ENDANGERED ANTARCTIC ENVIRONMENTS

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Abstract  The Antarctic continent harbors a range of specialized and sometimes highly localized microbial biotopes. These include biotopes associated with desiccated mineral soils, rich ornithogenic soils, glacial and sea ice, ice-covered lakes, translucent rocks, and geothermally heated soils. All are characterized by the imposition of one or more environmental extremes (including low temperature, wide temperature fluctuations, desiccation, hypersalinity, high periodic radiation fluxes, and low nutrient status). As our understanding of the true microbial diversity in these biotopes expands from the application of molecular phylogenetic methods, we come closer to the point where we can make an accurate assessment of the impacts of environmental change, human intervention, and other natural and unnatural impositions. At present, it is possible to make reasonable predictions about the physical effects of local climate change, but only general predictions on possible changes in microbial community structure. The consequences of some direct human impacts, such as physical disruption of microbial soil communities, are obvious if not yet quantitated. Others, such as the dissemination of nonindigenous microorganisms into indigenous microbial communities, are not yet understood.

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INTRODUCTION

The Antarctic continent offers a range of extreme climatic conditions that constitutes one of the harshest environments on Earth. Extremes of temperature, low atmospheric humidity, low liquid water availability, and high periodic incident radiation with long periods of complete darkness all contribute to rendering the continent relatively inhospitable for the development of biological communities.

We must remember that the concept of an extreme environment is, in part, anthropogenic and therefore artificial. The discomforts and difficulties that the mesophilic mammal Homo sapiens experience in Antarctic conditions are not a good yardstick for assessing the success, or otherwise, of microbial existence. Nevertheless, the Antarctic environment does impose real thermodynamic and kinetic limitations on microbial growth. This is evident in that higher eukaryotes are restricted to the more northern latitudes (the Antarctic peninsula) and that both microbial biomass levels and species diversity are significantly lower in the most extreme ice-free region of Antarctica, the McMurdo Dry Valleys, than in temperate environments. However, where suitable niches are found, microbial life exists. The presence of liquid water stimulates the most productive and diverse microbial communities: in shallow lake margins, glacial and snowfield melt water
TABLE 1  Impacts on Antarctic microbial biotopes and communities

<table>
<thead>
<tr>
<th>Source</th>
<th>Nature</th>
<th>Effect(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthropogenic</td>
<td>Movement, transport, physical</td>
<td>Physical disturbance to soil surfaces; dissemination of nonindigenous</td>
</tr>
<tr>
<td></td>
<td>activities</td>
<td>microorganisms</td>
</tr>
<tr>
<td></td>
<td>Production of waste materials</td>
<td>Chemical contamination/eutrification of soil and water systems</td>
</tr>
<tr>
<td>Climatic</td>
<td>Temperature rise</td>
<td>Loss of ice; increased microbial growth; increased water availability</td>
</tr>
<tr>
<td></td>
<td>Temperature decrease</td>
<td>Increase in ice cover; reduced microbial activity; decreased water availability</td>
</tr>
<tr>
<td></td>
<td>Elevated UV radiation</td>
<td>Changes in microbial distribution</td>
</tr>
</tbody>
</table>

streams and “flushes,” and meltwater pools in glacial ice. Elsewhere, microbial communities are more physically restricted. Endolithic microbial communities, taking shelter under stones, in cracks in rock strata, and even within the interstitial spaces in crystalline rocks, have achieved a fine balance between the limitations of light availability and desiccation.

Many of the Antarctic microbial communities are potentially sensitive to external impacts (Table 1). The physical fragility of the Dry Valley soils and Antarctic peninsular fellfields makes their microbial communities susceptible to physical and climatic deterioration. The extent to which the structures of these communities might be modified by the impact of nonindigenous microbial contamination remains to be evaluated. Others, such as ice, lake, and flush communities, are obviously susceptible to regional temperature changes.

It is important to understand the immediacy, significance, and ultimate consequence of these natural (climatic) and unnatural (anthropogenic) impacts. However, this will be possible only when we have a detailed understanding of the biological complexity of each habitat, and the way in which the community structures and relationships respond to environmental changes and impositions. We review the current state of knowledge of the microbiology of major Antarctic habitats (see Figure 1 for principal locations), and consider these microbial communities in light of known and projected environmental impacts.

COLD DESERT MINERAL SOILS

The Antarctic Dry Valleys

Ice-free regions represent less than 2% of the total land area of the Antarctic continent (35). The McMurdo Dry Valleys of Eastern Antarctica comprise much of the total ice-free land, although ice-free regions are also found in the Vestfold Hills, the Bunger Hills, and at various sites in the Transantarctic mountains and
on the Antarctic Peninsula. The Dry Valleys are the coldest and driest deserts on Earth and experience a variety of harsh environmental conditions (Table 2). The extremely low temperatures, low precipitation, low humidities, high salt content, katabatic winds, steep physical and chemical gradients in the terrestrial habitats, and low organic matter content impose major limitations on microbial growth and survival (74, 165).

The McMurdo Dry Valleys are not homogeneous systems. They offer a range of widely differing microbial biotopes that includes lakes (both freshwater and saline), freshwater streams, and at least two types of soil, moist soils that are exposed to glacial meltwater and desiccated mineral soils (153).

Dry Valley Mineral Soils: The Physical and Chemical Environment

Dry Valley mineral soils are the most barren soils of the snow-free regions of the Antarctic continent (Figure 2). The upper horizon of mineral soils typically has a low water content (0.5%–2% wt) due to the low level of precipitation and exposure to the desiccating atmosphere. Low humidity (<10% RH in winter), low precipitation and strong katabatic winds (especially during winter) result in long periods of desiccation (74). The mean annual precipitation of 15 g cm$^{-2}$ year$^{-1}$
TABLE 2 Ecological factors in Antarctic cold deserts (reproduced from Reference 165 with permission)

<table>
<thead>
<tr>
<th>Favorable conditions</th>
<th>Unfavorable conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>North-south orientation of valley (across katabatic wind direction)</td>
<td>East-west orientation of valley (along katabatic wind direction)</td>
</tr>
<tr>
<td>Northern exposure</td>
<td>Southern exposure</td>
</tr>
<tr>
<td>Gentle north-facing slope</td>
<td>Flat or south-facing slope</td>
</tr>
<tr>
<td>High solar radiation</td>
<td>Low, sporadic solar radiation</td>
</tr>
<tr>
<td>Microclimate above freezing</td>
<td>Microclimate below freezing</td>
</tr>
<tr>
<td>Absence of wind</td>
<td>High winds</td>
</tr>
<tr>
<td>Northerly winds</td>
<td>Southerly winds</td>
</tr>
<tr>
<td>High humidities</td>
<td>Low humidities</td>
</tr>
<tr>
<td>Slow or impeded drainage</td>
<td>Rapid drainage</td>
</tr>
<tr>
<td>Lengthy duration of available water</td>
<td>Short duration of available water</td>
</tr>
<tr>
<td>Translucent pebbles</td>
<td>Opaque pebbles</td>
</tr>
<tr>
<td>Nonsalty soils, balanced ionic composition</td>
<td>Salty soils, unbalanced ionic composition</td>
</tr>
<tr>
<td>Approximately neutral pH</td>
<td>High (or low) pH</td>
</tr>
<tr>
<td>Organic contamination (e.g., skuas, seals)</td>
<td>No organic contamination</td>
</tr>
</tbody>
</table>

is entirely in the form of snow. However, because of the low atmospheric humidity, much of the snow sublimes with little moisture penetrating the upper soil horizon.

A cemented permafrost layer is present at the base of the mineral soil profile (as little as a few centimeters below the soil surface) (Figure 3). Despite the presence of the permafrost layer, insufficient liquid water is obtained from the melted permafrost interface (owing to the steep desiccation gradient) to support consistent microbial growth in the surface soils (164).

The Dry Valleys of Antarctica experience extremely low temperatures, the mean annual air temperature ranging from –20 to –25°C (164). In summer, the mean air temperature is ∼0°C, while surface ground temperatures average around +15°C during periods of direct sunlight. Prolonged periods of extremely low temperatures (–55°C) prevail during winter (159). Cameron (27) reported that a Ross Desert soil experienced a temperature change from –15 to +27.5°C within 3 h. Such temperature fluctuations lead to freeze-thaw cycles that are potentially lethal to soil microbiota. The survival of microorganisms in Dry Valley mineral soils depends on their hydration state, their compatible solute content, and their ability to switch metabolism to synthesize cryoprotectants (24).

Besides tolerating the desiccating conditions and extreme temperatures, microorganisms inhabiting the mineral soils are subjected to osmotic stress due to high salt concentrations from accumulated sodium, calcium, magnesium, chloride,
sulphate, and nitrate (74). The high salt concentrations within the mineral soils result from upward transport from the substratum as well as surface supplementation resulting from sea spray blown inland by onshore winds (153, 165). The soluble nitrogen (N) concentrations measured in desert soils range from 0 to 1250 µg g⁻¹ soil in the form of NO₃⁻-N and from 0.3 to 40 µg g⁻¹ soil in the form of NH₄⁺-N (153). Nitrate concentrations in Antarctic mineral soils are the lowest reported for terrestrial soils (such as forest and cultivated soils) and are derived primarily from atmospheric precipitation (154). Soluble phosphorus (P) concentrations in Antarctic desert soils are between <0.01 and 120 µg g⁻¹ soil (153).

The Dry Valley mineral soils contain low levels of organic matter (an average of 0.064 ± 0.035% total organic carbon) (93). Soil organic matter in the Taylor Valley region arises from several sources, such as marine-derived organic matter, lacustrine-derived organic particulates, cryptoendolithically derived organic matter, and airspora (22). Strong katabatic winds aid the dispersal of organic matter from inland lakes (lacustrine-derived particulates) and marine environments onto mineral soil surfaces. Physical abrasion of rocks by wind-blow sand allows the distribution of organic matter from endolithic microbial communities.

### Cold Desert Microbial Communities

Microbial abundance and diversity in Antarctic desert soils depend on a number of specific ecological factors (29) (Table 1). This is evident from comparisons of habitat composition and associated microbial composition in Ross Desert soils collected from four different locations (all experiencing different edaphic characteristics) (Table 3) (24, 25, 28, 165). For example, soil water content and cell numbers are positively correlated; low-organic-content saline soils contain lower numbers of culturable microorganisms than nonsaline soils (29). However, caution must be exercised when interpreting quantitative data from culture-dependent enumeration studies, which have repeatedly shown that Dry Valley mineral soils contain low levels of microorganisms [e.g., 10²–10⁴ g⁻¹; (24, 25, 28)]. However in situ ATP analysis data have indicated that Dry Valley mineral soils contain three to four orders of magnitude higher levels of microbial biomass than previously reported (41).

