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Crystal ball – 2009

In this feature, leading researchers in the field of environmental microbiology speculate on the technical and conceptual developments that will drive innovative research and open new vistas over the next few years.

Microbial observatories in the sea

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All marine habitats support diverse and dynamic assemblages of microorganisms, including bacteria, archaea, eukarya and their viral and metazoan predators. These

complex communities interact through a variety of genetic, metabolic and ecological processes to sustain life in the sea. Recent discoveries of novel microbes, new metabolic pathways and their intimate interrelations have challenged pre-existing paradigms and have led to a renewed commitment to a comprehensive study of the biology and ecology of marine microorganisms from genomes to biomes (e.g. <http://cmore.soest.hawaii.edu>).

Our general understanding of the structure, function and regulation of microbial communities in the sea has changed radically during the past three decades but is still fragmentary. Currently, we are woefully ignorant of the time–space domains of microbial processes in the sea, in large part because of the extreme magnitudes of scale (seconds to millennia for the temporal domain and micrometre to ocean basin for the spatial domain). Because most marine ecosystems are remote and out of direct human sight, they are sparsely observed and grossly under-sampled; indeed, the scales that matter for microorganisms may be far removed from the scales that our own senses can perceive. Furthermore, anthropogenic forcing of the Earth since the dawn of the industrial revolution has created a ‘no analogue’ new world and we may be altering the ocean habitat in ways that we do not understand. The changing ocean may lead to different, perhaps novel, marine habitats that can select for new microbial assemblages. The lack of comprehensive temporal observation and facilities for long-term field experimentation currently limit and will ultimately restrict our rate of progress in the field of marine microbial ecology, in my opinion. There is no substitute for at-sea observation and experimentation, and no short cuts either. This situation needs to change, and it will improve in the near future according to my crystal ball!

Much of our extant knowledge concerning the role of microorganisms in the sea is based on either laboratory study of selected isolates or the results obtained during oceanographic research expeditions. The latter are, at best, single freeze frames of what are probably full-length motion pictures. Consequently, this expeditionary mode of data collection provides an incomplete account of the dynamic and stochastic nature of microbial life in the sea. Marine microbial community structure and the ecosystem services that they support are complex, time-varying, non-steady-state features of a changing planet, and must be studied as such. This demands a financial commitment for the establishment of microbial observatories for long-term observation of oceanic phenomena, an intellectual investment in the establishment of transdisciplinary research teams and the development of novel instrumentation for continuous, remote observations of marine microbes. Above all, there must be sustained ‘access to the sea’, not in the international political sense of Hugo Grotius’ classic treatise *Mare Liberum* (1609), but in a modern ecological research sense.

Long-term ecological studies are common in terrestrial and limnological research. They are ideally suited for investigation of subtle habitat changes, irregularly spaced stochastic events and complex interdependent phenomena. In 1988, two open ocean observatories were established to track the temporal changes in a variety of microbial processes in response to physical and chemical dynamics of the selected habitats. The two study sites, one in the North Atlantic Ocean near Bermuda (Bermuda Atlantic Time-series Study, BATS) and the other in the North Pacific Ocean near Hawaii (Hawaii Ocean Time-series, HOT), were initially focused on the ocean's carbon cycle from solar energy-based carbon dioxide reduction to particulate matter export and deep-sea carbon sequestration. At the time of their creation, there were no marine analogues of the atmospheric $p\text{CO}_2$ record (the so-called Keeling Curve) and no microbial-based ecosystem models for accurate predictions of carbon fluxes in the sea. To put our ignorance into proper context, *Prochlorococcus* – a tiny marine photoautotroph now recognized as the most abundant plant on Earth – had just been discovered, and the 'marine microbial genomics revolution' had not yet begun (the first full genome sequence of a marine microorganism was not available until 1996).

