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# The hydrochemistry of Lake Vostok and the potential for life in Antarctic subglacial lakes

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## Abstract:

Our understanding of Lake Vostok, the huge subglacial lake beneath the East Antarctic Ice Sheet, has improved recently through the identification of key physical and chemical interactions between the ice sheet and the lake. The north of the lake, where the overlying ice sheet is thickest, is characterized by subglacial melting, whereas freezing of lake water occurs in the south, resulting in ~210 m of ice accretion to the underside of the ice sheet. The accreted ice contains lower concentrations of the impurities normally found in glacier ice, suggesting a net transfer of material from meltwater into the lake. The small numbers of microbes found so far within the accreted ice have DNA profiles similar to those of contemporary surface microbes. Microbiologists expect, however, that Lake Vostok, and other subglacial lakes, will harbour unique species, particularly within the deeper waters and associated sediments. The extreme environments of subglacial lakes are characterized by high pressures, low temperatures, permanent darkness, limited nutrient availability, and oxygen concentrations that are derived from the ice that provides the meltwater. Copyright © 2002 John Wiley & Sons, Ltd.

KEY WORDS Lake Vostok; hydrochemistry; Antarctic subglacial lakes

## THE PHYSICAL SETTING OF LAKE VOSTOK

The base of the central East Antarctic Ice Sheet is warm, due to the combined effect of geothermal heating (of about 50 mW $m^{-2}$) and the insulation caused by the overlying ice, despite surface air temperatures commonly less than −60 °C. The production and flow of water at the ice-sheet bed leads to its accumulation within topographic hollows and, hence, the formation of subglacial lakes (Figure 1). Around 70 lakes have been identified beneath the Antarctic Ice Sheet (Siegert *et al.*, 1996; Dowdeswell and Siegert, 1999), of which Lake Vostok is by far the largest (Kapitsa *et al.*, 1996; Siegert and Ridley, 1998; Siegert, 2000) (Figure 2). The glaciological setting of Lake Vostok has been broadly established and attention is switching to understanding the physical and chemical environments within the lake, which help define the environmental envelope within which any microbiota present must function (Siegert *et al.*, 2001).

Lake Vostok is at least 240 km long and 50 km wide, and lies between 3750 m (over the south of the lake) and 4150 m (over the north) beneath the central East Antarctic Ice Sheet (Figures 2 and 3). The surface of Lake Vostok (i.e. the ice–water interface) slopes downwards from south to north with a gradient of about 0·002, which is roughly 11 times greater than the slope at the ice-sheet surface, but in the opposite direction. The lake is located within a very large subglacial topographic basin, similar to a rift valley. The basin has a crescentric shape, and the sidewalls are relatively steep (with gradients up to ~0·1) and high (up to ~1000 m

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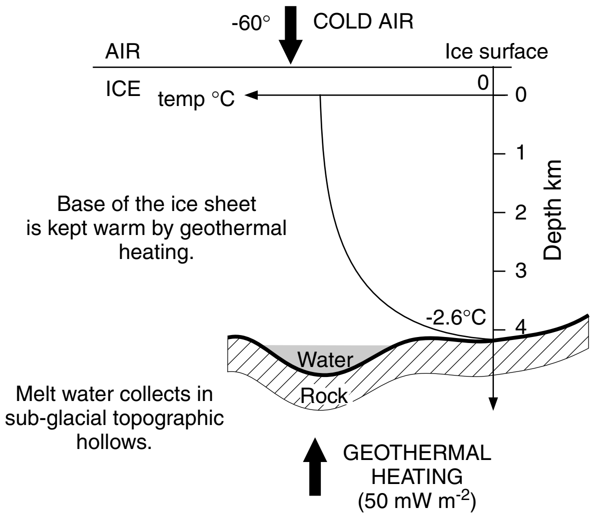

Figure 1. Ice sheet temperatures and the maintenance of warm subglacial conditions in East Antarctica due to geothermal heating

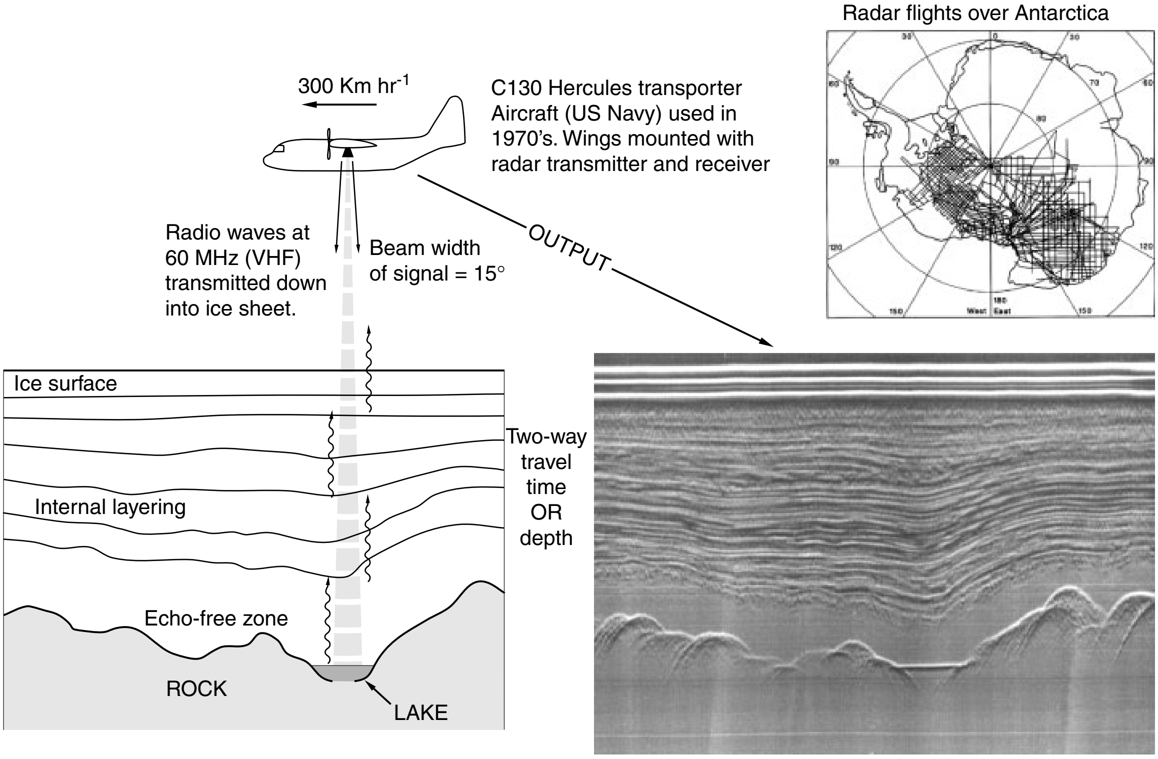

Figure 2. The technique of airborne radar sounding, and its application to identifying Lake Vostok and other subglacial lakes. In the 1970s, airborne radar surveys were undertaken with a C130 Hercules transporter aircraft, with the wings mounted with the radar transmitter and receiver. Aircraft navigation was accurate to around 5 km in the centre of Antarctica. Today, most radar surveys use smaller aircraft and GPS to navigate. Subglacial lakes are easily identified on airborne radar records owing to their uniformly strong and flat appearance. Bedrock perturbations are recorded as hyperbolae in radar data

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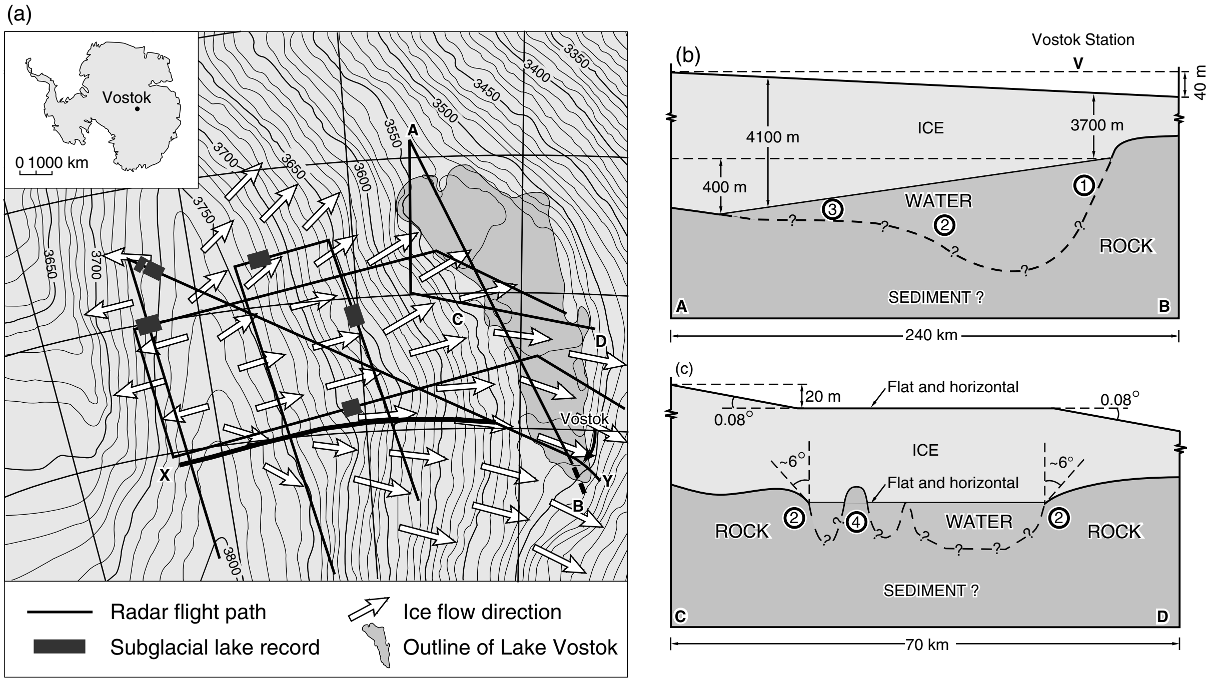