Most microorganisms isolated from mineral soils are psychrophilts, perhaps not surprisingly because these organisms are better adapted to survive the temperature cycling of surface soils than true psychrophiles. Psychrophiles are more abundant in the permafrost layer, where temperature fluctuations are low. Most of the viable (i.e., culturable) bacteria in Ross Desert soils are found in the permafrost layer and toward the surface (30). Chromogenic bacteria colonize soil surfaces, whereas nonpigmented bacteria were mainly found below the soil surfaces (30). Antarctic soils are largely aerobic and most microorganisms isolated from this habitat are aerobic heterotrophs. Although a few anaerobic bacteria have been isolated from
### Table 3
Soil edaphic and microbial characteristics at four Dry Valley sites (reproduced from References 24, 25, and 28 with permission)

<table>
<thead>
<tr>
<th>Properties</th>
<th>Victoria Valley</th>
<th>Coalsack Bluff</th>
<th>Barwick Valley</th>
<th>Wheeler Valley</th>
</tr>
</thead>
<tbody>
<tr>
<td>Position</td>
<td>77° 20′S</td>
<td>84° 14′S</td>
<td>77° 20′S</td>
<td>77° 12′S</td>
</tr>
<tr>
<td>Substratum</td>
<td>Dune sand</td>
<td>Sand on Berg Moraine sand</td>
<td>Pattern ground sand</td>
<td>Gray-brown sand</td>
</tr>
<tr>
<td>Moisture (% dry wt)</td>
<td>0.14</td>
<td>1.58</td>
<td>1.74</td>
<td>4.30</td>
</tr>
<tr>
<td>pH</td>
<td>8.0</td>
<td>6.5</td>
<td>8.3</td>
<td>8.1</td>
</tr>
<tr>
<td>Organic C (% wt)</td>
<td>0.02</td>
<td>0.38</td>
<td>0.02</td>
<td>0.17</td>
</tr>
<tr>
<td>Organic N (% wt)</td>
<td>0.003</td>
<td>0.024</td>
<td>0.004</td>
<td>0.024</td>
</tr>
<tr>
<td>Inorganic ions (ppm dry wt)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>140</td>
<td>50</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>NH₄</td>
<td>1.0</td>
<td>0.1</td>
<td>0.8</td>
<td>ND</td>
</tr>
<tr>
<td>NO₃</td>
<td>2</td>
<td>742</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Cl</td>
<td>835</td>
<td>110</td>
<td>5</td>
<td>41</td>
</tr>
<tr>
<td>PO₄</td>
<td>0.05</td>
<td>0.00</td>
<td>0.15</td>
<td>0.20</td>
</tr>
<tr>
<td>SO₄</td>
<td>6</td>
<td>120</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>CFU (G.D.W.)⁻¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacteria</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2–5°C</td>
<td>50</td>
<td>29,000</td>
<td>52,000</td>
<td>120,000</td>
</tr>
<tr>
<td>10–22°C</td>
<td>12,000</td>
<td>400</td>
<td>85,000</td>
<td>1.3 × 10⁶</td>
</tr>
<tr>
<td>Yeasts</td>
<td>0</td>
<td>5100</td>
<td>300</td>
<td>2</td>
</tr>
<tr>
<td>Microfungi</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>200</td>
</tr>
<tr>
<td>Algae</td>
<td>0</td>
<td>0</td>
<td>0100</td>
<td>6.4 × 10⁶</td>
</tr>
</tbody>
</table>

ND, not determined

Antarctic mineral soils, attempts to isolate anaerobic sulphate reducers from Ross Desert soils have been unsuccessful (25). No anaerobic bacterial or archaeal 16S rRNA gene signals have been observed in extensive phylogenetic studies of Dry Valley mineral soils (J.J. Smith, L. Ah Tow & D.A. Cowan, unpublished results).

Both cosmopolitan and indigenous fungal, yeast, and protozoan species have been isolated from McMurdo Dry Valley mineral soils (Table 4). Filamentous fungal cell counts of less than 200 cfu per gram of soil were obtained from Ross Desert samples, the lowest reported counts for the various Antarctic soil environments (25). Yeasts are relatively abundant in the surface horizons of certain moist Antarctic soils (4, 26). The predominant algae isolated from Antarctic soil were the oscillatorioids, *Microcoleus* sp., *Schizothrix* spp., *Anacystis* spp., and *Coccolchloris* spp. Flagellated and amoeboid protozoa have also been isolated from moist Antarctic soils (29). Thus while a few endemic microbial species have been isolated (78, 102, 128), most bacteria isolated from Antarctic soil
TABLE 4  Microbial species isolated from Antarctic Dry Valley soils (summarized with permission from Reference 153)

<table>
<thead>
<tr>
<th>Microorganism</th>
<th>Indigenous to Antarctica</th>
<th>Cosmopolitan genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fungi</td>
<td>Monodictys australia,</td>
<td>Acremonium, Alternaaria,</td>
</tr>
<tr>
<td></td>
<td>Chrysosporium verrucosum,</td>
<td>Aspergillus, Aureobasidium,</td>
</tr>
<tr>
<td></td>
<td>Acrodictium antarcticum,</td>
<td>Beauveria, Botrytis, Camposporium,</td>
</tr>
<tr>
<td></td>
<td>Chalara antarctica,</td>
<td>Chrysosporium, Cladosporium,</td>
</tr>
<tr>
<td></td>
<td>Philohora dancoii,</td>
<td>Epicoccum, Exophiala, Fusarium,</td>
</tr>
<tr>
<td></td>
<td>Thelebolus microsporus</td>
<td>Geotrichum, Gymnascella,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Helminthosporium, Hormoconis,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Myceliophthora, Nectria, Paecilomyces,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Penicillium, Phialophora, Phoma,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Racodium, Scedosporium, Sporothrix,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sporotrichum, Stephanosporium,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trichoderma, Trichophyton,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tritirachium, Verticillium, Wadomycyes,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mortierella, Mucor, Rhizopus</td>
</tr>
<tr>
<td>Yeasts</td>
<td>Cryptococcus consortions,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C. lupi, C. socialis,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C. vishniacii, Leucosporidium</td>
<td></td>
</tr>
</tbody>
</table>

have been found to be cosmopolitan in distribution (Table 4). Bacteria isolated from McMurdo Dry Valley soils most commonly belong to the following genera: Achromobacter, Arthrobacter, Bacillus, Corynebacterium, Flavobacterium, Micrococcus, Planococcus, Pseudomonas, Streptomyces, and Nocardia (23). Coryneforms are the most abundant bacteria isolated from Dry Valley soils (85% of which were represented by Corynebacterium sepedonicum) (23).

It is widely accepted that culture-dependent methods are strongly biased and that the 1% to 10% of microorganisms that can be detected by culture-dependent techniques (70) are not representative of the natural population (3). Culture-independent techniques such as small subunit (ssu) rRNA gene sequence analysis and in situ hybridization (2, 3) have proved to be invaluable in phylogenetic studies of soil microbiota (including viable, nonviable, and dormant microorganisms). It is highly revealing that sequences retrieved from environmental clone libraries are most often not represented by any cultivated organisms (156).

Although there have been numerous phylogenetic surveys of microbial species present in various temperate and tropical soils (86, 92, 109), few published data yet exist from phylogenetic studies of Antarctic Dry Valley mineral soil communities. Phylogenetic analysis of DNA extracts from mineral soils collected from the slopes of the Miers Valley (Ross Desert) indicated that as many as 50% of the retrieved sequences are from uncultured bacteria (J.J. Smith, L. Ah Tow & D.A. Cowan, unpublished data). Most of the remaining sequences are from bacteria
belonging to the Actinobacteria (27%), Bacteroidetes (11%), Acidobacteria (6%), and Verrucomicrobia (6%). In a separate phylogenetic study performed on mineral soil collected from heavily impacted gravels from McMurdo station, bacteria were identified as belonging to the following phylogenetic groups: Actinobacteria (12.5%), Bacteroidetes (25%), Firmicutes (12.5%), Planctomycetes (12.5%), and Proteobacteria (37.5%) (E.M. Kuhn & D.A. Cowan, unpublished data). The observation that a high percentage of bacteria inhabiting Antarctic mineral soils has not been assigned to a phylogenetic group, let alone identified at the genus level, is entirely consistent with phylogenetic data from many other microbial biotopes.

Sensitivity to Environmental Impacts

The Dry Valleys and other ice-free regions of the Antarctic continent have a history of human intervention of a little over a century. The combination of geographical isolation and environmental extremes provides some protection against direct human impacts, but little against global or regional climatic change. The former is further controlled by the existence of international treaties and by the designation of particularly sensitive areas as Sites of Special Scientific Interest. The sum of these factors means that much of the ice-free land area of the Antarctic continent can still be regarded as pristine.

However, our fascination with this continent results in a continued increase in human activities (research, exploration, tourism) on the continent. The impact of these activities is by no means homogeneous: Research bases now constitute sizeable towns, field research concentrates on a relatively limited number of sites (such as the Taylor Valley, the Wright Valley, and Mars Oasis), and current tourist activity is localized to sites of interest such as penguin colonies and historic hut sites. All these activities impose physical, chemical, and biological burdens on the local environment (see Table 1).

Possibly the most damaging effects resulting from increases in human activity in the ice-free areas of Antarctica are from physical (in the form of physical abrasion, compaction, trampling, and disturbance of soils) and chemical (for example, eutrophication, fuels spills, chemical debris) impacts. Physical disturbance of the mineral soils lead to some disruption of stratified microbial communities. In addition, the movement of individuals from one area to another results in cross-contamination of microorganisms between niches. Such impacts tend to invalidate phylogenetic studies performed on so-called pristine environments. There is also an increased risk of contamination at the macroscopic level, for example, by fuel-spill contamination (48). Although typically localized, such gross contamination is expected to have a dramatic and disruptive effect on the extant microbial community.

