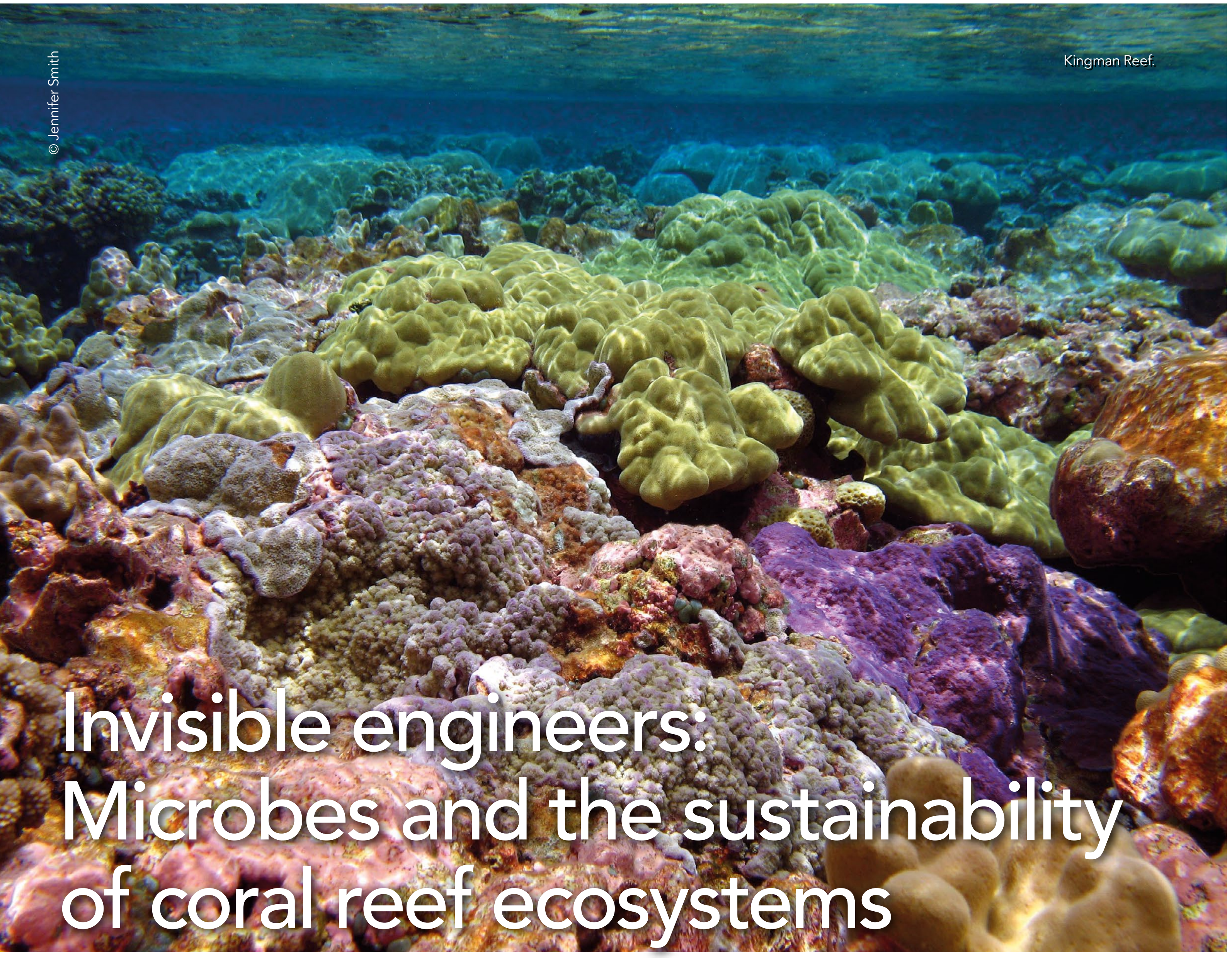


Kingman Reef.

