Species interactions are fundamental to understanding communities. Increasingly, we are encouraged to think of an organism as more than just the host, as most species also include microbial partners. These microbes define the extended phenotype of their host. Through this lens, I examine how microbes influence the nature of their host's interactions with other species to influence the population and community ecology of marine organisms. I integrate host-microbe dynamics into the more traditional (i.e., microbe-free) approaches to marine population and community ecology by conducting field surveys, manipulative experiments, mechanistic studies and molecular analyses. My research has four themes: 1) the role of microbial-host phenotypes in determining host growth, survival and population dynamics; 2) microbially mediated species interactions; and microbes as host traits that underlie 3) cryptic diversity and 4) adaptive plasticity.

Past and Current research

Marine macroalgae play a major role in coral dynamics, in part through classic competition for space, but also because algae release organic carbon which provides a substrate for microbial growth leading to local hypoxia and changes in the coral microbiome. My initial research, using in-situ and flume studies, showed that water flow modulates coral-algal interactions by reducing bacterial concentrations and normalizing oxygen concentrations on coral surfaces (Brown and Carpenter 2013, 2014). These interactions are further modulated by the presence of sessile marine snails (vermetid gastropods) that cast out mucus nets that cover coral tissues (Brown and Osenberg 2018). I demonstrated that both the presence of algae and snails lead to small-scale lowering of water flow near the coral surface that shifts the coral microbiome towards more pathogenic and anaerobic taxa; as well as lower coral calcification and linear extension (Brown 2018, Brown and Osenberg 2018, Brown et al. 2019). As a John J and Katherine C Ewel Postdoctoral Fellow at the University of Florida (UF), I continued to study coral-algal interactions and showed coral microbial diversity and composition changed across regions that vary in algal cover, islands and ocean basins.

Over 8 years of field research, my colleagues and I witnessed varied effects of vermetids on corals through space and time. From these observations, I hypothesized this variation resulted from the phenotypic plasticity of the corals: prior vermetid exposure reduced the vermetid effect modulated through traits changes, e.g., through the coral microbiome. To test this hypothesis, I conducted a reciprocal transplant experiment in Moorea, French Polynesia where I found that vermetids reduced coral skeletal growth, tissue thickness, *Symbiodinium* density, and, critically, altered coral microbiomes in favor of taxa associated with anaerobic environments (Brown et al. 2020). However, these traits (including their microbiome) were also greatly influenced by a coral's history with vermetids and previously unrecognized genetic variation among the corals. Thus, these cryptic coral genotypes gave rise to phenotypic differences that either facilitated or inhibited colonization by vermetids, which then led to cascading indirect effects resulting from the presence vs. absence of the coral-vermetid interaction (Brown et al. 2020). My work suggests that subtle genotypic and phenotypic differences among corals may lead to very different trajectories of reef communities.

I am currently leading and involved in collaborative efforts at the University of Florida and at Woods Hole Oceanographic Institution to investigate the indirect effects of microbes and other species in modulating host phenotypes. These collaborations are the result of two competitive post docs I earned, and involve diverse activities such as monitoring genotypic and phenotypic response of corals to disease; studying host-microbial interactions with cleanerfish and their role in shifting coral microbiomes; and developing temperate coral systems to study how bacterial communities impact the coral host during recovery from thermal stress. My work had and has direct implications for conservation efforts and informing critical questions in ecology and evolution, such as how corals, as foundation species and ecosystem engineers can become more resistant to abiotic stressors and disease. These projects are helping to accomplish some of my long-term goals to develop a broader understanding of how species

interactions and abiotic stressors modulate host phenotypes, including their inherent microbiomes, and how this influences the future responses of host-microbe interactions to environmental conditions.

Planned Research

At UC Davis and the Bodega Bay Marine Laboratory, I will extend my research program on microbially-mediated species interactions, cryptic phenotypes and host-microbial interactions by specifically understanding the role of extended phenotypes of marine species in systems dominated by foundation species, such as corals (the focus of much of my prior research) and seagrasses (my planned study system at BML). Seagrasses, like corals, are ideal systems to determine how extended phenotypes create cryptic diversity, influence trait-mediated species interactions, drive community trajectories and show an increase in adaptive capacity due to microbes. As foundation species, seagrasses have vast effects on their community, and because they are clonal, I can easily track genotypes. We already know that seagrasses are ecosystems that experience similar stressors to coral reefs, including disease. Furthermore, we know that genotypic variation in seagrasses influences population and community resistance to disturbance and that species interactions influence community structure of seagrass ecosystems. My research will expand the excellent research being done on seagrasses at Bodega Bay by incorporating microbes and the consequences of extended phenotypes in seagrass communities. I envision four major themes to my research over the next 5 years. For all of these themes, I plan to use a combination of subtidal field surveys, manipulative field experiments and lab experiments at the BML wet lab and sequencing through the College of Biological Sciences DNA Sequencing facility.