Cold desert soils, once thought to be sterile, are now known to be inhabited by a wide variety of microorganisms (55). Many of these microbial species appear
to belong to cosmopolitan taxa (153), although some are apparently endemic. Natural vectors aid the dissemination of microbes into and within the Antarctic continent (151). These include atmospheric circulation, oceanic circulation, and migratory mammals, birds, and fish, all of which contribute directly or indirectly to the introduction of nonindigenous microorganisms. Given that natural processes continuously seed nonindigenous microorganisms into the Antarctic continent, researchers might argue that additional dissemination of bacteria from human activities is of little significance.

That human activities do contribute nonindigenous microorganisms to the local environment has been clearly established by a number of recent studies that show contamination by human commensal and fecal microorganisms of mineral soils and aquatic systems in the vicinity of permanent bases and temporary camps (5, 19, 20, 49, 97, 132, 143). Regardless if the human-derived contaminants can survive the harsh environmental conditions in Antarctica, these results should be considered in the context of lateral gene transfer (LGT) between nonindigenous and indigenous organisms. Naked microbial DNA survives for long periods in Dry Valley soils (L. Ah Tow & D.A. Cowan, unpublished results). LGT between bacteria in the soil environment is a relatively common event (50, 71, 84). Evidence shows that LGT can occur over large geographic distances owing to particulate dispersal (71, 151). To date, there is no direct evidence for LGT in the Antarctic environment, nor is it clear whether such a process would be relevant, advantageous, or disadvantageous to Antarctic microbial communities.

Regional or global climate change has the potential to dramatically impact Antarctic environments. Interestingly, the hole in the South Polar ozone layer and its associated increase in incident UV radiation may not have a direct impact on Dry Valley mineral soil communities, which are thought to avoid the exposed upper surfaces of mineral particles. However, the dependence of mineral soil communities on lacustrine-derived organic material as a key source of C or N suggests that secondary effects from changes in lake productivity might be important. These arguments may also be applied to a range of other climatic changes, including regional temperature regimes. A net cooling of Eastern Antarctica during summer and autumn periods between 1966 and 2000 (47) appears to coincide with a warming of the western side of the Antarctic Peninsula, especially in winter (1951 to 2000) (141), with an increase of 1.09°C per decade during winter and 0.56°C per decade annually. Such regional differences suggest that it may be impossible (and unwise) to assume any continent-wide climate changes. Nevertheless, temperature increases in ice-free areas are expected to increase the availability of liquid water (from glacial and permafrost melting, and possibly from precipitation), with possibly dramatic changes in microbial biomass, microbial productivity, and community structure. Ross Desert soils subjected to temperatures above 0°C show large increases in culturable bacteria (11), while the enclosure of Dry Valley desiccated mineral soils under transparent plastic cloches resulted in the rapid growth of moss and cyanobacterial consortia (D.D. Wynn-Williams, personal communication).
LITHIC MICROBIAL COMMUNITIES

Introduction

The harsh ground surface environment associated with the ice-free area of Antarctica, characterized by high seasonal radiation, low water activity, and extremely low temperatures with high daily temperature fluctuations, has generated a variety of highly specific biotopes. One of the more obvious examples of exploitation of a biotope specifically to avoid climatic extremes is the existence of microbial communities associated with porous and translucent rocks (endoliths).

Although endolithic microbial communities are distributed worldwide, including in hot deserts (62), they have been most intensively studied in the Antarctic Dry Valleys through the efforts of Imre Friedmann and his coworkers. Several comprehensive reviews of this work are available (108, 130, 165).

The Physical and Chemical Environment

The endolithic microbial communities of the McMurdo Dry Valleys are restricted to rock types that offer suitable microhabitats. The most important physical characteristics are porosity (providing interstitial spaces for microbial colonization) and translucence (facilitating photosynthetic activity in the endoliths). These properties are found in the fine-grained Beacon sandstones, the dominant substratum of the Dry Valleys (108), but are also characteristic of coarse-grained quartzites (165) and limestones (57).

Organisms inhabiting rock surfaces and shallow cracks are subject to physical abrasion (from wind-blown sand) and rapid thermal fluctuations (165). However, endolithic microbial communities, even if only a few millimeters below the rock surface, are largely protected from extreme temperature fluctuations because of the thermal buffering of the rock. Nevertheless, the endolithic microenvironment is in equilibrium with the external temperature for much of the Antarctic year. Friedmann and coworkers (61) have estimated that metabolism is possible in endolithic microbial communities for less than 1000 h per annum, based on an assumption that the lower limit for endolithic metabolism is between –6 and –8°C (144).

Water supply is generally thought to be limiting in endolithic environments, particularly during the short summer period, when the elevated temperatures and presence of sunlight are conducive to photosynthesis. Intermittent snowfalls may be the only source of water (60), although the possibility that the upward diffusion of water vapor or transport of liquid water from a melting ice–permafrost interface can support microbial growth in hypolithic biotopes should not be discounted.

Endolithic communities wholly depend on photoautotrophic energy capture (108). Substrate enrichment, culturing, and phylogenetic studies have provided no reliable evidence for chemosynthesis (45, 144, 165). The light-attenuating effect of the crystalline rock strata is substantial (165), in which the surface photon density may be reduced by three orders of magnitude at a depth of 2 mm (the
upper surface of the lichen zone) and four orders of magnitude at a depth of 3 mm (the green algal zone). Low light intensities notwithstanding, endolithic growth may not be light limited (81). Instead, the limited availability of CO₂, resulting from its low atmospheric concentration (153), compounded by the low diffusion rates into crystalline rock strata, suggests that C availability is the major factor limiting productivity. The availability of CO₂ is not expected to be limited in cryptoendolithic communities that occupy marbles and other carbonate-rich rock types because of solubilization by excreted organic acids (79).

Although N₂ fixation in endolithic communities has been reported to be rare (59), the failure of exogenous N additions to stimulate respiration has been taken as an indication that N is not limiting. Fixed N in snow meltwater may be the dominant supplement to the endolith community N cycle.

Composition of Lithic Communities

Rock-based microbial communities have been defined (58) on the basis of localization. Chasmoendolithic organisms inhabit cracks in weathering rocks (Figure 4a), and cryptoendolithic organisms exist in the interstices of crystalline rock structures (Figure 4b). Hypolithic microbial communities reside on the underside of translucent stones (Figure 4c). The upper or exposed surfaces of rocks are thought to be essentially abiotic, at least as assessed by culture-based studies (108) and ATP analysis (D.A. Cowan, unpublished results).

Chasmoendolithic microbial communities are widespread in ice-free areas around the Antarctic continent, since freeze-fracturing of rock strata is a common occurrence. These biotopes are principally occupied by endolithic lichens (fungal hyphae with the green algal symbiont *Trebouxia*) and cyanobacterial associations (*Chroococcidiopsis* or *Gloeocapsa* species) (108). Little is known of the diversity of nonphotosynthetic prokaryotes that is almost certainly associated with these photoautotrophic communities. To the authors’ knowledge, no phylogenetic studies have focused on chasmoendolithic microbial communities.

The cryptoendoliths have been extensively studied, originally by microscopic, chemical, and culture-based methods (108), and only recently by the use of phylogenetic tools (45). Two dominant community types have been identified: lichen-dominated and cyanobacteria-dominated assemblages. The different communities generally have a clear zonal stratification where, for instance, the lichen-dominated community has an upper layer of lichenized fungal mycobionts in intimate association with the phycobiont *Trebouxia*, while the lower zones are dominated by cyanobacteria. Culture-dependent studies of heterotrophic bacteria associated with lichen-dominated endolithic communities showed a dominance of gram-positive cocci (129, 130) and various actinomycetes (108).

A recent comprehensive phylogenetic study of both lichen- and cyanobacteria-dominated communities, in which more than 1100 individual 16S rDNA clones were analyzed (45), has shown that these biotopes contain an extensive and varied bacterial population. Community DNA extracts were PCR amplified by both eukaryal and universal bacterial primer sets, and over 50 groups of phylotypes
(at greater than 98% identity, equivalent to species similarity) were identified. In the lichen-dominated community, three phylotypes accounted for over 70% of the clones: the fungus *Texosporium sancti-jacobi* (29%), the green alga *Trebouxia jamesii* (22%), and chloroplast-related sequences (22%). Both *Texosporium* (mycobiont) and *Trebouxia* (phycobiont) form lichenized associations (56) and together almost certainly represent the dominant *Buellia* lichen constituent of the endolithic community. Other fungal and algal phylotypic signals represented only a minor proportion of the total clones (<2%). Bacterial phylotypes comprised over 15% of the clones sequenced, with members of the order Cytophagales dominating. Phylotypes belonging to the class Actinobacteria (*Blastococcus* sp., *Microsphaera* sp., *Sporichthya* sp., *Rhodococcus* sp.), to the α-proteobacteria (*Sphingomonas* sp., uncultured clones), to the γ-proteobacteria (*Actinobacter* spp.), and to the Planctomycetales were identified by BLAST analysis, though all at relatively low frequency.

In the cyanobacteria-dominated community sample, cyanobacterial phylotypes (principally from the *Leptolyngbya-Phormidium-Plectonema* group) (34) constituted over 30% of clones sequenced. *Phormidium* species have been widely identified in moist Antarctic environments (135) and constitute dominant phylotypes in high-altitude and the (rare) carbon-rich McMurdo Dry Valley mineral soils (D.A. Cowan, L. Ah Tow & J.J. Smith, unpublished results). Heterotrophic bacterial phylotypes represented nearly 60% of the clones tested, falling into two major groups: the α-proteobacteria (~34%, virtually all *Blastomonas* sp.) and the *Thermus-Deinococcus* group (26%). The latter sequences showed an Antarctic-specific clade within this group, treeing with other uncultured Antarctic phylotypes (45). The presence of the putative *Blastomonas*-like phylotypes suggests that the cyanobacteria are not the sole contributors to primary productivity, as previously suggested (108). *Blastomonas* and related species are aerobic anoxygenic phototrophs (166) that possess functional light-harvesting complexes. The authors (45) also make the intriguing suggestion that the quantitative equivalence of cyanobacterial, α-proteobacterial, and *Deinococcus*-like clones implied that these organisms were involved in a “tightly regulated syntrophic relationship.” The existence and nature of this relationship can be addressed by culture and consortium assembly approaches (probably with difficulty, given that members of this consortium have so far proven to be unculturable) or by substrate labeling/tracing techniques.