Figure 3. The dimensions of Lake Vostok. (a) ERS-1 altimetry of the Antarctic Ice Sheet between Ridge B and Dome C. The location of Lake Vostok can be identified from the anomalous flat ice-surface region. SPRI radar flight lines and the location of all known subglacial lakes around Lake Vostok (denoted as black squares) are provided. The surface ice-sheet elevation, derived from the ERS-1 altimeter, is also shown. The contour interval is 10 m; arrows denote the direction of surface flow of ice over Lake Vostok calculated from InSAR (Siegert *et al*., 2000; Siegert and Kwok, 2000). (b) Cross-section from north to south along the 200 km length of the lake. (c) Cross-section from west to east along the 50 km width of the lake. The depth of Lake Vostok can be estimated by: (1) seismic information, which has revealed a water depth of >500 m beneath Vostok Station; (2), side-wall bedrock gradient adjacent to the lake of 0·1, which indicates several hundred metres of water depth in the centre of the lake; (3) radio-wave reflections from the lake floor, showing the water depth to be between 10 and 20 m in the north of the lake; and (4) bedrock 'islands' measured by radar. Taken from Siegert *et al*. (2001)

above the surface of the lake). Lake Vostok is at least 1000 m deep in the south (Figure 3), and relatively shallow in the north and extreme southwest. There may be several hundred metres of glacial sediments draped over its floor (Lukin *et al*., 2000). This suggests that the basement may be as much as 2500 m below the top of the sidewalls and over 5000 m below the surface of the ice sheet. Although there are several similar subglacial basins in East Antarctica (e.g. the Adventure Subglacial Trench and the Astrolabe Subglacial Basin), only Lake Vostok's basin is filled with deep water.

Most subglacial lakes probably formed in the last few million years, during which time the ice sheet has been at the current or greater thickness. However, because of its uniquely large size and central location in East Antarctica, Lake Vostok is thought to have existed for as long as the ice sheet has been at a continental scale (∼15 million years). This is because the ice thickness and subglacial conditions would not have changed significantly even over glacial–interglacial cycles (e.g. Salamatin, 2000). Some argue for a stable East Antarctic Ice Sheet over the last 15 million years (e.g. Summerfield *et al*., 1999). If this is correct, Lake Vostok may have been in continual existence across the youngest third of the Cenozoic and the entire Quaternary. It is also possible that: (1) a large lake occupied this basin before the glaciation of Antarctica 33 million years ago; (2) sediments deposited across the floor of the valley may not have been completely scoured by the glacial advance of the infant Antarctic ice mass (Barrett, 2001; Barrett, personal communication); and, because of this, (3) a historical record and biotic reservoir from the Mid Cenozoic is present at the base of the current lake sediment profile.

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## ICE FLOW OVER LAKE VOSTOK AND SUBGLACIAL MELTING AND FREEZING

Ice flows onto Lake Vostok from the Ridge B ice divide, located between 200 and 250 km from the lake's western margin (Kapitsa *et al.*, 1996; Siegert and Ridley, 1998; Kwok *et al.*, 2000). ERS-1 satellite altimetry shows the ice-sheet surface above Lake Vostok to be unusually smooth and virtually flat (Figure 3) (Kapitsa *et al.*, 1996; Siegert and Ridley, 1998; Rémy *et al.*, 1999). This morphology is caused by the different dynamics of ice that is grounded compared with floating ice. The basal shear stress across the ice–water boundary above the subglacial lake is effectively zero, so the ice sheet should flow over the lake by vertically uniform longitudinal extension (Paterson, 1994). However, numerical ice flow modelling shows that the effect of longitudinal extension is small, due to buttressing at the downstream lake shore (Mayer and Siegert, 2000). Instead, the flow of the floating ice is controlled more by the base-parallel shear deformation of the adjacent grounded ice. Surface ice motion across Lake Vostok has been measured using repeat-pass synthetic aperture radar interferometry (InSAR) from ERS-1 (Kwok *et al.*, 2000). The regional flow of the ice sheet upstream of the lake is from west to east, perpendicular to the surface elevation contours. As the ice flows past the grounding line on the lake's western margin, a noticeable southward component is added to the ice velocity (Bell *et al.*, 2002). At Vostok Station, the surface ice velocity is measured at 4·2 m year$^{-1}$ in the direction 130 °N (Kwok *et al.*, 2000), which compares with an astronomically based measurement of 3·7 ± 0·7 m year$^{-1}$ towards 142 ± 10 °N (Kapitsa *et al.*, 1996), but is noticeably higher than the value ~2·0 m year$^{-1}$ measured by Australian polar explorers (Neal Young, personal communication). Bell *et al.* (2002) calculate that surface ice will take between 16 000 and 20 000 years to cross the lake. It could take much longer for basal ice to make this journey, however, because ice flow may be inhibited when crossing grounding lines and 'islands' (local topographic high spots within the lake) (Figure 4b).

Borehole temperature measurements along the full length of the Vostok ice core have been used to establish the energy balance between the ice sheet and the lake (Salamatin *et al.*, 1998; Salamatin, 2000). The mean basal temperature gradient is ~0·02 °C m$^{-1}$, which relates to a heat flux through the ice from the lake ceiling of 46 mW m$^{-2}$, indicating that rates of subglacial freezing above Lake Vostok are most likely to be ~4 mm year$^{-1}$ (Salamatin *et al.*, 1998). In the extreme case where ice at −10 °C flows over the western lake margin, rates of melting and freezing beneath Vostok Station will probably not be higher than about 11 mm year$^{-1}$ (Salamatin, 2000).

The spatial distribution of subglacial melting and freezing can be estimated theoretically from isochronous internal radar layering, by observing the loss or gain of basal ice along a flowline. Using this technique, it has been shown that subglacial melting occurs in the north of Lake Vostok (Siegert *et al.*, 2000), and freezing (accretion) takes place in the south (Bell *et al.*, 2002).

## THE VOSTOK ICE CORE

Several deep ice cores have been extracted from the ice sheet at Vostok Station (at the southern end of Lake Vostok) since drilling began in the mid-1960s (the first 500 m deep dry borehole was extracted in 1965), providing important information about the climate during the last glacial cycle. The most recent and deepest (3623 m) ice core terminated ~120 m from the base of the ice sheet. The upper 3310 m of the ice core provides a detailed palaeoclimate record spanning the past 420 000 years (Petit *et al.*, 1997, 1999). In addition, microbiological analysis of the ice core has revealed a range of microbiota, including bacteria, fungi, and algae, some of which have been reported to be culturable in the laboratory (Abyzov *et al.*, 1998; Priscu *et al.*, 1999a; Karl *et al.*, 1999).

