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Challenges and Opportunities in Marine Chemical Ecology

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Where We Started

Marine chemical ecology is only a few decades old. Prior to the 1980s, chemists were discovering novel, bioactive molecules and hinting at their ecological function *via* bioassays with minimal ecological reality, while ecologists were conducting experiments that suggested chemically-mediated mechanisms, but they lacked the expertise to address the chemical underpinnings. This has changed and progress is now rapid due to critical collaborations between chemists and ecologists and to younger scientists being trained across borders of the old disciplines.

Where We Are

As humans we are poorly equipped to understand the omnipresent and critical importance of chemical cues and signals in regulating biotic interactions in marine and aquatic systems. Most organisms have neither eyes nor ears and thus must decide whether to eat, mate with, escape from, defend against, or settle alongside a neighboring organism based on chemical cues. These cues constitute the language in which the “instructions” for biotic interactions are written for most marine organisms. The goal of chemical ecology is to understand and translate this language from chemistry into ecology and to use this deeper understanding as a window into: (i) the processes that have selected for critical sensory abilities, (ii) understanding how these chemical cues change organism behavior, (iii) how these behaviors affect populations and interactions among species, and (iv) how a mechanistic-level understanding of behavioral cues can be scaled-up to better understand (and potentially conserve and manage) the structure and function of communities and ecosystems. Progress in this endeavor has been dramatic for marine systems. Future developments are likely to include advances in the fundamental chemistry, molecular mechanisms, and chemical complexity of these interactions (addressed by Professor Kubanek in this series of notes) and the scaling-up of this fundamental understanding to focus on impacts on populations, communities, and ecosystems (which I address here).

Over the past 2–3 decades, a combination of field and laboratory studies have demonstrated the roles of marine secondary metabolites in: (i) defense against diverse groups of generalist consumers, (ii) the evolution of feeding preferences, feeding specialization, and the role of

tri-trophic interactions in selecting for feeding ecologies and for resistance to host chemical defenses by small, less mobile consumers, (iii) antifouling and allelopathy, (iv) defenses against pathogens, and (v) generating complex interactions that impact both target and non-target species and that affect population regulation, community organization, biogeochemical cycles, and the maintenance and function of marine biodiversity.

Studies have included demonstrations of spatial patterns in selection for, and production of, chemical defenses that range from within individual allocation, to among individual and population allocation, to evolution and allocation of compounds across geographic scales from the tropics to the Antarctic. Similar patterns in consumer resistance to these defenses also have been demonstrated. Exciting examples of the dynamics of these chemically-mediated interactions have emerged demonstrating that prey can use chemical cues alone to detect consumers, identify those consumers to species, and induce appropriate chemical or physical defenses to specific consumers.

Chemical responses to competitors also can be nuanced and dynamic. Recent studies have elucidated roles of allelopathic interactions in both benthic and pelagic systems. Examples include: i) phytoplankton having their allelochemicals inactivated by other species, ii) corals chemically cuing mutualistic fishes to remove allelopathic seaweed competitors based on recognition of their chemistry alone, and iii) seaweeds responding to adjacent competitors by inducing greater allelopathy, but at a cost of reduced chemical defenses against other enemies. These chemically nuanced dances of offense and defense and constraints imposed by multiple natural enemies interacting simultaneously are only beginning to be understood. There is continued scope for growth in this area.

A recent focus of prominent ecological studies is determining the functional role of primary producer and consumer biodiversity in affecting community organization and ecosystem function. A common finding is that biodiversity *per se* is critical, but the mechanisms underlying this effect are rarely elucidated. Recent studies demonstrate a critical role for chemically-mediated interactions in connecting biodiversity to ecosystem function. As an example, studies on coral reefs show that herbivore diversity, as opposed to biomass or density alone, is critical for controlling seaweeds and preventing their suppression of corals and of reef degradation in general. This occurs because seaweed chemical defenses are differently effective against various herbivorous fishes, and as herbivore diversity rises the probability of any seaweeds escaping control by all fishes declines. Thus, the interaction between seaweed chemical defense and herbivore tolerance generates the functional role of consumer diversity in preserving coral cover and reef function. Similar chemically-mediated mechanisms are likely important to a broad range of community-level and ecosystem-level functions.

