Decoding virus-host interactions in the oxygen-starved ocean

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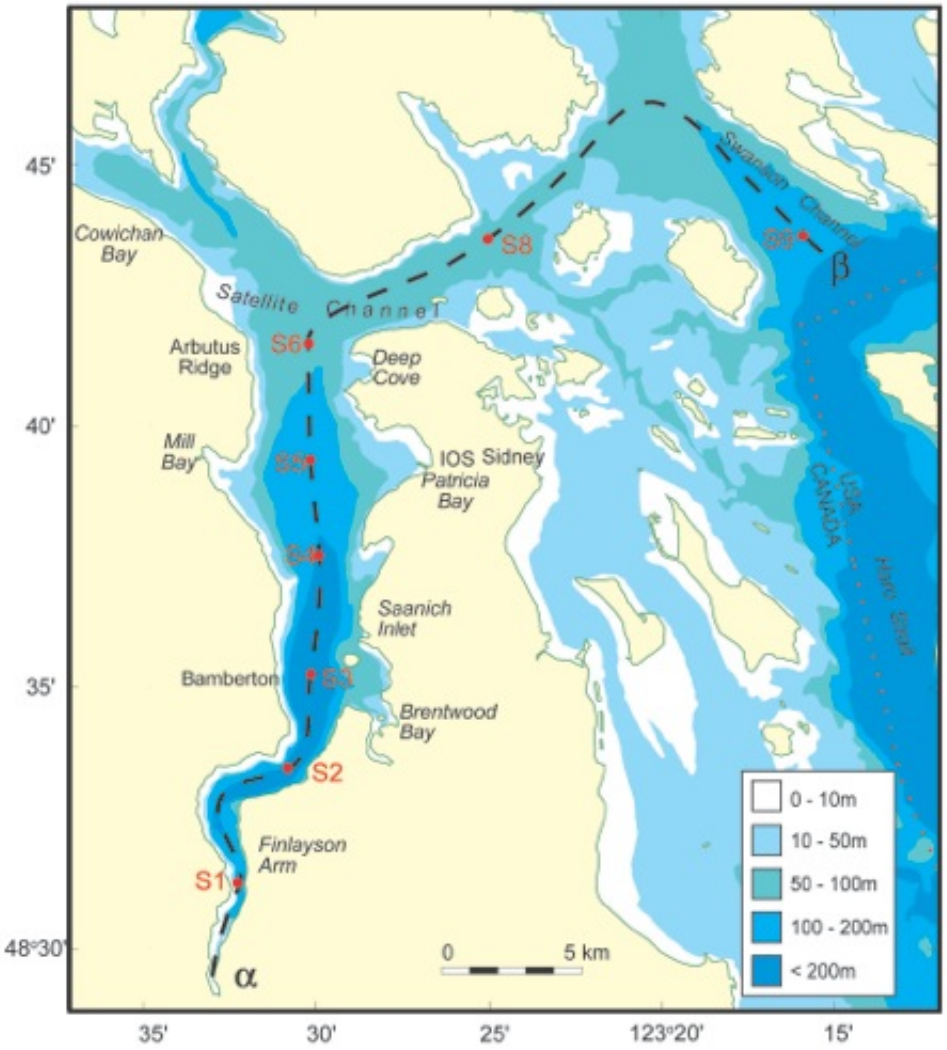

Map of Saanich Inlet with water depths denoted in color. Credit: Hallam lab

For multicellular life—plants and animals—to thrive in the oceans, there must be enough dissolved oxygen in the water. In certain coastal areas, extreme oxygen-starvation produces "dead zones" that decimate marine fisheries and destroy food web structure. As dissolved oxygen levels decline, energy is increasingly diverted away from multicellular life into microbial community metabolism resulting in impacts on the ecology and biogeochemistry of the ocean.