Sensitivity to Environmental Impacts

The sensitivity of Antarctic endolithic microbial communities to climatic, human, and other impacts cannot readily be quantitatively assessed. A qualitative analysis may suggest that these communities, which have adopted an avoidance rather than adaptive survival strategy (165), are rather delicately poised, both spatially and metabolically, with respect to their requirements for adequate supplies of light, water, and nutrients. Estimates of the low rates of photosynthesis may suggest that any climatic changes that reduced the immediate ambient temperature (including indirect effects such as an increase in cloud cover) may have drastic consequences.
in terms of primary productivity. Similarly, a significant reduction in atmospheric humidity or in annual snowfall, both potential products of a fall in mean temperatures on the Antarctic plateau, may disturb the delicate balance in subsurface positioning of endolithic communities. Should an increase in atmospheric desiccation reduce the viability of the upper layers of the community, total productivity could be substantially reduced owing to the greater attenuation of light at increased depth.

Endolithic communities are probably not at any particular risk from physical impacts, either from an increase in human activities or from changes in the degree of abrasion induced by wind-blown sand. Most principal sites of Antarctic endoliths are relatively remote from coastal areas, are at high altitude, are inaccessible other than by helicopter, and are therefore unlikely to suffer from excessive physical impact by humans, even with the inevitable future expansion of nonscientific Antarctic activities. Key sites (such as Battleship Promontory) can readily and effectively be protected if designated as Sites of Special Scientific Interest.

LAKE COMMUNITIES

Introduction

Antarctica contains numerous high-latitude continental lakes (such as Lake Vanda in the McMurdo Dry Valleys; Figure 5a), most of which have existed for very long periods. For example, lakes in the Taylor Valley are estimated to be 10,000–24,000 years old. Lakes arise from the collection of summer meltwater in catchment basins. It has been proposed (119) that sand particles blown onto glacial ice could act as solar collectors that initiate melting of the ice that surrounds the sand particles. As a depression forms, more sand accumulates, enlarging the depression, until a proglacial lake is formed. Many of the Antarctic lakes have a thick perennial ice cover (Figure 5b).

In contrast to the ice-covered lakes, Antarctic hypersaline lakes and ponds are not ice-covered. An example of such a hypersaline pond is Don Juan Pond (Figure 6, follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org). This water body is thought to have arisen owing to deposition of sea spray on snow and glacial ice. Meltwater transports the sea salts into the Dry Valleys, producing water with an ionic composition similar to seawater. Evaporation and sublimation of the water lead to concentration of the salts, particularly calcium chloride (157). The extremely high salt concentration in the Don Juan Pond (∼33%) lowers the freezing point of this water body to −53°C (31).

The Physical and Chemical Environment

Unlike the harsh environmental conditions experienced in the Dry Valley mineral soils, Antarctic lakes provide a buffered and protected aquatic environment
to aquatic microbiota. Not uncommonly, Antarctic lakes are meromictic (stratified, nonhomogeneous) in nature because of a combination of factors that include proximity to the sea, presence of an ice cover, the surrounding arid environment, and inflowing streams (131).

A major physical factor contributing to the environmental buffering of the lakes is the presence of ice cover. Ice cover prevents wind turbulence and reduces temperature fluctuations (68). During summer, peripheral moats (melting of the peripheral ice cover) allow the inflow of water from the melt streams, which results in steep salt gradients in the water column that in turn produce specific niches that are occupied by different aquatic biota.

Light penetration to the water column depends on the thickness of the ice cover (112). For example, Lake Vanda has a thin ice cover that allows transmission of solar radiation (18% of incident photosynthetically active radiation) through the ice to heat the underlying water. Absorption of incident infrared radiation by the benthic sediment results in temperatures at the bottom of the lake being warmer than the overlying water (14). In lakes with thick (e.g., 4–6 m) ice cover, much less light (<1% of incident photosynthetically active radiation) penetrates to the water column.

Ice cover also restricts gaseous exchange between the atmosphere and the water column (159). Microbial mat photosynthesis and oxygenated inflow water at peripheral moats contribute to the dissolved O2 content of lake waters. Owing to stratification in most Antarctic lakes, a dissolved O2 gradient forms, ranging from 400% supersaturation immediately underneath the ice cover to anoxic conditions near the bottom. Thin ice cover results in cracks that facilitate gas permeation, reducing the O2 supersaturated zone.

One of the major environmental regulators of microbial activity in high-latitude lakes is the deposition of sediment (107). Sediment cores collected from the bottom of the Dry Valley lakes show alternating layers of organic and inorganic material. Reduction in ice cover results in an increase in sediment deposition and an increased rate of burial of microbial mats (131). The trapping and binding of precipitated sediment by the microbial mats, particularly cyanobacterial mats, results in benthic mat structures that resemble stromatolites (165).

A combination of salinity, temperature, and chemical stratification plays vital roles in the microbial ecology of Antarctic lakes. Salt content of Antarctic lakes originates from chemical weathering of rocks as well as from the marine environment (66). Lakes of marine origin such as Ace Lake and Deep Lake in the Vestfold Hills possess ionic compositions similar to seawater (54), while others such as Lakes Hoare, Fryxell, and Vanda, which are not of marine origin (66), have ionic compositions consistent with glacial meltwater inflow (94).

Stratification within the lakes allows the formation of inorganic and organic nutrient gradients, and different Antarctic lakes have widely differing nutrient levels. For example, Lakes Hoare and Fryxell contain low concentrations of fixed N and P, similar to the levels found in their input streams (63). Fixed N (mainly in the form of urea) is added into the lakes via glacial melt streams (at 100–200 mg N m−3),
with ~10% of the total N budget attributable to N fixation by cyanobacteria (75). In contrast, Lake Vanda has a high N concentration but a low P concentration (32), the latter precipitating as hydroxyapatite. Nitrifying bacteria contribute to N stratification in lake water columns (145).

In general, Antarctic lakes are rich in dissolved organic compounds compared with temperate-latitude lakes (131). Total organic carbon and dissolved organic carbon vary with depth, and values as high as 110 and 186 mg C l\(^{-1}\), respectively, have been determined (95).

### Microbial Lake Communities

The presence of lake ice cover results in stratifications along the underlying water column, producing unique niches that are occupied by various microbiota. Bacterial cell densities in four Dry Valley lakes (Lakes Hoare, Vanda, Fryxell, and Miers) ranged between \(10^5\) and \(10^6\) cells l\(^{-1}\) and generally occupied the zones of maximum photosynthesis (145, 148), while zooplankton seemed to be absent (114). In contrast, zooplankton were found in many lakes in the Vestfold Hills. A summary of the planktonic and associated microbiota in several lakes in southern Victoria Land can be found in the review by Simmons et al. (131). Bacterial isolates representing new genera or species from the various Antarctic lakes have been reported (Table 5).

<table>
<thead>
<tr>
<th>Lake</th>
<th>New bacterial species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water column</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ekho Lake (East Antarctica)</td>
<td><em>Antarcobacter heliothermus</em></td>
<td>(87)</td>
</tr>
<tr>
<td></td>
<td><em>Roseovarius tolerans</em></td>
<td>(88)</td>
</tr>
<tr>
<td></td>
<td><em>Staleya guttiformis</em></td>
<td>(90)</td>
</tr>
<tr>
<td></td>
<td><em>Sulfito bacter brevis</em></td>
<td>(90)</td>
</tr>
<tr>
<td></td>
<td><em>Saccharospirillum impatiens</em></td>
<td>(89)</td>
</tr>
<tr>
<td></td>
<td><em>Friedmanniella lacustris</em></td>
<td>(91)</td>
</tr>
<tr>
<td></td>
<td><em>Nocarioi des aquaticus</em></td>
<td>(91)</td>
</tr>
<tr>
<td></td>
<td><em>Nesterenkonia lacusekhoensis</em></td>
<td>(40)</td>
</tr>
<tr>
<td>Lake Vanda (S. Victoria Land)</td>
<td><em>Carnobacterium</em> strain</td>
<td>(14)</td>
</tr>
<tr>
<td>Organic Lake (Vestfold Hills)</td>
<td><em>Flavobacterium gondwanense</em></td>
<td>(46)</td>
</tr>
<tr>
<td>Ace Lake (Vestfold Hills)</td>
<td><em>Salegentibacter salegens</em></td>
<td>(46)</td>
</tr>
<tr>
<td>Sediments/mats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyanobacterial mat</td>
<td><em>Methylophaera hansonii</em></td>
<td>(9)</td>
</tr>
<tr>
<td>Pond sediment (McMurdo Ice Shelf)</td>
<td><em>Flavobacterium tegetincola</em></td>
<td>(96)</td>
</tr>
<tr>
<td>Pond sediment (McMurdo Ice Shelf)</td>
<td><em>Planococcus antarcticus</em></td>
<td>(124)</td>
</tr>
<tr>
<td></td>
<td><em>Planococcus psychrophilus</em></td>
<td>(124)</td>
</tr>
<tr>
<td></td>
<td><em>Psychromonas antarcticus</em></td>
<td>(105)</td>
</tr>
</tbody>
</table>
Water Column Communities

Lake Vanda (Figure 5a) is the most oligotrophic lake in the world but nevertheless supports three distinct algal communities distributed in the water column (148). An algal community was found to occupy a large thermal convection cell, while a microflagellate community is present immediately beneath the ice cover. Most plankton occupy the bottom of the water column at the oxic-anoxic interface. This planktonic community is called the deep chlorophyll maximum and coincides with maximum biomass and photosynthesis in the lake (131, 165). In Lake Fryxell (Taylor Valley) an abundance of Pyramimonas sp. and Chroomonas lacustris was reported to coincide with the zone of maximum production (145). Protozoans and rotifers were reported at the oxic-anoxic zone of Lake Fryxell.

Ace Lake (Vestfold Hills) is a seasonally ice-free meromictic lake. Only four flagellate species from this lake have been reported: Pyraminosa gelidicola, Cryptomonas sp., a dinoflagellate, and a microflagellate (21). The major bacterioplankton were the photosynthetic green sulfur bacteria Chlorobium vibrioforme and C. limnicola. Photosynthetic purple bacteria, methanogenic bacteria, and sulfate-reducing bacteria were also identified, which suggests the presence of a complex and sophisticated trophic structure.

