Dry Valley Streams in Antarctica: Ecosystems Waiting for Water

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ECOLOGICAL LEGACIES ALLOW ABUNDANT CYANOBACTERIAL MATS TO OCCUR IN DRY VALLEY STREAMS

In the McMurdo Dry Valleys of South Victoria Land, Antarctica, the striking features of the stark landscape include the wide expanses of barren ground patterned with large hexagonal shapes created by periglacial (freeze–thaw) processes, the high mountains interspersed with alpine glaciers, and the large, permanently ice-covered lakes in the valley floors. For most of the year, it is the cold winds descending from the polar plateau that gradually shape the dry valley landscape. The dominant influences of wind erosion and cold temperatures on the landscape are less potent during the austral summer, when the temperatures become warm enough for melting to occur on the surface and face of the glaciers (Fountain et al. 1999). During runoff, streams flow down the sides of the valleys, carrying water, solutes, and sediments to the lakes.

Since the first exploration of the McMurdo Sound region of Antarctica by Robert Scott's expedition in 1904–1906, the dry valleys, which are located across the sound from Scott's base, have intrigued scientists from many disciplines. The McMurdo Dry Valleys are the coldest and driest deserts in the world and are representative of the 2% of the Antarctic continent that is ice free. The valleys encompass an area of approximately 4000 km^2. This region has experienced a warming trend since it was first explored, and most lakes have risen more than 1 m since 1968, when the New Zealand Antarctic Research Program began monitoring lake levels (Chinn 1993).

The biota that grow in the soils, lakes, and glacial meltwater streams of this harsh environment are primarily cyanobacteria, eukaryotic algae, mosses, and heterotrophic and chemoautotrophic bacteria. The multicellular organisms representing higher trophic levels are generally low in diversity and abundance. Aside from the occasional skua gull, the largest animals in the dry valley ecosystems are nematodes.

Streams in the McMurdo Dry Valleys region are very different from most streams on the planet. Dry valley streams are fed by melting glaciers and flow only for up to 10 weeks each year. They vary in length from less than 1 km to 30 km, in the case of the Onyx River in Wright Valley. Because of the lack of precipitation and terrestrial runoff, there are limited interactions between streams and the surrounding barren landscape. For example, because there are no vascular plants in the region, there is no leaf litter input to the streams. One might expect these streams to be relatively barren of life, and some of them are (Alger et al. 1997); however, in many streams diverse microbial communities persist despite the extreme conditions.

The microbial communities present in the dry valley streams consist primarily of cyanobacteria, although chlorophytes and diatoms are also common. The harsh conditions limit stream fauna to nematodes, rotifers, and tardigrades. There are no insects or other macroscopic stream consumers, which are common in most temperate streams. Algal communities grow in the streams as mats and have different colors because of photosynthetic and accessory pigments. These perennial algal mats can survive long periods of desiccation, allowing high biomass to develop, even by temperate-zone standards (McKnight and Tate 1997). Consequently, these streams can be hotspots of life in an otherwise barren landscape.

Research on dry valley streams has been conducted primarily in Wright Valley, Taylor Valley, and Miers Valley. Canada Stream, a productive stream in the Lake Fryxell basin of Taylor Valley (Figure 1), has been studied most thoroughly (Vincent and Howard-Williams 1986, Vincent 1988). Since 1993, additional research on the stream ecosystems has been conducted as part of the McMurdo Dry Valleys Long-Term Ecological Research (LTER) project, which is one of a network of LTER projects located in

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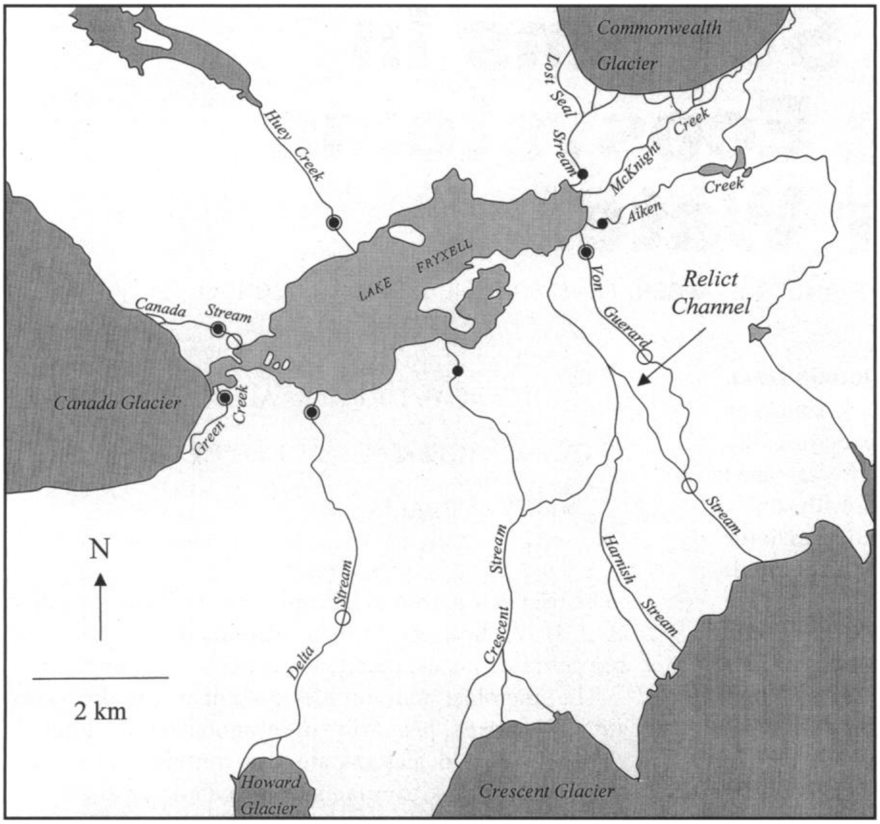


Figure 1. Map of the Lake Fryxell basin in Taylor Valley, McMurdo Dry Valleys region, Antarctica. Solid circles indicate stream gauging stations, and open circles indicate the locations of algal transect stations.