Over the past 50 years, oxygen minimum zones (OMZs) have expanded due to climate change and increased waste run-off from farms and cities. There are currently more than 500 OMZs worldwide, encompassing roughly eight percent of ocean volume that is considered oxygen-starved. Microbial community metabolism in these oxygen-starved waters directly impacts nutrient and energy conversion processes, including the production and consumption of the greenhouse gases carbon dioxide, methane, and nitrous oxide. Knowing how microbial interactions change in response to OMZ expansion is crucial to understanding the organizing principles underlying coupled nutrient and biogeochemical cycling in the ocean and the balance of greenhouse gases in the atmosphere.

Collaborating with the U.S. Department of Energy Joint Genome Institute (DOE JGI), a DOE Office of Science user facility, Steven Hallam's lab at the University of British Columbia has been studying a microbial community dominated by SUP05, an currently uncultivated group of microorganisms, related to gill symbionts of deep-sea clams and mussels that thrive in the most oxygen-starved regions of the water column. In a recent study published online August 29, 2014 in the journal *eLife*, Hallam teamed up with another DOE JGI collaborator, Matt Sullivan of the University of Arizona, to investigate marine viruses infecting SUP05 to better understand how viral infection influences SUP05 ecology and metabolic potential.

"This study represents the first of its kind, exploiting the unique strength

of single-cell genomics to explore virus-host dynamics, including viral co-infections, in a completely cultivation-independent manner," noted Tanja Woyke, head of the DOE JGI Microbial Program and co-author of this study. "The resulting data provide a very robust foundation for future experimental work," she added. Woyke is also excited about the expansion of this work into dark matter branches of the microbial tree of life.

In work supported by a Gordon and Betty Moore Foundation Investigator Award, postdoctoral researcher Simon Roux led an effort to develop a novel method to identify viral sequences in microbial datasets, an approach that combines single-cell genomics with viral and microbial metagenomic sequencing to explore virus-host interaction dynamics over space and time. A principal conclusion of this study is that viruses appear to be much more important to marine microbial ecology below sunlit surface waters than earlier suspected.

For the Hallam lab, the research vessel MSV John Strickland provides an ideal sampling platform in the still waters of Saanich Inlet. Credit: Hallam lab

The Hallam lab studies the SUP05-dominated community in Saanich Inlet, a seasonally anoxic (oxygen deficient) fjord on the coast of Vancouver Island, British Columbia, Canada that is a natural laboratory for studying OMZs. Recent studies in Saanich Inlet estimated that SUP05 bacteria could be responsible for as much as five percent of global primary productivity, making them key players in ocean carbon cycling.

"Whenever you sequence a genome from an isolate or single-cell, you're potentially sequencing infecting viral genomes at the same time, and for a long time those viral sequences have been ignored given the focus on cellular genomes," Hallam said. "Through the single-cell genomics approach, we're able to define lineage-specific infections in natural populations of uncultivated microorganisms opening an unprecedented window on microbial and viral evolution and ecology." The Hallam Lab single-cell sequencing efforts were supported by grants from the Tula Foundation, the G. Unger Vetlesen Foundation and the Ambrose Monell Foundation.

In the study, the team collected several thousand individual bacterial cells from three depths spanning the Saanich Inlet oxygen gradient (at 100, 150 and 185 meters). Nearly 130 SUP05 single amplified genomes (SAGs) were recovered from this collection by the Bigelow Laboratory for Ocean Sciences and sequenced at the Genome Sciences Centre in Vancouver British Columbia. The sequences were then assembled, quality checked and annotated at the DOE JGI. Forty-two of the sequenced SUP05 SAGs were found to contain a total of 69 viruses

representing five new genera. These viral sequences provided new reference genomes and enabled a number of eco-evolutionary inquiries including lineage-specific viral infection and mortality estimates, biogeography and accessory metabolic gene potential. For example, using the new viral genomes as "hooks," Roux and colleagues queried 186 viral and microbial metagenomic datasets, many of which were generated through DOE JGI Community Science Program (CSP), to demonstrate that while SUP05 viruses were locally restricted to OMZs they persisted in the environment over several years, with some viruses evolving over that time interval.