Microbial Mats

Microbial mats, which develop on the upper surface of lake sediments (Figure 7), are formed from filamentous matrices of cyanobacteria, particularly Phormidium frigidum and Lyngbya martensiana (53). Heterotrophic bacteria, fungi, protozoa, and eukaryotic algae are also present in these mats (160). P. frigidum is ubiquitous in southern Victoria Land and has been isolated from various terrestrial and aquatic environments. Five benthic mat morphologies have been identified thus far. The three major morphologies are pinnacle mats (found in Lakes Bonney, Hoare, and Vanda), “lift-off” mats (found in all Dry Valley lakes except Lake Vanda), and prostrate mats (found in all Dry Valley lakes, especially Lakes Chad, Fryxell, and Hoare) (115).

Pinnacle mats (Figure 8) are 2–5 cm high and 3–5 cm wide at the base and consist of alternating translucent light-brown and greenish-purple layers, interspersed with sand and calcite crystals. Lift-off mats occur because of high concentrations of dissolved gases in shallow waters (160) and the genesis of gas bubbles within the benthic mat. Lift-off mats remain fixed and form columnar calcite structures (see Figure 7) or tear loose and float to the top of the water column (160) (Figure 8), eventually penetrating the overlying ice to be dispersed by wind to the surrounding environment as an inoculum or nutrient source. Phylogenetic studies performed on mineral soils collected from the shores of an ice-covered lake in Miers Valley showed a predominance of cyanobacteria (43%) including Phormidium, Oscillatoria, Cylindrospermum, and Nostoc species (J.J. Smith, L. Ah Tow & D.A. Cowan, unpublished data), some of which are likely to be of lake origin.
Prostrate mats include both aerobic and anaerobic microniches. An actively photosynthesizing aerobic layer is located toward the upper surface of the mat. The microbial diversity in the aerobic layer is similar to that found in pinnacle and lift-off mats (131). Anaerobic prostrate mats contain *Leptothrix* sp., *Achroonema* sp., *Planctomyas* sp., *Thiothrix* sp., *Clostridium* sp., as well as the anaerobic photosynthetic green sulfur bacterium, *Chloroflexus* (131).

Phylogenetic studies on Antarctic benthic mats have shown that they contain a high microbial diversity (10, 13, 133, 138) (Table 6). A high diversity of purple nonsulfur bacteria in Lake Fryxell was also observed (83). Phylogenetic studies
TABLE 6  Microorganisms isolated from or detected in microbial mats from Lake Fryxell (Taylor Valley)

<table>
<thead>
<tr>
<th>Phylogenetic taxa</th>
<th>16S clone library</th>
<th>Microbial isolation</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clostridium-Bacillus [24]</td>
<td>Clostridium-Bacillus [10]</td>
<td></td>
</tr>
</tbody>
</table>

Numbers in brackets in columns 2 and 3 indicate the number of different species identified within the given phylogenetic groups.

on Bratina Island meltwater pond sediments revealed the presence of sulfate-reducing δ-proteobacteria, an indication of the low redox potential of the sediment core fractions (133). Archaea belonging to the Crenarchaeota and Euryarchaeota groups have also been detected in microbial mats by culture-independent methods (10, 13, 133).

Sensitivity to Environmental Impacts

Temperature change potentially offers one of the major environmental impacts on the lake systems in Antarctica. A continued decrease in atmospheric temperature (47) may lead to a decrease in glacial melt streams, reduced inflow into the lakes, and a reduction in lake volumes. Ice volume and coverage should increase, further reducing free water volumes. Thicker ice cover reduces light penetration to the water column. Although the planktonic communities in Dry Valley lakes are adapted to low photosynthetic photon flux densities, photosynthetic C fixation is linearly related to light intensity (144). A reduction in photosynthetic capacity clearly interferes with microbial community structure and nutrient cycling within Antarctic lakes.

Conversely, a net warming such as that reported for the western side of Antarctica (141), leads to an increase in glacial meltwater volumes. Increased water flow rates increase sediment scouring and transport. The effect of higher sediment loads in lake water columns and enhanced deposition onto the lake floor is expected to reduce lake productivity, possibly outweighing the positive effects of higher atmospheric mean temperatures.
FLOWING WATER SYSTEMS

Introduction

Antarctic streams and rivers originate from melting snow, ice fields, and glacial ice. Flowing waters occur only seasonally for limited periods, from a few weeks to a few months, depending on the warmth of the season. Coastal continental Antarctica contains numerous flowing water systems that can be divided into three types: percolating flows, melt-streams, and rivers (67, 152). Percolating flows generally flow over rock faces, down glaciers, and through saturated soils. However, the major type of flowing water in Antarctica is melt streams. Numerous meltwater streams, flowing in well-defined perennial channels in ice-free ground, have been observed in southern Victoria Land and on Ross Island during the summer season periods (66). Small streams have also been observed flowing across the surface of glaciers and ice shelves on the McMurdo Ice Shelf (75) and the Amery Ice Shelf (100). Flow rates may be considerable. The Onyx River (Wright Valley) discharges into Lake Vanda at a rate of up to 14 m$^3$s$^{-1}$ with an annual discharge of 2 × 10$^6$m$^3$ (37).

Stream flow rates are primarily controlled by solar radiation, which controls the melting of snow and glacial ice. In southern Victoria Land, the glacier-fed streams experience a short period of high discharge associated with early season melt (76, 146). The sediment loads of input streams range from <1 to >1000 g m$^3$, depositing mineral particulates and micronutrients into lake systems (99). Streams flowing out of lakes, such as the Miers River (147), contain lower sediment loads because of prior settling.

Nutrient availability in Antarctic streams is subject to considerable seasonal variation and is associated with freeze-thaw cycles. The highest nutrient concentrations correspond to the first flow. For example, the Onyx River contained three times more nitrate and twenty times more dissolved reactive P on the first day of flow than at any other time of the season (146). High concentrations of dissolved organic nutrients have also been reported. In the Fryxell Stream (southern Victoria Land), the dissolved organic nutrient concentration increased with distance downstream, possibly owing to extracellular release by the streambed microbial mat communities (75). Other sources include wind-blown organic matter deposited on glacier surfaces during winter, streambed soils, autochthonous algal production, and ornithogenic deposits (152).

Microbial Communities in Aquatic Systems

Microalgae and cyanobacteria are the predominant biota found in Antarctic flowing waters. However, most of the microbial studies performed on Antarctic flowing waters have focused on phototrophs, and microbial heterotrophs have received little attention.

In shallow meltwater channels flowing over glacial ice, Prasiola calophylla (Carmichael) meneghini is the dominant green alga. The cyanobacteria Gloeocapsa
kuetzingiana Naegeli and Nostoc are frequently associated with *P. calophylla* (18). On the McMurdo Ice Shelf, a more complex microflora associated with ice channel streams is observed, including benthic diatoms and Oscillatoriaceae (75).

Flushed mineral soils (flushes) are regions subject to periodic rather than continual inundation by meltwater. These soils develop surface microbial mats dominated by cyanobacteria, including Oscillatoriaceae and *Nostoc*. Flush communities in continental coastal regions, in nunataks (52), and in maritime Antarctica (72) have been observed. Various potential N-fixing cyanobacteria [*Nodularia harveyana* Thuret, *Scytonema myochrous* (Dillw.) Agardh, *Calothrix parietina*, and *Tolyphothrix tenuis* Kützing], oscillatoriacean genera (*Oscillatoria*, *Lyngbya*, *Phormidium*, *Schizothrix*, and *Microcoleus*), and *Gloeocapsa* spp. are all associated with microscopic mats in the Vestfold Hills. Flushed soils at Cape Bird (Ross Island) are dominated by *Calothrix parietina* and diatoms [*Navicula muticopsis* van Heurck and *Achnanthes brevipes* var. *intermedia* (Kützing) Cleve] (17). Flushed soils exposed to saline aerosols contain *Urospora* sp. (a filamentous chlorophyte), while flushed soils of lower salinity contain *P. calophylla* (17).

The macroscopic *Prasiola crispa* (Lightfoot) meneghini is a prevalent colonizer of water-flushed ornithogenic soils. *P. crispa* has been isolated from flushed soils around penguin colonies in the Vestfold Hills (16) and on Ross Island (18). Flushed soils are subject to drying (Figure 9, follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org) and the microbial mat communities may be dispersed as dry particulates and act as sources of nutrient for surrounding oligotrophic mineral soils.

Perennial streams and rivers in Antarctica are colonized by the different groups of phototrophic organisms: cyanobacteria, green algae, diatoms, mosses, and associated and epiphytic species (153). The most common cyanobacterial communities consist entirely of Oscillatoriaceae (146). An alternative type of cyanobacterial community identified in the streams of the McMurdo Sound region is mainly composed of *Nostoc commune* Vaucher. The *N. commune* communities form a thick (20 mm) black surface layer and are sometimes associated with mosses.

Many Dry Valley streams support rich growth of the chlorophytes *Binuclearia tectorum* (Kützing) Beger and *P. calophylla*, as well as smaller growths of the chrysophyte *Tribonema elegans* Pascher (147). *Zygmena* and *Mougeotia*, which are not found in Dry Valley streams, are dominant, together with *Klebsormidium*, in streams on Signy Island (maritime Antarctica) (69).

Diatoms are found mainly on alluvial sands and gravels in streams. Adams Stream (Miers Valley) is colonized by *Hantzschia amphioxys* (Ehrenberg) Grunow and *Navicula* spp. (76). The sands of the Onyx River (Wright Valley) are colonized by the diatoms *H. amphioxys*, *N. muticopsis*, *N. cryptcephala* Kützing, *Stauroneis anceps* Ehrenberg, and *Tabellaria* sp. (76).

Mosses are commonly found on the margins of streams and in flushes (99). Epiphytes associated with mosses include bacteria, yeasts, filamentous fungi, and microalgae (*Nostoc* is a common epiphyte of mosses) (42).
Unlike the microbial mats found in maritime streams and rivers (e.g., Signy Island), the epilithic mats, cyanobacterial films, and chlorophytes found in southern Victoria Land streams (continental Antarctica) can withstand the freezing winter conditions (147). Processes such as photosynthesis occur only at low rates within the microbial mat communities in continental streams. The low photosynthetic rates are attributable to low ambient stream temperatures and to low viable chlorophyll a contents (147).