The design of the sampling and core measurement programme for HOT and BATS was based on the best information at that time; an approximately monthly frequency, ship-based programme lasting for at least one decade was believed to be a minimum investment for establishing the seasonal climatologies and variability spectra for most key physical, biogeochemical and microbial processes. Now, 20 years later, the data from these ocean time-series programmes continue to reveal previously unrecognized phenomena including, but not limited to, novel ecological processes and unpredicted climate-driven biogeochemical connections. These microbial ocean time-series programmes have attracted the interest of collaborators who have benefited from the existing core measurement programmes and from shared and leveraged access to the sea. The new knowledge gained is being used to improve existing ecosystem-based models, and to develop new ones.

At the beginning of the HOT programme, we had no idea that our efforts would facilitate the discovery of novel microorganisms, unexpected metabolic pathways and new ecological insights. We also had no idea that a monthly sampling frequency would be deemed inadequate for all key microbially mediated biogeochemical processes that we had endeavoured to understand. For example, it is now known that stochastic physical processes with time scales of less than 1 month can trigger a pulsed delivery of nutrients, resulting in changes in microbial community structure and a cascade of independent ecological processes. Higher temporal frequency microbe

detection to track these rapid perturbations will require the development of new sensors and sampling procedures since it is impossible to sustain continuous human presence at this remote field location. Significant microbial and biogeochemical changes have also been observed on decadal time scales, possibly triggered by large-scale changes in the coupling of the ocean to the atmosphere (e.g. El Niño) or by secular changes in habitat due to greenhouse gas-induced climate warming. Ultimately, these long-term changes are the result of processes taking place over a broad range of scales eventually propagating into the habitat that impacts microbial processes. Understanding how marine microbial assemblages in different oceanic habitats may evolve over time in response to climate change will require not only a characterization of the microbes' response to physical and chemical changes but also the development of how interactions among microbes contribute to the metabolic plasticity and resilience of the biome as a whole. Prior to the start of the HOT programme, the North Pacific subtropical gyre – Earth's largest contiguous biome – was thought to be relatively stable in time and coherent in space, a habitat supporting a climax-type microbial community that was well tuned to its environment and resistant to change. We now recognize a fundamentally different biome, one that is dynamic, variable and poised for ecological opportunity. The design of future ocean time-series programmes and field experiments can benefit from lessons learned in HOT and related time-series programmes.

In summary, marine microbial communities are genetically gifted, metabolically talented and functionally literate. All microbial and biogeochemical processes in the sea reside in a temporal domain, and each process has a characteristic time scale of variability. A major achievement of the HOT programme is an improved understanding of the time-varying changes in microbial community structure and fluxes of energy and carbon at a key, open ocean site. If the ultimate goal of ecological research is to understand how organisms regulate metabolism and growth, coexist in complex and diverse assemblages, and respond to various environmental forces, then the future research prospectus needs to be comprehensive, ranging from extensive field observations, to well-controlled laboratory studies using model microorganisms, to whole ecosystem experiments. The design and conduct of meaningful field experiments demands an *a priori* understanding of habitat dynamics and metabolic controls, which ultimately requires extensive at-sea observations in advance of formulating the specific research question. The emergent HOT data sets are serving as the basis for the generation of new ideas, improved models, controlled experiments and other forms of hypothesis testing. Future ecological research will focus on the interrelationships among climate,

habitat, microbes and their collective metabolic function. Most important to our success will be continued, indeed enhanced, access to the sea for sustained observation and experimentation. By the next year of the dog, I predict that at least a dozen new ocean time-series programmes will have emerged with a collective focus on the key roles that microbes play in sustaining planetary habitability. These comprehensive, transdisciplinary field programmes will fully integrate physical and chemical oceanography with theoretical ecology and modelling into the wonderful world of marine microbes. It should be a very exciting decade of discovery.

This article is dedicated to the past, present and future scientists, students and technical staff of the Hawaii Ocean Time-series programme on their 20th anniversary (1988–2008) of successful field operation (<http://hahana.soest.hawaii.edu>).