The age of the basal ice in the Vostok ice core is an important constraint on the age of the youngest water within the lake. Preliminary examination of the isotope record (Jouzel *et al.*, 1999), estimates of the air-hydrate crystal growth rates (Lipenkov *et al.*, 2000) and ice flow modelling (Barkov *et al.*, submitted), provide evidence that the basal ice, 230 m beneath the 3310 m level, is up to 1 000 000 years old. This marks the age of the youngest lake water. The mean age of the water within Lake Vostok is also a function of the

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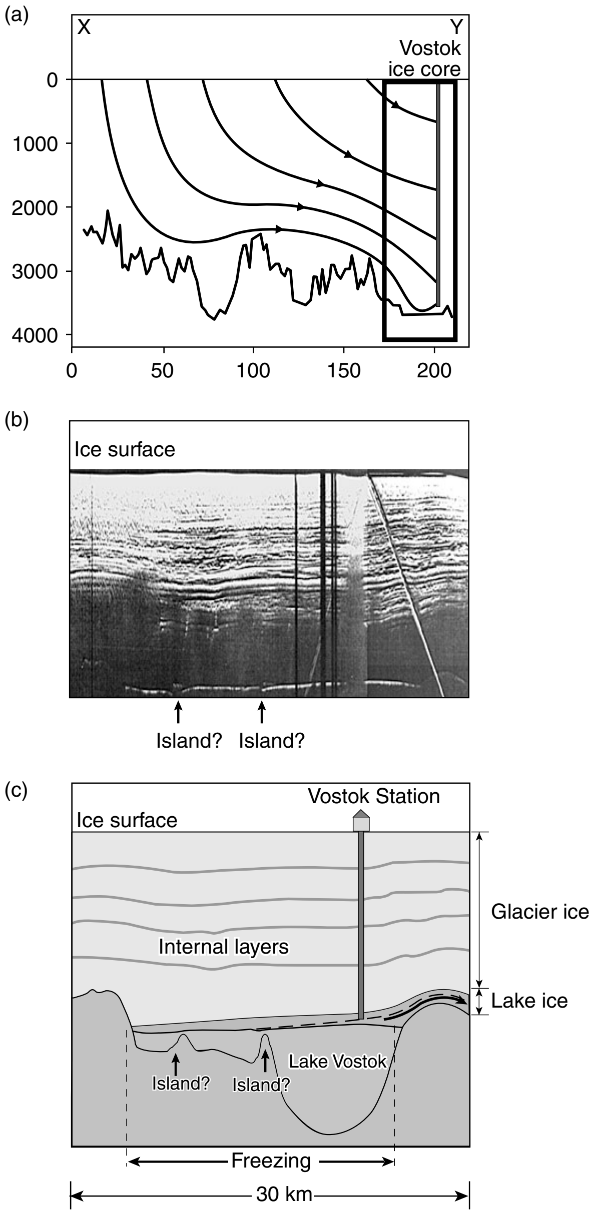

Figure 4. (a) Ice particle flowpaths between Ridge B and the southern end of Lake Vostok (Figure 2a). The bedrock elevation has been measured from airborne radar (Siegert and Kwok, 2000). (b) Raw radar records along an ice flowline across Lake Vostok, showing the pattern of internal layering. Also shown are disturbances to the otherwise smooth ice-sheet base above the lake, which may reflect shallow lake conditions and ice-sheet grounding. (c) Ice flow across a continuous zone of subglacial freezing, followed by transfer of the entire ice column over the eastern lake margin. Evidence in support of this process comes from the internal layering in the radar data (b)

residence time of the lake water and how well the meltwater mixes with the existing water. We hypothesise that if 20% of the annual meltwater mixes with the resident lake water before refreezing, then the residence time of Lake Vostok would be around 100 000 years or greater. Hence, the mean age of Lake Vostok water could be up to 1·1 million years. This effectively marks the time since the waters of Lake Vostok were last in direct contact with biotic or chemical constituents in the Earth's atmosphere. Even if the residence time were low (as suggested by Bell *et al.* (2002)), the age of the lake water would still be of the order of a million years.

### *Accreted ice at the base of the ice core*

Typical glacier ice contains a record of gases and isotopes from which palaeoclimate information is inferred. In the Vostok ice core, this type of ice exists to a depth of 3310 m. Lower layers of ice, between depths of 3310 and 3538 m, are reported to have been reworked, making the extraction of palaeoclimatic information difficult to establish (Figure 5). The basal 84 m of the ice core, from 3539 to 3623 m (Figure 5), has a chemistry and crystallography that are distinctly different from the 'normal' glacier ice above. The basal ice has an extremely low conductivity, huge (up to 1 m) crystal sizes, and sediment-particle inclusions (in the upper half) (Jouzel *et al.*, 1999). The mineral composition of ice-bound sediments below 3539 m is dominated by micas and is clearly different than typical crustal composition and particles within the overlying glacial ice (Priscu *et al.*, 1999a, 2001). Its isotopic composition, distinct from the 'meteoric' ice above, suggests that it formed by the refreezing of lake water to the underside of the ice sheet. Thus, there is ~210 m of accreted Lake Vostok ice beneath Vostok Station (Jouzel *et al.*, 1999) (Figure 5). The accreted ice below 3608 m (and presumably extending to the ice–water interface) contains no sediment-particle inclusions, implying that it formed over the lake proper rather than along the shoreline.

Ice flows from west to east across Lake Vostok, and the accreted ice containing sediment particles must have formed across the western side of the lake at the first contact between ice and water. Airborne radar data from across Lake Vostok and seismic information suggest that the lake may be shallow across the western side compared with the 510–1000 m water depth recorded beneath the station (Kapitsa *et al.*, 1996; Lukin *et al.*, 2000) (Figure 4). There are two ideas linking water depth to the entrainment of material into the accreted ice. The first is that the basal ice 'scrapes' against the shallow floor of the lake across the western side, picking up debris as it does so (Jouzel *et al.*, 1999). The second is that 'anchor ice' (particles on the floor of the lake that float to the surface after becoming attached to ice crystals) forms over the lake floor in the west. In both cases, it follows that basal material is no longer incorporated into the accreted ice when the ice flows across deeper water.

Helium can be readily incorporated into ice crystalline structures and $^3$He/$^4$He ratios from accreted ice in the Vostok ice core clearly indicate a signature typical of old continental cratonic geology rather than the much higher $^3$He/$^4$He ratios typically associated with high enthalpy mantle processes (Jean-Baptiste *et al.*, 2001). Hence, data from the surface waters of Lake Vostok suggest (1) the lake is not situated in an active rift valley and (2) a lack of significant hydrothermal activity contributing to the lake's energy budget. However, if the lake water is vertically stratified, helium signals from deep hydrothermal activity may not be reflected accurately in accretion ice. Until vertical profiles of helium isotopes and related constituents are made throughout the Lake Vostok water column, the magnitude of deep-water hydrothermal input and associated biota remains unclear.

## MICROBES IN THE ACCRETED ICE

The accreted ice offered the first opportunity for aquatic biologists and geochemists to investigate material derived from a subglacial lake. Two recent independent studies of accreted ice subsampled from different depths (3590 and 3603 m) near the base of the Vostok ice core (maximum depth 3623 m) have shown that these samples contain both low numbers and low diversity of bacteria (Karl *et al.*, 1999; Priscu *et al.*, 1999a). The low diversity (seven phylotypes) may reflect the small sample size analysed (~250 ml of melt) and should be considered as a lower limit. Low concentrations of 'growth nutrients' and evidence of mineralization of $^{14}$C-labelled organic substrates were also found—though activity was measured under potentially more benign laboratory conditions of +3 °C and 1 atm pressure (Karl *et al.*, 1999). Since the accreted ice has been frozen from Lake Vostok water, the inference is that these microbes were present in the lake water, at some point, and viable prior to freezing. Priscu *et al.* (1999a), using ice–water partitioning coefficients from the permanently

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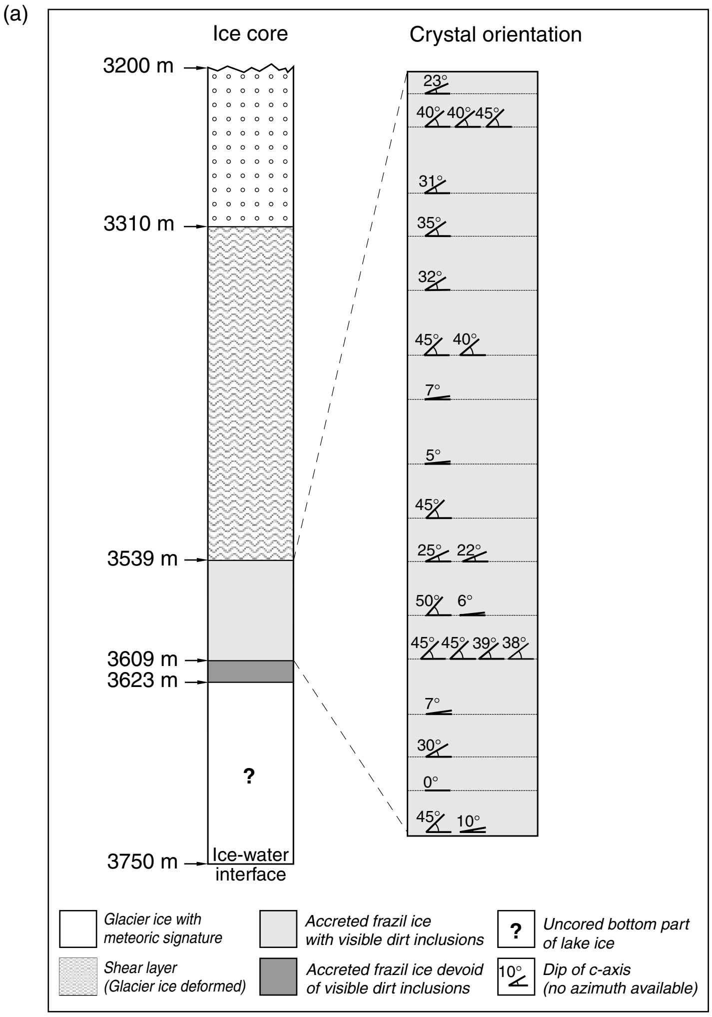