Sensitivity to Environmental Impact

Antarctic streams arise from melting snow and glacial ice. The melting of snow and ice is highly dependent on solar radiation and ambient temperature. Any significant change in mean annual temperature obviously has a dramatic effect on stream volumes. Decreased stream volume, probably also associated with lower average meltwater temperatures, is expected to reduce microbial productivity in streams. Conversely, increased stream volumes are expected to increase transport and scouring processes. Together these reduce the physical stability and longevity of stream ecosystems. Because streams and rivers are the main source of water and nutrients to the Antarctic lakes, factors affecting streams and rivers ultimately have an effect on the lake systems.

ICE MICROBIOLOGY

Introduction

It is arguable whether ice should be considered as a viable microbial biotope at all. On one hand, glacial ice and snowfields may be considered as no more than entrapment and storage systems. Microorganisms enter these systems as vegetative and resting cells, transported by wind-blown particulates, aerosols, and ice crystals, and as unsupported cells. They are trapped by the further addition and compaction of snow, to be finally released to the surrounding environment by surface melting or ablation (for terrestrial glaciers), by melting at the glacial underside-rock interface, or by calving and melting (for marine glaciers). The timescales of this process can be short (for seasonal snowfields) or extremely long (e.g., for the Antarctic continental ice cap). It is not clear whether, during the intervening period, these entrapped cells have significant metabolic activity. Certainly, they have no community structure and should best be described as assemblages (73).

Conversely, there is good evidence that lake, glacial, and sea ice harbor microniches where, at least during the Antarctic austral summer periods, active metabolism and cell division occur. These microniches, even if transitory, may be validly considered to be communities. There is evidence that even under the most severe Antarctic conditions, viable microbial cells maintain a slow rate of metabolic activity (33).
Sea Ice

Sea ice differs substantially from terrestrial (glacial) ice in terms of its origin, composition, and biology. It is formed by the freezing of seawater, accompanied by a salting out process, whereby marine salts are excluded from the nascent crystals and concentrated in brine pockets. The ice composition is not homogeneous; columnar crystals, brine pockets, and brine channels introduce a variety of microenvironments of various temperatures, light intensities, and salt and nutrient concentrations. In addition, the underside of the sea ice is in intimate association with the nutrient-rich and biologically active marine biosphere.

Sea ice offers a range of microbial habitats. The lower face of the ice sheet provides an adhesion surface that is colonized by a wide variety of microorganisms, collectively known as the Sea Ice Marine Communities (137), that consist of a complex and trophically dependent collection of bacteria, microalgae, zooplankton, and higher eukaryotic grazers (krill). Brine pockets and channels in the ice interior provide a separate, but interconnected, microbial community and are usually highly vertically stratified (85). In a detailed culture-based study of sea ice microbiology, Bowman et al. (7) noted that “a variety of taxa were observed in sea ice samples which have not been generally observed in open sea water samples.”

The physical, chemical, and microbiological composition of sea ice has been the subject of several comprehensive and recent reviews (15, 111, 137, 149) and is not discussed here in more detail.

Polar and Glacial Ice

With the exception of cryoconite holes (see below) and saline pond systems such as in the vicinity of Bratina Island, polar cap and glacial ice is essentially liquid-water free, other than from transitory melting. More than in any other Antarctic ice system, these structures act merely as repositories for wind-transported microorganisms. Indeed, microbial counts have been correlated with dust content in Antarctic ice cores (117). The interest in the microbiology of glacial ice therefore lies not in the development and function of microbial communities, but in the survival and stability of deposited microorganisms. Continental glaciers (Figure 10) and ice caps develop by accumulation and compaction of snow, and entrapped particulates undergo slow downward transport, driven by further accumulation and lower face attrition (as a result of pressure-dependent melting). Depth is therefore linked directly to age, and ice cores can be dated by counting annual depositional layers (140) or chemical analysis (6).

Extensive culture-based studies of Antarctic polar ice cap microbiology have been undertaken (reviewed in Reference 1). The 2.5 km of Vostok Station ice cores, recovered during 1974–1989, represent an age period of some 200 kya (1). Younger samples showed higher viable cell counts than old samples (Table 7). A wide variety of bacteria, yeasts, and fungi have been isolated, with spore-forming organisms dominating in older core samples.
TABLE 7  Microbial isolates from the Vostok ice cores (reproduced with permission from Reference 1)

<table>
<thead>
<tr>
<th>Depth of core sample (m)</th>
<th>Approximate age of core samples (year)</th>
<th>Number of inocula tested</th>
<th>Percentage of positive inocula</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–105</td>
<td>0–3000</td>
<td>144</td>
<td>20</td>
</tr>
<tr>
<td>105–208</td>
<td>3000–7400</td>
<td>129</td>
<td>14</td>
</tr>
<tr>
<td>208–320</td>
<td>7400–12,500</td>
<td>250</td>
<td>6</td>
</tr>
<tr>
<td>330–1500</td>
<td>12,500–107,000</td>
<td>207</td>
<td>6</td>
</tr>
<tr>
<td>1500–2400</td>
<td>107,000–200,000</td>
<td>176</td>
<td>3</td>
</tr>
</tbody>
</table>

Renewed interest in ice microbiology has come from the discovery that enclosed lakes lie beneath the Antarctic ice sheet. The largest, Lake Vostok (14,000 km², maximum depth 670 m), has attracted particular attention because it has been proposed that the lake waters have been isolated from liquid interchange for at least 1 million years (80). The ice above the lake has been cored to 3623 m, approximately 120 m above the lake level, at least 200 m into transitional ice, and some 84 m into refrozen lake water (accretion ice). A series of microscopic (116), isolation (39), and phylogenetic studies (39, 120) showed viable microorganisms, particularly members of the Brachybacterium, Methylobacterium, Paenibacillus, and Sphingomonas lineages, and phylotypes assigned to the β-proteobacteria (Acidovorax and Comamonas), α-proteobacteria (Afopia), Actinomyces, low and high G+C gram positives, and the Cytophaga/Flavobacterium/Bacteroides lineage. Cell densities in accretion ice samples have been estimated at between $2 \times 10^2$ and $3 \times 10^2$ mL$^{-1}$, and thought to be dominated by gram negatives (on the basis of the quantitation of the lipopolysaccharide biomarker) (82).

It seems reasonable to assume that microorganisms entrapped in glacial ice are metabolically inert. Ambient temperatures on the surface of the polar ice cap rarely exceed $-25^\circ$C and have been recorded as low as $-88.3^\circ$C at Vostok Station (131). Mid-winter temperature measurement in deep boreholes at the South Pole indicated a surface temperature of $-52^\circ$C, rising to $-21^\circ$C at a depth of 2350 m (118). Extrapolation of temperature-depth profile gave a predicted temperature of $-9^\circ$C at the 2810-m base of the ice cap. Under such low temperatures, both the possible freezing of the cytoplasm and the temperature-dependent rigidification of intracellular enzymes suggest that intracellular catalytic processes might be halted. However, such a view is at odds with the apparent anomaly of long-term survival of vegetative cells in ice cores, which intrinsically requires some degree of metabolic turnover for molecular repair. Indeed, Deinococcus-like organisms identified in South Polar snow (33) appear to maintain low levels of metabolic activity (measured by incorporation of tritium labeled thymidine and leucine) at ambient temperatures of $-12$ to $-17^\circ$C, and photosynthetic activity in lichens has been detected at $-17^\circ$C (126). From a simply enzymological viewpoint, this is
not so surprising because Arrhenius rate law predicts that catalytic (enzyme) rates should be decreased by only a factor of about 6 from optimum (assuming a $T_{opt}$ of 15°C and the presence of fluid zones in the cytoplasm). Daniel and coworkers (12) have measured in vitro enzyme activity as low as −100°C, demonstrating that, at least under artificial reaction conditions, some enzymes do not undergo any dramatic conformational switch-off transitions.

Lake Ice

Lake ice differs substantially from glacial ice. The permanent floating ice caps of the Dry Valley lakes (Figure 5b), typically between 3 and 6 m in depth, exist in a dynamic equilibrium owing to freezing of lake water on the underside and ablation from the upper surface (98). Only the marginal areas melt during the summer season, to refreeze over winter. The upper surfaces of the permanent ice are subject to constant seeding by particulates of eolian origin (121) and typically contain a layer of sand and organic matter within the ice profile. Priscu and coworkers, who have extensively studied the physical, chemical, and biological characteristics of Antarctic Dry Valley lake ice (65, 110, 121), have demonstrated that liquid water inclusions within the ice during the summer months (due to solar heating of the sediment layer) can constitute as much as 40% of the total ice volume. Measurements of photoautotrophic and heterotrophic activity, biomass, and chemistry in the sediment layer of Lake Bonney ice indicated that the sediment layer supports an active microbial assemblage (110, 121). Microscopic analysis showed bacterial and cyanobacterial cells, the latter dominated by *Phormidium* with lower numbers of *Chamaesiphon* and the N₂-fixing *Nostoc*. 16S rRNA sequence-based phylogenetic analysis showed numerous clones identified as *Leptolyngbya*, *Chamaesiphon*, and *Phormidium*. Several phylogenetic clades showed less than 93% identity with sequences in the public databases, indicating the possible presence of novel cyanobacterial genera (121). Bacterial clones were identified as members of the genus *Rhodoferax*, the *Acidobacterium/Holophaga* group, the Planctomycetales, and an unnamed green nonsulfur bacterial isolate (65). While the cyanobacterial phylotypes were similar, and therefore probably derived from those found in the nearby terrestrial mats, novel bacterial phylotypes were also identified. However, a much more comprehensive survey of Dry Valley microbiology is necessary before any statement can be made on whether these organisms are truly unique to either lake or ice habitats.

Cryoconites Holes

The deposition of solid particulates [e.g., stones (cryoconites), dust, desiccated algal mat fragments] on the surface of glacial or lake ice is the precursor to the formation of a unique glacial habitat, the cryoconite hole (Figure 11a). Solar warming of the particulate body gradually melts the underlying ice, forming a liquid inclusion in the surrounding solid ice (64). Each hole is spatially separate, and therefore potentially a unique microcosm.
The physical and chemical characteristics of Antarctic cryoconite holes are well suited to biological activity. During the brief summer period, the holes contain liquid water several degrees above freezing point. Nutrients accessed from melting ice, biological N fixation, and fixed carbon from phototrophic activity provide the basis for a complex community. Isolation and microscopic studies have identified a wide range of bacteria, algae, diatoms, fungi, and rotifers that inhabit cryoconite hole waters. This habitat may be one of few in Antarctica inhabited by metazoan life (158).

