# Polar Lakes and Rivers

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**Warwick F. Vincent and Johanna Laybourn-Parry**

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CHAPTER 7

# Antarctic subglacial water: origin, evolution, and ecology

**John C. Priscu, Slawek Tulaczyk, Michael Studinger, Mahlon C. Kennicutt II, Brent C. Christner, and Christine M. Foreman**

## Outline

Recent discoveries in the polar regions have revealed that subglacial environments provide a habitat for life in a setting that was previously thought to be inhospitable. These habitats consist of large lakes, intermittently flowing rivers, wetlands, and subglacial aquifers. This chapter presents an overview of the geophysical, chemical, and biological properties of selected subglacial environments. The focus is on the large subglacial systems lying beneath Antarctic ice sheets where most of the subglacial water on our planet is thought to exist. Specifically, this chapter addresses the following topics: (1) the distribution, origin, and **hydrology** of Antarctic **subglacial lakes**; (2) Antarctic ice streams as regions of dynamic liquid-water movement that influence ice-sheet dynamics; and (3) subglacial environments as habitats for life and reservoirs of organic carbon.

## 7.1 Introduction

Over the last decade, interest in **subglacial lakes** and rivers has matured from a curiosity to a focus of scientific research. The earliest evidence of large **subglacial lakes** was provided by Russian aircraft pilots who flew missions over the Antarctic continent in the 1960s (Robinson 1964). Speculation about the presence of lakes was verified by airborne radio-echo soundings collected during the 1960s and 1970s (Drewry 1983) in which flat reflectors at the bottom of ice sheets were interpreted as indicating subglacial accumulations of liquid water (Oswald and de Robin 1973; de Robin *et al.* 1977). However, it was Kapitsa's description of subglacial Lake Vostok in Antarctica that convinced the scientific community of the existence of major reservoirs of water beneath thick ice sheets (Kapitsa *et al.* 1996). We now know that more than 150 lakes exist beneath the Antarctic ice sheets (Priscu *et al.* 2003, 2005; Siegert *et al.* 2005) and that many may be connected by networks of subglacial streams and rivers (Gray *et al.* 2005; Wingham *et al.* 2006; Fricker *et al.* 2007; see Plate 1). Recent evidence also indicates that **subglacial lakes** may initiate and maintain rapid ice flow and should be considered in ice-sheet mass balance assessments. Liquid water had previously been documented beneath Antarctic ice streams (Engelhardt *et al.* 1990), the Greenland ice sheet (Fahnestock *et al.* 2001; Andersen *et al.* 2004), and smaller continental glaciers (e.g. Mikucki *et al.* 2004; Bhatia *et al.* 2006). Estimates indicate that the volume of Antarctic **subglacial lakes** alone exceeds 10 000 km$^3$ (Dowdeswell and Siegert 1999), with Lake Vostok ($\approx$5400 km$^3$; Studinger *et al.* 2004) and Lake 90°E (1800 km$^3$; Bell *et al.* 2006) being the largest.

Subglacial environments were originally speculated to be devoid of life (e.g. Raiswell 1984). However, discoveries of microbial life in McMurdo Dry Valley lake ice (Priscu *et al.* 1998), **accretion ice** above Lake Vostok (Priscu *et al.* 1999; Christner *et al.*

2006), within Greenland and Antarctic glacial ice (e.g. Christner *et al.* 2006), at the beds of alpine (Sharp *et al.* 1999) and High Arctic glaciers (Skidmore *et al.* 2005), in subglacial volcanic calderas (Gaidos *et al.* 2004), and in outlet glaciers draining the polar plateau (Mikucki and Priscu 2007) have all provided information about the expected diversity and biogeochemical importance of biology in subglacial environments. It is now known that subglacial biology plays a role in geochemical processes, offering new insights into the evolution and biodiversity of life on our planet (Priscu and Christner 2004). The discovery of viable organisms in subglacial environments has extended the known limits of life on Earth, providing strong evidence that life has successfully radiated into virtually all aquatic habitats on Earth that contain 'free' liquid. Subglacial liquid environments are an exciting frontier in polar science and will provide an improved understanding of the coupling of geological, glaciological, and biological processes on our planet.

This chapter presents an overview of the geophysical, chemical, and biological properties of selected aquatic subglacial environments. The focus is on the large subglacial systems lying beneath Antarctic ice sheets where most of the subglacial water on our planet is thought to exist (e.g. Siegert *et al.* 2006; Priscu and Foreman, 2008). This chapter addresses the following specific topics: (1) the distribution, origin, and **hydrology** of Antarctic **subglacial lakes**; (2) Antarctic ice streams as regions of dynamic liquid-water movement that influence ice-sheet dynamics; and (3) subglacial environments as habitats for life and reservoirs of organic carbon. Surface ice-based ecosystems are discussed in Chapter 6.

## 7.2 Antarctic subglacial lakes and rivers: distribution, origin, and hydrology

### 7.2.1 Distribution

The analysis of airborne surveys collected between 1967 and 1979 (Siegert *et al.* 1996) initially revealed at least 70 **subglacial lakes** beneath the Antarctic ice sheet. Dowdeswell and Siegert (2002) categorized these **subglacial lakes** as: (1) lakes in subglacial basins in the ice-sheet interior; (2) lakes perched on the flanks of subglacial mountains; and (3) lakes close to the onset of enhanced ice flow. Lakes in the first category are found mostly in and on the margins of subglacial basins. Lakes in this category can be divided into two subgroups. The first subgroup is located where subglacial topography is relatively subdued; the second subgroup of lakes occur in topographic depressions, often closer to subglacial basin margins, but still near the slow-flowing center of the Antarctic ice sheets. Where bed topography is subdued, deep **subglacial lakes** are unlikely to develop. Lake Vostok is the only subglacial lake that occupies an entire subglacial trough. Other troughs, such as the Adventure Subglacial Basin, contain several smaller lakes (e.g. Wingham *et al.* 2006). 'Perched' **subglacial lakes** are found mainly in the interior of the ice sheet, and on the flanks of subglacial mountain ranges. In several cases, small **subglacial lakes** (<10 km long) have been observed perched on the stoss face (i.e. facing the direction from which a glacier moves) of large (>300 m high), steep (gradient >0.1) subglacial hills. At least 16 **subglacial lakes** occur at locations close to the onset of enhanced ice flow, some hundreds of kilometers from the ice-sheet crest (Siegert and Bamber 2000). About 20 other lakes have also been reported by Popov *et al.* (2002), who analyzed radio-echo sounding data collected between 1987 and 1991 by Russian Antarctic Expeditions in central Antarctica between Enderby Land and 90°S. Radar surveys carried out in 1999 and 2001 by the Italian Antarctic Program over Aurora and Vincennes Basins and over Belgica Highlands revealed 14 **subglacial lakes** in addition to the original Siegert inventory (Tabacco *et al.* 2003). The Italian survey defined the boundary conditions of a relatively large lake (Subglacial Lake Concordia) located in the Vincennes Basin, at 74°06'S, 125°09'E. The ice thickness over Lake Concordia ranges from 3900 to 4100 m, the surface area is greater than 900 km$^2$, and the water depth is estimated to be about 500 m in the central basin (Tikku *et al.* 2005). The high density of lakes in the Dome C region suggests that they are hydrologically connected within a watershed, making them an important system for the study of subglacial **hydrology**, and biological and geochemical diversity. The recent discovery of four large lakes with surface areas of

3915, 4385, 1490, and 3540 km² near the onset of the fast-flowing Recovery Ice Stream, a catchment that compromises 8% of the East Antarctic Ice Sheet and contributes 58% of the flux into the Filchner Ice Shelf, has led to the suggestion that these lakes may be responsible for the initiation of the ice stream (Bell *et al*. 2007). If this is true, then basal **hydrology** should be taken into consideration in numerical models of ice-sheet motion.