Figure 2. A dry valley stream (Priscu Stream, in the Lake Bonney Basin of Taylor Valley). The dark bands of the water-saturated hyporheic zone are visible along the stream. Stream width in the photograph is approximately 1–3 m.

22 diverse regions across the globe. In our research, we use descriptive measurements of hydrology, chemistry, and biology in combination with short- and long-term stream-scale experiments. In this article, we discuss the dynamic interactions between cyanobacterial mats in the dry valley streams and the physical and geochemical processes of the stream ecosystems. We also discuss the persistence of algal mats despite the long periods of desiccation and extreme cold and emphasize the ecological legacies (Moorhead et al. 1999) that control the response of stream ecosystems to the changing climate.

Characteristics of dry valley stream habitats

In the extreme environment of the McMurdo Dry Valleys, physical and chemical factors determine biological presence and activity. Therefore, characterization of the unusual hydrology, geomorphology, and geochemistry of dry valley streams provides a foundation for understanding the ecology of these streams.

Hydrology. The drainage of meltwater from the alpine glaciers into meltwater streams supports the brief annual productivity of the stream ecosystems. For 4–10 weeks during the austral summer, the meltwater streams become a distinctive feature of the barren landscape. The land surface is composed of an unconsolidated sediment that has large (5 m), hexagonally patterned ground features caused by periglacial processes. A layer of active permafrost, which freezes and thaws annually, begins 0.1 m below the surface layer and extends to approximately 0.5 m in depth. The true permafrost layer then begins at 0.5 m beneath the surface. The streambeds vary in width from 1 m to 30 m. Because the streambank vegetation is limited to small patches of moss, the stream banks consist of steeply sloped, poorly sorted sediment and are generally unstable. Undercutting of the banks during high streamflow periods can result in 1–2 cm deposits of sediment in lower reaches of the streams (Diane M. McKnight, personal observation).

During the austral summer, dark bands that border the streams can be seen (Figure 2); these moist areas, which develop as the summer progresses, are the surficial manifestations of the hyporheic zone. The term "hyporheic zone" refers to the area adjacent to and underneath the stream, in which water flows through the streambed in the downstream direction and exchanges with water in the main channel (Figure 3). In Huey Creek in the Lake Fryxell basin (Figure 1), the high permeability of the hyporheic zone sediment and the steep gradient of the stream result in exchange rates of water with the main channel that are more rapid than exchange rates measured in temperate streams at similar flows (Figure 4; Runkel et al.

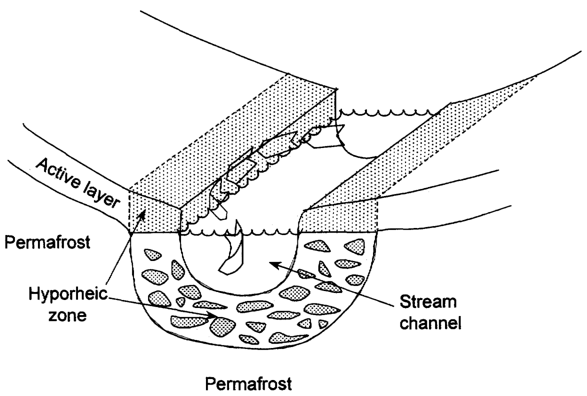


Figure 3. Schematic diagram illustrating the hyporheic zone in dry valley streams. Water leaves the main stream channel and passes through the substrate on the sides and below the stream and then may return to the main channel. Solutes also pass through the streambed and may undergo reactions that affect their transport. The hyporheic zone may also be a source of some nutrients to the water in the main stream channel.

1998). Measurements at low flow in Green Creek in the Lake Fryxell basin (Figure 1), which has a shallow gradient, yielded exchange coefficients that are at the high end of the range measured in temperate streams (Figure 4).

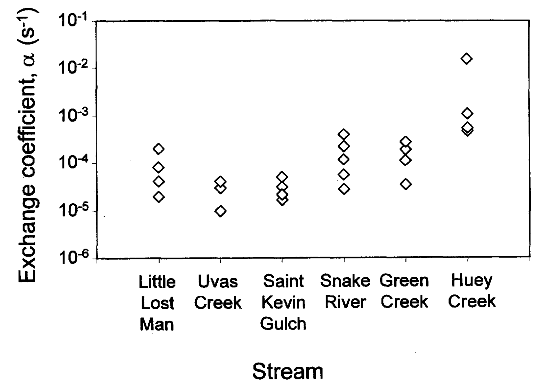
The rapid exchange rates and the absence of lateral inflows from shallow groundwater result in a substantial lateral extent of the hyporheic zone. For long streams during low-flow years, water storage in the hyporheic zone can account for a significant portion of the annual meltwater from the glacier (Bomblies 1998, Conovitz et al. 1998). The depth of the hyporheic zone is controlled by the thaw depth of the active permafrost layer (Figure 3), which extends to a greater depth throughout the valleys as the summer progresses. Measurement of the active-layer thaw depth at 18 transects on three different streams indicated that the depth was 5–10 cm at the beginning of summer and increased to 50–60 cm by the end of the summer (Conovitz 1999). Both the rapid exchange rates and the increasing volume through the summer indicate that hyporheic zone processes are potentially important in these stream ecosystems.

The measurement of stream flow provides a context for understanding interannual changes in the streams. The flow of the Onyx River in Wright Valley has been monitored at two gauging sites since 1968, and data for annual discharge to Lake Vanda indicate considerable interannual variation (Figure 5a). Because the Onyx River receives drainage from Lake Brownsworth, which abuts a piedmont glacier, as well as from tributary streams draining alpine glaciers, its flow may be affected by climatic conditions in McMurdo Sound in addition to those in Wright Valley. A network of stream gauges was established in the Lake Fryxell basin in 1990 (von Guerard et al. 1994) and was extended to include the entire Taylor Valley in 1993. Taylor Valley streams also have as much as a fivefold interannual variation in stream flow (Figure 5b; House et al. 1995).