Figure 5. (a) Ice stratigraphy of the basal 550 m of ice beneath Vostok Station determined from analysis of the Vostok ice core (after Souchez *et al.* (2000)). (b)–(d) Chemical records of the basal 90 m of the ice core. (b) $\delta$D with the frequency of rock particle inclusions, (c) $\delta^{18}$O, (d) deuterium excess (Souchez *et al.*, 2000)

ice-covered lakes in the McMurdo Dry Valleys, estimated that the bacterial density within the Lake Vostok water column is on the order of $10^6$ ml$^{-1}$. It is important to note that the studies of Karl *et al.* (1999) and Priscu *et al.* (1999a) were conducted on accretion ice that is thought to have formed along the shoreline of the lake. A better estimate of actual conditions within the main water body of Lake Vostok will become available once microbial measurements are made on the clear accreted ice below 3608 m, which was formed over the main water body of the lake and is anticipated to be unaffected by rock–water–ice interactions.

The ice drilling operations were not undertaken with sterile procedures, and hence the possibility exists that the accreted ice microbes are contaminants from the drilling fluid, and associated core handling, despite the care taken to obtain clean samples from the centre of the ice cores under ultra-clean laboratory conditions. Although there was clearly a high potential for contamination, all laboratory-based contamination controls[†]

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[†] The contamination controls used by Priscu *et al.* (1999a) are as follows. Ice core sections were cut for analyses using a saw sterilized with ethanol. Samples were processed under a laminar flow hood; gloves, clean clothing, and hair covering were worn during handling. Ion and

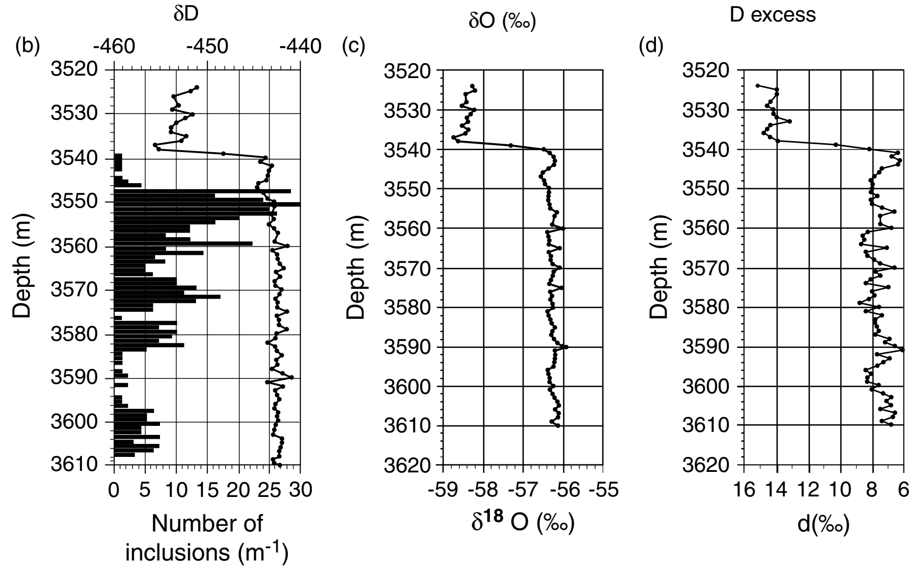

Figure 5. (*Continued*)

proved negative (Priscu *et al.*, 1999a). A number of laboratories have documented and cultured microbes from Vostok ice (Karl *et al.*, 1999; Priscu *et al.*, 1999a; Christner *et al.*, 2001), which suggests either that contamination is pervasive through all samples collected, or that microbes representative of those in the waters of Lake Vostok are captured by the accreted ice. Molecular profiling of accreted ice microbes using 16S rDNA techniques (Priscu *et al.*, 1999a) show a very close agreement with present-day surface microbiota. Phylotypes have mapped closely to extant members of the alpha- and beta-Proteobacteria and to Actinomycetes (the latter also isolated in Vostok glacial ice; Abyzov *et al.*, 1998). If the accreted ice microbes are representative of the lake microbiota, this would imply that microbes within Lake Vostok do not represent an evolutionarily distinct subglacial biota. The time scale of isolation within Lake Vostok (which could be ~15 million years) is not long in terms of prokaryotic evolution compared with their $3{\cdot}7 \times 10^9$ year history on Earth, and studies of species divergence of other prokaryotes have shown that species level divergence may take ~100 million years (Lawrence and Ochman, 1998). However, other mechanisms of genetic change, such as recombination and mutator genes, could allow more rapid alteration of organism phenotype (Page and Holmes, 1998) to adapt to conditions within Lake Vostok. As the microbes currently studied are all from accreted ice probably formed at the edge of the lake relatively close to a melting zone, it seems probable that these microbes have spent little time within the actual lake water itself (few, if any cell divisions occurring) before being frozen within the accretion ice. The microbes within the main body of the lake may have originated primarily from basal sediments and rocks and, if so, their period of isolation could certainly be adequate for significant

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trace chemical samples were rinsed thoroughly with 0·2 μm filtered Barnstead-nanopure™ water. The samples were then melted at room temperature in clean high-density polyethylene jars. Ions in filtered (0·2 μm) and unfiltered samples were analysed by ion chromatography; trace elements in unfiltered melt were determined by inductively coupled plasma mass spectrometry . Stable isotope samples were melted without rinsing and analysed by mass spectrometry. Scanning electron microscopy (SEM) and atomic force microscopy (AFM) samples were rinsed and melted as for ion chemistry. Melted SEM and AFM samples were filtered onto sterile 0·2 μm filters using cleaned and sterilized equipment. A control was prepared using 0·2 μm filtered nanopure water frozen in a clean 10 cm diameter polycarbonate tube. The control core was melted, filtered and analysed by SEM and AFM using methods identical to that of the sample. Mineral and biological particles from the sample were unique with respect to that observed in the control core. Cryogenic SEM (JEOL-6100) and energy dispersive spectrometry were used to image and analyse biologic and geologic particles. AFM imaging was obtained with a Digital Instrument's Dimension 3100 system in tapping mode.

evolutionary divergence, particularly given the potential selection pressures that exist within the subglacial environment.

Accreted ice could offer a unique habitat for microbes (Price, 2000) in veins of relatively solute-rich water that can exist between crystals (Mader, 1992a,b), and that intersect at triple junctions. If veins are present in the Vostok accreted ice, microbes may exist within them, since the liquid water would contain nitrate, sulphate, and simple organic molecules, which could support a geochemically driven microbial habitat. Water inclusions within ice might similarly offer a habitat, but it must be recognized that the salinity and pH potentially present in inclusions or veins could constitute a stressful and highly selective environment for life. To date, metabolic activity has been observed in melted accretion ice at 3 °C and 1 atm (Karl *et al.*, 1999), viable microbes have been found at depth in the Vostok ice core (Abyzov *et al.*, 1998), and microbes active at sub-zero temperatures have been reported in South Pole snow (Carpenter *et al.*, 2000). Recent data on the isotopic composition of nitrous oxide in Vostok ice cores suggest that this gas has been biologically modified within the ice (Sowers, 2001), providing indirect evidence for active metabolism within solid ice. These findings suggest the potential for accreted ice vein or water inclusion habitats to be populated with living biota, but this has yet to be confirmed by direct examination of these habitats for the presence of metabolizing cells at *in situ* temperatures and pressures.

## WATER CIRCULATION WITHIN LAKE VOSTOK

The zones of subglacial melting in the north and freezing in the south of Lake Vostok are thought to be controlled by the slope of the ice–water interface, since the thickness of ice dictates the pressure-melting temperature and the density of meltwater. Melting and freezing induce circulation in the lake, and the salinity of Lake Vostok will also have a strong control on the form of circulation.

### *Circulation in Lake Vostok assuming no chemical stratification*

Since the surface of Lake Vostok is inclined, the pressure-melting point in the south will be slightly (~0·3 °C) less than that in the north. The circulation of pure (non-saline) water in Lake Vostok will be driven by the differences between the density of meltwater and lake water. Geothermal heating will warm the bottom water to a temperature higher than that of the upper layers. The water density will decrease with increasing temperature because Lake Vostok is in a high-pressure environment, resulting in an unstable water column (Wüest and Carmack, 2000). This leads to convective circulation conditions in the lake in which cold meltwater sinks down the water column and water warmed by geothermal heat ascends up the water column (Figure 6a). However, a pool of slightly warmer and stratified water may occur below the ice roof in the south, where the ice sheet is thinner and subglacial freezing takes place (Wüest and Carmack, 2000). Here, the water would not be involved in convective motion, as heat is transferred from the ice towards the lake (i.e. the temperature will decrease with depth).