Where We May Go

Much of marine chemical ecology has focused on large organisms that we can collect, manipulate, and extract for adequate quantities of secondary metabolites. Chemically mediated interactions are even more important for marine microbes (all microbial ecology is chemical ecology), and those microbes are now known to play roles in producing secondary

metabolites that defend the larvae, embryos, and adults of numerous macro-organisms. It is likely that the microbiome of macro-organisms also produces compounds that play roles in “labeling” members of family or social groups vs. foreign group members, in indicating the physiological or sexual status of potential mates, and in protecting the host from a broad range of potential pathogens and competing organisms. They might also play roles in chemically cuing various group behaviors like swarming and migration. With recent advances in culture-independent molecular methods, meaningful studies of chemically-mediated interactions among marine microbes or between microbes and hosts are now possible. Understanding chemical mediation of host microbiomes is likely an important area of growth for chemical ecology.

As we understand more about the mechanisms of chemically-mediated interactions, it will be an exciting challenge to understand how these interactions, which are usually studied between pairs of interacting species, scale-up and cascade to produce impacts at the scales of communities and ecosystems. This is already being done, but can be improved. Examples include: i) marine birds that use dimethyl sulfide coming from phytoplankton as a chemical cue to aid foraging over a scale of 1000s of square kilometers, bring marine resources back to terrestrial systems, and *via* fertilization impacting terrestrial populations as diverse as cacti, beetles, lizards, and coyotes, ii) chemically mediated interactions between phytoplankton and zooplankton of different size classes that may determine whether atmospheric carbon is buried in the deep sea or cycled between shallow waters and the atmosphere where it can affect global climate, iii) dynamic responses of toxic harmful algal species that can result in the deaths of millions of fishes and fundamentally alter marine food webs, and iv) instances where the chemical cues from consumers have as much impact on trophic cascades and community structure as do predation events themselves.

As a final possibility, it is well-known that larvae of ecosystem engineers like tropical corals settle in response to chemical cues from specific benthic organisms, and it recently has been discovered that juvenile reef fishes appear to be “smelling” their way back to home reefs. Thus, marine larvae may be exquisitely tuned to use chemical cues to seek out appropriate habitats and avoid habitats that constrain their fitness. Our present reliance on Marine Protected Areas (MPAs) to produce excess larvae that will be exported to damaged areas to help “rescue” populations in those degraded areas may be ineffective if coral and fish juveniles reject these areas as unsuitable based on chemical cues. Such chemically-cued larval behavior could help explain the phenomena of ecosystem tipping-points or alternative stable states where a community shifts dramatically from one state to another (*e.g.*, coral reefs to seaweed beds) and then fails to rebound to its original state. Such discoveries could fundamentally alter strategies for conservation and management of marine systems.

The above predictions are best guesses. Some will work out, some won't. However, the most important future breakthroughs are unlikely to be listed above. The most enlightening discoveries are the ones that are complete surprises; these provide insights we never considered. To some extent, all science is driven by its history, present technology, models, and culture, but the individual creativity and imagination of key individuals also play critical roles in breaking new ground. In chemical ecology, like most fields, one can look to a small number of critical individuals and collaborative partnerships and see that without them, the

field would not exist in its present form. Somewhere out there is a student or post-doc who is the next Tom Eisner, Jerrold Meinwald, or Bill Fenical (a list that would include the other authors of these essays). It is these innovative, insightful, risk takers who are disproportionately important in generating new insights. To the students and post-docs reading this, I challenge you to use the firm ground these individuals have produced, to push to the forefront of present knowledge, but to then push beyond this known border, to the forefront of ignorance where the most exciting discoveries occur. When you are being productive and most things are going well, occasionally jump into the unknown and try the project that is just-too-cool to work. Sometimes it will.