In addition to showing interannual variation, average streamflow rates can show considerable daily variation during the summer, depending on insolation and air temperature. Hydrologic data indicate that stream flow can vary as much as 5–10-fold during a single day, depending on the orientation of the source glacier with respect to the solar trajectory (Conovitz et al. 1998). For example, the flow in Huey Creek can range from a trickle of clear water at 5 L/s in the early morning to a surging flow of turbid, sediment-laden water at 80 L/s by the afternoon. During cold periods, when there is no meltwater source from the glacier, the recession of the hydrograph is controlled primarily by drainage of the hyporheic zone (Conovitz et al. 1998).

To understand climatic responses of streams throughout the McMurdo Dry Valleys, it is important to know what causes variation in climate–stream flow relations. Our analysis (Bomblies 1998) indicates that, in addition to being related to variation in meltwater generation associated with characteristics of the glacier, some of the interstream variation is related to stream length and geomorphology, which affect the storage of water in the hyporheic zone. Because the physical processes that control the flow in the stream channels and hyporheic exchange have a high degree of temporal variability during a single day,

Figure 4. Comparison of hyporheic exchange rate among temperate and dry valley streams. The exchange rate is a measure of how fast water exchanges between the main stream channel and the hyporheic zone and is estimated from conservative tracer profiles. Diamonds indicate values estimated for individual reaches at each stream. Little Lost Man and Uvas Creeks are in California; Saint Kevin Gulch and Snake River are in Colorado; and Green and Huey Creeks are in Taylor Valley, Antarctica (data from Runkel et al. 1998, Diane M. McKnight, Robert L. Runkel, John H. Duff, Cathy M. Tate, Daryl L. Moorhead, unpublished manuscript).



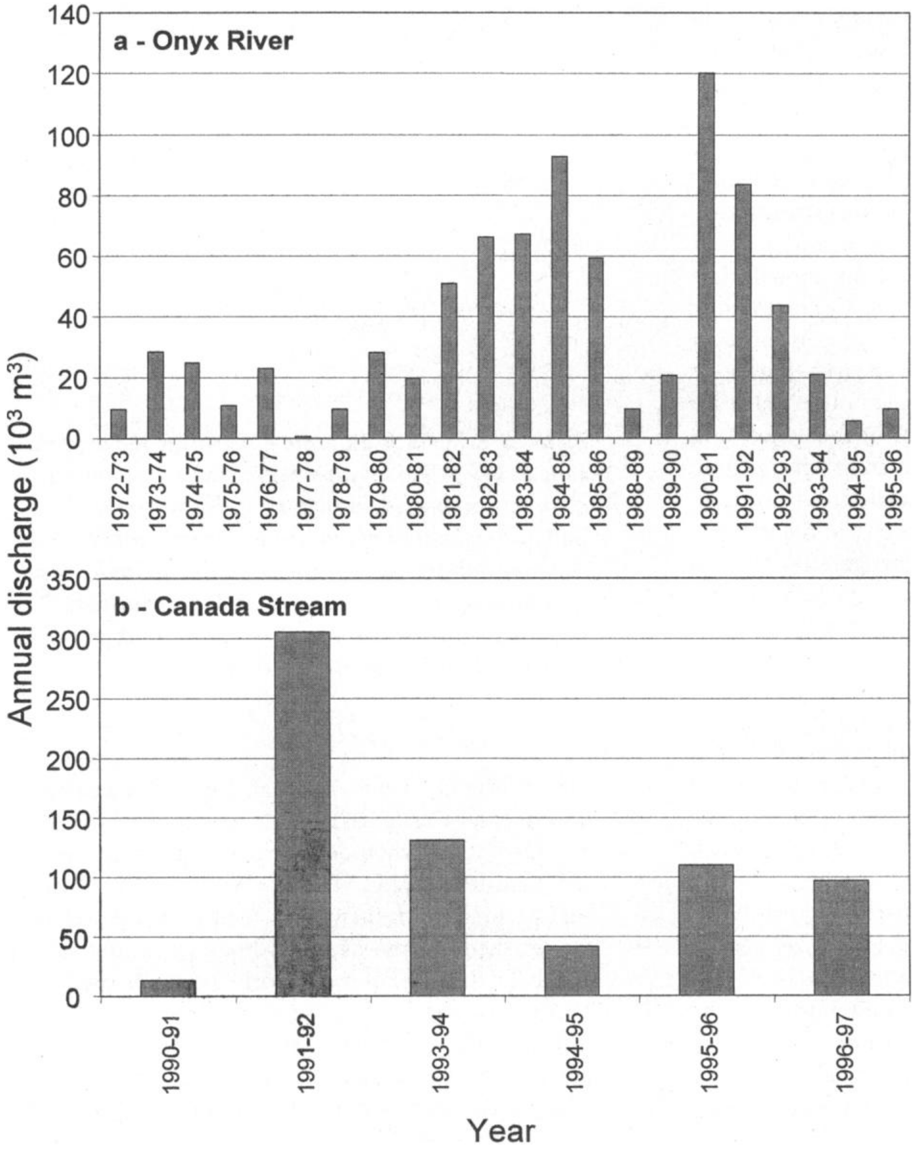


Figure 5. Annual variation in stream discharge for two of the McMurdo Dry Valley streams. (a) Onyx River, at Vanda Station in the Wright Valley (north of Taylor Valley). (b) Canada Stream, in the Lake Fryxell basin in Taylor Valley (see Figure 1).

within a summer, and among years, the stream habitat is dynamic during the brief summer period of flow. Thus, stream ecosystems contain algal species that must not only survive the long period of desiccation during fall, winter, and spring but also sustain primary production under a highly variable flow regime.