There have been three models from which the circulation of pure water in Lake Vostok can be evaluated (Wüest and Carmack, 2000; Williams, 2000; Mayer *et al.*, submitted) (Figure 6a). The models indicate that meltwater will be colder and denser in the northern area of Lake Vostok, where the ice is thickest, than both the surrounding lake water and meltwater in areas with thinner ice cover. It appears, therefore, that this region is the main zone of downwelling of pure water. However, the circulation is complicated by the geometry of the lake cavity and the Coriolis force. This means that circulation in Lake Vostok will include horizontal transfer and, to a lesser extent, vertical overturning. The models agree that northern meltwater will sink and be transported horizontally to the south, via a clockwise circulation system, to a region where the pressure-melting point is higher, allowing refreezing to occur (Figure 6a).

### *Circulation in Lake Vostok assuming chemical stratification*

An alternate point of view is that the lake is saline to a small extent (Souchez *et al.*, 2000). The fresh glacier meltwater will, therefore, be buoyant compared with the resident, more saline, lake water (Figure 6b).

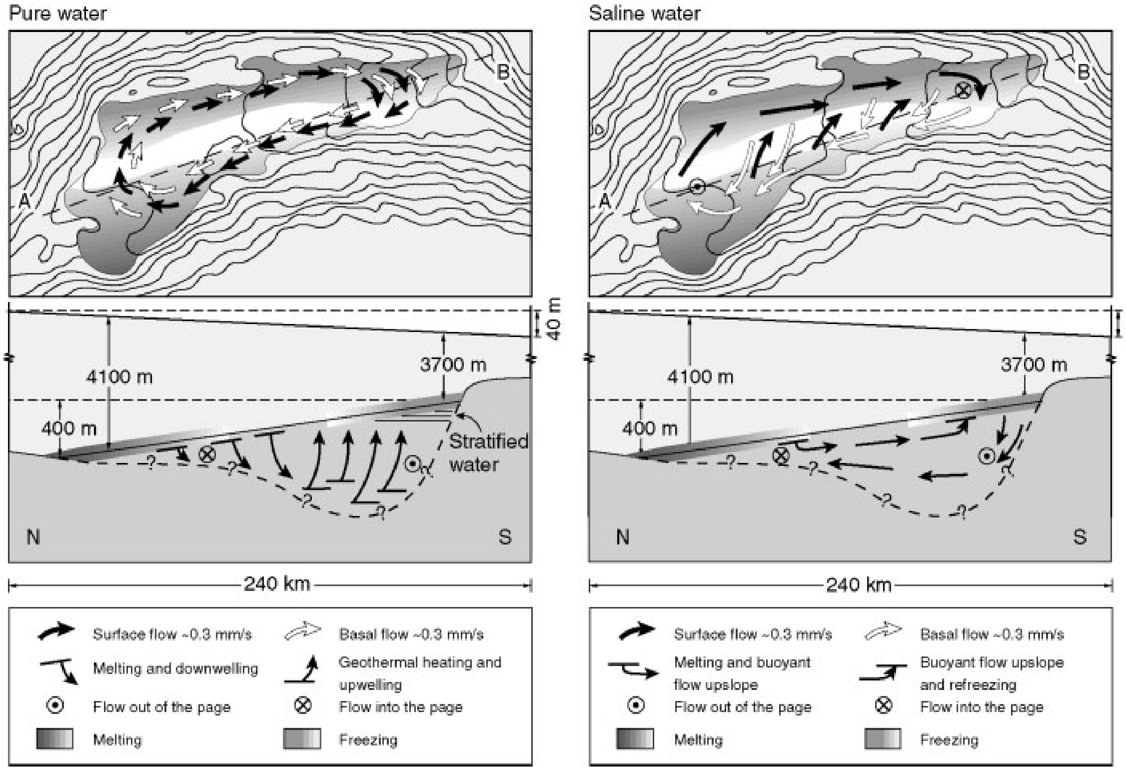

Figure 6. Water circulation within Lake Vostok. (a) Circulation calculated by numerical modelling, assuming that the water is pure (Williams, 2001; Wüest and Carmack, 2000; Mayer *et al.*, submitted). The white arrows show the bottom water circulation and the black arrows denote the higher level circulation close to the ice base. Dots refer to up-welling of lake water; crosses denote down-welling. There are two clockwise circulation paths in the upper and lower regions of the lake. Most of the vertical mixing takes place in the southern two-thirds of the cavity, but this exchange is rather limited. Blue Darkgrey Shading refers to predicted zones of subglacial freezing; lightgrey shading indicates subglacial melting. (b) Circulation of Lake Vostok thought to occur as a result of saline conditions (Souchez *et al.*, 2000) (i.e. 1·2–0·4‰)

The northern meltwater likely spreads southwards and upwards, travelling into regions of progressively lower pressure and displacing lake water in the south if the horizontal salinity gradient (north–south) is high enough to compensate for geothermal warming. The possibility of such a regime is controlled by (1) the melting–freezing rates, (2) the rates of mixing between the fresh ascending meltwater layer and the underlying saline water, and (3) vertical free convection driven by the geothermal heating of water at the lake bottom. The cold northern water will eventually enter a region where its temperature is at, or below, the pressure-melting point, if the heat flux from the basal water is not sufficiently high. The water will then refreeze back onto the ice-sheet base some distance away from where it was first melted into the lake. In this case, a conveyor of fresh cool meltwater is established that migrates from north to south immediately beneath the ice sheet, which causes displacement of warmer dense lake water from south to north. In contrast, if the bulk salinity is not high enough, a stable stratification will develop in the upper water layers below the tilted lake ceiling, with more-saline warmer water in the south and fresher, cooler water in the north (Wüest and Carmack, 2000). The deep-water stratum will be subject to vertical thermal convection because, for any reasonable level of salinity, the temperature at the lake bottom will be high enough to start the convection.

### *Biological and chemical implications of circulation*

Regardless of whether Lake Vostok is chemically stratified or not, the models predict that meltwater from the north will be transferred towards the freezing zone in the south. In the saline case, this circulation may effectively separate meltwater near the ice–water interface from the underlying main body of lake water. Thus, microbes melted out of the ice sheet in the north would be transported along the ice–water interface southward within relatively short time scales, where they can be refrozen to the underside of the ice sheet without necessarily having significant opportunities for exchange with the main lake-water body. There will be some exchange between the upper meltwater layer and lake water as a consequence of turbulence and diffusion at water body boundaries in each of these scenarios, but more sophisticated modelling, which also accounts for mixing between saline lake water and fresh meltwater, will be needed to quantify this exchange.

On the basis of existing circulation models, the meltwater appears more intimately linked with the ice sheet than with the underlying lake water mass and sediments. If so, the accreted ice microbes are essentially glacial melt-derived organisms restricted to the meltwater zone and would not be necessarily representative of the microbiota of the major part of Lake Vostok. A more appropriate location to find the lake's 'natural' biota may be in the deep-water column or at the water–sediment interface at the lake floor, where numerous surfaces and significant chemical energy sources are likely to occur. Current estimates of inputs to the whole lake have invariably focused on that material originating from the glacial ice and neglected the likely much larger contributions of glacial scour material. If the circulation models prove correct, the chemistry of the accreted ice essentially reflects chemical (and potential biological) processes occurring in the upper water column, whereas, in the main lake water body, geochemistry would be driven by chemical (and biological) weathering processes acting on glacial scour material deposited in the bottom sediments.

