Metabolic cascades in marine microbial communities

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It is 3:00 AM and a thousand-pound rosette is swinging off the back of the ship. The rosette cradles dozens of Niskin bottles that contain water samples retrieved from various depths. As the crew laboriously secures all moving parts, you get soaked with 4 °C seawater setting up filters to capture the viruses and microbes in the water samples, the efforts hindered by the ship plowing through 25+-foot swells. Conical tubes roll around the bench and the microscope has been slammed so often that it is almost impossible to check that the filters are working. Two hours later the ship has arrived at the next station and the rosette is dropped back into the deep. This is your chance to catch some hours of sleep before doing it all over again. Only 3 weeks more to go. Drifting off in the bunk, you dream of sending undergraduate “volunteers” on the next research cruise.

In PNAS, Aylward et al. (1) describe a different type of microbial oceanography:

one where scientists need not be doused with frigid waters and deprive themselves of sleep to obtain valuable samples. Enter the semiautonomous Environmental Sample Processors (2), which gather high-resolution spatiotemporal samples for metatranscriptome analyses. Unlike ships, which steam from station to station, these Lagrangian drifters move with the water mass and repeatedly sample the same microbial community. Two drift tracks, one off the northern California coast and the other in the North Pacific Subtropical Gyre, have shown that the dominant photoautotrophic primary producers differ between the two habitats: *Ostreococcus*, a micro-Eukaryotic green algae was located near the coast and *Prochlorococcus*, a small cyanobacteria, preferred the open ocean. Not surprisingly, expression of photosynthesis-related genes was strongly circadian. However, the fine-scale temporal sampling showed that carbon dioxide accumulation (a.k.a. carbon fixation)

occurred just before sunrise in the open ocean and just after sunrise in the coastal system. In both cases carbon fixation ceased before peak solar irradiation. This decoupling of carbon dioxide concentration from the light-driven parts of photosynthesis reminds us that, despite the valid concerns about burning fossil fuels and ocean acidification, primary producers are often CO₂-limited.

Gene-expression data also show that heterotrophic microbes keep up their end of the bargain by producing the CO₂ as they feast daily on dissolved organic matter (DOM) that mostly contains sugars and polysaccharides produced by the photosynthesizers. So turns the oceanic carbon cycle. The most interesting finding from Aylward et al. (1) is that these heterotrophs succeeded each other in the same order in both systems; *Roseobacter* spp → SAR116 → SAR11 → SAR86 (Fig. 1). For example, once *Roseobacter* finished consuming its favorite DOM component, it slowed down its heterotrophic metabolism and let SAR116 gobble up its favorite DOM goodies. This rhythm is driven by DOM availability and community succession and is probably tuned by an autotrophic circadian clock (3).

Aylward et al.’s (1) observation of parallel heterotroph successional dynamics in coastal and open ocean waters is compelling because *Ostreococcus* and *Prochlorococcus* release very different types of DOM. Typically, microbial ecologists assume that the chemical composition of the DOM determines microbial community structure and metabolism. This has been shown in tropical coastal systems where macrobial primary producers (e.g., coral or algae) are the main source of DOM (4, 5). Consistent with Aylward et al.’s results (1), McCarren et al. (6) showed that the oxidative state of DOM dictated patterns of resource partitioning by different bacterial species, resulting in a temporal cascade of taxa and metabolic pathways. This means

Fig. 1. Overview on transcriptional cascades for key metabolic processes (carbon fixation, photosynthesis, translation, and oxidative phosphorylation; ox phos) in the microbial communities of California coastal waters and the North Pacific Subtropical Gyre (transcriptional maximas not shown). Diurnal photosynthetic active radiation and transcriptomic modules identifying the governing physical and chemical parameters in each system are shown along suggested factors triggering the onset of photosynthetic (light), carbon fixation (biological clock), and heterotrophic respiratory (DOM) metabolism. Note that the ΔG (J/mol) of DOM decreases during the heterotrophic cascade (figure modified from ref. 1).

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that the taxonomic structure and number of species in a community are determined by the redox state of the metabolized substrate. An emerging generalization resulting from these and other studies (4, 7, 8) is that the heterotrophic community and the associated core metabolic genes are structured by organic energy provisioning, whereas the inorganic nutrients determine the identity of the photosynthetic community.

These types of community successional dynamics have been observed on a wider temporal scale in the Sargasso Sea (7). In this case, the annual pattern starts with blooms of *Synechococcus* during water column stratification in late spring, followed by successive maximas of *Roseobacter* and SAR11, and finally a return to a *Prochlorococcus*-dominated system. Each stage of this succession was strongly correlated with changes in viral

predation and it was hypothesized that nutrients released from the lysed cells increased the rate at which one community replaced the other. Aylward et al. (1) do not report on viral dynamics. However, they did observe that the microbial populations were largely nonoverlapping, which suggests predation is driving strain diversification. Future analysis of their datasets should help us better

understand the role predators play in community succession on diurnal time scales. Now that scientists can use new tools like the Environmental Sample Processors to study marine microbiology and oceanography, we won't be up in the middle of the night filtering seawater while being hit in the head with airborne conical tubes. Now what to do with those undergraduates?

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6 McCarren J, et al. (2010) Microbial community transcriptomes reveal microbes and metabolic pathways associated with dissolved organic matter turnover in the sea. *Proc Natl Acad Sci USA* 107(38):16420–16427.

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