Geomorphology. Geomorphological features of the dry valley streams also control the suitability of streams for supporting algal mats. Algae are generally abundant in many moderate-gradient stream reaches, in which the rocks of the streambed are arranged in a stone pavement. These stone pavements are similar to those commonly found along the shores of alpine lakes, which form through periglacial processes. We infer that the stone pavements in dry valley streams are also a result of periglacial processes acting over long periods of time, perhaps centuries or longer. We propose that as the saturated alluvium freezes, the expansion of the alluvium surrounding a rock rotates the rock until the largest flat side is upward. This process, which occurs across the streambed, wedges the rocks together, creating the appearance of a flat pavement. The stone pavement configuration may limit sediment transport and scour and create smooth flow conditions, thereby providing a favorable habitat for algal mats (Alger et al. 1997). Thus, we propose that these stone pavements are an important physical legacy from past summers that promotes the current growth of cyanobacterial mats and shape the ecological system.

In contrast to their abundance in reaches of moderate gradient, algae are scarce in steep reaches of dry valley streams, where the rocks are uneven and jumbled, and in shallow gradient reaches, where the streambed consists of moving sand. In steep reaches, algal growth is present as sheets of the chlorophyte *Prasiola* on the underside of rocks. High stream velocities, turbulence, and abrasion may limit growth of other taxa in these steep reaches (Vincent et al. 1993a, Alger et al. 1997). Stone pavements probably do not form in steep reaches because the alluvium drains rapidly, before freeze–thaw processes move the rocks into a stone pavement formation. Furthermore, high-flow events may remove sand and smaller rocks in these reaches. In shallow reaches, which are common near the outlet to lakes, the instability of the sand substrate is most likely the limiting factor for algal growth (Alger et al. 1997). In both steep- and shallow-gradient reaches, rivulets of water occur on the sides of the active channel and are important habitat for algal mats. The rivulets, which are called parafluvial seeps, appear to drain the hyporheic zone. In shallow-gradient reaches, the algal mats in the parafluvial seeps may represent most of the algal biomass (Alger et al. 1997).