1) **The role of microbial-host phenotypes in determining host growth, survival and population dynamics** Understanding how changes in the microbiome modulate host responses on an organismal, and by extension, population, scale is the proverbial "white whale" of host-microbial ecology. Within this theme, I ask what influences the onset and maintenance of microbial associations? And, how do disruptions to host-microbial relationships affect microbial community stability, and what does this mean for host populations? ***My aim is to use microbial changes in response to stressors, to better understand how microbes modulate host responses.*** These effects, in addition to the effects of host genotype, can scale up, to influence population-scale dynamics. Using abiotic or biotic stressors (such as disease or temperature stress), I will determine how changes in microbial associations influence seagrass growth, survival and resistance to stressors. My work will first document the specificity of host genotype-microbial associations, then explore how specific stressors and seagrass genotype influence the seagrass-microbial relationships.

2) **Incorporating microbes in our understanding of species interactions** Although species interactions are the foundation of community ecology, our understanding of how microbes associated with hosts mediate species interactions is a nascent field. ***My research emphasizes that microbes are a fundamental feature of the host phenotype that mediates its effect on, and response to, other species. This adds a new dimension to our understanding of how species both compete and form mutualisms***. This perspective can provide new insight then on competitive interactions, mutualisms, and trait-mediated direct and indirect effects (as I've shown in my previous work). For example, the mutualism between seagrasses and lucinids, which has already shown to be microbially-mediated by the gill bacteria of the clam. To elucidate microbially mediated relationships, my students and I will assess seagrass host and microbial trait changes in response to interactions with members of the seagrass community.

3) **Microbes as host traits associated with cryptic diversity: implications for communities and ecosystems** Building on themes 1 and 2, I am excited to integrate the relationships between host genotypes, phenotypic traits (classic host traits and their microbes), and species interactions to

better understand cascading changes in marine communities and ecosystems. ***Variation in genotypes (e.g., cryptic genotypes), that are associated with different phenotypes, which lead to different outcomes of species interactions can likely help explain heterogeneity across communities***. These are examples of community phenotypes; which researchers have shown in terrestrial systems and have only recently demonstrated in marine systems (Brown et al. 2020). Using field surveys and manipulative experiments, I will measure ecological changes (e.g., associated community assemblages) that are likely to change as the result of genotypic/phenotypic trait variation.

4) **Adaptive plasticity** Because microbial communities change on such fast time scales, they can lead to changes in the host more quickly than evolution traditionally allows. Adaptive plasticity is an ecological concept in which prior exposure to a stressor (or a biotic interaction) can lead to phenotypic changes that decrease the effect of the stress in the future. This concept, ***when extended to hosts and their associated microbiomes, can allow for the relatively rapid adaptation of a species to stressor conditions.*** By exposing species to stressors initially (as in themes 1 and 2), I hope to gain a better understanding in how shifts in microbiomes feedback to influence how seagrasses subsequently respond to those stressors. Shifts in microbiomes via the extended phenotype can facilitate (or impede) a host's ability adapt to environmental change. This form of phenotypic plasticity likely plays a critical role in species responses to stressors and environmental change yet remains largely ignored by ecologists. Using lab and field experiments, I plan to not only understand how prior exposure influences a species' response to stressors, but to induce changes via microbial addition and removal experiments (if the adaptive response is mediated through microbial changes).

The ecological importance of these themes makes them competitive for funding by NSF (Biological Oceanography and Integrated Organismal Systems), Sea Grant, and Environmental Protection Agency grants. In collaboration with Julie Meyer at UF, we have already submitted a grant for the "Understanding the Rules of Life: Microbiome Theory and Mechanisms" call, which builds on the post-doctoral studies I started in her lab. That project will also be appropriate for the IOS division at NSF. Once in a tenure-track position, I will be competitive for the NSF Faculty Early Career Development (CAREER program) grant.

My expertise in marine communities at both macroscopic and microscopic scales will complement the existing research strengths at BML. I am eager to collaborate with colleagues working in other empirical systems, who develop population and community models, or who have expertise in ecosystem processes. Combined, we can (1) better understand host-microbial relationships and their response to stressors through the use of diverse methodologies, including different -omic techniques, (2) extrapolate my insights about host-microbial relationships to population and community dynamics, and (3) expand population and community level changes into understanding ecosystem-level effects that arise from environmental change. Overall, I am excited for the opportunity to be part of the exciting research group at BML to further understand the ecology and evolution of marine species.