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## **SPOTLIGHT**

## DIATOM ECOLOGY AND MICROBIAL MAT STRUCTURE AND FUNCTION IN ANTARCTIC DRY VALLEYS

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Streams in the McMurdo Dry Valleys of Antarctica (MDV) are harsh habitats for life. Months of perpetual darkness and subzero temperatures are punctuated by months of perpetual sunlight, intense UV radiation, and temperatures that hover around freezing. The availability of liquid water regulates biological activity and limits the growing season to 6–10 weeks each year. These harsh conditions likely allow perennial microbial mats to persist in this freshwater environment (Fig. 1), as the rates of biomass accumulation exceed losses due to grazing metazoans and scouring (McKnight and Tate, 1997).

Despite the extreme selective conditions, MDV microbial mats harbor a diverse diatom flora. Diatoms comprise a large lineage of eukaryotic algae that are broadly distributed in aquatic habitats and contribute significantly to global primary productivity (Tréguer et al., 1995; Field et al., 1998). Their cell walls, or frustules, are constructed out of biogenic silica (SiO<sub>2</sub>), which can persist as a biosignature in sediments and the rock record for millions of years (Kooistra et al., 2007). The morphology of the frustule is generally species specific and is, therefore, relied upon for taxonomic identification, although cryptic species do exist (Beszteri et al., 2005). In MDV streams, approximately 42 species belonging to 17 genera have been taxonomically described. Phylogenetically, all of these species belong to the relatively young (30–50 Ma [Kooistra et al., 2007; Sorhannus, 2007]) group of bilaterally symmetric, raphid pennates that dominate in both modern marine and freshwater habitats.

Diatom remains are frequently used as paleoecological indicators, and we confer ecological preferences of ancient diatoms based on the ecological preferences of their modern counterparts. Understanding modern diatom ecology is therefore essential for constraining diatom-based paleoreconstructions. In the MDVs, for example, glaciologists have concluded that diatom assemblages from ancient stream-delta microbial mats indicate that the sea level during the late Quaternary Period was ~300 m higher than today (Miagkov et al., 1976). A later study revisited this analysis and found that the previous study incorrectly characterized the ecology of the diatom assemblages as marine when they were in fact inland species (Kellogg et al., 1980). This latter study concluded that the diatom assemblages reflect the occurrence of an ice dam that raised lake levels in the MDVs during the late Quaternary.

Characterizing the ecological preferences of diatoms in MDV streams is valuable not only for constraining paleoclimate studies, but also as a proxy for the function of microbial mats in the current state of rapid environmental change in the Antarctic. Physical processes have long been suspected to exert strong influences on MDV diatoms (McKnight et al., 1999). Recent studies have corroborated this assertion, showing that the duration and intensity of stream flow drives variation in

\* Corresponding author. Published Online: May 2013 diatom communities (Esposito et al., 2006; Stanish et al., 2011, 2012). Diatoms that inhabit MDV streams break into two groups: one is more abundant in fast-moving water with a stable flow regime; the other is more abundant in slow-moving, hydrologically unstable streams. The underlying mechanism for such habitat preferences is not understood, although size may be important (Stanish et al., 2011), as smaller, faster growing species can outcompete larger, slower growing species in a more stable environment.

Microbial mats typically contain consortia of bacteria, Archaea, and Eucarya that interact with both the external environment and their microbial neighbors (Spear et al., 2003; Ley et al., 2006; Feazel et al., 2008; Robertson et al., 2009). The first traces of cellular life on Earth are recorded in ancient stromatolites—laminated, lithified microbial mats—where oxygenic photosynthesis is thought to have evolved (Buick, 1992, 2008). Consideration of the relative importance of





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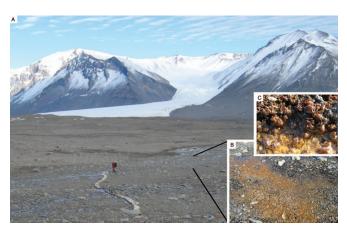


FIGURE 1—Harnish Creek Tributary in the McMurdo Dry Valleys of Antarctica. A) Glacial meltwater flows into stream channels that drain into closed-basin lakes on the valley floors. The unconsolidated sediments in this image represent much of the ground surface, while a stable stone pavement is found in numerous stream channels, which results from freeze-thaw action over many years. Large seepage areas and a wide hyporheic zone develop as meltwater infiltrates the unconsolidated sediment. Close-up of area. C) Vibrant black and orange colors are UV-protective pigments produced by filamentous cyanobacteria, which form the matrix. Gas bubbles within the microbial mat demonstrate the high photosynthetic rates that can be achieved. Photo credit: Breana Simmons.

physical versus biological processes in directing the formation of microbial consortia through time is therefore interesting, both from a practical and philosophical perspective. A mounting body of evidence supports the role of species interactions between bacteria and diatoms (Murray et al., 1986; Grossart, 1999; Bruckner et al., 2008). Consider, for example, that marine diatoms can produce reactive oxygen species that affect microbial Fe metabolism (Kustka et al., 2005). There are numerous reasons why microbes might want to interact mutualistically, such as when the byproducts of one species benefit the other (e.g., Orphan et al., 2001). Thus, species interactions within and between all three domains of life play an important role in microbial mat development, and possibly even in the evolution of new species (Hansen et al., 2007).