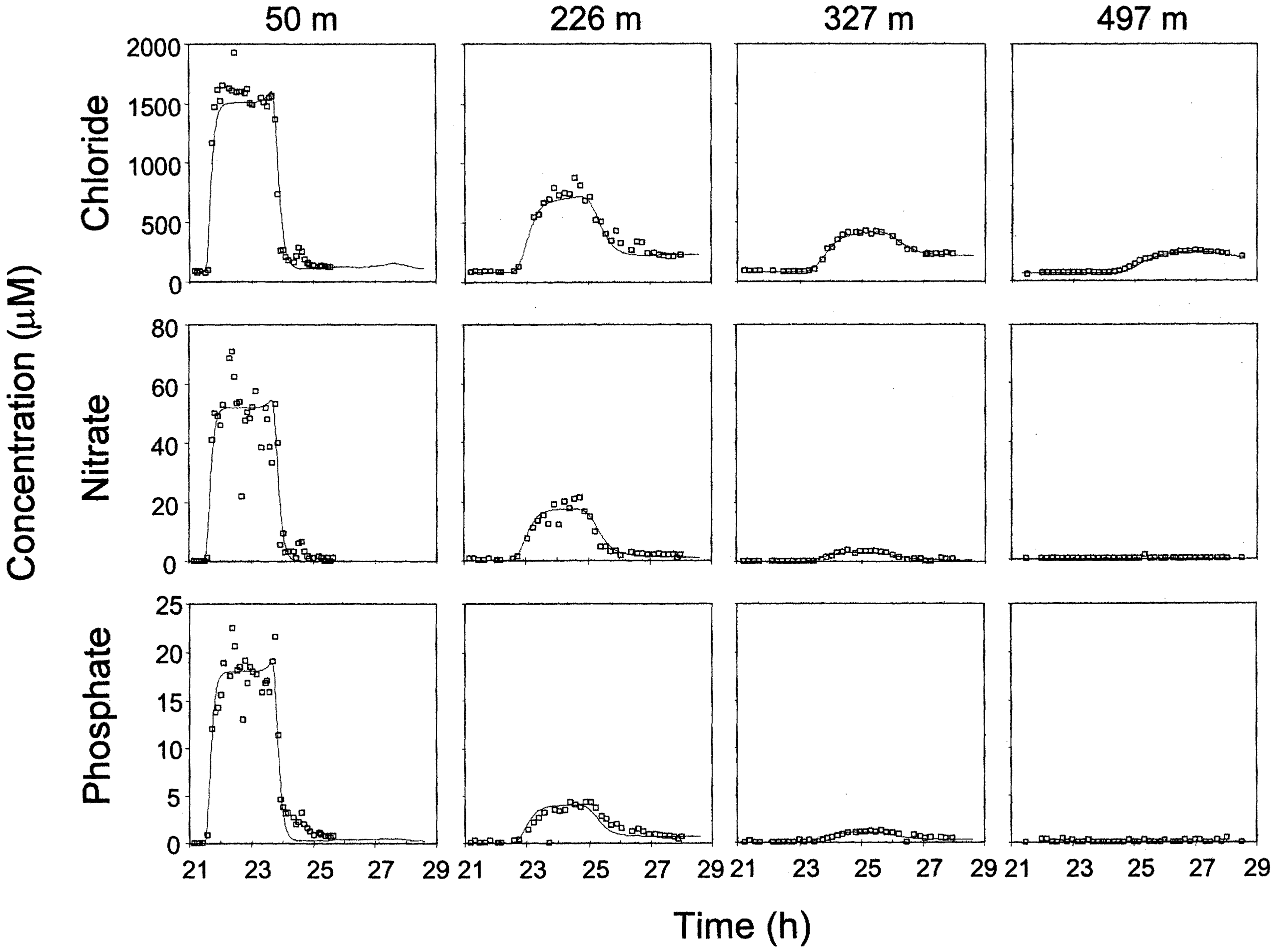


Figure 6. Concentration profiles at four sites below an experimental injection point of chloride (conservative tracer), nitrate, and phosphate. A solution of nutrients and chloride salt was injected into the stream for 4 hours (starting at 21 hours). Distance downstream from injection location is shown above panels. At the site 497 m downstream from the injection point, the absence of detectable concentrations of nitrate and phosphate indicates the rapid uptake of these nutrients by stream biota. The open squares represent actual data points, whereas the solid lines represent simulations using a hyporheic exchange model with variable flow and first-order uptake of nutrients (Diane M. McKnight, Robert L. Runkel, John H. Duff, Cathy M. Tate, Daryl L. Moorhead, unpublished manuscript). If the nutrients had behaved conservatively, their concentration profiles would be similar to the chloride profile at each site. The slight increases in concentrations at 50 m at the end of the injection result from a decrease in stream flow during that time.

Currently active streams in the dry valleys constitute only a subset of the fluvial features of the landscape. Satellite images reveal what appear to be relict stream channels in the McMurdo Dry Valleys region. Furthermore, approximately 50% of the streams marked on the topographic maps of the region do not appear to be flowing during the 1990s. Some of these "streams" may represent subglacial flowpaths that were carved out when terminal glaciers extended farther down the valleys (David R. Marchant, Boston University, personal communication). Other relict channels may have lost their water source after the retreat of alpine glaciers, which now feed new stream channels, or they may have been cut off from meltwater by upstream sediment deposition that formed a barrier to flow. Future field studies may reveal which of these features are truly relict stream channels, as opposed to subglacial flowpaths, and may indicate whether stone pavements were common habitats when the channels were active.

Biogeochemistry. Streams in the dry valleys link the glaciers and the lakes. Several abiotic and biotic processes in stream ecosystems affect the sources, sinks, and transport of chemicals along these flowpaths. These processes may occur not only along the streambed but also in the hyporheic zone below and alongside the active channel.

A role for hyporheic zones in biogeochemical cycling has been documented in many streams (e.g., Triska et al. 1993, Holmes et al. 1994, Jones et al. 1995, Mulholland et al. 1997). As discussed by Vervier et al. (1992), hyporheic processes are likely to play an important biogeochemical role in streams under conditions of high permeability. As water in the hyporheic zone exchanges with water in the main stream channel, solutes are also exchanged (Runkel et al. 1998). Examination of major cation and silicate data for many Taylor Valley streams indicates that weathering of silicate rocks and other minerals occurs in the hyporheic zone at surprisingly high rates (Lyons et al. 1998a, 1998b). This conclusion is further supported by observations that in von Guerard Stream in the Lake Fryxell basin, concentrations of major ions, including silicate, increase with distance downstream (Alexander Blum, Michael Gooseff, W. Berry Lyons, Diane McKnight, unpublished data). Similarly, Green et al. (1988) proposed that in dry valley streams, weathering of apatite is the source for phosphate, and leaching of atmospheric deposition is the source for nitrate. Thus, dissolved nutrients can be released through hyporheic zone reactions. Primary weathering reactions and dissolution of marine aerosols probably occur in the hyporheic zone, greatly modifying the chemical composition of glacial meltwater within the streams as water flows to the lakes (Lyons et al. 1998a).

Biologically controlled processing of stream solutes is also evident in dry valley streams. Mats of *Nostoc* cyanobacteria fix atmospheric nitrogen, accounting for as much as 10% of the nitrogen inputs in streams (Howard-Williams et al. 1989). Howard-Williams et al. (1989, 1998) reported that algal communities may transform inorganic nitrogen in dry valley streams to organic forms of nitrogen that are then transported to the lake ecosystems. Monitoring of stream chemistry has shown that nitrate and phosphate concentrations are higher in streams without algal mats than in streams with mats, indicating that algal uptake of nutrients in streams regulates inorganic nutrient flux to the lakes (Diane M. McKnight, Robert L. Runkel, John H. Duff, Cathy M. Tate, Daryl L. Moorhead, unpublished manuscript). Howard-Williams et al. (1998) also reported that nitrate concentrations decreased across the boulder pavement in the Onyx River, an area of extensive algal mats; concentrations of dissolved organic nitrogen increased across this reach. Moreover, in streams that have algal mats, nutrient concentrations in the hyporheic zone are higher than those in the stream water, indicating that there is a constant nutrient supply to the mats through hyporheic weathering and exchange with surface water. At the end of the austral summer, drainage from the hyporheic zone therefore becomes a source of nutrient-rich water to the algal mats.

To examine the controls on dissolved nutrient flux to the lakes, we conducted a nutrient injection experiment in Green Creek (Figure 1), a stream that has abundant algal mats. The injectate concentrations corresponded to drainage of nutrient-rich hyporheic water into the stream in late summer (55 μM nitrate and 18 μM phosphate; Diane M. McKnight, Robert L. Runkel, John H. Duff, Cathy M. Tate, Daryl L. Moorhead, unpublished manuscript). Chloride was injected and monitored as a conservative (i.e., nonreactive) tracer, and chloride data were used to model hydrologic exchange. Unlike chloride, nitrate and phosphate did not behave conservatively; concentrations of these solutes at the downstream sites were much lower than those of chloride (Figure 6). During the arrival of the chloride tracer at a site 497 m downstream of the injection point, nitrate and phosphate remained below detection (less than 1–2 μM), indicating rapid nutrient removal from the stream water (presumably because of algal uptake). Moreover, the production of nitrite at two intermediate sites (226 m and 327 m downstream of the injection point) indicates that other nitrogen cycling processes, in addition to uptake, were occurring during the injection of nitrate. Incomplete nitrification or denitrification could account for the nitrite production (Diane M. McKnight, Robert L. Runkel, John H. Duff, Cathy M. Tate, Daryl L. Moorhead, unpublished manuscript). We used a solute-transport model (Runkel 1998), in which nutrient uptake was represented as a first-order process, to determine reach-scale parameters for nitrate and phosphate uptake. The best match to the experimental data was provided by a model in which phosphate uptake occurs in the main channel and nitrate uptake occurs in the main channel and the hyporheic zone, possibly representing loss due to denitrification (7–16% of total nitrate uptake).