Siegert *et al.* (2005) combined radar-sounding interpretations from Italian, Russian and US researchers to revise the number of lakes known to exist beneath the ice sheet from 70 to 145. Approximately 81% of the detected lakes lie at elevations less than a few hundred meters above sea level whereas the majority of the remaining lakes are 'perched' at higher elevations. Lake locations from the new subglacial lake inventory are shown in Figure 7.1 relative to local 'ice divides' calculated from the satellite-derived surface elevations of Vaughan *et al.* (1999) and their spatial relationship to subglacial elevation and hydraulic fluid potential. Most of the lakes identified (66%) lie within 50 km of a local ice divide and 88% lie within 100 km of a local divide. Even lakes located far from the Dome C/Ridge B cluster and associated with very narrow catchments lie either on or within a few tens of kilometers of the local divide marked by the catchment boundary. The hydraulic potential reveals that some of the lakes along the divide could be hydraulically connected, whereas others located on either side of the divide may not be in communication as the divides tends to follow the line of maximum fluid potential.

### 7.2.2 Origin

The association of **subglacial lakes** with local ice divides and regions of high hydraulic fluid potential leads to a fundamental question concerning the evolution of subglacial lake environments: does the evolving ice sheet control the location of **subglacial lakes** or does the fixed lithospheric character necessary for lake formation (e.g. basal morphology, geothermal flux, or the nature of sub-ice aquifers) constrain the evolution of ice-sheet catchments? With the exception of central West Antarctica (e.g. Anandakrishnan *et al.* 2007) little is known about either the lithospheric character along these catchment boundaries or the history of

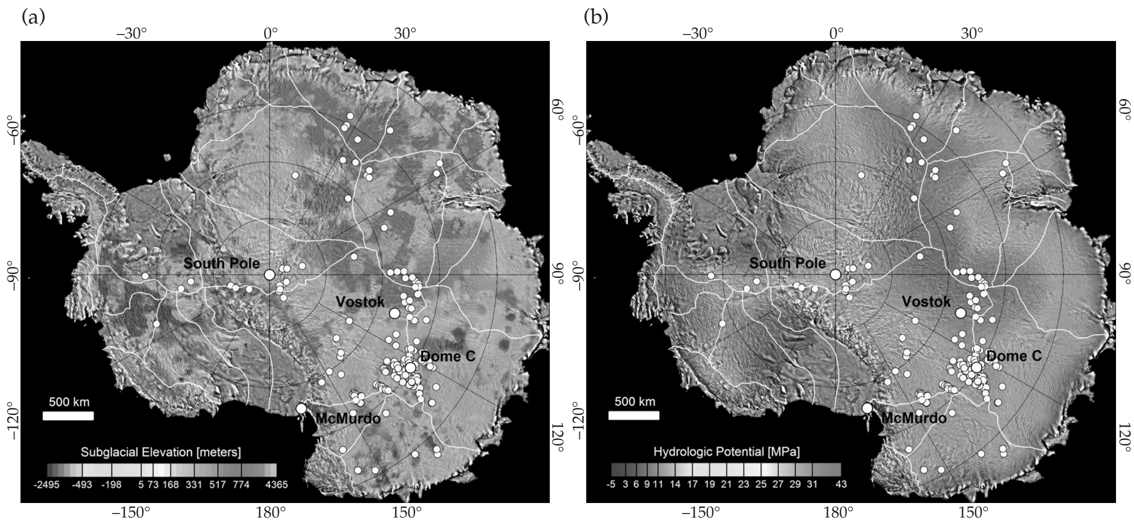


**Figure 7.1** Distribution of Antarctic subglacial lakes in relation to the ice divides (light lines in both panels), subglacial elevation (a) and hydraulic fluid potential (b). The base map is a MODIS image mosaic. The water should flow from lakes with high fluid potential to lakes with lower potential, assuming that there is a connection. The white circles indicate the locations of major field stations. A colour version is shown in Plate 1.

their migration as discerned from layering within the ice sheet.

Together with Lake Vostok (14 000 km²; >800 m deep), the 90°E and Sovetskaya lakes define a province of major lakes on the flanks of the Gamburtsev Subglacial Mountains (Bell *et al.* 2006) (Figure 7.2). The estimated water depths of the 90°E (2000 km²; ≈900 m deep) and Sovetskaya (1600 km²; >800 m deep) lakes are similar to the maximum water depths deducted from seismic and gravity inversions over Lake Vostok and are also similar to other tectonically controlled lakes such as fault-bounded lakes including Tahoe, USA (501 m) and Issyk-kul, Kyrgyzstan (668 m), as well as rift lakes including Tanganyika, Africa (1479 m), Malawi, Africa (706 m), and Baikal, Siberia (1637 m) (Herdendorf 1982). With the exception of Great Slave Lake, Canada (624 m), glacially scoured lakes tend to have maximum water depths of less than 420 m (Herdendorf 1982). Whereas the majority of surface lakes are glacial in origin (75%) (Meybeck 1995), most (85%) of the deep lakes (>500 m) are tectonic in origin (Herdendorf 1982). The steep, rectilinear morphology of Lakes Vostok, 90°E, and Sovetskaya indicate a tectonic origin (see Figure 7.2 and Bell *et al.* 2006). Tectonic control of these basins is not indicative of active tectonics or elevated geothermal heat flow, but the basin-bounding faults may provide conduits of active fluid flow rich in dissolved minerals into the lakes (Studinger *et al.* 2003). These deep elongate basins probably pre-date the onset of Antarctic glaciation and were likely surface lakes before becoming overlain by glacial ice. The tectonically controlled depth of these lakes should provide relatively constant water depths through changing climatic conditions over the past 10–35 million years (Bell *et al.* 2006). Deep **subglacial lakes** are likely to have been stable through many glacial cycles and may have developed novel ecosystems, in contrast to the shallower lakes. This contention is corroborated by recent evidence from Great Slave Lake, Canada, which showed that the **benthic** sediments were undisturbed by the retreat of the Laurentian ice sheet across the lake basin (S. Tulaczyk, unpublished results).