"At this point, there's a lot of microbial community sequence data out there, but it's a lot harder to get the viral sequence data," said Sullivan. "What we've done is leverage the microbial datasets being generated for microbial ecology and automate the process to be able to see the viruses in that data. Here, the results surprised us as it appears that while viruses in sunlit surface ocean waters kill about a third of cells and keep organic carbon available for smaller cells, the same appears to be true in OMZs – even hundreds or thousands of meters below the ocean's surface. Further, the nature of the data mean that we can, for the first time, look at a single group's viral mortality, not just community-wide numbers. This is critical for specifically examining virus-host interaction dynamics, and reveals that viruses are playing a big role in OMZ biogeochemistry."

SUP05 breathes nitrate and exhales nitrous oxide. This respiratory process is coupled to carbon dioxide fixation and the removal of toxic hydrogen sulfide. The presence of SUP05 in non-sulfidic oxygen minimum zones prompted the description of a cryptic sulfur cycle linking the metabolic activities of SUP05 with other microorganisms involved in nitrogen and sulfur cycling. "What we're ultimately interested in understanding is how different microbial groups interact to drive carbon, nitrogen and sulfur cycling in OMZs," said Hallam.

"SUP05 is a hub for metabolic coupling in OMZs. By studying viruses that infect SUP05, we're beginning to recognize that viruses can alter the network properties of microbial communities with resulting feedback on nutrient and energy conversion processes, including the production and consumption of climate active gases. That's where one interesting twist to the story can be found. Given that a third of SUP05 cells may be infected at any given time, to what extent is carbon fixation and energy metabolism modulated by viral lysis or reprogramming?"

While the team is still trying to figure out how much carbon SUP05 is fixing, and how much of the greenhouse gas nitrous oxide the bacteria are releasing, Hallam pointed out that the work has provided tools allowing researchers to look at these interactions in a way that could lead to better ecosystem models. Sullivan noted that another research direction is to "go global and go dark," scaling up the datasets they're looking at to explore both viral and microbial dark matter.

Both Hallam and Sullivan credit their collaborations with the DOE JGI, particularly through the CSP, for both the opportunity and the capability to study virus-host interactions in OMZs. "These CSP opportunities are critical for building community resources. For example, when researchers isolate a new virus and want to know whether it exists in the world and where, it helps to compare its genome to available viral metagenomic datasets. Right now, at least half of these came out of two of our CSP projects to form the 'Pacific Ocean Virome' dataset," Sullivan said. "For viromics, at the moment this is the only systematically and quantitatively prepared dataset available, so the results provide a strong basis for making ecological inferences. This scale of data is critical, and such CSP deliverables are fundamental for the viral ecology community or anyone who wants to contextualize their favorite new virus."

Hallam noted that through the CSP program, his lab has been able to

generate 340 human genome equivalents of time-resolved microbial metagenome, and metatranscriptome data from OMZs. "That's the largest data set in existence specifically focused on OMZs," Hallam said. "The resulting open access archive promotes integrated science. When we wrote those initial CSP proposals, we didn't envision this kind of synthesis. However having the archive in place gives us the benefit of hindsight as new scientific questions come into focus."

Hallam also said that the data their labs have generated through the CSP has enabled them to conduct collaborative projects with the Environmental Molecular Sciences Laboratory, a DOE Office of Science user facility at Pacific Northwest National Laboratory. "Genomic and transcriptomic data generated in one national lab is empowering hypothesis-driven research in another focused on proteomic and metabolomic information. These collaborations between people, projects and platforms is opening the floodgates for systems biology in natural and engineered ecosystems in new and unexpected ways."

Provided by DOE/Joint Genome Institute

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