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Editorial

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Editorial: special issue on sponge microbiome

Sponges, the oldest extant multicellular animals (i.e. more than 600 million years old), are holobionts comprised of the host and its symbiotic microbes. Marine sponges are ecologically important components of coral reef ecosystems where they provide habitat for a wide range of species and couple the benthic and pelagic zones through their high seawater filtration capability. Sponge holobionts are also a hotspot for bioactive molecule discovery as they produce a rich source of marine natural products.

Symbiotic microbes in sponges are ecologically important due to their interactions with the sponge host and the environment. A number of characteristics that were originally attributed to the host sponge (e.g. nutrient cycling, secondary metabolite production) have now been shown to be capabilities of the symbiotic microbial community. As a result, sponge microbiology has become an active research area within marine microbiology and marine biotechnology. During recent decades, the field of sponge microbiology expanded quickly, particularly with studies that elucidated the composition and functional potential of the sponge microbiome using next generation sequencing technologies. In 2016, the Global Sponge Microbiome Project, a part of the Earth Microbiome Project, was announced. Soon afterwards, the first comprehensive dataset of sponge microbial populations was published (Moitinho-Silva *et al*. 2017).

In 2011, Ute Hentschel and Michael Taylor organized the 1st International Symposium on Sponge Microbiology (ISSM) in Würzburg, Germany. This was followed by the 2nd ISSM in Baltimore, USA, in 2014 hosted by Dr. Russell T. Hill. To provide another forum to exchange the latest achievements in sponge microbiology, Dr. Zhiyong Li organized the 3rd ISSM in Shanghai, China, Oct. 25–29, 2018, at the Shanghai Jiao Tong University. More than 100 participants from the United States, Germany, Britain, Switzerland, Australia, Israel, Netherlands, Japan, Estonia, Bangladesh and India, as well as nearly 80 participants from China, attended the 3rd ISSM. A total of 35 speakers gave presentations across two sessions, one focused on the sponge microbiome and sponge-microbe symbiosis, the other on sponge microbial natural products biosynthesis. This thematic issue on the Sponge Microbiome was compiled in connection with the 3rd ISSM, including one mini-review as well as 12 original research articles contributed by scientists worldwide. These contributions cover how sponge-associated microbial diversity varies with geography and host phylogeny as well as the contributions of sponge symbionts to nutrient cycling, chemical defense and environment acclimatization.

One reason for the success of sponges as one of the most dominant organisms in marine ecosystems is their close association with microorganisms. Sponges have generally been classified as either high microbial abundance (HMA) or low microbial abundance (LMA) species, according to their symbiont abundance and diversity. Cleary *et al*. (2019) found that a number of sponge species did not fit neatly within the HMA/LMA dichotomy and instead contained prokaryote communities intermediate between HMA and LMA species. Interestingly, Yang *et al*. (2019) demonstrated that both the diversity and structure of sponge microbiomes were highly specific to the host phylogeny at the order and family levels.

To better understand how geography and host phylogeny cause variation in the sponge microbiome, Swierts, Cleary and de Voogd (2018) compared the prokaryotic communities of 44 giant barrel sponges (*Xestospongia* spp.) and suggested that the variation in these communities was primarily associated with geography as opposed to phylogenetic relatedness. Knobloch, Jóhannsson and Marteinsson (2019) observed a single, dominant bacterial taxon, '*Candidatus* Halichondribacter symbioticus', which was both a highly abundant specialist in *Halichondria panicea* and a low abundant opportunist in other sponge species. Furthermore, Wu *et al*. (2018) described a detailed profile of sponge-associated microbiomes at different life stages of the sponge *Tedania* sp., where some bacterial species were recovered only at particular life stages, e.g. Synechococcales in adults and Enterobacteriaceae in larvae.

An overview of the recent advances in understanding microbially-mediated carbon (C), nitrogen (N), phosphorus (P) and sulfur (S) cycles in sponge holobionts was summarized in the mini review from Zhang *et al*. (2019), and a conceptual model that described potential interactions and constraints in the major nutrient cycles was proposed. Compared with nitrogen cycling, microbial roles in carbon utilization in sponge holobionts have been rarely identified. Feng *et al*. (2019) evaluated functional gene transcripts for CO_2 assimilation and CO oxidation in the sponges *Theonella swinhoei*, *Plakortis simplex* and *Phakellia fusca* Transcribed genes for autotrophic CO_2 assimilation (*rbcL* and *rbcM*), anaplerotic CO_2 assimilation (*accC*) and aerobic CO oxidation (*coxL*) were identified and assigned to a wide variety of bacterial lineages. Some of these carbon metabolism genes demonstrated specificity for particular sponge species. Using genomic comparisons of uncultured Rhodospirillaceae from *Spongia officinalis* and free-living taxa, Karimi *et al*. (2018) showed that the major contribution of microbial symbionts to host fitness likely related to nutritional exchange and host detoxification (through e.g. ammonium assimilation).