## HYDROCHEMISTRY OF LAKE VOSTOK

Solutes are added to the lake water during ice melt and via chemical weathering of debris in and around the base of the lake. The average chemistry of the meltwater entering Lake Vostok can be inferred from Legrand *et al.* (1988), assuming that ice from glacial periods makes up 85% of the melt and that from interglacials makes up 15%. The average initial melt water has the following composition: $Na^+ = 4{\cdot}0$ μeq $l^{-1}$; $K^+ = 0{\cdot}19$ μeq $l^{-1}$; $Mg^{2+} = 1{\cdot}4$ μeq $l^{-1}$; $Ca^{2+} = 2{\cdot}1$ μeq $l^{-1}$; $NH_4{}^+ = 0{\cdot}21$ μeq $l^{-1}$; $H^+ = 2{\cdot}4$ μeq $l^{-1}$ (pH 5·6); $Cl^- = 4{\cdot}4$ μeq $l^{-1}$; $NO_3{}^- = 1{\cdot}2$ μeq $l^{-1}$; and $SO_4{}^{2-} = 4{\cdot}9$ μeq $l^{-1}$. This is equivalent to a very dilute mix of marine-derived aerosol, calcium-rich dust, and strong acids (i.e. $HNO_3$ and $H_2SO_4$). Solutes are rejected from the ice lattice during refreezing (Killawee *et al.*, 1998), and hence there should be an accumulation of nutrients, gases, and solutes in the lake water over time. The isotopic and major ion composition of Lake Vostok has been inferred from the composition of the accreted basal ice in the Vostok ice core. The accreted ice is enriched in $^{18}O$ and $^{2}H$ compared with the Vostok precipitation line (Jouzel *et al.*, 1999; Priscu *et al.* 1999a). This is because there is isotopic fractionation during water freezing, but none during melting (Souchez *et al.*, 1988, 2000). The accreted ice has values of $\delta^{18}O$ and $\delta D$ that differ from the time-averaged melting ice by only 60% of the theoretical fractionation, and it has been suggested that 30–58% of unfractionated lake water is entrained in the accreted ice during freezing, so helping to maintain less extreme values of $\delta D$ and $\delta^{18}O$ (Souchez *et al.*, 2000). The total capture of significant quantities of lake water and solute confounds existing calculations of the chemical composition of the lake water based on accreted ice chemistry (Jouzel *et al.*, 1999, Souchez *et al.*, 2000), as we detail below.

The first estimate of the chemical composition of Lake Vostok (Priscu *et al.*, 1999a) was derived from the chemical composition of the accreted ice (Table I) from above 3608 m, using ice–water partition coefficients (the ratio of the concentration of a particular solute in ice relative to that in water) obtained from surface lake ice and the underlying waters of perennially ice-covered Lake Hoare, a surface water body located in the southern Victoria Land Dry Valleys of Antarctica. Unfortunately, the inferred water chemistry has a significant charge imbalance (Table I), which may relate to the differences in both accretion rate (30 cm year$^{-1}$ in Lake Hoare and up to 4 cm year$^{-1}$ in Lake Vostok) and in ice crystal structure. A second estimate (Souchez *et al.*, 2000) has been derived from knowledge of typical partition coefficients between ice and water, which are assumed to be 0·0008 and 0·0028 (Gross *et al.*, 1977; Eicken, 1998). These partition coefficients, when applied

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Table I. The chemical composition of accreted ice (upper) and estimates of the chemical composition of Lake Vostok water (lower). It should be noted that $HCO_3^-$ concentrations are derived from charge balance

| Depth (m) | Ion concentration (μeq $l^{-1}$) | | | | | | | Comment | Source |
|---|---|---|---|---|---|---|---|---|---|
| | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Cl^-$ | $SO_4^{2-}$ | $HCO_3^-$ | | |
| 3550 | 25.2 | 0.17 | 11.0 | 0.83 | 19.2 | 7.50 | 10·5 | Accreted ice with visible dirt inclusions (all samples) | Souchez *et al.* (2000) |
| 3590 | 1.26 | n/a | 0.49 | 0.63 | 1.06 | 0.79 | 0·52 | Filtered sample; values consistent with Souchez *et al.* (2000) | Priscu *et al.* (1999a) |
| 3590 | 1.09 | n/a | 1.07 | 2.39 | 0.83 | 3.44 | 0·28 | Unfiltered sample | Priscu *et al.* (1999a) |
| 3601 | 13.0 | 0.14 | 1.00 | 7.50 | 10.7 | 9.20 | 1·70 | Lowest sample; closest to inclusion-free ice (below 3609 m) | Souchez *et al.* (2000) |
| Estimate | | | | | | | | | |
| Current | 200 | | 115 | 275 | 54 | 1150 | n/a | From Priscu *et al.* (1999a). There is a surplus of negative charge in this estimate | |
| Modified current | 700 | | 270 | 350 | 461 | 444 | 289 | Derived from the filtered sample at 3589 m above, with an ice–water partition coefficient of 0·0018 (after Souchez *et al.* (2000)) | |
| Minimum | 5.0 | | 1.2 | 1.6 | 2.1 | 2.0 | 1·3 | Derived from the filtered sample at 3589 m, and assuming that 40% of lake water is completely trapped and all solute frozen into the accreted ice (after Souchez *et al.* (2000)) | |
| Maximum | 10 600 | | 3330 | 2320 | 8330 | 4640 | 3390 | Derived from the average composition of samples from 3550 and 3601 m above, with an ice–water partition coefficient of 0.0018 (after Souchez *et al.* (2000)) | |
| | | | | | | | | ~1‰ salinity water would contain ~17 mM of anions. This composition is ~16 mM of anions | |

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to the chemical composition of the accreted ice, suggest that the salinity of the lake water is in the range of 0·4–1·2‰, which is an upper limit of estimates to date. Table I gives an indication of the ionic composition this implies. Both the Priscu *et al.* (1999a) and Souchez *et al.* (2000) calculations are inaccurate if there is significant incorporation of lake water into the accreted ice and solute cannot diffuse back into the lake during the subsequent freeze. Most of the solute in the ice will be derived from the captured lake water solutes, and application of the partition coefficients to concentrations in the ice will lead to an overestimation of the true lake water composition.

If the accreted ice (see Table I) does contain 30–58% of frozen lake water, from which no solute escaped back into lake water during freezing, then the lake-water composition will be ~1·72–3·33 times that of the accreted ice composition (Table I). This is a minimum estimate of lake-water composition to date. There is reasonable agreement between the Priscu *et al.* (1999a) estimate and a modified estimate obtained if a partition coefficient of 0·0018 (after Souchez *et al.* (2000)) is applied to the filtered accreted ice concentration at 3590 m (Priscu *et al.*, 1999a). The water has an ionic composition that is ~1 mM in terms of total dissolved anions (Table I). This water composition is similar to those sampled directly from subglacial environments elsewhere, which are often characterized by rock–water interactions (Tranter *et al.*, 2002).

Most of the accreted ice studied to date comes from the zone containing mineral debris (Souchez *et al.*, 2000). This debris potentially interacts with the ice meltwater during sample processing to generate additional solute. The filtered accreted ice sample, shown in Table I, has the lowest solute concentrations of those measured in the accreted ice that contains visible dirt inclusions, being approximately one order of magnitude lower than the other samples (Souchez *et al.*, 2000). This order of magnitude difference accounts for the seemingly high solute concentrations in water of salinity ~1‰ (Table I), which is ~16 mM in anions, and could represent an upper estimate of the lake-water composition. Preliminary studies of the 'gem' ice below 3608 m, however, show it has a lower ionic strength than the overlying 'dirty' accreted ice, which probably formed in proximity to the lake perimeter (Montagnat *et al.*, 2001). These new data appear to rule out the upper estimate of the lake's hydrochemistry (Table I).

Recent studies of microbially mediated chemical weathering in subglacial environments have shown that environments out of free contact with the atmosphere, and without an alternative supply of oxygen, become progressively anoxic over time (Tranter *et al.* 2002; Bottrell and Tranter, 2002) as sulphide oxidation and microbial respiration of organic matter deplete the $O_2$. It is interesting to note that the chemical composition of the filtered accreted basal ice with the lowest solute concentrations (Table I) has an anion stoichiometry consistent with sulphide oxidation and carbonate dissolution being dominant chemical reactions. Sulphide oxidation and carbonate dissolution produce equal equivalents of $SO_4^{2-}$ and $HCO_3^-$ and the proportion of $SO_4^{2-}$ to $HCO_3^-$ increases if there is a paucity of carbonate in the bedrock. The accreted ice has an $SO_4^{2-}$ concentration of 0·79 μeq $l^{-1}$, and the negative charge balance deficit suggests that the $HCO_3^-$ concentration is 0·52 μeq $l^{-1}$, giving a $SO_4^{2-}$: $HCO_3^-$ ratio of ~1·5 : 1. The cation chemistry suggests that other more complex chemical reactions also take place. In particular, it appears that $Na^+$ and $Mg^{2+}$ are enriched with respect to $Ca^{2+}$, suggesting that feldspars, such as albite, and ferromagnesium minerals supply new solute to the lake water.