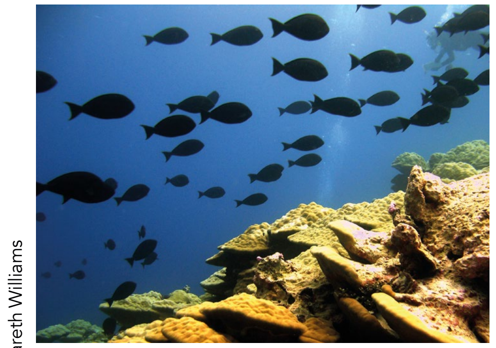
Invisible engineers: Microbes and the sustainability of coral reef ecosystems

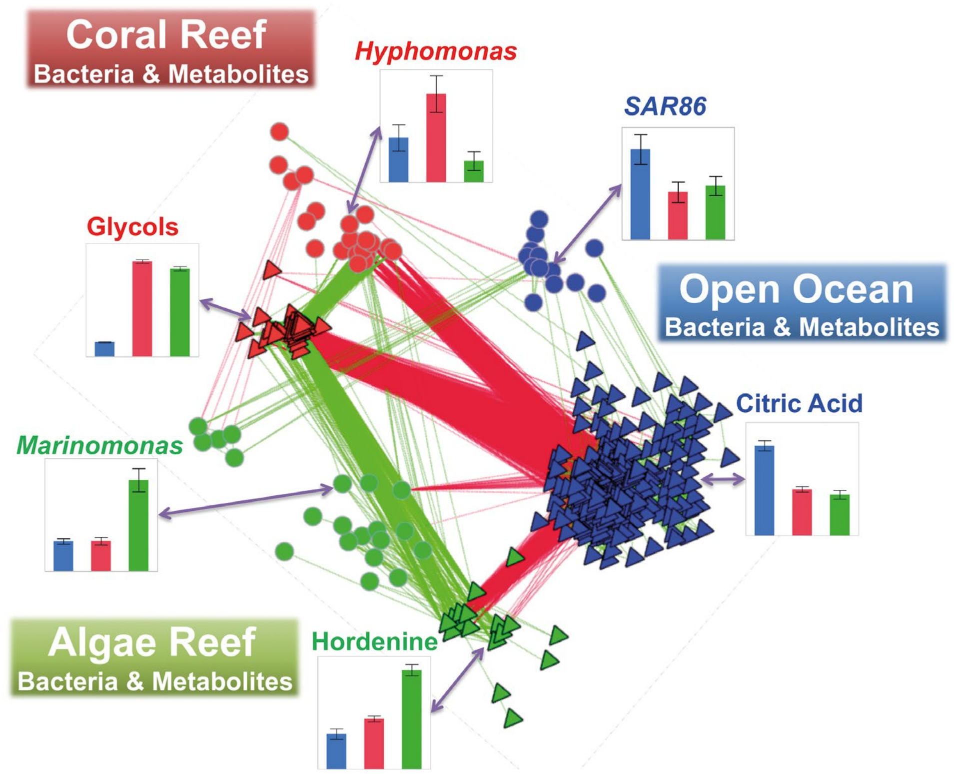
Coral reefs are oases of biodiversity and productivity that flourish in some of the most dilute waters on earth. Reefs worldwide are changing as human activities shift the balance in dominant organisms and corresponding ecosystem processes. Microbes living in water or symbiotically with coral play a major role in the function and fate of tropical reefs. **Professors Linda Wegley Kelly** of San Diego State University and **Craig Nelson** of the University of Hawaiʻi at Mānoa are investigating the genetics and ecology of these microbial communities.

Anyone who descends into a coral reef can see the complexity and diversity of life in these vibrant ecosystems: towering mounds of coral skeleton surrounded by schools of brightly coloured fish nibbling at wispy algae or tiny invertebrates hiding in the intricate reef architecture. What we can't see with our eyes are the microbes: millions of bacteria, archaea and viruses in every teaspoon of water and ten times that many on the surface of every nook and cranny. Corals, algae, sponges, fish, sand and rock are all coated (inside and out) with symbiotic microbial communities (what we now call the "microbiome") that play a key role in the health, metabolism and interactions of reef denizens. The water too is packed with microbes that seed and respond to the symbionts associated with larger reef organisms. Molecular techniques have long established that these microbes play a key role in structuring reef communities and driving ecosystem processes. Professors Linda Wegley Kelly and Craig Nelson are studying the significance of these microbial communities in the processes and interactions that govern coral reef resilience, health and function using a breadth of interdisciplinary methods, spanning genomics and molecular biology to ecosystem ecology and biogeochemistry.