The role of species interactions is poorly understood, however, due primarily to the complexity of potential interactions: first, you must

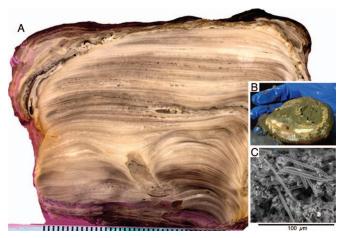


FIGURE 2—Cross section of a stromatolite from Obsidian Pool Prime, Yellowstone National Park, Wyoming. A) diatom-rich drape facies is observed as a prominent cleft in the upper left tracing under the top (itself, a second drape facies) and down to the right. The bulk of the image shows the main body facies with its stromatolitic fine laminae of silicified cyanobacteria (Berelson et al., 2011; Pepe-Ranney et al., 2012). Scale bar on bottom of image is in mm. B) view of an intact living stromatolite from the hot spring. C) Scanning electron micrograph that shows diatoms in tight association with the cyanobacteria-rich microbial mat of the drape facies.

tease apart which organisms are interacting; then, you attempt to determine the mechanism describing that interaction. Further complications are added when you consider microbial interactions occurring at the nanoscale (e.g., viruses) and at the molecular scale (e.g., hydrogen utilization [Spear et al., 2005]). The disconnect between the scale of interactions and the analytical scale becomes even greater if these interactions occur between many different species simultaneously. Technology, for example next-generation, high-throughput DNA sequencing techniques (e.g., pyrosequencing and Illumina sequencing), has allowed community ecologists to approach these questions with newly developed computational tools; however, as of yet, fine-scale analytic tools remain elusive.

Questions in microbial ecology can be daunting in new environments where little is known about species composition and function. Fortunately, a wealth of information exists on diatom ecology and species composition in MDV stream microbial mats. Recently, the relationships between diatoms and bacteria were examined from a bacterial pyrosequencing dataset and a corresponding diatom morphological dataset (Stanish et al., 2013). We found significant relationships between diatom and cyanobacterial-heterotrophic bacterial communities, and co-occurrence analysis identified numerous correlations between the relative abundances of individual diatom and bacterial taxa. Future studies could delve into these findings to formulate hypotheses and design experiments that uncover the mechanisms that drive these relationships and determine whether they result from species interactions

Additionally, the strength of correlations between heterotrophic bacteria and diatoms varied along a hydrologic gradient, indicating that flow regime can influence bacterial community structure just as it influences diatoms. This study reminds us that we can learn much more about microbes in new environments when we consider that they live as interacting consortia, in an ecosystem with applied chemical-physical forces, and that the ecology of seemingly unrelated organisms can provide useful insights into the ecological processes that influence microbial community structure. A second example of a diatom-rich microbial ecosystem is a living stromatolite from Yellowstone National Park (Fig. 2). Berelson et al. (2011), describe a finely laminated stromatolite with two facies of growth: a main body and a drape facies. The main body is made up of a novel cyanobacterium that constructs the stromatolite (Pepe-Ranney et al., 2012), and the drape facies is primarily composed of heterocystous cyanobacteria with a large number of pennate diatoms. The co-occurrence of diatoms with cyanobacteria in the drape facies may be due to atmospheric exposure of the drape facies. Alternatively, the heterocystous cyanobacteria could have a symbiotic association with the diatoms by fixing nitrogen, thereby feeding the stromatolite construction happening under the drape facies.

To conclude, the ecology of MDV diatoms informs our understanding of both modern and ancient processes, and we can uncover important ecological processes that drive species distributions using cross-species (and cross-domain) relationships. These relationships are apparently not unique to MDV mats, as living stromatolites in Yellowstone National Park also have unique diatom distribution patterns. While these large-scale community analyses can inform us about the processes that are likely present, examining species interactions remains difficult to definitively describe. The value in community-level analyses lies in their ability to screen overall patterns in community assembly under natural conditions. Thus, such studies provide a foundation for asking focused questions that allow us to understand the role of diatom-bacterial interactions in structuring microbial mat habitats.

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