimentation, pollution, and ocean acidification pose a significant threat to their survival (van Oppen and Blackall 2019; Vanwonterghem and Webster 2020; A. R. Mohamed et al. 2023). If you wish to learn more about the coral anatomy, habitat, and distribution of stony corals in Florida, see EDIS publication #FA210, "A Guide to Common Stony Corals of Florida." This publication will focus on the intricate relationship between corals and their microbiomes and how microbes help corals cope with environmental stress.

What is a microbiome?

A microbiome is defined as a complex community of microorganisms, including bacteria, archaea, viruses, and fungi, that inhabit a specific environment such as the human gut, skin, soil, or air (Shanahan, Ghosh, and O'Toole 2021; Berg et al. 2020). Microbes exist virtually everywhere and provide functions that drive whole ecosystems as well as influence the health of living organisms. For example, some microbes that live in soil turn gaseous nitrogen from the air into usable nitrogen for plants (Chen, Zhu, Zhang 2003). Microbes associated with the human skin can help defend the body against pathogens or even influence the amount of acne a person may have (Egert, Simmering, and Riedel 2017). In humans, the gut microbiome plays a crucial role in maintaining human health and well-being. It aids in digestion, creates vitamins, and regulates the immune system (Shanahan, Ghosh, and O'Toole 2021; Lacruz-Pleguezuelos 2022). An imbalance in the microbiome, known as **dysbiosis**, is associated with conditions that affect the gut and immune system, such as irritable bowel syndrome (IBS) or certain cancers (Bramhachari et al. 2021; Libertucci and Young 2018). A healthy human gut microbiome is increasingly recognized as a key factor in promoting and preserving overall human health. This same concept can be applied to corals, as they also have an associated internal and external microbiome that play important roles in coral health, environmental adaptation, and disease defense.

The Coral Microbiome

The coral microbiome includes microalgal **symbionts**, bacteria, viruses, fungi, and other microorganisms (van Oppen and Blackall 2019; Peixoto, Rosado, et al. 2017; Voolstra et al. 2021). The host coral and its microbiome together make up the **coral holobiont** (Figure 1), with these microorganisms existing throughout different tissues of the coral animal (Figure 1C) (Peixoto, Rosado, et al. 2017; Vanwonterghem and Webster 2020). Each of these microbial groups impacts the coral in various ways that influence the health of the coral and aid in resistance to disease and environmental stress.

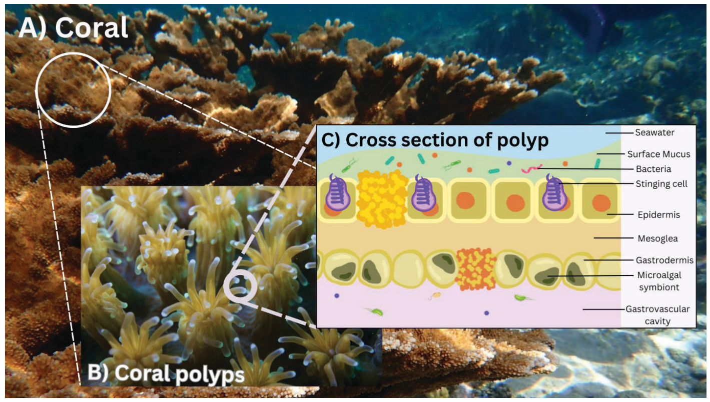

Figure 1. The coral microbiome. An individual coral colony is composed of the coral animal and its microbiome, which is collectively referred to as the coral holobiont. A) Photograph of an Elkhorn coral (Acropora palmata), a large branching Caribbean coral. B) Close-up photograph of the polyps that make up the coral colony. C) Schematic representation of an individual coral polyp showing a cross section of the tentacle with coral microbes, including bacteria and the microalgal symbiont among various tissue layers.
Credits: (A) Rachel D. Howard, University of Florida; (B) Public Domain; and (C) Monica D. Schul, University of Florida

The Microalgal Symbiont

Perhaps the most well-studied relationship between corals and their microbial symbionts is the interaction between corals and their microalgae in the family Symbiodiniaceae. Corals have a mutually beneficial relationship with these tiny, photosynthetic microalgae, whose partnership is essential for the survival of corals (Ceh et al. 2013; Goodson, Whitehead, and Douglas 2021). Corals protect and provide a habitat for Symbiodiniaceae within their gastrodermal cells (Figure 1C), offering them access to sunlight for photosynthesis (Ceh et al. 2013; Goodson, Whitehead, and Douglas 2021). In return, the microalgae produce oxygen and provide corals with energy by producing carbohydrates through photosynthesis (Ceh et al. 2013; Goodson, Whitehead, and Douglass 2021). This partnership not only fuels coral growth but also provides their vibrant colors and protection from harmful UV radiation (Salih et al. 2000). However, corals exist in a delicate balance with these microalgal symbionts. In the presence of environmental stressors, like rising sea temperatures or pollution, corals will expel their microalgal symbionts and appear lighter or stark white in color (AGRRA 2022; Buerger et al. 2020). This event is called **coral bleaching**, in which the coral animal remains alive but loses the coloration and health benefits of the microalgal symbiont. Without their microalgal symbionts, corals lose energy and UV protection, and coral health will quickly decline. Once the temperature cools, the corals can take up new microalgal symbionts from the surrounding water and incorporate them back into the cells of their gastrodermis (Figure 1C) (Barott et al. 2015). If the high temperatures are long-lasting and corals are without their microalgae for too long, it can result in a widespread coral bleaching event and coral death (AGRRA 2022).