In summary, once the stream ecosystem has been "turned on" by the arrival of water, there will be some nutrient supply to algal mats through primary weathering, leaching of deposited aerosols, and internal nutrient transformations within the hyporheic zone. Algal mats take up inorganic nutrients from the stream but release dissolved organic nutrients, which are then transported to lakes. Scouring of the algal mats from the streambed during high flows then provides a source of particulate organic carbon, nitrogen, and phosphorus as well as microbiota to the lakes, but this flux has not been quantified.

Algal communities. The cyanobacterial mats in dry valley streams are essentially perennial, growing at a slow rate during the summer flow period and overwintering in a freeze-dried state. The abundance of cyanobacteria in dry valley streams is to be expected because cyanobacteria dominate the microbial populations of many extreme environments (Potts 1994). Furthermore, the survival of cyanobacteria in a freeze-dried state is not surprising; for example, freeze-drying is used for the preservation of bacterial samples in culture collections (Potts 1994). Previous ecological studies of dry valley algal communities have focused on the algal mats and mosses in Canada Stream, located in Taylor Valley (Figure 1; Howard-Williams et al. 1986, Vincent and Howard-Williams 1986, Vincent 1988). One remarkable observation is that some algal mats begin photosynthesizing within 10–20 minutes of being rewetted after desiccation (Vincent and Howard-Williams 1986,

*Figure 7. Algal mats growing in an area of stone pavement in Green Creek in the Lake Fryxell basin. Orange mats are present in the main channel (approximately 1 m across) and black (*Nostoc*) mats grow as tufts near the edges of the main channel.*

Hawes et al. 1992).

Compared to stream ecosystems at other sites in the LTER network, dry valley streams represent several extremes—they lack terrestrial inputs of coarse organic matter, they have high standing algal biomass, they have low primary productivity, and they have low grazing losses (McKnight and Tate 1997, Webster and Meyer 1997). The high standing biomass is a result of the perennial nature of the mats as well as the lack of macroinvertebrate grazing, which in turn is related to the harshness of the climate. Algal mats of filamentous cyanobacteria in the main channel usually consist of an orange upper layer that is enriched in accessory pigments, and a green lower layer that has greater chlorophyll *a* content and greater photosynthetic activity (Vincent et al. 1993b). The relatively low rates of primary productivity per unit streambed area and per unit chlorophyll reflect the fact that growth in the mats is restricted to the layer of algae on the underside of the mats.

The dry valley streams have widely varying productivity, in part because of variations in algal mat biomass. For example, whereas mats are abundant in Canada Stream, chlorophyll is nearly indetectable in House Creek, a stream in the Lake Hoare basin in Taylor Valley that flows through an ice-bound moraine (Alger et al. 1997, McKnight et al. 1998). Net primary production rates range from 0.6 ± 0.1 $\mu g \cdot cm^{-2} \cdot h^{-1}$ of carbon (mean ± 1 SE) for sediment at House Creek to 12.2 ± 1.3 $\mu g \cdot cm^{-2} \cdot h^{-1}$ of carbon for black *Nostoc* mats in the relict channel in the Lake Fryxell basin (Diane M. McKnight, Cathy M. Tate, Dev K. Niyogi, unpublished data). Primary production rates reflect differences in where algae occur. In streams that have abundant algae, the mats form extensive, blanketlike coverage over most of the streambed (Figure 7), whereas in streams that have sparse mats the algae occur as patches at the margins of the active channel or as smooth sheets on the sides and undersides of jumbled rocks, receiving sunlight when the sun is low on the horizon (Vincent 1988, Alger et al. 1997). Mosses occur farther up the stream banks, where they are wetted for short periods of the austral summer, or in flat areas that become damp but where open water flow does not occur (Alger et al. 1997).

To document the range of biomass content in the stream ecosystems, we collected samples of algae at 16 stream sites containing permanently established transects. At each site, we had delineated a transect across the stream and mapped a reach of approximately 40 m encompassing the transect; locations of topographic features, stream banks, thalweg (lowest point on channel bed), stream edges, wetted-zone edges, and distribution of algal mats had been recorded (Alger et al. 1997). Within each transect, algal mats were visually identified as either orange, red, black, or green, although not all types of algal mat were found at every site. Black mats are found near the channel margins, and green mats are attached to large rocks in the main channel. Orange and red mats occur in flowing water habitats, either in the main channel or in rivulets draining the hyporheic zone at the stream margins. Therefore, it is similarities in physical characteristics of the stream habitat, rather than differences in water quality, that determine the occurrence of the different algal mats in streams.

A total of 30 taxa of cyanobacteria and chlorophytes were present at the 16 stream sites, and the species composition of the different mat types was consistent among sites, even sites that differed widely in productivity (Alger et al. 1997). Evenness values (Zar 1996), which indicate homogeneity expressed as a ratio of diversity to maximum possible diversity, were calculated from the algal species composition of each community type (McKnight et al. 1998). The black algal mats were dominated by *Nostoc* sp. and had a low evenness of 0.13 ± 0.07 (mean ± SD). The green algal mats were also made up of essentially one species, being composed chiefly of *Prasiola calophylla* or *Prasiola crispa*, and had an evenness of 0.17 ± 0.10. The orange and red algal mats were composed of species of *Oscillatoria* and *Phormidium* and had more diverse assemblages of species. For the orange and red algal mats, the evenness values were 0.55 ± 0.16 and 0.48 ± 0.21, respectively. The orange and red mats also had a high degree of intrasite heterogeneity in species distribution, as indicated by data from five samples of orange mats collected within a 20 m reach in Green Creek (Figure 8). Based on the uniformity of the algal species across streams that range widely in productivity, we propose that the limited set of algal species that are found in dry valley streams represents a second major legacy (along with the first legacy, stone pavements) for the stream ecosystems.