Dissolved oxygen will be found in the Lake Vostok water column since gas hydrates are released from the melting glacial ice. Gas hydrates (or clathrates) are crystal lattices formed by water molecules around gas molecules under conditions of low temperatures and high pressures. High pressures result in substantial volumes of gas being compressed and trapped within these lattice structures. Air hydrates are known to be present in the glacial ice above Lake Vostok (Uchida *et al.*, 1994). This is because gases cannot dissolve in the solid ice, and hence all of the air is subject to the confining pressure of the ice. Some of the gases in the air clathrates that enter the lake can dissolve in water, and hence the air clathrate may completely or partially dissolve, dependent on the concentration of dissolved gases already present in the lake water. Lipenkov and Istomin (2001) calculate that the minimum oxygen concentration in Lake Vostok waters is ~17 μM, just under twice that of water saturated with oxygen at the surface, whilst the maximum concentration is ~850 μM. The oxygenation of lake water by dissolution of the clathrate will most likely occur near the surface of the lake,

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proximal to the supply of hydrates from the melting ice sheet base. Water circulation will then allow the transfer of oxygenated water to other parts of the lake, including the southern side, where subglacial freezing occurs, and the deeper regions. It is also likely that the concentration of dissolved oxygen will decrease with distance from the source of hydrates, if there is microbial respiration in the lake water (see below) and if there is oxidation of sulphides, ammonium, or other metabolic electron donors in the glacial debris. This may mean that some regions, such as the floor of the lake and the lake-floor sediments, may be depleted in dissolved oxygen, potentially making the environment there anoxic.

Clearly, the oxygen concentration in the lake water is a function of the magnitude of the oxygen source (from clathrate dissolution) and oxygen sinks (oxidation of reduced compounds and incorporation in refrozen meltwater). Anoxia will occur in regions of the lake where the flux of oxygen is less than the potential oxygen demand. A third factor that may control oxygen concentrations, if the oxygen source exceeds the oxygen sink, is the saturation limit. The oxygen concentration of the lake water will gradually increase over time until the maximum oxygen concentration is reached. Then, additional oxygen is retained as clathrate, which may effectively buffer variations in oxygen concentrations in the water column against short-term variations in oxygen supply and sinks. Oxygen concentrations are calculated to reach saturation levels in a minimum of 0·2–1·6 million years if there are no sinks of oxygen from the lake (Lipenkov and Istomin, 2001). The time scale of $N_2$ saturation is of a similar magnitude, and it is likely that nitrogen clathrates will be found in the lake given the age of the lake and the lack of obvious $N_2$ sinks. Our current lack of an oxygen mass balance for the lake prevents us from having an unequivocal position on both the distribution of oxygen concentrations throughout the lake and the presence or absence of oxygen clathrates.

## APPLICATION OF PHYSICAL AND CHEMICAL PROCESSES TO OTHER SUBGLACIAL LAKES

All subglacial lakes have an ice–water interface sloping at $-11$ times the ice surface gradient, if they are in hydrostatic equilibrium. Thus, there are likely to be temperature and density contrasts between meltwater and the main lake water body, and possibly zones of subglacial melting and freezing, that may lead to water circulation within even small lakes. Lake Vostok is the only subglacial lake *known* to have a substantial water depth of the order of hundreds of metres. Maximum depths of other lakes are yet to be established, but minimum water depths of at least five further lakes have been shown to be between 10 and 20 m (Gorman and Siegert, 1999). These depths were determined from radar reflections off the floors of the lakes. Such reflections are possible if the water conductivity is of the order of $10^{-4}$ mhos $m^{-1}$ (Gorman and Siegert, 1999). If the conductivity is higher by, say, an order of magnitude, as it certainly would be if the water is saline even to a small extent, the radio waves would attenuate instead of propagating and reflecting off the lake floor. Water depths of less than 10 m are likely to result in the break up of the smooth flat ice–water radar recording that is used as an identification criterion for subglacial lakes. All the known subglacial lakes have been identified from a smooth flat radar signal, so it can be concluded that these lakes have water depths of at least 10 m. The bedrock slopes at the edges of subglacial lakes are often similar to those bordering Lake Vostok, and hence the water depths of smaller lakes may be significantly greater than 10 m. It is likely that the deep circulation caused by melting and freezing along a sloping ice roof, as conceptualized in Lake Vostok, is applicable in other subglacial lakes with significant water depths. The implications of freezing and melting zones within subglacial lakes and of possible gas hydrate persistence outlined above should also equally apply to these smaller systems.

## IMPLICATIONS FOR LIFE IN SUBGLACIAL LAKES

Microbes have developed biochemical, physiological, and morphological diversity to facilitate their growth in most, if not all, environments on Earth containing liquid water (Rothschild and Mancinelli, 2001). This diversity encompasses organisms with novel redox couples for the production of energy, adaptations to

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extremes of temperature, pressure, salt, and pH, of novel energy acquisition mechanisms, and unique strategies for withstanding starvation (Madigan and Marrs, 1997). There seems little doubt, therefore, that some form of microbial life will be found in Lake Vostok. Existing studies of the accreted ice (Priscu *et al*., 1999a; Karl *et al*., 1999; Christner *et al*., 2001), deep glacier ice (Abyzov *et al*., 1998; Christner *et al*., 2000), and permanent lake ice in the McMurdo Dry Valleys (Priscu *et al*., 1998; Gordon *et al*., 2000) have each reported prokaryotes of the domain Bacteria (no Archaea were detected) and eukaryotes. It is anticipated that viruses will also occur in Lake Vostok, since an enormous diversity of viral particles has been detected in Antarctic surface lakes (Wilson *et al*., 2000), and preliminary results from electron microscopy have indicated the presence of viruses in Vostok glacial and accretion ice (Young and Priscu, unpublished data).

A microbial presence in the water column can be inferred from existing accreted ice data and from studies of cold aquatic environments elsewhere (Vincent, 2000; Ellis-Evans, 1996; Priscu *et al*., 1999b). Microbes favour colonizing surfaces and environments with strong chemical gradients, and significant colonization of the lake sediments seems likely. Though the composition, activity, and distribution of lake microflora remain unknown, knowledge of the physical and chemical environment of the lake (given above) does, however, provide an insight to the microbes that may live there.

Assuming that appropriate partition coefficients have been used to calculate concentrations of chemicals in lake water from accreted ice chemistry, the lake waters will have adequate nutrients to support a heterotrophic microbial assemblage. Karl *et al*. (1999) and Priscu *et al*. (1999a) reported dissolved organic carbon (DOC) levels in accretion ice between 79 and 510 $\mu$g $l^{-1}$. Based on the upper limit of this range, Priscu *et al*. (1999a) have estimated that Lake Vostok will have a DOC level of 1200 $\mu$g $l^{-1}$, which is adequate to support heterotrophic growth. Karl *et al*. (1999) also reported total nitrogen levels in accretion ice ranging from 0·972 to 2·577 $\mu$M, which would fuel a well-developed microbial assemblage within the lake supporting the estimates of $10^6$ cells $ml^{-1}$ in the Vostok water column made by (Priscu *et al*., 1999a). Measurements of nutrient loads to the lake based on the Vostok watershed and estimated melting rates are currently under way to corroborate these claims.

Growth and activity need not be limited at the relatively low temperatures ($-3$ to $-4$ °C) experienced in subglacial lakes, since microbial activity has been reported at ambient temperatures below $-12$ °C in Antarctic snow (Carpenter *et al*., 2000) and in sea ice (Bowman, 1998; Bowman *et al*., 1998). The vast majority of microbes isolated from Antarctic soils, freshwater, marine, and air samples to date are psychrotolerant rather than psychrophilic (Ellis-Evans, 1996; Fritsen and Priscu, 1998; Vincent, 2000), which implies that selection pressures for optimal growth at low temperature are often less important than other constraints in these extreme environments. Psychrophilic forms are more prevalent in permanently cold environments, such as sea ice and the marine abyssal, but the influence of temperature in subglacial environments may prove to be primarily manifested in dampening of overall rates of activity. More significant determinants of the diversity and physiological characteristics of the lake microflora could be the environmental stresses associated with reaching these lakes and the different time scales available for colonization, particularly when considering the time scales over which Lake Vostok may have existed when compared with other subglacial environments. Comparison of molecular profile diversity from accreted ice with Antarctic aeroflora and glacial ice flora could feasibly provide some insights to these potential selection pressures.

In Lake Vostok it is possible that oxic conditions exist near the surface, while the mid-depths are more sub-oxic, and the lake base and lake-floor sediments are anoxic. This sequence favours the presence of aerobic microbes near the surface with facultative and strict anaerobes present in deeper waters. Both facultative and obligate anaerobes can undertake a wide range of geochemically relevant processes as listed in Table II.