Although arguments have been made for the tectonic origins of deep **subglacial lakes** (Studinger *et al.* 2003; Bell *et al.* 2006), there continues to be debate about whether **subglacial lakes** in Antarctica reside in active tectonic basins or along old inactive zones of structural weakness that once provided guidance for subglacial erosion. Much of East Antarctica, where the majority of **subglacial lakes** have been found so far (see Figure 7.1), is thought to have assembled between 500 and 800 million years ago. However, our knowledge of the interior of the continent, the distribution of major tectonic boundaries and old zones of structural weakness is limited due to a paucity of data. In regions were geophysical data, such as surface and airborne

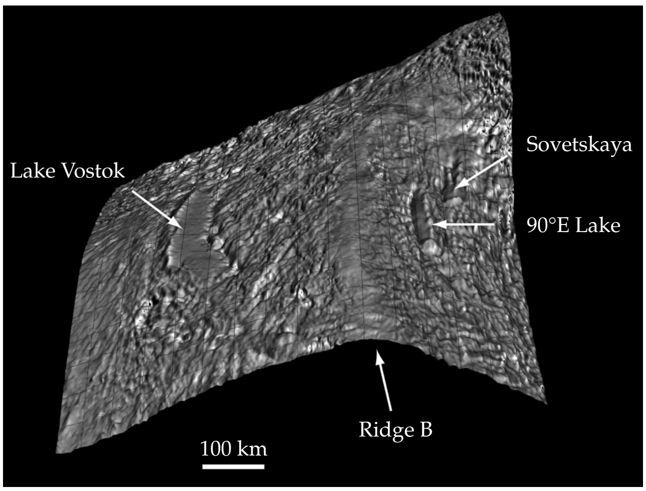


**Figure 7.2** MODIS mosaic of Ridge B region including the 90°E and Sovetskaya lakes as well as Lake Vostok. Geographic north is to the bottom. See Bell *et al.* (2006) for details.

geophysics, and continent-wide geodetic networks can be combined, it is possible to discern whether tectonically controlled basins or zones of structural weakness are the preferred sites of **subglacial lakes** (SALE 2007). Views of the origins of structures that bisect the interior of the East Antarctic continent continue to evolve. Further knowledge based on high-resolution dating techniques will be needed to clarify whether **subglacial lakes** preferentially form along major tectonic boundaries when water is available.

### 7.2.3 Hydrology

For over 30 million years the Antarctic continent has had a hydrologic system in which redistribution of atmospheric precipitation is accomplished predominantly through flow of ice. When observed from the surface, Antarctica lives up to its reputation as a 'frozen continent'. However, recent scientific observations indicate the existence of a dynamic subglacial system of liquid-water generation, storage, and discharge in Antarctica, which is similar in some ways to river and lake systems on the other continents. Understanding the physical, chemical, and biological properties of this liquid subglacial water is currently one of the most exciting frontiers in Antarctic science and has the potential to change our basic understanding of the coupling of geological, glaciological, and biological processes in Antarctica.

Although the **hydrology** of certain alpine temperate glaciers have been studied for some time, knowledge of sub-ice-sheet **hydrology** in Antarctica is rudimentary. We can put only loose quantitative constraints on the dynamics of sources and sinks of water beneath the ice. To date, our understanding of the topology, geometry, and efficiency of subglacial drainage networks in Antarctica is based mostly on models. We know more about drainage channels on Mars than about liquid-water flow features in Antarctica. Subglacial Antarctic lakes provide the most impressive evidence for the presence and importance of subglacial water in Antarctica. Antarctic lakes may hold over 8% of all lacustrine fresh water on Earth, enough to cover the whole continent with a uniform water layer approximately 1 m deep. These estimates of water volumes in **subglacial lakes** are surprising given the fact that rates of subglacial water production are 100–1000 times slower than mean effective precipitation rates on other continents ($\approx$0.001 compared with $\approx$0.3 m year$^{-1}$, respectively). This means that average water residence time in the subglacial zone of Antarctica is equal to approximately 1000 years, which is likely a reflection of the slow rates of drainage of liquid water through subglacial environments. From other glacial drainage systems we know that water drainage often involves long periods of water accumulation, punctuated by dramatic flood events, known typically under their Icelandic name, *jökulhlaups*. Such floods could modulate ice flow rates, be significant agents of geomorphic change, and may release living organisms and organic carbon from **subglacial lakes.**

Despite the dearth of information on the subglacial **hydrology** in Antarctica, there is a growing appreciation that the origins and cycling of water in these systems plays an important role in continent-wide hydrological processes. Recently, Gray *et al.* (2005) and Wingham *et al.* (2006) presented evidence for large discharges of water ($\approx$0.3 km$^3$, $\approx$5 m s$^{-1}$; and $\approx$1.8 km$^3$, $\approx$50 m s$^{-1}$, respectively) beneath ice sheets occurring over a period of months. These processes appear to extend over distances of tens or even hundreds of kilometers. Wingham *et al.* (2006) and Fricker *et al.* (2007) further hypothesized that subglacial basins may be flushed periodically. This has important ramifications for the residence time of water and water-circulation patterns in **subglacial lakes**. Mixing and transport processes within lakes established by *in situ* chemical, geothermal, and biogeochemical activities, or by pressure melting of ice, would be disrupted by the rapid throughput of water. Periodic discharges would also alleviate or reduce gas pressure build-up from the disassociation of gas hydrate during the melting of basal ice and exchange resident biota between **subglacial lakes**. If these hydrologic processes occur on a large scale, solute and microbial redistribution throughout the subglacial water environment may occur frequently. Understanding the parameters that control subglacial water balances will be a major challenge for future subglacial environment research.

Evidence is emerging that **subglacial lakes** may also drain catastrophically to the ocean. Lewis *et al.* (2006) demonstrated recently that the dramatic morphology of the Labyrinth in the Wright Valley and the drainages associated with the Convoy Range, both located in the McMurdo Dry Valleys along the Trans-Antarctic Mountain front, may be the result of large floods during the mid-Miocene era. The mid-Miocene was a period when the Antarctic climate cooled and the East Antarctic Ice Sheet experienced a major expansion, growing far beyond its present limits. The ice-free regions of southern Victoria Land exhibit extensive bedrock-channel networks most probably carved during catastrophic outbursts of **subglacial lakes** (Denton and Sugden 2005). The sudden and repeated drainage of the subglacial lake system through the Labyrinth/Convoy regions occurred between 12.4 and 14.4 million years ago when the East Antarctic Ice Sheet was larger and the melting-ice margins terminated in the Southern Ocean. During this period, a significant addition of freshwater from subglacial floods ($\approx$6000 km$^3$, $\approx 2\times10^6$ m$^3$ s$^{-1}$, sea level rise $\approx$1.6 cm; Lewis *et al.* 2006) could have triggered alternate modes of ocean circulation within the Ross Sea and Southern Ocean (e.g. Mikolajewicz 1998). The results of recent climate modeling suggest that regional and global climate are sensitive to freshwater influx into the Ross Embayment. This flux can alter thermohaline circulation, disrupt deep-water formation, and impact sea-ice extent (Mikolaiewicz 1998; Lewis *et al.* 2006). Such changes, if they were rapid, could influence climate on a global scale.