Numerous severe bleaching events have occurred in the Caribbean since 1995, with the intensity and frequency of the events increasing over time (AGRRA 2022; Muñiz-Castillo 2019). Since 2011, mild to moderate bleaching has occurred each year in Florida, greatly reducing the health of Florida reefs (Muñiz-Castillo et al. 2019). With hundreds of species of Symbiodiniaceae, some corals can adapt to these increased temperatures by switching their microalgal symbiont for a more heat-tolerant species (Buerger et al. 2020; Muñiz-Castillo et al. 2019). However, microalgal stress tolerance limits are not well understood, and more tolerant species may not be readily available or accepted by the coral host (Voolstra et al. 2021). Recent advancements in coral research have investigated using assisted evolution techniques to enhance the heat-stress tolerance of microalgal symbionts in the laboratory and offer a potential solution to bolster coral resilience against rising ocean temperatures (Buerger et al. 2020). Laboratory heat-evolved microalgal species show promising results in increasing the holobionts' bleaching tolerance. However, conducting long-term field studies on these evolved microalgal species is essential to assess their compatibility with various coral hosts and to confirm whether their heat tolerance remains consistent after prolonged exposure to cooler temperatures that are brought about by seasonal variations. Thus, understanding the intricate relationship between corals and their microalgal symbionts is crucial for determining coral adaptation and response to heat stress and other environmental factors. Such information can be further applied to coral conservation efforts and for mitigating the impact of environmental stressors on these vital ecosystems.

Coral Bacteria

Bacteria also play a pivotal role in the coral microbiome and coral health. When people think of bacteria, they often think of infections, disease, and other negative connotations related to bacterial functions. However, just as good bacteria exist in the human gut and aid in digestion and nutrient uptake, beneficial bacteria exist in or on corals to perform similar functions. Figure 1C illustrates the bacteria that exist within various tissues of the coral animal, including the surface mucus layer and the coral gut (gastrovascular cavity). One crucial role that bacteria play in the coral microbiome is the acquisition and cycling of nutrients. Bacteria help break down complex compounds into forms that corals can use for growth and energy (Peixoto, Rosado, et al. 2017; Buerger et al. 2020; H. F. Mohamed et al. 2022). This recycling process is especially important in nutrient-poor tropical waters where coral reefs often thrive.

Additionally, bacteria in the coral microbiome are important for protecting corals from harmful pathogens and diseases. Unlike humans, corals do not have an adaptive immune system, which means they do not have specialized immune cells capable of recognizing and defending against specific pathogen invaders (Peixoto, Rosado, et al. 2017; Reshef et al. 2006). An adaptive immune system provides the body with a "memory" of pathogens it has seen, allowing the immune system to fight off the foreign invader faster and easier for future infections. Without this adaptive immune response, microbes in the surface mucus of corals can act as a first line of defense (Shnit-Orland and Kushmaro 2009; Vilas Bhagwat, Ravindran, and Irudayarajan 2023). They do so by competing for resources with potential pathogens or by producing antimicrobial compounds that inhibit the growth of other harmful microorganisms (Peixoto, Rosado, et al. 2017; Shnit-Orland and Kushmaro 2009; Vilas Bhagwat, Ravindran, and Irudayarajan 2023).

Influences on the Microbiome

The composition of coral microbiomes can be influenced by both host and environmental factors (Figure 2). For example, the geographic location of the reef may impact salinity levels around river outflows, the depth of the reef, and proximity to human influences. In addition to coral bleaching events resulting from rising ocean temperatures, land-based pollution like fertilizer and sewer runoff can disrupt the delicate balance of the coral microbiome and lead to dysbiosis (Figure 2) (A. R. Mohamed et al. 2023; Thurber et al. 2020). This can cause potentially harmful shifts in bacterial communities and increased susceptibility to diseases or bleaching. Coral genetics, mode of reproduction, and age also influence the microbiome (Figure 2) (van Oppen and Blackall 2019). For example, brooding corals that release fertilized larvae into the water column can pass beneficial bacteria from parent to offspring (van Oppen and Blackall 2019; Ceh et al. 2013).