Assuming low concentrations of dissolved oxygen, oxidants such as nitrate and sulphate will acquire greater significance as metabolic electron acceptors (Table II). Low levels of nitrate, relative to concentrations in the overlying glacial ice, have been recorded from accreted ice (Priscu *et al*., 1999a). This suggests some form of biologically mediated nitrogen cycling within the lake (or at least in the meltwater) as the nitrogen cycle is essentially biologically driven. The sulphate and bicarbonate concentrations in accreted ice are consistent with the occurrence of yet other geochemical processes, though these may be located within the lake sediments

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Table II. Bacterial metabolic processes that may operate in the presence (aerobic) or absence (anaerobic) of oxygen within subglacial lakes

| Conditions | Electron (energy) donor | Electron acceptor | Metabolic process |
|---|---|---|---|
| Aerobic | $H_2$ | $O_2$ | H oxidation |
| | $HS^-$, $S^0$, $S_2O_3^{2-}$, $S_4O_6^{2-}$ | $O_2$, $NO_3^-$ | S oxidation |
| | $Fe^{2+}$ | $O_2$ | Fe oxidation (low pH) |
| | $Mn^{2+}$ | $O_2$ | Mn oxidation |
| | $NH_4^+$, $NO_2^-$ | $O_2$ | Nitrification |
| | $CH_4$ and other C-1s | $O_2$ | (C-1) oxidation |
| | $CH_4$ | $O_2$ | Methane oxidation |
| | Organic compounds | $O_2$ | Heterotrophic metabolism |
| Anaerobic | $H_2$ | $NO_3^-$ | H oxidation |
| | $H_2$ | $S^0$, $SO_4^{2-}$ | $S^0$ and sulphate reduction |
| | $H_2$ | $CO_2$ | Acetogenesis |
| | $H_2$ | $CO_2$ | Methanogenesis |
| | $S^0$, $SO_4^{2-}$ | $NO_3^-$ | T. denitrificans |
| | Organic compounds | $NO_3^-$ | Denitrification |
| | Organic compounds | $S^0$, $SO_4^{2-}$ | $S^0$ and sulphate reduction |
| | Organic compounds | | Fermentation |

rather than within the main lake water column. Microbially mediated reduction/oxidation (redox) reactions are important at alpine glacier beds (Sharp *et al.*, 1999) and in polythermal Arctic subglacial environments (Skidmore *et al.*, 2000). Such environments challenge the view that chemical weathering in subglacial systems could be purely abiotic.

Mineral analysis of sediment particles in accretion ice from 3590 m (Priscu *et al.*, 1999a) revealed that biotite (73%), quartz (13%), potassium feldspar (9%), plagioclase (2%), muscovite (2%), and iron oxide (1%) were the primary minerals. The distribution of mineral phases in these sediments does not reflect the expected proportions of minerals observed in common crustal granitoid rock types (biotite: $<20\%$; quartz 20–55%; potassium feldspar + plagioclase: 40–80%; and muscovite and iron oxide: trace amounts). The results indicate that both mechanical sorting processes and, more importantly, differential sedimentation rates are operating to concentrate biotite to relatively high levels in Vostok accretion ice. These processes will be located in the shallow region of the lake where accretion has been initiated and glacial meltwater and bedrock debris are in close proximity; a situation comparable to that described in alpine and polythermal arctic glaciers (Sharp *et al.*, 1999; Skidmore *et al.*, 2000). It has been suggested that the dissolution of micas, such as biotite and muscovite, may be a source of $NH_4^+$ in temperate watersheds of the USA (Holloway *et al.*, 1998). Hence, dissolution of micas in the basal sediment may be providing an additional source of nitrogen to the lake waters.

Solar radiation through photosynthesis is, directly or indirectly, the major source of energy for most organisms on Earth, and a major driver of processes in surface Antarctic lake ecosystems (Ellis-Evans, 1996). In its absence, microbes in subglacial lakes would have to utilize chemical energy to power biological processes. This situation is typical of sub-seafloor and other subterranean environments (Parkes *et al.*, 2000), and a substantial diversity of microbes have the necessary chemolithotrophic capability to utilize inorganic energy sources (Table II). A source of recalcitrant organic carbon in subglacial debris would enable a strategy of high biomass and low growth rate to be possible, as is often the case in deep marine sediments (Parkes *et al.*, 2000). Current experience of extreme environments suggests that a range of redox-related processes utilizing inorganic energy sources are likely in subglacial lakes, and these will be rate limited by the availability of reduced compounds, such as sulphides, ammonium, and organic carbon, and of oxidants, such as those outlined in Table II. Such processes give rise to relatively low energy yield in comparison with photosynthesis. In the permanent absence of solar radiation inputs, substantial biomass and diversity of microbes needs to be

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supported either by geothermal energy and/or a readily available supply of reduced compounds, similar to that produced at hydrothermal sites (Karl, personal communication). Helium isotope data (Jean-Baptiste *et al.*, 2001) indicate that hydrothermal activity is unlikely in Lake Vostok, suggesting that exploration of subglacial lakes will reveal microbial populations adapted to an existence within a low energy flux environment. Nevertheless, sub-seafloor sediments and subterranean environments with similar low energy flux systems have revealed a widespread occurrence of intact high molecular weight prokaryotic DNA, unique 16S-rRNA gene sequences, and a range of physiologically adapted or optimized microbes (Bidle *et al.*, 1999; Parkes *et al.*, 2000). The potential for finding novel microbes in subglacial environments, therefore, clearly exists.

The proposed suite of biogeochemical reactions that could occur in the water column and sediments, which include sulphide oxidation, nitrate respiration, sulphate respiration, and methanogenesis (Table II), are ultimately dependent on the supply of oxidants. These can be provided primarily only via melting of the glacial ice sheet and secondarily by chemical weathering of sediments, so their rate of supply will be critical for rates of biological activity in both the water column and within the lake sediments. It has been postulated that extreme oxidant depletion could occur in a 'Snowball Earth' scenario, where access to solar radiation and the supply of atmospheric oxidants to aquatic environments is prevented by an ice sheet of global scale present for millions of years (Gaidos *et al.*, 1999). This would eventually lead to anoxia and the virtual annihilation of ecosystems on time scales of tens of millions of years. The possibility that Lake Vostok could have existed for a comparable time scale since the onset of Antarctic glaciation ($\sim$33 million years ago) has prompted comparison with the Snowball Earth hypothesis (Hoffman *et al.*, 1998). However, the presence of microbes and of oxidants, such as nitrate and sulphate, as well as their apparent utilization in modern-day Lake Vostok, suggests that the lake is a functioning ecosystem despite its long isolation beneath the ice. The extreme oxidant depletion postulated in a Snowball Earth scenario is attributed to extensive hydrothermal activity in areas such as the mid-Atlantic Ridge. The presence of a range of oxidants in Lake Vostok would support the conclusion from $^3$He/$^4$He data that there is no substantial mantle activity in the lake.

## CONCLUSIONS

The base of the Vostok ice core comprises accreted ice that has been refrozen to the underside of the ice sheet from the lake water. This ice is, effectively, a sample of Lake Vostok. Geochemical analysis of the accreted ice, combined with airborne geophysical reconnaissance, has prompted the following ideas about the lake's physical environment and hydrochemistry, and their implications for life in Antarctic subglacial lakes.

- In the north of the lake, subglacial melting occurs, which releases solute and gas hydrates into the lake.
- Near-surface water at the southern end of Lake Vostok has a composition similar to water sampled *directly* from Alpine and Arctic subglacial environments (i.e. $Na^+ = 200-700$ μeq $l^{-1}$; $Ca^{2+} = 115-270$ μeq $l^{-1}$; $Mg^{2+} = 275-350$ μeq $l^{-1}$; $Cl^- = 54-461$ μeq $l^{-1}$; $SO_4{}^{2-} = 444-1150$ μeq $l^{-1}$; $HCO_3{}^- \cong 300$ μeq $l^{-1}$). This suggests that the principal reactions that supply solute to the lake water include carbonate hydrolysis, carbonation, sulphide oxidation, and oxidation of organic carbon.
- Nitrogen hydrates are likely to be present within the lake. The presence of oxygen hydrates depends, first, on the flux of oxygen from melting ice being greater than potential oxygen sinks and, second, on there being sufficient time available for oxygen to become saturated in the lake water. Water near the melt zone will contain oxygen, derived from the dissolution of air hydrates from the melting ice.
- The concentration of dissolved oxygen is likely to decrease with distance from the melt zone. This may leave the upper regions of Lake Vostok with a higher concentration of oxygen than mid-depths and the lake floor, which may become suboxic or anoxic.
- The lake biota must survive in an environment of permanent darkness, high pressure (350 atm) and low temperature ($-3\,^\circ$C). Oxidation of sulphides and organic matter will, in the likely absence of hydrothermal activity, provide a major source of energy, but chemolithotrophic utilization of iron, manganese, sulphate,

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and carbon dioxide by microorganisms, particularly in anoxic sediments, are also likely to play a role, as already demonstrated in permanently cold polar surface lakes.

- Microbes have been found in the accreted ice. Molecular profiling of accreted ice microbes using 16S-rDNA techniques show a very close agreement with present-day surface microbiota. This is consistent with the idea that the microbes found in accreted ice originate from deep glacial ice, are transported towards the south of the lake after melting out at the north end, and consequently spend little time in the lake prior to refreezing.
- These modern biota may be unrepresentative of lake microbes that could feasibly originate from lake floor sediments and the subglacial geology. Lake-floor biota, if they exist, may show significant evolutionary divergence, since their period of isolation has been of the order of tens of millions of years.

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