## 7.3 Antarctic ice streams: regions of dynamic liquid water movement that influence ice-sheet dynamics

Antarctic **subglacial lakes** tend to be located in the central parts of the ice sheet, where ice becomes thick enough to provide sufficient thermal insulation for the basal thermal regime to melt ice in contact with the bedrock. As the ice sheet thins towards the edges, increasing basal shear heating in zones of fast ice sliding becomes the primary mechanism maintaining basal melting (Llubes *et al.* 2006). In these fringe regions, basal melting rates (>10 mm year$^{-1}$) may be several times greater than in the deep interior ($\approx$1 mm year$^{-1}$). Average basal melting on the continental scale is approximately 2 mm year$^{-1}$ (Vogel *et al.* 2003; Llubes *et al.* 2006).

The combination of relatively abundant fresh water associated with fine-grained sediments that typify the subglacial and basal zones of ice sheets may provide an important habitat for life in addition to **subglacial lakes**. Whereas the total area of **subglacial lakes** is estimated to cover less than 1% of Antarctica (Dowdeswell and Siegert 1999), the zone of saturated sediments is likely to extend over most of the continent forming what can be considered as our planet's largest wetland. It is unlikely that basal meltwater is confined only to the pore spaces of glacial sediments immediately underlying the ice base (typically 1–10 m; Alley *et al.* 1997). In North America, glacial meltwater penetrated the upper 100's of meters of rocks and sediments (e.g. McIntosh and Walter 2005). Even making the conservative assumption that basal meltwater infiltrated just the top approximately 0.1 km beneath the Antarctic ice sheet, the volume of subglacial groundwater is likely to fall in the range of $10^4$–$10^5$ km$^3$ (assuming $\approx 10\times10^6$ km$^2$ for the area and average porosity ranging between 1 and 10%). This volume would increase to $10^6$ km$^3$ assuming basal meltwater infiltration of 1 km and a porosity of 10%, which is consistent with the formerly glaciated portions of North America (McIntosh and Walter 2005). Based on these estimates, the volume of subglacial groundwater beneath the Antarctic ice sheet would be 100 times greater than that estimated for **subglacial lakes**, an order of magnitude greater than all nonpolar surface fresh water (e.g. atmosphere, surface streams, and rivers), and would account for almost 0.1% of all water on our planet (Table 7.1).

Subglacial zones of West Antarctic ice streams represent an important example of potential freshwater-saturated subglacial wetlands. Their physical and chemical characteristics have been studied during recent decades through geophysical and glaciological investigations (e.g. Alley *et al.* 1987; Tulaczyk *et al.* 1998; Gray *et al.* 2005). Existing predictions of basal melting and freezing rates in the drainage basin of Ross ice streams indicate a predominance of melting in the interior with melting rates decreasing downstream. This region has an area of approximately $0.8\times10^6$ km$^2$ has an average net

**Table 7.1** The major water reservoirs on Earth. Data for the polar ice sheets and Antarctic groundwater are shown in bold. Compiled from Wetzel (2001) and Gleick (1996). Antarctic groundwater volume assumes a surface area of $10 \times 10^6$ km$^2$, depth of 1 km, and porosity of 10% (see text for details).

| Reservoir | Volume (km$^3$×10$^6$) | Percentage of total |
|---|---|---|
| Oceans | 1370 | 96.94 |
| **Antarctic ice sheet** | **30** | **2.12** |
| Groundwater | 9.5 | 0.67 |
| **Greenland Ice Sheet** | **2.6** | **0.18** |
| **Antarctic 'groundwater'** | **1** | **0.07** |
| Lakes | 0.125 | 0.009 |
| Soil moisture | 0.065 | 0.005 |
| Atmosphere | 0.013 | 0.001 |
| **Antarctic subglacial lakes** | **0.010** | **0.001** |
| Streams and rivers | 0.0017 | 0.0001 |

melting rate of about 3 mm year$^{-1}$ (≈2.5 km$^3$ year$^{-1}$) (Joughlin *et al.* 2004).

Recent observations indicate the presence of small **subglacial lakes** (≈5–10 km diameter) beneath ice streams that exchange water at rates of about approximately 100 m$^3$ s$^{-1}$ (Gray *et al.* 2005). These findings imply the presence of a highly dynamic subglacial water drainage system, which is consistent with borehole observations of temporally (and spatially) variable subglacial water pressure (Engelhardt and Kamb 1997). A borehole camera deployed on one of the ice streams revealed the presence of an approximately 1.6-m-deep cavity of liquid water, which may be part of a more widespread water-drainage system. In the same area, the camera imaged an approximately 10–15-m layer of refrozen water, which possesses a record of changes in subglacial **hydrology** over time scales ranging between decades and millennia (Vogel *et al.* 2005). In addition to basal water flow, the subglacial sediments themselves experience deformation and horizontal transport, associated with fast ice flow (Alley *et al.* 1987; Tulaczyk *et al.* 2001).

Samples collected from the subglacial environment beneath the West Antarctic ice streams have revealed the widespread presence of porous subglacial till (Tulaczyk *et al.* 2000a, 2000b). Subglacial core samples recovered from dozens of locations on three different ice streams permitted investigation of both the mineral component and pore water in these cores. The subglacial sediment is spatially uniform, presumably because it is generated by erosion of relatively homogeneous, widespread Tertiary glaciomarine sediments (Tulaczyk *et al.* 1998). This material contains many unstable minerals, which are susceptible to chemical weathering, such as pyrite and hornblende. The sediments are saturated by fresh water (dissolved solids <0.5 g l$^{-1}$), contain approximately 0.2% (by weight) of organic carbon, and contain ions that can act as redox couples capable of supporting chemotrophic life (Vogel *et al.* 2003).

## 7.4 Subglacial environments as habitats for life and reservoirs of organic carbon

As discussed in previous sections of this chapter, there is a diverse range of subglacial environments on our planet ranging from the relatively small liquid-water habitats that exist beneath polar and temperate glaciers to the systems we now know are present beneath the Antarctic ice sheet. Life in all of these must proceed without immediate input from the atmosphere and in the absence of light. Space constraints do not allow us to discuss all of these environments in detail so we have chosen to focus on what is known about Lake Vostok, the largest subglacial lake, located beneath the East Antarctic Ice Sheet.

### 7.4.1 Lake Vostok

Much attention is currently focused on the exciting possibility that the subglacial environments of Antarctica may harbor microbial ecosystems under thousands of meters of ice, which have been isolated from the atmosphere for as long as the continent has been glaciated (20–25 million years, Naish *et al.* 2001). The discovery during the early 1970s and subsequent inventory of **subglacial lakes** in Antarctica (Kapitsa *et al.* 1996; Siegert *et al.* 1996) rarely mentioned their biological potential until Priscu *et al.* (1999) and Karl *et al.* (1999) showed the presence, diversity, and metabolic potential of bacteria in frozen lakewater (accreted ice) overlying the liquid waters of Lake Vostok. Owing to differences in the pressure melting point caused by the tilted ice ceiling, lakewater refreezes (accretes) at the base of the ice sheet in the central and southern regions of Lake Vostok, removing water from the lake (e.g. Studinger *et al.* 2004). Hence, constituents in the **accretion ice** should reflect those in the actual lakewater in a proportion equal to the partitioning that occurs when water freezes (Priscu *et al.* 1999; Siegert *et al.* 2001; Christner *et al.* 2006).

