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New insights and research prospects from the ocean microbiome

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A Viewpoint on the Frontiers in Science Lead Article

Metagenomic probing toward an atlas of the taxonomic and metabolic foundations of the global ocean genome

Key points

- While providing outstanding opportunities for genomic discovery within the ocean microbiome, the KAUST Metagenomic Analysis Platform (KMAP) Global Ocean Gene Catalog 1.0 provides a baseline for the changing microbial communities and activities of the ocean as they react to global warming, ocean acidification, and pollution.
- Considering the diversity of life in the ocean, the KMAP Global Ocean Gene Catalog 1.0 showcases underexplored marine viruses and fungi with novel roles in organic matter degradation, scavenging, and turnover.
- Ultimately, the KMAP platform used to assemble and analyze the Global Ocean Gene Catalog 1.0 will prove its worth empirically through researchers, with emerging agendas and new questions, who utilize this resource. Intercalibration and comparability of its taxonomy and functionality pipelines with other genome analysis platforms will be crucial for its wider adoption.

Researchers with a certain amount of experience cannot help noticing the fast turnover of software tools and databases in the bioinformatics landscape. In order to thrive, metagenomic analysis and annotation tools have to remain up to date in terms of content, organization, and taxonomy; they have to be maintained by a devoted team of curators; and they should offer access and handles for a diverse and active user community that prevents them from falling into disuse (1). Finally, long-term institutional support is essential for staying power and longevity in this ever-changing field. The KAUST Metagenomic Analysis Platform (KMAP) appears among the latest entries within the field of large-scale metagenomic analysis and annotation. In their *Frontiers in Science* article, Laiolo and colleagues deliver an impressive rollout for the KMAP by assembling and analyzing an extensive global marine metagenome dataset, the Global Ocean Gene Catalog 1.0, which represents over 2,000 metagenomic

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samples predominantly from the open ocean and, to a smaller extent, from coastal waters and benthos (2). Numerous marine metagenomic samples from the European Nucleotide Archive (ENA; www.ebi.ac.uk/ena) were extracted as of May 2018 for processing in the KMAP, which includes quality control of readings and assembly of metagenomes (3). The large volume of this marine gene survey imposes some limits on the level of phylogenetic and functional detail that can be accommodated in a paper of reasonable length; therefore, this study emphasizes broad occurrence patterns of microbial classes and phyla, and major metabolic pathways.

When trying to assess potential trajectories of the KMAP, which range from a strictly in-house tool at KAUST to a more widely used metagenomic analysis platform, it certainly helps to look at the results of this global marine survey and to comment on outcomes that will capture the attention of researchers today and tomorrow. First and foremost, this survey provides a benchmark for the global ocean microbiome in the early 21st century, as environmental change-heat uptake and warming of the water column, increased ocean stratification and development of water column anoxia, increased acidification and dissolution of calcareous plankton, and spread of pollution and pathogens-is engulfing the ocean and its microbiome on all fronts (4). This survey captures anaerobic microbial pathways (sulfate reduction, anammox, and nitrate reduction) that are becoming more widespread in response to increasing eutrophication, water column stratification, and suboxic or anoxic conditions in the water column; thus, changing microbial community and pathway profiles act as indicators of global change. Metagenomic samples, which are time-stamped and precisely localized, provide an archive of the ocean microbiome that will extend into the future. While microbial taxonomy and functional annotation in future databases and pipelines will evolve, archived metagenome data provide a baseline against which newly added metagenomes will be compared to record microbial ecosystem change over time. Of course, keeping such efforts on track is not just a challenge for the KMAP but for all metagenomics platforms, and it requires intercomparability and standardization of annotation pipelines.

