

important thing now is to seize the moment and move forward gathering more data, depositing it in the central CAMERA databank (<http://camera.calit2.net/>), and working to describe the marine ecosystem as the complex system it is.

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Soaking it up: the complex lives of marine sponges and their microbial associates

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Marine sponges (phylum Porifera) are among the oldest multicellular animals (metazoans), the sea's most prolific producers of bioactive metabolites, and of considerable ecological importance due to their abundance and ability to filter enormous volumes of seawater. In addition to these important attributes, sponge microbiology is now a rapidly expanding field.

In the 1970s and 1980s, Clive Wilkinson and Jean Vacelet set the benchmark for sponge microbiology, describing dense and diverse microbial communities comprising up to 40% of total 'sponge' volume (Vacelet and Donadey, 1977; Wilkinson and Fay, 1979; Wilkinson, 1983). Advances in molecular techniques have, over the past decade, taken the field to a new level, revealing new and exciting research opportunities. The catalyst for this article was a recent roundtable session, 'Marine sponges as microbial fermenters', held under the auspices of the *11th International Symposium on Microbial Ecology*, Vienna, Austria. Scientists from many different backgrounds (biotechnology, ecology, evolution, microbiology, organic chemistry) were brought together, stimulating wide-ranging

discussions across normal discipline boundaries. Based on these discussions and key recent findings, we chart a course for future research in the field, identifying as key focal points the evolution of symbiont diversity, microbial metabolism, host–microbe interactions and the potential biotechnological implications (Table 1).

The microbial consortia present in many sponges (Figure 1) span all three domains of life, with at least 18 bacterial and archaeal phyla now known from these hosts (Taylor *et al.*, 2007) (Figure 2). Interactions between sponges and microbes are also diverse, ranging from mutualistic to commensalistic and exploitative (parasitism/pathogenesis). A major challenge in sponge symbiont biology, and a key theme to emerge from the roundtable, is how best to handle this diversity. Although the study of simple systems offers valuable insights into host–microbe interactions (the squid–*Vibrio* symbiosis (Nyholm and McFall-Ngai, 2004) is a prime example), we suggest that this scenario is not the norm in nature, at least for the marine environment. Rather, most prokaryote–eukaryote associations in the oceans are probably a complex mix of stable and transient associates, as exemplified by the sponge–microbe model. Embracing the complexities of the sponge system will thus lead to its establishment as an

important model for the study of prokaryote–eukaryote interactions, providing valuable clues about how higher organisms cope with, and benefit from, the presence of diverse microbial communities. An urgent challenge for those working in this field is to determine which, among the detected microorganisms, represent stable members of the community.

Remarkably, distantly related sponges from across the world appear to share a substantial proportion of their microbiota (Hentschel *et al.*, 2002). The apparent absence of these same microbes from

seawater and other marine hosts raises interesting questions about the origin, evolution and maintenance of sponge–microbe associations. Molecular techniques including denaturing gradient gel electrophoresis and fluorescence *in situ* hybridization revealed that highly diverse microbial assemblages are transmitted between sponge generations via the reproductive stages (Enticknap *et al.*, 2006; Schmitt *et al.*, 2007; Sharp *et al.*, 2007). The potential for host–symbiont co-evolution in such systems is clear, with evidence of this for sponges and their cyanobacterial associates (Thacker and Starnes, 2003). However, the poorly resolved phylogenies of many sponge taxa play a confounding role (Boury-Esnault, 2006), and additional emphasis on both sponge and symbiont evolution is urgently required.