Profiles of prokaryotic cell abundance through the entire Vostok core reveal a 2–7-fold higher cell density in **accretion ice** than the overlying glacial ice, implying that Lake Vostok is a source of bacterial carbon beneath the ice sheet (Figure 7.3). Cell densities ranged from 34 to 380 cells $ml^{-1}$ in the glacial ice between 171 and 3537 m and the concentration of total particles of more than 1 µm ranged from 4000 to 12 000 particles $ml^{-1}$, much (30–50%) of which was organic in origin (Royston-Bishop *et al.* 2005; Priscu *et al.* 2006; Christner *et al.* 2008). A 6-fold increase in bacterial cell density was detected in samples of ice core from depths of 3540 and 3572 m where glacial ice transitions to **accretion ice**. Measurements of membrane integrity indicated that that the majority of cells were viable in both the glacial and **accretion ice** (Christner *et al.* 2006). The **accretion ice** below 3572 m contained fewer particles than glacial ice and the deepest **accretion ice** (3622 m) had the lowest number of total particles of all accretion-ice samples. Bacterial density followed the same trend as the density of mineral particles within the ice core (Royston-Bishop *et al.* 2005). These results, in concert with geophysical data from the lake basin led Christner *et al.* (2006) to contend that a shallow embayment located in the southwestern portion of the lake supports higher densities of bacteria than the lake proper. Christner *et al.* (2006), using partitioning coefficients obtained from lakes in the McMurdo Dry Valleys (see also Priscu *et al.* 1999), estimated that the number of bacteria in the surface waters of the shallow embayment and the lake proper should be approximately 460 and 150 cells $ml^{-1}$, respectively. These concentrations are much lower than those found in the permanently ice-covered lakes in the McMurdo Dry Valleys ($\approx 10^5$ $ml^{-1}$; Takacs and Priscu 1998), indicating that Lake Vostok is a relatively unproductive system.

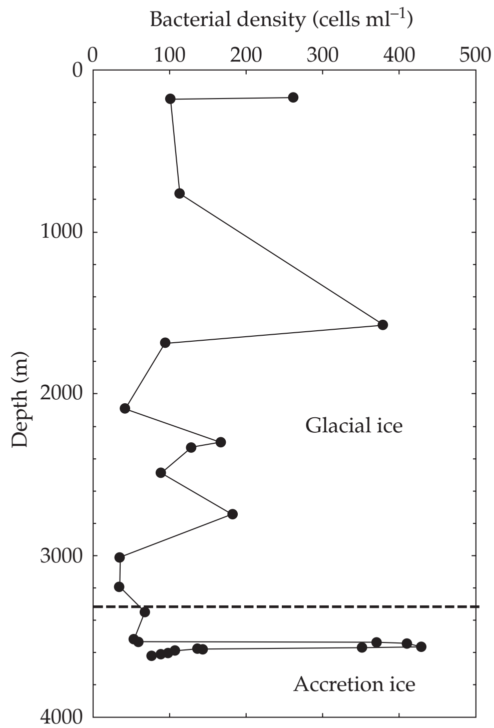


**Figure 7.3** Vertical profile of bacterial cell density in the Vostok ice core. The horizontal dashed line denotes the transition from glacial ice to accretion ice. Cell density was determined on melted ice treated with the DNA stain SYBR Gold and counted by epifluorescence microscopy. Modified from Christner *et al.* (2006).

Sequence data obtained from DNA encoding for small-subunit ribosomal RNA (16S rDNA) revealed phylotypes that were most closely related to extant members of the alpha-, beta-, and gamma-Proteobacteria, Firmicutes, Bacteroidetes, and Actinobacteria. If the accreted ice microbes are representative of the lake microbiota, these data imply that microbes within Lake Vostok do not represent an evolutionarily distinct subglacial biota (Christner *et al.* 2008). The time scale of isolation within Lake Vostok ($>15 \times 10^6$ years) is not long in terms of prokaryotic evolution compared with their $3.7 \times 10^9$-year history on Earth, and studies of species divergence of other **prokaryotes** have shown that species-level divergence may take approximately 100 million years (Lawrence and Ochman 1998). However, other mechanisms of genetic change (such as recombination) could allow more rapid alteration of organism phenotype allowing for adaptation to conditions within Lake Vostok (Page and Holmes 1998), which would not be reflected in evolutionary changes in the 16S rRNA gene. An alternative scenario is that glacial meltwater entering the lake forms a lens overlying the Vostok water column. If so, the microbes discovered within **accretion ice** would likely have spent little time in the lake water itself (few, if any, cell divisions occurring) before being frozen into the **accretion ice**. The microbes within the main body of the lake below such a freshwater lens may have originated primarily from basal sediments and rocks and, if so, their period of isolation may be adequate for significant evolutionary divergence, particularly given the potential selection pressures that exist within subglacial environments. PCR-based analyses of the microbial diversity in Lake Vostok **accretion ice** based on 16S rRNA genes (Christner *et al.* 2001; Bulat *et al.* 2004) has revealed two phylotypes closely related to thermophilic bacteria. One of them is related to a facultative chemolithoautotroph identified previously in hot springs and capable of obtaining energy by oxidizing hydrogen sulphide at reduced oxygen tension. Evidence for the presence of hydrothermal input is supported by the recent interpretation of $He^3/He^4$ data from **accretion ice** (Petit *et al.* 2005), which implies that there may be extensive faulting beneath Lake Vostok, which could introduce geochemical energy sources to the southern part of the lake**.** If this emerging picture is correct, Lake Vostok could harbor a unique assemblage of organisms fueled by chemical energy. Although it seems inevitable that viable microorganisms from the overlying glacial ice, and in sediment scoured from bedrock adjacent to the lake, are regularly seeded into the lake, the question remains of whether these or pre-existing microorganisms have established an ecosystem in Lake Vostok. If a microbial ecosystem were found to exist within the water or sediment of these subsurface environments, it would be one of the most extreme and unusual ecosystems on Earth.

The 16S rRNA gene sequence data from the Vostok **accretion ice** allow comparisons to be made with physiologically well-characterized organisms that exist in public databases. In addition to the data of Bulat *et al.* (2004), suggesting the presence of thermophiles that may use hydrogen for energy and carbon dioxide as a carbon source, several of the phylotypes reported by Christner *et al.* (2006) are most closely related to aerobic and **anaerobic** species of bacteria with metabolisms dedicated to iron and sulphur respiration or oxidation. This similarity implies that these metals play a role in the bioenergetics of microorganisms that occur in Lake Vostok. As cautioned by Christner *et al.* (2006), these metabolic estimates were made on relatively distant phylogenetic relationships (<95% identity); hence, these conclusions remain tentative until the organisms are characterized physiologically. Given this caveat, Figure 7.4 shows the possible chemoautotrophic metabolic pathways that may occur in Lake Vostok. Importantly, the substrates involved can be supplied to the lake by physical glacial processes and do not require geothermal input. These pathways could supply organic carbon and support heterotrophic metabolisms that use $O_2$, $NO_3^-$, $SO_4^{2-}$, $S^0$, or $Fe^{2+}$ as electron acceptors.