During the Antarctic winter, cryoconite hole liquids freeze completely (38). At some point in the evolution of the hole, the cryoconite will be at sufficient depth
such that the summer solar heating will fail to open the hole to the atmosphere, thereby generating a liquid inclusion. In a further evolutionary stage, the inclusion remains permanently frozen, thereby acting as a nondepositional mechanism for seeding glacial ice with local concentrations of microorganisms.

A comprehensive analysis of the diversity of microorganisms inhabiting Antarctic cryoconite holes, based on phylogenetic analyses of isolated organisms and community DNA extracts, has recently been reported (38). Isolated bacteria were identified as members of the $\beta$-proteobacteria, Cytophagales, and Actinobacteria (Table 8), while PCR amplification with universal 16S rRNA gene primers yielded phylotypes showing high identity with members of the cyanobacteria, $\gamma$-proteobacteria, Acidobacterium, Cytophagales, Planctomycetes, $\alpha$-proteobacteria, Gemmimonas, Verrucomicrobia, and Actinobacteria (Table 8). Many of the sequences and some of the isolates were similar to organisms identified in other

**TABLE 8** Organsims identified from culturing studies or inferred from phylogenetic analysis of cryoconite hole community DNA (adapted with permission from Reference 38)

<table>
<thead>
<tr>
<th>Cultured isolates</th>
<th>Phylotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group</strong></td>
<td><strong>Organism</strong></td>
</tr>
<tr>
<td>Bacteria</td>
<td></td>
</tr>
<tr>
<td>$\alpha$-Proteobacteria</td>
<td>Pseudomonas sacchariphila</td>
</tr>
<tr>
<td>$\beta$-Proteobacteria</td>
<td>Janthinobacterium lividum</td>
</tr>
<tr>
<td>$\gamma$-Proteobacteria</td>
<td></td>
</tr>
<tr>
<td>Acidobacterium</td>
<td>None</td>
</tr>
<tr>
<td>Cytophagales</td>
<td>Flavobacterium ferrugineum</td>
</tr>
<tr>
<td></td>
<td>Haloanella gallinarum</td>
</tr>
<tr>
<td></td>
<td>Flavobacterium sp.</td>
</tr>
<tr>
<td></td>
<td>F. succinicans</td>
</tr>
<tr>
<td>Planctomycetes</td>
<td>None</td>
</tr>
<tr>
<td>Gemmimonas</td>
<td>None</td>
</tr>
<tr>
<td>Verrucomicrobia</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Cryobacterium psychrophilum</td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Eukarya</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Fungi</td>
<td>n/a</td>
</tr>
<tr>
<td>Viridiplantae</td>
<td>n/a</td>
</tr>
<tr>
<td>Alveolata</td>
<td>n/a</td>
</tr>
</tbody>
</table>

*Genospecies showing highest percent identity in comparison of 16S rDNA sequences with Ribosomal Database and GenBank sequences. Numbers in brackets indicate numbers of similar clones identified. n/a, not attempted.
glaciers of the Taylor Valley. In no instance were members of the same genera observed in both isolate and clone libraries. Amplification of community DNA with 18S (eukaryote)-specific primers yielded a single algal phylotype and clones from tardigrades, rotifers, fungi, and ciliates (Table 8), emphasizing the complex trophic structure contained within the cryoconite hole environment. There was, however, little evidence of species uniqueness: Virtually all clones were closely related to previously identified Antarctic sequences, supporting the view that glacial ice microbiology is seeded from the immediate surroundings. Nevertheless, this conclusion is worth a cautionary note. This phylogenetic study had certainly not accessed the full microbial diversity, and probably not even a minor fraction of it. Unique (endemic) microbial species might be present in low numbers, which would be detected only by examining much larger clone libraries (e.g., in excess of 1000 clones) from several cryoconite holes.

A variant of the cryoconite hole is observed in Dry Valley lake ice. The transmission of light through the surface ice layer promotes growth of substantial cyanobacterial mats on the surface of the underlying sediment (160). At depths of less than 10 m, bubble formation on the underside of the mats causes lift-off (158), in which portions of the mat break free and float to the underside of the ice (Figure 11b). The mat fragments freeze into the ice, move upward by a combination of surface ice ablation and melting, and eventually melt through the upper surface. In the latter stages of the process, solar radiation generates a liquid inclusion around the mat fragment. The cyanobacterial mat consortia remain viable (131) and presumably support an active microbial community during the progression of the inclusion.

Sensitivity to Environmental Impacts

Ice microbiology populations, whether unique or cosmopolitan, are clearly susceptible to regional warming and the concomitant loss of ice volume. In the context of terrestrial ice bodies (glaciers, ice caps), this may be of little relevance to microbiology per se. The broader environmental and climatic consequences of this process are, of course, a separate issue of real importance.

The Dry Valleys are considered to be sensitive to climatic shifts (161). Meteorological data spanning 1966–2000 show a significant degree of cooling (0.7°C per decade) in the Dry Valleys, with an associated decrease in soil water content, reduced glacial melting, reduced lake input flows, increased lake ice thickness, reduced primary productivity, and declining numbers of soil invertebrates (47). One of the many consequences of the continuation of this trend is a dramatic impact on sensitive lake ice microbial communities, for example, by decreasing the extent and duration of the liquid-phase inclusions in ice and thereby limiting the seasonal metabolically active period. More dramatically, a significant decrease in glacial melting may substantially alter lake levels and lake ice dynamics, possibly shifting the equilibrium between ice formation and ablation.

Contamination of Antarctic glacial and lake ice systems with nonindigenous microorganisms and xenobiotic chemicals (from human activities rather than
natural transport processes; 151) are potential future problems that require international awareness and legislative control. The current stipulations of the Antarctic Treaty (http://www.nsf.gov/od/opp/antarct/anttret.htm) provide a framework for such control. However, this issue has become a focal point in the context of Lake Vostok, where the deep drilling project has penetrated into lake accretion ice, within \( \sim 120 \) m of the surface of the lake. The open drill hole is maintained by the presence of drilling fluid, some 60 tonnes of aviation fluid, and freons (150). As a water body that may have been isolated for more than a million years, Lake Vostok represents “one of the last remaining pristine bodies of water on the planet” (150). It may also harbor genetically unique microorganisms. It is therefore imperative that further drilling is not commenced until technologies have been developed to (a) prevent the pollution of the lake water by organic drilling fluids, and (b) minimize the transfer of nonindigenous microorganisms into a potentially unique microbial environment.

**FELLFIELD COMMUNITIES**

**Introduction**

Maritime and continental fellfield soils (i.e., moist high-silt-content soils and drier sand or gritty ash soils, with discontinuous cryptogamic vegetation; 165) are largely restricted to the warmer, more northerly regions of the Antarctic continent (the Antarctic peninsula) and to offshore islands (such as Signy and Marion Islands). The physical topology of fellfields is governed by climatic factors, frost-heave and particle sorting (36), desiccation, meltwater, and wind erosion (165). The particle sorting action of the freeze-thaw process generates semiregular surface structures including polygons (36). Unlike Dry Valley mineral soils, maritime fellfield soils are generally not saline, because of regular leaching (165). N/P nutrient contents are typically high compared with desert mineral soils (Table 9). Measurements of organic C in fellfield soils (Table 9) showed widely differing levels (>50% under moss cover compared with 1%–2% in visually bare sites) (134), but in all cases several orders of magnitude higher than measurements in Ross Desert soils (0.064% ± 0.035%) (93).

Antarctic fellfields are dominated by cryptogams (mostly mosses and lichens), but areas of visually barren soil fines also occur (165). The carpet of cryptogams has a limited depth profile and is generally poorly anchored to the underlying sand-, ash-, or peat-dominated soils (165). These ecosystems are therefore physically unstable and highly susceptible to physical disturbance and erosion.

**Fellfield Microbiology**

The fellfield soils of the Antarctic Peninsula support a structurally complex but low diversity vegetation that is composed of mosses, liverworts, lichens, and algae. In more sheltered areas, two flowering plants, the grass *Deschampsia antarctica*...
and the herb *Colobanthus quitensis*, are found. The Signy Island eukaryotic plant community supports extensive microbial populations, in particular the cyanobacteria *Phormidium autumnale* and *Pseudoanabaena catenata* with subdominant populations of the diatom *Pinnularia borealis* (43). Other species identified include *Nostoc* sp., *Achnanthes lapponica*, *Clamydomonas chlorostellata*, *Planktosphaerella terrestris*, *Cylindrocystis brebissonii*, *Cosmarium undulatum*, and *Netrium* sp. Species distribution within the polygon structure typical of fellfields was not homogeneous: Most cyanobacterial cells were found in the top 1 mm of the soil profile, and nonmotile species were more dominant at the edges of the frost polygons (43). Filamentous microorganisms may be particularly important in stabilizing soil structure. The filamentous morphology and the production of extracellular glycoprotein (165, 127) are thought to bind soil particles and aid in the production of stabilized microbial mats.

The continental and maritime fellfield communities support substantial heterotrophic microbial populations (44, 163, 164). A variety of bacterial (103), yeast (104), and filamentous fungal (127) isolations have been reported. However, these studies provide little information on the nature of the microbial community structure and on the trophic interactions within the community. To the authors’ knowledge, no comprehensive analyses of microbial distribution in fellfield habitats have been undertaken. For example, the extent to which the vegetative components of the community possess unique microbial associations (e.g., rhizospheric species) is currently not known.