A GLOBAL SHIFT

Scleractinian corals form mutualistic relationships with single-celled algae, called zooxanthellae, and associate with a suite of other microorganisms such as bacteria, archaea, protists, fungi, and viruses. These symbiotic partnerships are collectively referred to as the coral holobiont. Alongside planktonic microbes, holobiont microbes influence reef processes, particularly the carbon fixation that supports reef productivity, the calcification that corals carry out to build reef structure, and the tight recycling of nutrients critical to sustaining reefs in dilute tropical waters. The latter is particularly important given that coral reefs maintain astoundingly high biomass and diversity in oligotrophic or low nutrient tropical waters, structuring oases of life on which more than 25% of the world's people rely for food and protection.





Above: Two reefs, one dominated by calcifying coral and the other by fleshy algae. Network analysis shows microbes respond to distinct organic compounds enriched by these different reef types compared with the surrounding ocean.

Anthropogenic (human-driven) impacts are causing shifts in the structure of tropical reefs worldwide. Overfishing and nutrient pollution encourage algal growth while global warming and acidification of the oceans further weakens coral reef communities. Microbial ecosystems science is important in understanding the resilience of coral reefs to these changes because microbial communities play a key role in the ecological consequences of shifts in coral systems to algal-dominated reefs. For example, transitions towards algal dominance can create hypoxic conditions due to enhanced oxygen consumption by microbes (which grow on algal-derived sugars exuded into the surrounding water). When reefs succumb to higher proportions of fleshy algae (seaweeds), ecosystem metabolisms are changed including net carbon fixation and carbonate accretion; both of which influence the exchange of carbon dioxide with the atmosphere, the rate at which reefs grow and their ability to support diversity and biomass.

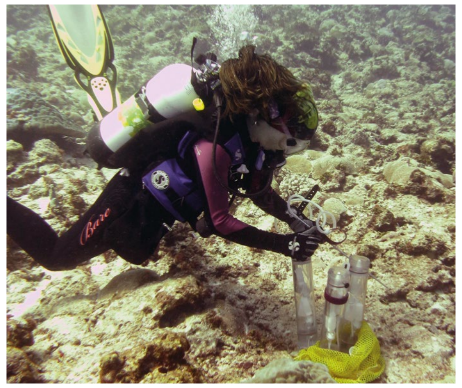
FROM GENOMICS TO GEOCHEMISTRY

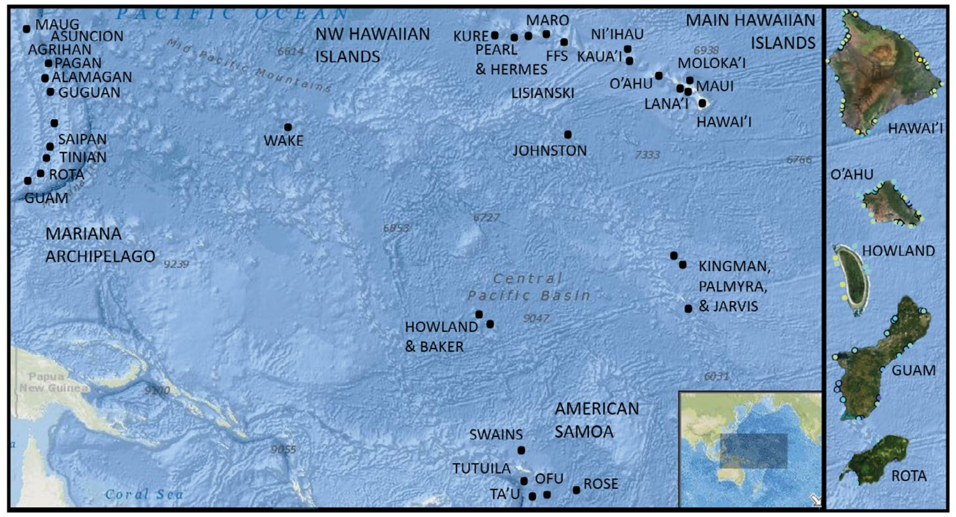
Elucidating the identities, ecological roles and biogeochemical mechanisms of microbial organisms in coral ecosystems is the central research focus of Professors Kelly and Nelson. Molecular techniques (biomarker profiling and shotgun sequencing of nucleic acids) have defined the taxonomic diversity, dynamics and genomic structure of microbes in coral communities. Professors Kelly and Nelson simultaneously strive to employ a variety of methods to make sense of the microbial influences on reef biogeochemistry, including nutrient recycling and the balances of both organismal and ecosystem-level production, calcification and respiration. Linking these molecular and biogeochemical dynamics Kelly believes will allow researchers to better explain ecosystem level changes occurring on reefs that cannot be seen with your eyes.