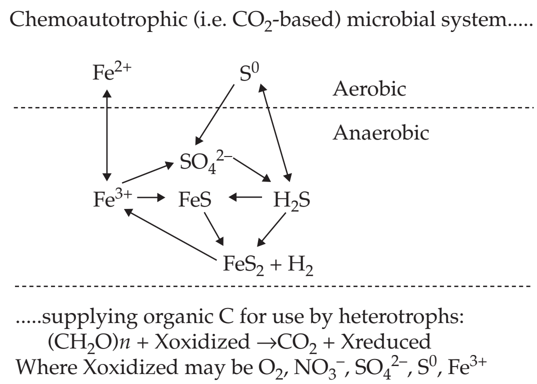


**Figure 7.4** Diagram showing the potential biogeochemical pathways that may be important in the surface waters of Lake Vostok based on 16S rDNA sequence data. This pathway involves chemoautotrophic fixation of carbon dioxide using iron and sulphur as both electron donors and electron acceptors. The pathway also shows the potential transformations that may occur across an aerobic/**anaerobic** boundary (the sequence data revealed the presence of both aerobic and **anaerobic** bacteria). Organic carbon produced by chemoautotrophic metabolism could then fuel heterotrophic metabolism within the lake.

### 7.4.2 Microbial ecology of icy environments

A major question that arises in the study of subglacial and other icy environments concerns the role of microorganisms in terms of ecosystem structure and function. Stated more succinctly: are the organisms we observe 'freeloaders' or are they actively involved in ecosystem processes? If the latter, we would expect to observe distinct biogeographical distributions of organisms within icy environments, much like those observed in cyanobacteria in hot springs (Papke and Ward 2004). Microbiological surveys of icy environments have identified common bacterial genera from global locations (e.g. Priscu and Christner 2004; Christner *et al*. 2008). We have used data from these surveys to show that more than 60% of these isolates group into only six genera (Figure 7.5), implying that icy habitats are indeed selecting for specific groups of microorganisms and that these organisms may be actively growing within icy environments. Caution should be taken when applying the results summarized in Figure 7.5 to **subglacial lakes** because there is an emerging view (discussed previously in this chapter) that many of the lakes are connected by advective flow, which could disperse gene pools within and perhaps across watersheds. The balance between growth rates and rates of advection must be known before subglacial biogeography can be understood. We must further know if the microorganisms within the subglacial environments were derived solely from the overlying glacial ice or from the sedimentary environment underlying the ice sheet. This has important implications for the evolutionary times scales involved. If derived from the overlying ice sheet, the organisms would only have about 1 million years to evolve, a time scale that is highly unlikely to lead to evolution, particularly at the slow growth rates expected. If the organisms were derived from the sediment environment, their lineages could have evolved over perhaps 30 million years, which approximates the time when the first major glaciations were thought to have occurred in Antarctica.

Before we can understand unequivocally the biology and selection pressures within subglacial

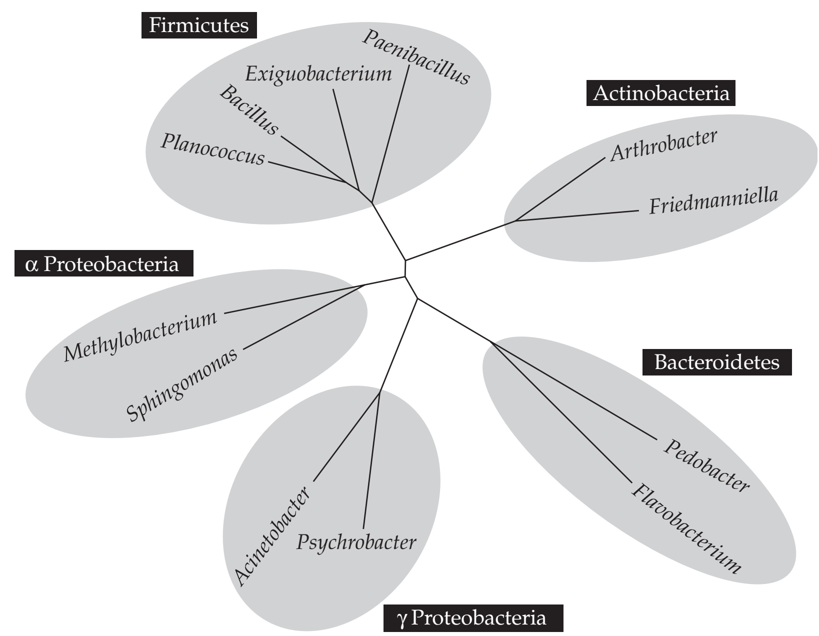


**Figure 7.5** The most frequently recovered genera from glacial ice and subglacial environments based on the phylogeny of the 16 S rRNA molecule . The various source environments in which these genera have been documented are quite diverse and share little in common except that all are permanently frozen. See Priscu and Christner (2004) and Christner *et al.* (2007) for details.

environments, the habitat must be defined precisely. For example, most of what we know about Lake Vostok comes from **accretion ice**, which formed from near-surface lake water. Physical **limnology** models that assess water circulation in Lake Vostok have been reviewed recently by Siegert *et al.* (2005). Lake Vostok circulation is predicted to be a consequence of differences in the pressure melting point between the north and south ends of the lake. In a freshwater (i.e. low ionic strength) lake, geothermal heating will warm bottom waters to a temperature higher than that of the upper layers. The water density will decrease with increasing temperature, resulting in an unstable water column leading to convective circulation where cold meltwater sinks and water warmed by geothermal heat ascends. Conversely, if the lake is slightly saline, the fresh glacier meltwater will be buoyant relative to bulk lake water, and the northern meltwater would spread southward and upward. If the horizontal salinity gradient is great enough to compensate for geothermal warming, water would move into regions of progressively lower pressure, displacing lake water in the south. The cold northern water would eventually refreeze onto the ice sheet base some distance from where it first melted. In this case, a conveyor of fresh cool meltwater would migrate from north to south beneath the ice sheet, causing displacement of warmer dense lake water from the south to the north. If the lakes are vertically chemically stratified, an upper layer of cold fresh water can circulate over a deep layer of warm saline water. The heat in the deep saline water may originate from biogenic processes as well as geothermal heating.