In addition to microbially-mediated nutrient cycling, chemical defense is another important role played by some sponge symbiotic microorganisms to ensure the survival of sponges in complex ocean ecosystems. Helber *et al*. (2019) showed that sponges from Zanzibar hosted diverse prokaryotic communities

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that were host species-specific and enriched in various pathways responsible for secondary metabolite production. In the biosynthesis of brominated and chlorinated secondary metabolites, halogenases were found to be key enzymes. Gutleben *et al.* (2019) proposed that sponge-associated Chloroflexi and Actinobacteria were the putative producers of halogenases which may contribute to the chemical defense of their host. To characterize microbial contributions to other classes of secondary metabolites, the diversity of PKS/NRPS genes from bacteria isolated from 49 sponge species from the Beibu Gulf, South China Sea was presented by Liu *et al.* (2019).

Distinct microbial populations (e.g. *Candidatus Entotheonella*) with no significant differences among chromotypes and/or sites were found in the cave dwelling sponge *Plakina kanaky* (Porifera, Homoscleromorpha) that may be linked to its ecological success in dark and oligotrophic environments (Ruiz *et al.* 2020). Kandler *et al.* (2018) discovered that microbial flexibility did not underpin host survival under ocean acidification by performing a reciprocal transplantation of the sponges *Coelocarteria singaporensis* and *Stylissa* cf. *flabelliformis* between a control reef site and an adjacent CO_2 vent site in Papua New Guinea.

These contributions to this special volume showcase considerable progress in the broad field of sponge microbiology but also highlight the key knowledge gaps in sponge microbiome research. An era of 'holobiont' research has emerged to investigate the intricate network of interactions between a host and its symbiotic microbial consortia. It is expected that sponge microbiology research will be greatly improved by future studies at multiple space and time scales using the ideas and techniques of systems biology and ecology. In order to move the field of sponge microbiology forward, the following research directions are suggested:

1. Research on sponge holobionts as both an individual as well as an interacting ecosystem. The sponge host provides a special habitat for its symbiotic microbiota, and the microbial processes in the sponge holobiont have an impact on the health of the host and the surrounding ecosystem. Accordingly, research on sponge holobionts needs to encompass the disciplines of biology, ecology, chemistry and pharmacognosy, applying and integrating techniques (e.g. laboratory and *in situ* analysis, deep-sea sampling, multi-omics) to greatly promote our understanding of sponge microbiology and symbioses.
2. Additional emphasis on the uncharacterised microbial community members in sponges. Since 2000, remarkable advances have been achieved in describing the microbial community, in particular the species-specific, core and abundant bacterial or archaeal components in sponge microbiomes. However, we still know little about the diversity and roles of viral and eukaryotic (e.g. fungi, protists) symbionts.
3. Studies on the function of the sponge microbiome. Some progress has been made in revealing the functional potential of sponge microbes, cultured or uncultured, by using traditional strategies or -omics approaches. However, our knowledge of the metabolic potential of most sponge symbionts remains limited, particularly with respect to uncultured microbes.
4. Symbiotic mechanisms based on interactions between/among members of the sponge holobiont. The understanding of host-microbe and microbe-microbe interactions and coevolution of sponge symbionts would illustrate the molecular mechanisms underpinning host-microbe symbiosis. In this respect, the role of natural products in signaling and chemical defense needs to be addressed.
5. The mechanisms shaping the ability of the sponge holobiont to acclimatize and adapt to global climate change. In an open ecosystem, sponge holobionts are increasingly threatened by anthropogenic stressors and environmental changes (e.g. seawater acidification, warming) which jeopardize the health and function of the sponge holobiont. Further research is needed to understand microbial contributions to holobiont acclimatization. To validate the role of the sponge microbiome in host health and environmental acclimatization represents one of the frontiers in sponge microbiome research.
6. Elucidation and characterization of natural products (NPs) from sponge microbes. Sponge holobiont-derived NPs, most of which are thought to be of microbial origin, account for nearly one quarter to one third of the total number of marine NPs. However, there is still a considerable bottleneck in our understanding of sponge holobiont NPs. Metagenomic strategies have revealed potential NPs from uncultured microorganisms in sponge holobionts, but successful heterologous expression of the gene clusters has remained challenging.

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Zhiyong Li
State Key Laboratory of Microbial Metabolism, School of Life Sciences & Biotechnology, Shanghai Jiao Tong University, Dongchuan Road 800, Shanghai 200240, P.R. China

Ute Hentschel
RD3 Marine Symbioses, GEOMAR Helmholtz Centre for Ocean Research Kiel, Du¨sternbrooker Weg 20, 24105 Kiel, Germany

Nicole Webster
Australian Institute of Marine Science, PMB 3, Townsville MC QLD 4810, Australia

Julie Olson
Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA

Max Häggblom
Department of Biochemistry and Microbiology, Rutgers University, School of Environmental and Biological Sciences, 76 Lipman Drive, New Brunswick NJ 08901, USA

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