One area where microbiologists have made rapid advances is in relating the collective genomic potential of reef microorganisms to critical processes that are changing in reefs. While the genome of any one bacteria is relatively small, microbial communities work in concert, and their collective genomes together can contain ten to one hundred times more metabolic genes than the human genome. Professors Kelly, Nelson and their colleagues have shown that as algae increase on reefs these microbial meta-genomes shift in concert, altering the rates and efficiency of bacterial metabolism and increasing pathogens in the reef water. In one example, Professor Kelly showed how the iron pollution from decades-old shipwrecks on several remote reefs increased algal growth but also threatened the reef by changing microbial communities: increasing the number of bacteria in the water, selecting for pathogenic species, and altering the community meta-genome by increasing particular genes, called virulence factors, that allow bacteria to attach to and potentially attack host organisms (including corals and fish). This study provided a tangible example of how a window into microbial genomes can help understand ecosystem-scale changes in reefs under threat from anthropogenic impacts.

Holobiont microbes influence reef processes, particularly the carbon fixation that supports reef productivity, the calcification that corals carry out to build reef structure, and the tight recycling of nutrients critical to sustaining reefs in dilute tropical waters ”

> **While coral communities are extraordinarily diverse and complex, our research and that of others has demonstrated the many ways in which microbes may facilitate reef resilience to the onslaught of anthropogenic change**





Reefs across the Pacific are surveyed for microbial dynamics and chemical components in partnership with NOAA's Coral Reef Ecosystem Program.

Another avenue of research is exploring the connection between microbial metabolism and energy in the form of organic carbon. Water throughout the world is imbued with a massive quantity of near-invisible dissolved organic matter (DOM) rivalling the amount of carbon dioxide in the atmosphere. Only microbes can consume DOM and recycle it into the food chain, therefore the transformations of DOM by microbes is a crucial piece of the tight resource management that maintains reef productivity in these blue deserts. In all ecosystems, available energy is partitioned according to the position it occupies in the food chain or rather, the trophic level. This energetic allocation ultimately shapes the structure of coral reef food webs; though little is known about the ecology and mechanisms involved in these trophic energy transfers. Changes in reef communities caused by humans can alter the type of DOM and the microbes that consume it, fostering pathogens and weakening transfer into the reef food chain. These processes require investigation into the chemistry of DOM and the genomics of microbes that use it to untangle how these relationships impact reef resilience to global change.

Linda Wegley Kelly and Craig Nelson (at right) with their field team in French Polynesia (from left: Zachary Quinlan, Daniel Petras, Andi Haas, Jacqui Comstock and Irina Köster).

PARTNERSHIPS ACROSS THE PACIFIC

In collaboration with the US National Oceanic and Atmospheric Administration Coral Reef Ecosystem Program (NOAA CREP), Professors Kelly and Nelson study the microbiology of coral reefs across the Pacific, including the Hawaiian Islands, American Samoa, Mariana Islands, and several remote islands and atolls largely untouched by humans. These collections allow us to evaluate microbial communities in a spatial context, but also to compare reef systems significantly impacted by urban human populations and commercial fishing with pristine or intact sites. This partnership also allows NOAA to combine measurements of microbial dynamics and the fluxes of matter and energy they facilitate with data on the benthic and pelagic macrobiota (corals, algae, fish, invertebrates, etc.), collected by CREP; providing a holistic characterisation of coral reefs from a molecular to ecosystem scale.