Air hydrate (a naturally occurring solid composed of crystallized water (ice) molecules, forming a rigid lattice of cages (a clathrate) with most of the cages containing a molecule of air) is suspected of playing a role in establishing the physical, chemical, and biological characteristics of **subglacial lakes**. Atmospheric air, captured in ice sheets, occurs exclusively as gas hydrate at an ice thickness of a few kilometers (Hondoh 1996). In large **subglacial lakes**, such as Lake Vostok, with a geometry that favors the establishment of a melt–freeze cycle, the melting of the ice sheet would release air hydrate to the water. Accretion ice is nearly gas-free relative to overlying glacial ice due to the exclusion of gas during refreezing (Jouzel *et al.* 1999). This exclusion would lead to increased dissolved gas concentrations in Lake Vostok (Lipenkov and Istomin 2001; McKay *et al.* 2003). Dissolved oxygen concentrations are predicted to be as much as 50 times higher than air-equilibrated water (McKay *et al.* 2003). Within 400 000 years (≈29 residence times), gas concentrations in the lake are predicted to reach levels that favor the formation of air hydrate. Air hydrate formed in the lake would float to the surface of the lake if formed from air or sink if it contains more than 10% carbon dioxide. The estimates of Lake Vostok water dissolved oxygen concentrations do not consider the effects of biological removal processes or hydrologic recharge (McKay *et al.* 2003). High oxygen levels can react with intracellular molecules to produce superoxides and hydrogen peroxide, the latter of which can generate free radicals following the reaction with certain intracellular metals (e.g. iron). These strong oxidants can degrade macromolecules and damage membranes. To combat the effects of these oxidants, we would expect the microorganisms within the lakes to contain antioxidants and other detoxifying agents such as superoxide dismutase and catalase.

Dissolved organic carbon (**DOC**) plays a key role in ecosystem carbon cycling owing to its role as an energy and carbon source for heterotrophic organisms. **DOC** concentrations in Lake Vostok **accretion ice** are low (<70 μM; Christner *et al.* 2006), implying that **DOC** concentrations in surface lake waters are low as well. Priscu *et al.* (1999) and Christner *et al.* (2006), using partitioning coefficients of **DOC** from McMurdo Dry Valley lakes, estimated **DOC** levels in the surface waters of Lake Vostok between 86 and 100 μM (160 μM for the shallow embayment). Although these **DOC** levels can support heterotrophic growth, molecular evidence from Lake Vostok **accretion ice** implies that carbon dioxide fixation by chemolithoautotrophs may also be an important source of new organic carbon in Lake Vostok (Christner *et al.* 2006). The new carbon produced by this process can then provide a substrate to support heterotrophic activity.

One must also consider the sediments that exist within subglacial environments in any discussion of metabolic activity, and distribution and evolution of microorganisms. Sediments have been shown to be hotspots for biological diversity and activity in most surface lakes on our planet, and they should have a significant role in all subglacial microbial processes. Lake sediments are generally organic, nutrient-rich, and support a wide range of reduction/oxidation conditions over relatively small spatial scales (e.g. Wetzel 2001). Consequently, sedimentary habitats can support diverse metabolic lifestyles. Data from Lake Bonney (McMurdo Dry Valleys) show that sediment bacterial diversity and metabolic activity exceed those in the overlying water column (J.C. Priscu, unpublished results), and preliminary data from the subglacial sediment environment beneath the ice streams of West Antarctica reveal that microbial density exceeds $10^7$ cells g sediment$^{-1}$ (B. Lanoil, unpublished results). Biogeochemical transformations produce chemical gradients within the sediments, which affect the properties of the overlying water column. For example, organisms utilizing oxygen as a terminal electron acceptor can produce **anoxic** or suboxic conditions within the sediments and the lower portion of the water column. Sediment biogeochemistry can also produce compounds (e.g. $CH_4$, $H_2S$, $NH_4^+$, $PO_4^{3-}$) that diffuse into the water column, supplying redox couples and **nutrients** to water column bacteria. As with surface lakes, sediments in **subglacial lakes** should play an important role in the lake ecosystem.

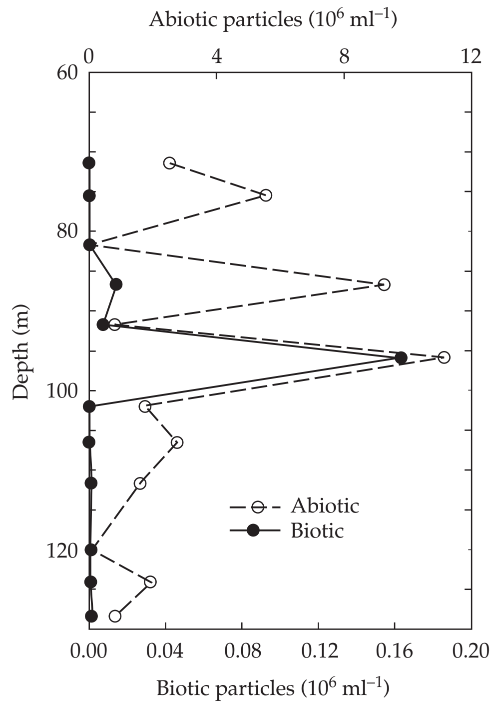


**Figure 7.6** Vertical profiles of biotic and abiotic particles in the 30–130-m (below the surface) glacial ice from the West Antarctic Ice Sheet divide core site. The data were obtained on melted samples processed with a flow cytometer. Biotic particles were determined by particle fluorescence following application of the DNA stain SYTO 60.

### 7.4.3 Subglacial environments as reservoirs of organic carbon

Snowfall typically accumulates on the Antarctic ice sheets at a rate of 2–10 cm year$^{-1}$ (accumulation of ≈22 cm year$^{-1}$ can occur near ice divides (e.g. www.waisdivide.unh.edu/) and carries with it a record of gases, ions, and particles present in the atmosphere at the time of snowfall (e.g. Priscu *et al.* 2006). An initial analysis of particle data collected with a flow cytometer from 70 to 130 m (which represents ≈1000 years of accumulation) at an ice divide in the West Antarctic Ice Sheet revealed total densities ranging from $2\times10^4$ to $1\times10^7$ particles ml$^{-1}$, with the highest densities occurring 94 m beneath the surface (Figure 7.6). Concentrations of bacterial-sized particles containing DNA (determined by staining samples with SYTO 60, a DNA-binding fluorescent dye) ranged from $2.1\times10^{-2}$ to $1.6\times10^5$ ml$^{-1}$, with the highest levels at 94 m, the depth with the highest abiotic particle density. Although these data from the West Antarctic Ice Sheet site represent only the near-surface ice, they do imply that biotic and abiotic particle densities at the West Antarctic Ice Sheet site are higher than in the Vostok core collected from the East Antarctic Ice Sheet (Christner *et al.* 2006). These ice entombed bacteria will eventually be released to the subglacial environment following a period of transit (hundreds of thousands of years). Owing to the large volume of Antarctic glacial ice (see Table 7.1), these ice-bound bacteria may represent an important reservoir of global organic carbon. Priscu and Christner (2004) first estimated the organic carbon reservoirs associated with the Antarctic ice sheet and associated