In addition to cyanobacteria, 38 species of diatoms were identified in dry valley streams (Alger 1999). Many of these species (e.g., *Hantzschia amphioxys*, *Stauroneis anceps*, and *Pinnularia borealis*) are cosmopolitan and are

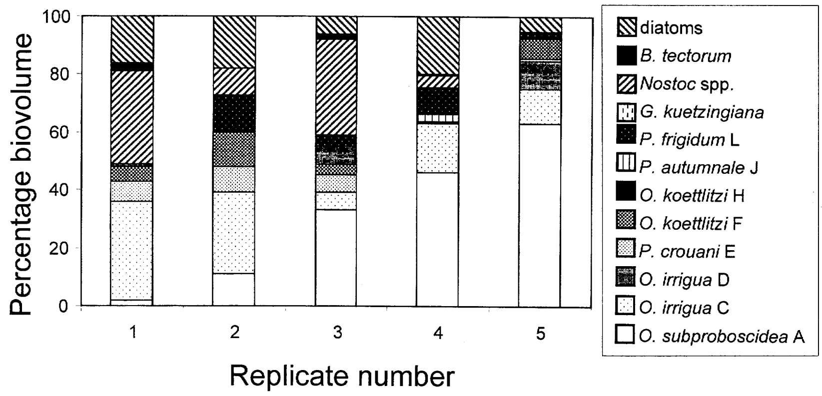


Figure 8. Species composition of orange algal mats from Green Creek in the Lake Fryxell basin. Five replicate samples, collected within 20 m of each other, highlight the intrasite variation in species composition in these communities. Genera are as follows: B.,* Binuclearia*; G.,* Gleocapsa*; O.,* Oscillatoria*; P.,* Phormidium*. Letters after species refer to morphotypes. Figure reprinted from Alger et al. (1997).

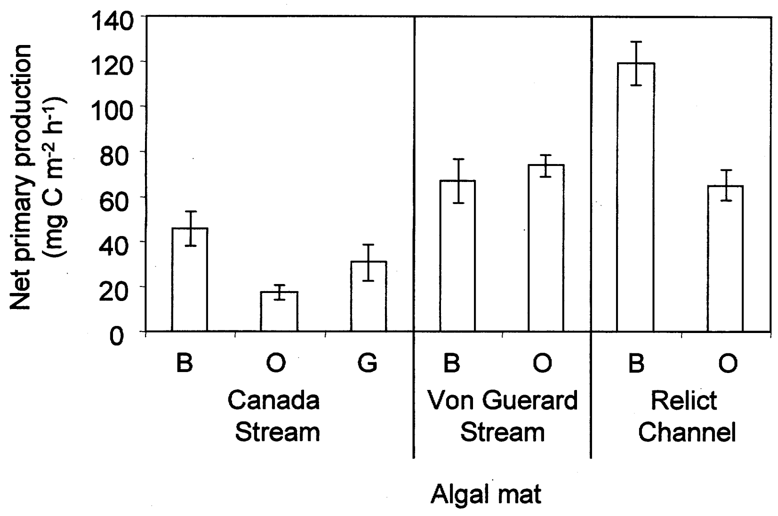
considered to be aerophilic or soil diatoms, whereas others (*Muelleria meridionalis* and *Muelleria peraustralis*) appear to be endemic to the Antarctic continent (Spaulding and Stoermer 1997). In fact, approximately 60% of the diatom species in dry valley streams may be endemic to Antarctica (Alger 1999).

Long-term persistence of cyanobacterial mats

To understand the basis for the long-term persistence of stream algal mats, we studied a relict stream channel for which sustained stream flow was last recorded in the summer of 1969 (Diane M. McKnight, Cathy M. Tate, Dev K. Niyogi, unpublished data). In January 1995, we constructed a sandbag control structure and routed meltwater to this relict channel (Figure 1). We discovered that both black and orange algal mats had persisted in the channel and that these mats grew rapidly within a few days of the arrival of flow. Because of the accumulation of aeolian material on the freeze-dried algae, these mats had not been apparent before flow was restored. Within 2 weeks, a full microbial ecosystem was active over the 1.5 km stream reach. Both mat types became quite extensive by the second week of flow. The species composing the black and orange mats were the same as those commonly found in similarly colored mats in other dry valley streams.

Experiments conducted during the second year after meltwater was rerouted to the relict channel indicated that the black mats in the relict channel had higher net primary productivity than black mats from streams that had consistent annual flow (Figure 9; Niyogi et al. 1998). The relict channel also had higher solutes, including nutrients, than other dry valley streams, which may account for the greater productivity of the mats (Diane M. McKnight, Cathy M. Tate, Dev K. Niyogi, unpublished data). This ongoing experiment has demonstrated that microbial stream ecosystems can persist in a cryptobiotic state for long periods and can respond rapidly to renewed flow. The tolerance of a cryptobiotic state, which allows the cyanobacterial mats to overwinter, also provides for the preservation of algal mats in inactive channels and their rapid response to climatic and geomorphological shifts.

Figure 9. Rates of net primary production of algal community types in three streams in the Lake Fryxell basin: Canada Stream, von Guerard Stream, and the relict channel. Mat types refer to colors, as follows: B, black algal mats (*Nostoc*); O, orange algal mats (*Phormidium*); G, green algal mats (*Prasiola*). Values are means ± 1 SE (from Niyogi et al. 1998).