The Microbiome and Future of Coral Health

By understanding the coral's microbial communities and the drivers shaping these communities, we can better determine the role of the microbiome in adaptation and defense to stressors. Thus, researchers will have a more comprehensive idea of a healthy coral microbiome and can make restoration strategies or decisions based on collective microbial and coral physiological data. This is especially prudent for corals facing persistent environmental stressors, in which efforts can be made to help corals adapt to a changing world.

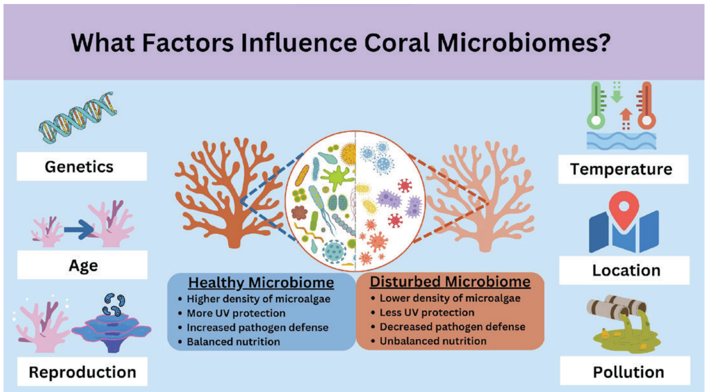

Figure 2. Many factors can influence the coral microbiome and lead to changes in coral health. The influences on the left include characteristics of the coral host such as the coral genetics, age or size of the colony, and style of reproduction. The influences on the right include environmental conditions like changes in water temperature, nutrient pollution, and the coral's geographic location. Each of these factors may influence changes in the microbiome from a healthy host-microbe relationship where the microbiome provides the coral with defense against pathogens and access to vital nutrients (center left), to an imbalanced host-microbe relationship (dysbiosis) that can lead to stress or disease (center right).
Credits: Monica D. Schul, University of Florida

Scientists are currently developing coral probiotics as a means of improving coral health through the introduction of potentially beneficial coral microbes. Just as humans ingest probiotics from yogurt to improve gut health, the application of probiotics to corals can improve coral fitness against disease and heat stress (Piexoto et al. 2021; Ushijima et al. 2023). Though probiotics show promise in relieving corals of such ailments, more research needs be done to increase probiotic effectiveness and application feasibility to wild corals (Peixoto, Sweet, et al. 2021). Moreover, we must understand the full effect of probiotics on corals, including how the introduction of more resilient microbial species will impact coral health and longevity.

Conclusions

It is important to study the microbiomes of stony corals to identify microbial community members and services that promote the health and resilience of these vital reef building organisms. When the corals' microbial ecology is not considered, we only gain a narrow perspective of the complex relationship between corals and their surrounding environment, making the efforts to manage or restore coral populations less effective and more time consuming. Thus, a multi-disciplinary approach is necessary as understanding the physiology and microbiology of corals, and the surrounding reef environment could help us to develop better conservation and restoration practices. Microbes are clearly important in maintaining health and promoting balance in ecosystems. Additionally, they provide similar functions and benefits to different living organisms (i.e., humans and corals). Here, we reviewed a few coral-microbial relationships to identify some of the beneficial roles that these microorganisms play in keeping corals healthy. However, there are many other microbes within the coral holobiont that benefit coral survival. It is evident that microbes are important in maintaining coral health and that when the delicate relationship between corals and their microbes is disturbed, it can lead to bleaching and disease. By continuing to explore the coral microbiome, researchers can more easily identify disease markers or associations, develop more effective treatments for diseased or bleaching corals, and even develop early interventions to allow corals to adapt to a changing climate. In conclusion, it is imperative for microbiome research in corals to be considered in current and future monitoring, research, and restoration practices as it sheds light on the impact of microbes on coral health and adaptation to stressors. Additionally, research on coral microbiomes paves the way for future interventions that may lead to higher success rates for coral restoration and the persistence of corals in the future.

Key Definitions

Cnidaria—A phylum containing species of animals such as stony corals, jellyfish, and sea anemones. All of these animals possess stinging cells, called nematocysts, that arm the cnidarians against predators or help them to catch prey.

Coral bleaching—A consequence of the explosion of the microalgal symbiont by the coral host when the host is under stress. Because the microalgal symbiont gives the coral its color, the loss of microalgae makes the coral appear paler or white in color.

Coral holobiont—The coral host and its associated microbial community, including microalgae, bacteria, viruses, and fungi.

Dysbiosis—Often referred to as an imbalance of microbes within a system. This ultimately leads to a shift in microbial groups present within the system and a change in microbial metabolic activity.

Ecosystem engineers—Species that modify, maintain, or create habitat for other species. Ecosystem engineers often change the physical resources around them.

Foundational species—Species that are typically abundant within an ecological system and control the biodiversity related to the system.

Symbiont—An organism that lives in a close relationship with another organism, and both partners often benefit from the relationship.

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