**Table 7.2** Summary of the prokaryotic cell number, prokaryotic carbon (Cell carbon), and dissolved organic carbon (DOC) computed for Antarctic subglacial lakes, the ice sheet, and the subglacial aquifer. Carbon concentrations are in Petagrams ($10^{15}$ g). Global estimates of cell number in freshwater lakes and rivers, the open ocean, the terrestrial subsurface and soils are from Whitman *et al.* (1998; Tables 1 and 5). Global cellular carbon reservoirs for the terrestrial subsurface and soils are also from Whitman *et al.* (1998); a carbon content of 11 fg C cell$^{-1}$ was used to obtain the carbon reservoirs in the freshwater lakes and rivers, and open ocean. DOC estimates for fresh waters, the open ocean, and the terrestrial subsurface assume average values of 2.2, 0.5, and 0.7 mg l$^{-1}$ for these systems (Thurman 1985) and volumes of $2.31 \times 10^5$, $1.37 \times 10^9$, and $6.00 \times 10^7$ km$^3$, respectively (Wetzel 2001). Cellular and DOC pools in subglacial lakes were estimated using values projected for the main body of Lake Vostok ($1.50 \times 10^8$ cells m$^{-3}$ and $1.03 \times 10^3$ mg m$^{-3}$, respectively (Christner *et al.* 2006), in concert with the volume for all subglacial lakes of 10 000 km$^3$ (Dowdeswell and Siegert 1999). Cellular and DOC data from ice cores collected below Vostok Station (Christner *et al.* 2006) were depth-weighted to yield average values of $1.34 \times 10^8$ cells m$^{-3}$ and $3.09 \times 10^2$ mg m$^{-3}$. These values were used with an ice-sheet volume of $3.01 \times 10^7$ km$^3$ (IPCC 1995) to compute the cellular reservoirs within the ice sheet. A subglacial aquifer volume of $10^7$ km$^3$ was computed assuming that depth equals 1 km and surface area equals $1.0 \times 10^7$ km$^2$. The aquifer volume was used with a cellular density obtained from samples collected beneath the Kamb Ice Stream ($2 \times 10^7$ cells g$^{-1}$) and a sediment density of 2 g cm$^{-3}$ to compute the number of total cells in the aquifer (B. Lanoil, unpublished results). The method used to determine cellular abundance includes cells attached to sediment particles and those residing within the pore waters. Hence, our results provide a bulk estimate of cells within the entire aquifer, not just the pore water. The DOC reservoir in subglacial groundwater was computed using a subglacial aquifer porosity of 10% and an average value for groundwater DOC of 700 mg m$^{-3}$ (Thurman 1985; assuming all DOC is in pore water). Cellular carbon in all Antarctic habitats was computed using a conversion factor of 11 fg C cell$^{-1}$, determined for bacteria from a permanently ice-covered lake in the McMurdo Dry Valleys, Antarctica (Takacs and Priscu 1998). NA, not computed owing to the large variation in published values.

| | **Antarctica** | | | | **Greenland** | **Both poles** | **Global** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Lakes** | **Ice sheet** | **Subglacial aquifer** | **Total** | **Ice sheet** | **Lakes, ice sheet and subglacial water** | **Fresh water** | **Open ocean** | **Terrestrial subsurface** | **Soils** |
| Cell number | 1.50 ($\times 10^{21}$) | 4.03 ($\times 10^{24}$) | 4.00 ($\times 10^{29}$) | 4.00 ($\times 10^{29}$) | 3.51 ($\times 10^{23}$) | 4.00 ($\times 10^{29}$) | 1.31 ($\times 10^{26}$) | 1.20 ($\times 10^{29}$) | 2.50 ($\times 10^{30}$) | 2.60 ($\times 10^{29}$) |
| Cell carbon (Pg) | 1.65 ($\times 10^{-8}$) | 4.43 ($\times 10^{-5}$) | 4.40 ($\times 10^{0}$) | 4.40 ($\times 10^{0}$) | 3.86 ($\times 10^{-6}$) | 4.40 ($\times 10^{0}$) | 1.44 ($\times 10^{-3}$) | 1.32 ($\times 10^{0}$) | 2.15 ($\times 10^{2}$) | 2.60 ($\times 10^{1}$) |
| DOC (Pg) | 1.03 ($\times 10^{-2}$) | 9.29 ($\times 10^{0}$) | 7.00 ($\times 10^{-1}$) | 1.00 ($\times 10^{1}$) | 9.50 ($\times 10^{-1}$) | 1.10 ($\times 10^{1}$) | 5.08 ($\times 10^{-1}$) | 6.85 ($\times 10^{2}$) | 4.20 ($\times 10^{1}$) | NA |
| Cell carbon+DOC (Pg) | 1.03 ($\times 10^{-2}$) | 9.29 ($\times 10^{0}$) | 5.10 ($\times 10^{0}$) | 1.44 ($\times 10^{1}$) | 9.50 ($\times 10^{-1}$) | 1.54 ($\times 10^{1}$) | 5.10 ($\times 10^{-1}$) | 6.86 ($\times 10^{2}$) | 2.57 ($\times 10^{2}$) | NA |

**subglacial lakes**, but they had relatively little data to work with. The recent publication by Christner *et al.* (2006) now provides the most complete dataset with which to estimate carbon reservoirs in the Antarctic ice sheet and **subglacial lakes**. Using these data, plus new values on subglacial groundwater and bacterial density in Antarctica as well as new data on **DOC** in Greenland ice, the density of bacterial cells, bacterial carbon, and **DOC** were estimated in (1) Antarctic **subglacial lakes**, (2) Antarctic and Greenland ice sheets, and (3) Antarctic and Greenland subglacial groundwater (Table 7.2). These calculations reveal that the largest bacterial carbon pool (>99%) occurs in subglacial groundwater, whereas the largest pool of **DOC** (93%) occurs within the glacial ice. These results reflect the relatively high prokaryotic cell densities used for the groundwater estimates ($2\times10^7$ cell g$^{-1}$) and the immense volume of the Antarctic ice sheet ($3\times10^7$ km$^3$), respectively. All carbon pools estimated for Greenland ice are about an order of magnitude below those for the Antarctic equivalents. The prokaryotic carbon pool from both poles exceeds that estimated in all surface fresh waters (rivers and lakes) by more than two orders of magnitude; this is equivalent to that in the open ocean but is 49 and six times lower than that in terrestrial groundwater and soils, respectively.

**DOC** levels within polar regions exceed those in surface fresh water by 20-fold, but are 63 and 38 times lower than **DOC** in the open ocean and terrestrial groundwater, respectively (global **DOC** pools were not computed for soils owing to the extreme site-specific variability observed in the literature). These comparisons indicate that Earth's polar regions contain a significant reservoir of prokaryotic carbon and **DOC**. This result should not be surprising given that more than 70% of our planet's fresh water resides in polar regions as ice and subglacial water. The estimates in Table 7.2 will continue to be refined as we learn more about the geophysical, chemical and biological properties on our polar regions. Data in Table 7.2 support the contention of Priscu and Christner (2004) that polar ice, particularly Antarctic ice, contains an organic carbon reservoir that should be considered when addressing issues concerning global carbon dynamics.

## Acknowledgments

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