While coral communities are extraordinarily diverse and complex, their research and that of others has demonstrated the many ways in which microbes may facilitate reef resilience to the onslaught of anthropogenic change. A variety of methods, applied at scales ranging from single corals to comparing reefs worldwide, will be needed to further elucidate their role in how reefs may respond and adapt to these changes. This, in turn, will hopefully provide novel insights into and future solutions to global reef degradation.

Q&A

Do all coral reef communities exhibit the same patterns of microbes?

The microbes living within and on the surfaces of corals and algae differ between functional groups of organisms (i.e. plants versus animals), but even different species of coral harbour unique microbial consortia that are consistent across geographic contexts. As one would expect, coral microbiomes are significantly altered when the animal is suffering from a disease or dying. The planktonic microbes (millions per teaspoon) are also highly diverse and very sensitive to the types and metabolism of the larger reef organisms. Exometabolites, compounds released by all marine animals and plants, interact with microbial plankton to change how they grow and process nutrients in the waters of reefs, with drastic changes even from day to night.

Is there any way to restore community structure after the algal shift has occurred?

Recovery of coral communities has been observed, some examples include the southern Great Barrier Reef after the massive bleaching event in 2006, algal dominated reefs in the Caribbean following the epidemic of a seaweed grazing urchin, and after remediation of nutrient pollution on Oahu and Maui in the US. Transitions back to coral-dominated states can take decades and often reef communities are rebuilt with different coral types. Our findings indicate that the proportion of corals or algae on the reef benthos strongly influences fluxes of organic compounds and nutrients through the microbial community. We hypothesise that these invisible components promote negative feedbacks to stabilise the existing dominant benthic constituents, either calcifying corals and coralline algae or fleshy algae, which inhibit shifts from one phase to another.

What methods do you hope to employ for predictive monitoring of coral reefs?

Microbial communities in all habitats are diverse and very sensitive to the environment, whether it be the physiology of a host organism or the chemistry of the water column. We believe that microbes and their metabolites can serve as a kaleidoscope window into the functioning of corals and reefs, informing us about processes that we cannot measure. As all the parameters in a blood test can tell a doctor nuances of disease, we hope that microbes can provide a complex predictive snapshot of reef states and trajectories, with potential for development of an early warning system for reefs that need a new management approach.

What are some of the key differences between microbes associated with coral reefs?

We find that the abundances (the number of microbes per litre of seawater) and species compositions are different across reefs. Many degraded or algae-dominated reef systems exhibit greater microbial biomasses and harbour more bacteria related to known pathogens. We predict that these microbes further diminish coral health directly by causing disease or indirectly by reducing water quality which can affect growth rates or calcification.

Are there any ways to increase reef resilience?

Any measure to reduce the growth of fleshy algae on reefs will protect the ecosystem. A reef may not be resistant to a mass bleaching event, but the reef could be resilient against significant coral mortality if local practices were in place to sustain good water quality in order to keep fleshy algae at bay while coral colonies recover.

> **Overfishing and nutrient pollution encourage algal growth while global warming and acidification of the oceans further weakens coral reef communities**

Detail

RESEARCH OBJECTIVES

Professors Linda Kelly and Craig Nelson study the genomics and ecology of reef microbial communities, combining laboratory experiments, *in situ* mesocosms, and surveys of reefs throughout the Pacific to understand how microbes control the health, resilience and function of coral ecosystems.

FUNDING

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COLLABORATORS

Andreas Haas (Netherlands Institute for Sea Research, NIOZ), **Craig Carlson** (UC Santa Barbara) , **Forest Rohwer** (San Diego State University), **Lihini Aluwihare, Pieter Dorrestein, Stuart Sandin, Jennifer E. Smith** (Scripps Institution of Oceanography & UC San Diego), **Rusty Brainard** (NOAA-Pacific Islands Fisheries Science Center).

BIO

Linda earned a PhD in Molecular Biology from SDSU-UC San Diego in 2013. Her research characterises microbial communities across coral reef systems. Craig joined the faculty at UH-Mānoa in 2013 after completing a PhD in Ecology, Evolution, & Marine Biology from UC Santa Barbara in 2008. His research focuses on the biogeochemistry and microbial ecology of aquatic ecosystems.

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