### TABLE 9 Nutrient levels in Antarctic soils (reproduced with permission from References 136 and 153)

<table>
<thead>
<tr>
<th>Soil/location</th>
<th>Soil water content (% wt)</th>
<th>Soluble NO$_3$-N ($\mu$g g$^{-1}$)</th>
<th>Soluble NH$_4$-N ($\mu$g g$^{-1}$)</th>
<th>Soluble P ($\mu$g g$^{-1}$)</th>
<th>Organic C (% wt)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fellfield soils</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marion Island</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Signy Island</td>
<td>10–20</td>
<td>1.9–6</td>
<td>3–4</td>
<td>40–80</td>
<td></td>
</tr>
<tr>
<td>Signy Island</td>
<td>0.1</td>
<td>0.1</td>
<td>40</td>
<td>1–50</td>
<td></td>
</tr>
<tr>
<td>Coastal Antarctica</td>
<td>1–20</td>
<td>15–20</td>
<td>4–45</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td><strong>Desert soils</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ross Desert</td>
<td>0.26–5</td>
<td>0–120</td>
<td>6–40</td>
<td>80–120</td>
<td>0.0037–0.32</td>
</tr>
<tr>
<td>Ross Desert</td>
<td>0.26–5</td>
<td>0–960</td>
<td>0–2.2</td>
<td>0–2.2</td>
<td></td>
</tr>
<tr>
<td>Pensacola Mountains</td>
<td>&lt;1–1250</td>
<td>&lt;1</td>
<td>0.25–0.5</td>
<td>0–2.2</td>
<td></td>
</tr>
<tr>
<td>Pensacola Mountains</td>
<td>0.7–6.4</td>
<td>0.3–1.1</td>
<td>&lt;0.01</td>
<td>0–2.2</td>
<td></td>
</tr>
<tr>
<td><strong>Ornithogenic soils</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marion Island</td>
<td>0–130</td>
<td>101–664</td>
<td>146–675</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Signy Island</td>
<td>90</td>
<td>1369</td>
<td>4600</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>S. Shetland Island</td>
<td>18.8–35</td>
<td>140–400</td>
<td>50–145</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Ross Island</td>
<td>20–35</td>
<td>0</td>
<td>6000</td>
<td>2400</td>
<td>21–24</td>
</tr>
</tbody>
</table>
Fellfield-like communities are uncommon in the more southerly regions of continental Antarctica. Only in localized and environmentally benign sites in the Dry Valleys such as Botany Bay (104) do moss-dominated fellfield-like communities exist.

Sensitivity to Environmental Impacts

Fellfield communities, which physically depend on the presence of macroflora (cryptogams) and filamentous microbiota (cyanobacteria), are potentially susceptible to physical impact. The relatively low eukaryotic species diversity and the physical structure of the community (a relatively thin biological layer overlying mobile gravels or peats) make these communities highly sensitive to physical disturbance [whether by human activities, local seal populations (155), or the actions of wind and water].

Increases in continental snowfall may also impact negatively on communities that depend on eukaryotic photosynthesis. Measurements of chlorophyll a fluorescence in continental lichen communities suggest that snow cover significantly reduces the period of active photosynthesis (113). This contrasts maritime Antarctic and European alpine environments, where snow cover acts as a protective cover, maintaining thallus hydration and extending the photosynthetic period (162).

ORNITHOGENIC SOIL ENVIRONMENTS

Introduction

Ornithogenic soils (i.e., soils modified or generated by the presence of birds; 142) offer localized and specialized environments that differ widely from other Antarctic microbial habitats. Such soils are generated by the deposition of guano in the vicinity of bird colonies; the most extensively studied are the Adelie Penguin colonies of Ross Island and the Vestfold Hills. These environments are unique among Antarctic microbial habitats in that they do not depend on in situ photoautotrophy, have continuous exogenous nutrient supplementation, and maintain high nutrient levels, in particular, inorganic nitrogen, phosphorus, and organic carbon.

Relic ornithogenic soils, resulting from the abandonment and subsequent maturation of rookeries, are widespread through maritime Antarctica. These soils provide localized regions of high nutrient concentration in an otherwise nutrient-poor environment (139).

The Physical and Chemical Environment

Ornithogenic soils (Figure 12) are characterized by high levels of inorganic and organic nutrients, compared with virtually any other Antarctic terrestrial environment (see Table 9). The soil profile is typically a compacted upper horizon, with an underlying moist, soft, and sandy loam horizon (136). Both horizons have a high
saturation level (up to 30% H2O by weight). The nutrient composition is a direct result of the continued deposition of guano (Figure 13) and shows the high uric acid and ammonia-N levels typical of guano deposits in other parts of the world (77). Uric acid degrades to allantoin, urea, and finally ammonia (77), accounting for the high NH4+ -N levels (~5% dry wt.) (136) in ornithogenic soils. Nitrate-N can also be present at significant levels, much higher than is typical of normal terrestrial soils (0.5% dry wt; compare with <0.001%) (136). Nitrites can derive from microbial nitrification, abiotic weathering processes, and auroral activity (154). Evidence for biological nitrate production in ornithogenic soils is currently indirect, and no culture-dependent or phylogenetic evidence for the presence of nitrifying bacteria has yet been published.

Ornithogenic soils also carry a high soluble salt load (>0.7% dry wt; (136)), levels which are thought to be deleterious to plant growth (101). This may account for the virtual absence of lichen, moss, and algal growth within the bounds of active bird colonies, with the exception of ornithocoprophilous lichen growth on protruding rocks.

Microbiology of Ornithogenic Soils

The organic C contents of ornithogenic soils (Table 9) are high, particularly in comparison with Dry Valley mineral soils. The high levels of organic C are consistent with estimates of microorganisms by direct microscopic counts [2 × 10^10 cells g^-1; (8)] and by ATP analysis [5 × 10^7-7 × 10^8; (41)]. Interestingly, low levels of in situ 3H-glucose uptake have led to suggestions that ornithogenic soil bacteria are inactive (possibly because of the suppressive effect of organic molecules) or dead (122). A comparison of the microscopic- and ATP-derived numerical data suggests that a relatively high proportion of the visible cells may not be viable.

Microscopic examination of ornithogenic soils has shown that up to 50% of the microbiota are gram-negative nonmotile cocci (123). Although only a low proportion of the cell types were culturable (8), a high proportion of the isolates were phenotypically similar. Several new species of Psychrobacter were isolated, all of which could grow on urate as a sole C source. This study led to a proposal that the genus *Psychrobacter* predominates in ornithogenic soils (8). To date, no comprehensive phylogenetic analyses of the true microbial distribution in ornithogenic soils have been reported. More than in other more complex microbial ecosystems, such studies might be expected to provide useful guidelines for the pathways of nutrient cycling.

Sensitivity to Environmental Impacts

The dependence of ornithogenic soils, and their associated (possibly unique) microbial diversity, on a constant source of guano is obvious. Abandoned rookeries undergo a variety of chemical, physical, and biological successional changes (136, 139). Erosion and leaching processes reduce the inhibitory salt concentration, resulting in a proliferation of cryptogamic vegetation and, in maritime sites, plant
growth. The high level of easily available nutrients in relic ornithogenic soils might be maintained for centuries and even millennia (106). Although there have been no comparative studies reported on the microbial distribution in active and relic ornithogenic soils, the documented changes in nutrient profiles (such as the rapid loss of uric acid) (136) and the subsequent growth of fellfield-like cryptogamic and higher-plant-dominated communities suggest that major changes in microbial population distribution are inevitable.

Climatic change may be the major long-term factor in rookery abandonment (51), although disturbance caused by human activities has a major impact on penguin breeding and short-term colony viability (125). Given the attraction of penguin colonies as targets for tourist activity, careful control of these activities is critical to avoid detrimental impacts on both the penguin populations and their associated microbial communities.

CONCLUSIONS

To address the question of whether Antarctic microbial biotopes are truly endangered by human activities on the continent and by current and projected changes in climatic conditions, we must first ask ourselves if we understand sufficiently the true microbial diversity and microbial community structure in these biotopes to appreciate the effects of such impacts. The answer to this question is clearly negative, at least for most Antarctic biotopes. A large proportion of the many microbiological studies have either focused on macroscopic biota (such as cryptograms and cyanobacteria) or have addressed the issue of microbial diversity using culture-dependent methods. The latter are valuable, but may be highly misleading. Detailed phylogenetic studies of microbial diversity have only recently started to emerge and are currently restricted to some of the more specialized Antarctic communities (such as endoliths and lake ice and cryoconite hole communities). Other much more extensive microbial niches, such as cold desert soils and fellfields, have yet to be characterized in detail.

Understanding microbial community structure in detail is a precursor to meaningful studies of climatic and other impacts, based both in the field and in the laboratory. To date, such studies have monitored only gross biological changes (such as the development of moss and cyanobacterial consortia in cloche-enclosed desert soils, and the disintegration of fellfield mats by trampling) or gross metabolic changes (e.g., the reduction in lake productivity in response to atmospheric cooling). Though important, these studies reveal little of detailed effects at the level of microbial diversity, community structure, and trophic interactions.

Our current state of knowledge on Antarctic microbiology is incomplete. In consequence, our ability to accurately assess the sensitivity of Antarctic microbial communities is limited to the more obvious physical effects. It is clear that some Antarctic microbial communities are physically unstable (such as fellfield and flush mats, and moss communities) and steps have already been taken to minimize physical disturbance in these areas. For other communities and for other
impacts, we do not have the necessary data to assess the sensitivity of the first or the importance of the second. Therefore, until such data exist, it is appropriate to maintain a policy of considerable care and caution with respect to these communities. Where possible, the direct effects of human activities should be minimized: restricted access to particularly sensitive areas, control of nonscientific activities on and around continental and maritime Antarctica, and minimization of chemical and biological contamination. Together with a growing awareness of the consequences of climatic change, these restraints will help retain Antarctica as the last pristine continent.

ACKNOWLEDGMENTS

The authors would like to express their gratitude to those individuals, organizations, and agencies who have collaborated, supported, and funded our research on Antarctic microbial diversity. Particular thanks are extended to Professors Roy Daniel, Alan Green, and Craig Cary of the Waikato University Antarctic Terrestrial Biology Research Program, to Antarctica NZ, and to the South African National Research Foundation and the SA National Antarctic Program. The authors also wish to dedicate this article to friend and colleague David Wynn-Williams, who died tragically in 2002.

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Figure 2  Dry Valley mineral soils in the Miers Valley, Eastern Antarctica.

Figure 3  Depth profile of a west-facing Dry Valley mineral soil clearly showing the dry surface horizon (0–10 cm) overlying moist gravels (a depth of ~10–30 cm). The permafrost layer is at a depth of ~30 cm. Spatula scale: ~15 cm.
Figure 4  Lithic microbial community habitats. (a) Freeze-fractured rocks that provide chasmoendolithic habitats, (b) cryptoendolithic organisms in coarse sandstone, and (c) a hypolithic habitat.
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Figure 10  The Adams Glacier, Miers Valley. A typical hanging glacier of the Dry Valleys.
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**Errata**

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