Our burgeoning understanding of microbial diversity in sponges contrasts with our limited knowledge of symbiont function. An inability to cultivate many of these microbes – a phenomenon shared with other environmental microbiologists – has hampered efforts in this direction. What we do know, based largely upon measurements of micro-

Table 1 Focal points for future research in sponge microbiology

- Defining the members of the ‘stable’ vs ‘transient’ microbial communities
- (Co)evolution of sponges and microorganisms
- Physiology of sponge symbionts (including non-cultivated lineages)
- Accessing bioactive compounds from sponge symbionts via metagenomics and cultivation strategies
- Host–symbiont interactions (for example, signaling)

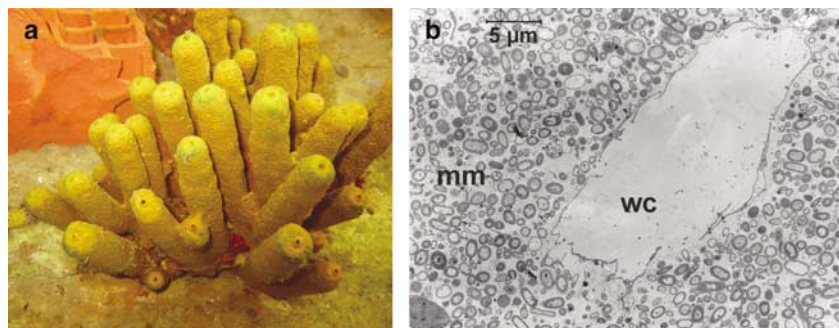


Figure 1 The Mediterranean sponge *Aplysina aerophoba*. Underwater photograph (a) and transmission electron micrograph (b) showing the microorganism-filled mesohyl matrix (mm) and a water channel (wc) (photography by K Bayer and M Wehrl, Würzburg, Germany, respectively).



Figure 2 The known phylogenetic diversity of bacteria and archaea in sponges, based on the 16S ribosomal RNA gene (Taylor *et al.*, 2007).

bially mediated processes within sponge tissue, is that symbionts provide sponges with an impressive metabolic repertoire (for example, photosynthetic carbon fixation, nitrification, sulphate reduction). Application of new technologies such as stable isotope probing, metagenomics and high-throughput cultivation strategies will greatly improve our understanding of symbiont function and host–symbiont interactions.

The immense numbers of microorganisms in sponges have led to their being labeled as ‘microbial fermenters’, capable of producing a wide range of chemicals with bioactive properties and pharmaceutical potential. The suspicion that many of these compounds are symbiont-derived sparked much of the recent interest in sponge microbiology. Although in most instances host or symbiont origin of key compounds remains debatable, in at least some cases this has been established. Metagenomic analysis of the Japanese sponge *Theonella swinhoei* indicated bacterial production of onnamides (Piel *et al.*, 2004), potent cytotoxins of the polyketide family. A related compound, pederin, is known only from a symbiont of terrestrial beetles, begging the question as to what evolutionary and ecological forces might have led to the presence of such similar substances in the symbionts of such dissimilar hosts. Harnessing the chemical potential of sponge-associated microbes could overcome the acknowledged supply problem with marine natural products and create an essentially inexhaustible source of novel drugs from the sea.

What makes a symbiont? Microorganisms are a major food source for filter-feeding sponges and yet, paradoxically, they thrive alongside phagocytic sponge cells within the host tissue. True symbionts may be shielded from sponge consumption due to specific recognition mechanisms or surface characteristics, for example, slime capsules. The recently published (meta)genome of ‘*Cenarchaeum symbiosum*’, the uncultivated archaeal symbiont of the Californian sponge *Axinella mexicana*, has yielded the first genomic insights into this issue (Hallam *et al.*, 2006). The ‘*C. symbiosum*’ genome contains many genes encoding cell surface, regulatory functions and defence mechanisms, some of which are absent from the ubiquitous free-living relatives of this species. Future genomic studies of sponge symbionts will revolutionize our understanding of a range of host–symbiont phenomena, such as signaling between partners, metabolic interdependencies and possible symbiont genome reduction.

The obvious appeal of sponges – and their microbes – to pharmacologists and biotechnologists will ensure future interest in this field. More basic aspects of sponge microbiology research, namely microbial function, (co)evolution and host–microbe interactions, should flourish as we seek to better understand this, perhaps the most ancient of all microbe–metazoan symbioses.

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