Metagenomic sequence analysis is perhaps the premier avenue for the discovery of unexpected diversity and new types of microbial life; without metagenomics, the rapid growth of the microbial tree of life would have been unthinkable. While the approximate outlines of the genomic bacterial and archaeal tree of life are becoming visible, this cannot yet be said for the vast domain of parasitic DNA and its viral carriers even after three decades of sequencing environmental genes and genomes. While Bacteria and Archaea get their due, the authors highlight viral diversity as one of the key results of their survey, noting that viral genomes contain far more genetic novelty than previously realized even considering that this DNA-based assessment of the global ocean genome omits RNA viruses. Given their sheer abundance in the ocean, viruses exert key controls on marine biogeochemical cycling (5). "Localized" studies of marine viruses that are associated with specific microbial lineages seek to narrow the field to make it manageable but have instead uncovered swarms of unexplored viral genes that surround their microbial hosts in veritable gene clouds; this is exemplified by two recent studies that limited the hunting grounds to very particular

Archaea but found much more than they had bargained for (6, 7). Looking beyond the constraints of a large-scale survey, more detailed functional, structural, and phylogenetic annotation of viral genes and gene products will remain an ongoing challenge.

Another major result that the authors have singled out (and for good reason) is the unexpected prominence of fungi in the mesopelagic water column. The mesopelagic zone is where the sinking biomass of photosynthetic organisms originating in the surface ocean undergoes degradation and remineralization, which is marked by slowing migration and high oxygen demand at the thermocline and pycnocline. Fungal infections of phytoplankton, for example, chytrids colonizing living diatoms, may play a previously underestimated role (8, 9). Diverse lineages of parasitic or free-living marine fungi may emerge as major catalysts of organic matter degradation and turnover. That said, taxonomy annotation pipelines and sequence databases have trouble when it comes to the classification of uncultured or barely cultured fungi. Likewise, this analysis stops at the threshold of pointing out "There be fungi!". Regardless of these limitations, it is becoming obvious that the contribution of marine fungi to carbon cycling can no longer be ignored, and this study calls attention to this important issue.

The fungal problem touches on a perennial database issue: the rapidly evolving taxonomy of microorganisms. To mention examples from relatively well-cultivated microbial lineages, the class Deltaproteobacteria has morphed into the phyla Deltaproteobacterota, Myxococcota, and Bdellovibrionota (10), and the class Epsilonproteobacteria has become the phylum Campylobacterota (11). Taxonomic turmoil has been particularly severe among uncultured Archaea and Bacteria, where revised class- and phylum-level lineages are proposed based on genomes and metagenomes (12). The resulting taxonomy developed by the Genome Taxonomy Database (GTDB) continues to evolve as new metagenomic branches of life are added (13). The KMAP Global Ocean Gene Catalog 1.0 largely uses the more traditional National Center for Biotechnology Information (NCBI) taxonomy that accommodates historically grown database structure and content (14). Future KMAP maintenance will require that a watchful eye be kept on the rapid development of microbial taxonomy. Finally, regular updates to KMAP will be needed for it to remain current and intercomparable, as outlined by the FAIR (Findable, Accessible, Interoperable, and Reusable) principles for scientific data management and stewardship (15).

Given the challenges of rapidly evolving microbial taxonomy, the limited number of benthic samples in this water columnfocused survey is probably a blessing in disguise since sedimentary habitats are generally anaerobic and harbor a distinct microbial biosphere of mostly uncultured bacterial and archaeal lineages that do not occur in the water column (16). Except for persistently anoxic basins and growing oxygen minimum zones, the water column of the modern ocean is a biosphere dominated by oxygen-respiring life, and it contains the lineages of life that have adapted to the presence of this strong oxidant. Diving into anaerobic waters and sediments, and their ancient microbial inhabitants, could provide an interesting challenge for the KMAP team, and it may serve as a welcome opportunity to keep the spotlight on the KMAP. Finally, intercalibration and comparisons with other metagenomic pipelines, for example, by working on shared datasets or emerging timelines of microbial ocean change at selected locations, should provide further avenues to integrate the KMAP into the global community of metagenomic researchers.

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Author contributions

AT: Writing – original draft, Writing – review & editing, Conceptualization, Data curation.

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Conflict of interest

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