Anthropogenic effects on stream communities

The long-term persistence of the stream ecosystems should be considered in the context of anthropogenic changes that may affect the dry valleys. The current and future effects range from local, apparently short-term site disturbances associated with scientists and tourists to the effects of climate and ultraviolet radiation associated with global processes.

The Antarctic Treaty System has adopted comprehensive protocols to limit environmental damage in the Antarctic by providing a system to assess environmental effects of planned activities. The stream research carried out by the McMurdo Dry Valleys LTER has been permitted after an environmental assessment process in which the activities were evaluated in the context of natural processes. The environmental protocols also apply to the activities of tourists visiting the dry valleys. During January 1995, the first visit of tourists to Taylor Valley—part of an overall increase in Antarctic tourism—brought several groups to the banks of Green Creek. Since then, tourist visits to the dry valleys have generally involved groups of 10–20 people brought in by helicopter from ships in McMurdo Sound. The environmental protocols for the dry valleys recommend several steps to minimize disturbance to the algal mats; these include crossing the stream at a perpendicular angle, avoiding stepping on the mats, and limiting activities on the banks that may deposit sediment into the stream. Tourists visiting the dry valleys may not be aware of the presence of algal mats and their perennial character, but the protocols will help them avoid disturbing the mats. While the streams are flowing, tourists probably would not choose to walk in the channel for any distance. However, before or after stream flow, the stream channels present easy pathways for foot travel and convenient flat places for helicopter landings. Extensive trampling of the freeze-dried algal mats in the channels could alter the stream ecosystems. The algal mats may be resilient to natural changes, poised waiting for water; however, they may not be resilient enough to withstand disturbance by modern-day tourists. Therefore, clear communication between scientists and tour operators in the dry valleys is essential for preservation of these unique ecosystems.

In addition, anthropogenic changes associated with the modification of the earth's atmosphere may result in changing temperatures and climate in the dry valleys. Nevertheless, because the interannual variation in climate and flow conditions is already very large, it is doubtful that the new mean climate would produce flow conditions outside the range observed in the past two decades. We hypothesize that the dry valley streams' response to climate is mediated by major ecological legacies, specifically the stable stone pavement of the streambed and the biodiversity of the algal flora. Although we would expect some change in spatial distribution of current mat types in the streams with a gradually changing climate, we would not expect dramatic shifts, such as loss of mat types.

The Antarctic has already experienced a change in the radiative environment associated with the springtime development of an ozone hole over the continent that allows penetration of ultraviolet radiation at intensities greatly exceeding those anywhere else on the planet (Jones and Shanklin 1995). This increased exposure to ultraviolet radiation occurs in August and September, well before the onset of stream flow. During these months, the freeze-dried cyanobacterial mats may be directly exposed to the increased ultraviolet radiation unless they are covered by accumulated snow or are shaded in an incised stream channel. The potential for damage to the mats and impairment of productivity in the following summer months will depend on the extent to which the radiation penetrates the upper layers of the mat to the lower layers, where active growth occurs (Vincent et al. 1993b). Cyanobacteria do have accessory pigments that limit damage from excess light and ultraviolet radiation (Vincent et al. 1993b, Hawes and Howard-Williams 1998), but the ability of these pigments to protect cells during prolonged desiccation is not known. For relict mats that go for many years without receiving flow, the damage from increased exposure to ultraviolet radiation may accumulate over time and could impair rapid regrowth once flow returns.

Summary and conclusions

An axiom of ecology is: "Where there is water, there is life." In dry valley ecosystems of Antarctica, this axiom can be extended to: "Where there has been and will be water, there is life." Stream communities in the dry valleys can withstand desiccation on an annual basis and also for longer periods—as much as decades or even centuries. These intact ecosystems, consisting primarily of cyanobacteria and eukaryotic algae, spring back to life with the return of water. Soil organisms in the dry valleys also have remarkable survival capabilities (Virginia and Wall 1999), emerging from dormancy with the arrival of water.

Streams in the dry valleys carry meltwater from a glacier or ice-field source to the lakes on the valley floors and generally flow for 4–10 weeks during the summer, depending on climatic conditions. Many of these streams contain abundant algal mats that are perennial in the sense that they are in a freeze-dried state during the winter and begin growing again within minutes of becoming wetted by the first flow of the season. The algal species present in the streams are mainly filamentous cyanobacteria (approximately 20 species of the genera *Phormidium*, *Oscillatoria*, and *Nostoc*), two green algal species of the genus *Prasiola*, and numerous diatom taxa that are characteristic of soil habitats and polar regions. Algal abundances are greatest in those streams in which periglacial processes, acting over periods of perhaps a century, have produced a stable stone pavement in the streambed. This habitat results in a less turbulent flow regime and limits sediment scour from the streambed.

Because dry valley glaciers advance and retreat over periods of centuries and millennia and stream networks in the dry valleys evolve through sediment deposition and transport, some of the currently inactive stream channels may receive flow again in the future. Insights into the process of algal persistence and reactivation will come from long-term experiments that study the effects of reintroducing water flow to channels in which flow has not occurred for decades or centuries.

The present work of the McMurdo Dry Valleys LTER has led us to conclude that the legacy of past conditions constitutes a dominant influence on present-day ecosystem structure and function in the dry valleys (Moorhead et al. 1999). For example, Virginia and Wall (1999) have found that soil nematodes are partly sustained by relict organic carbon from algae that grew during the high lake stands of 8000–10,000 years ago. Similarly, the growth of current algal populations in the lakes of the dry valleys is supported by diffusion of nutrients from relict nutrient pools in the deep bottom waters (Priscu et al. 1999). For the stream ecosystems, abundant algal mats are present in channels that have stable stone pavements, which formed through freeze–thaw cycles occurring over long periods, possibly hundreds of years. We hypothesize that these stone pavements are an important ecological legacy permitting the successful "waiting for water" strategy. Similarly, the biodiversity of algal species that can survive the harsh conditions in the streams of the dry valleys may be stable for centuries or more, representing a second important ecological legacy.

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