Physical, chemical and biological processes in Lake Vostok and other Antarctic subglacial lakes

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Over 70 lakes have now been identified beneath the Antarctic ice sheet. Although water from none of the lakes has been sampled directly, analysis of lake ice frozen (accreted) to the underside of the ice sheet above Lake Vostok, the largest of these lakes, has allowed inferences to be made on lake water chemistry and has revealed small quantities of microbes. These findings suggest that Lake Vostok is an extreme, yet viable, environment for life. All subglacial lakes are subject to high pressure (~350 atmospheres), low temperatures (about −3 °C) and permanent darkness. Any microbes present must therefore use chemical sources to power biological processes. Importantly, dissolved oxygen is available at least at the lake surface, from equilibration with air hydrates released from melting basal glacier ice. Microbes found in Lake Vostok's accreted ice are relatively modern, but the probability of ancient lake-floor sediments leads to a possibility of a very old biota at the base of subglacial lakes.

Only five years ago, Antarctic subglacial lakes were catalogued from airborne radio-echo sounding (RES) records collected in the 1970s (refs 1, 2) (Fig. 1). The largest of these, Lake Vostok, has generated a huge amount of scientific interest as a potential and unusual habitat for life. Quantification of the physical and chemical processes within Lake Vostok, and identification of life within the lake, requires samples of lake water. It was unclear in 1996 how, or even whether, water sampling could be performed. Recently, however, coring at Vostok station[3], located at one end of Lake Vostok, has sampled ice down to 150 m from the surface of the lake. The lower 60 m of the ice core, and therefore the basal 210 m of the ice sheet beneath Vostok station, comprises ice refrozen from lake water[4]. This basal ice is, essentially, a sample of Lake Vostok.

Several independent analyses of the accreted ice have revealed preliminary information about the lake's chemistry and biology[5–7]. However, these results, which need to be fully confirmed, have yet to be either integrated or interpreted with a full appreciation of the physical dynamics operating in Lake Vostok. It is therefore appropriate to review the recent research on Lake Vostok, in order to establish the main physical and chemical processes within the lake, and assess the implications of these for life in this extreme environment and in other subglacial lakes.

All subglacial lakes have an ice–water interface sloping at eleven times the ice surface gradient (but in the opposite direction), if they are in hydrostatic equilibrium. The pressure melting point along the upper boundary of the lake, which is dependent on the overlying ice thickness, therefore varies. For example, the pressure melting point in the south of Lake Vostok will be around 0.3 °C less than that in the north. This leads to density contrasts between meltwater and the main lake-water body, and water circulation even within small lakes. Lake Vostok is the only subglacial lake that is known to have a substantial water depth (hundreds of metres)[8]. The maximum depths of other lakes are yet to be established but minimum water depths of at least seven lakes have been shown to be between 10 and 20 m (ref. 9). The bedrock slopes at the edges of subglacial lakes are often similar to those bordering Lake Vostok, and hence the water depths of many of the smaller lakes may be significantly greater than 20 m (ref. 10). We therefore contend that the physical and chemical processes that occur in Lake Vostok are likely to be applicable in many other subglacial lakes.

Lake age and physiography

Lake Vostok is at least 240 km long and 50 km wide, and lies between 3,750 m (over the south of the lake) and 4,150 m (over the north) beneath the central east Antarctic ice sheet (Fig. 2)[11–13]. The lake is located within a very large subglacial topographic basin, similar to a rift valley, though it is unlikely that the rift valley tectonics remain active[14]. The basin has a crescent-like shape, and the side-walls are relatively steep (with gradients up to ~0.1) and high (up to ~1,000 m above the surface of the lake). Lake Vostok is at least 1,000 m deep in the south (Fig. 2), and relatively shallow in the north and extreme southwest. There may be several hundred metres of glacial sediments draped over its floor[15]. Although there are several similar subglacial basins in East Antarctica (for example, the Adventure subglacial trench and the Astrolabe subglacial basin), only Lake Vostok's basin is filled with deep water.

Lake Vostok is thought to have existed for as long as the ice sheet has been at a continental scale[16]. This is because, even over glacial–interglacial cycles, the ice thickness and subglacial conditions would not have changed significantly[17]. Some argue that the east Antarctic ice sheet has been stable for the last 20 million years at least[18]. If this is correct, Lake Vostok may have been in continual existence across the youngest third of the Cenozoic era and the entire Quaternary period. It is also possible that sediments across the floor of the valley may not have been completely scoured by the glacial advance of the infant Antarctic ice mass 33 million years ago[16]. This would mean that a historical record and biotic reservoir from the mid-Cenozoic is present at the base of Lake Vostok's sediment profile.

The age of the basal ice in the Vostok ice core is an important constraint on the age of youngest water within the lake. Preliminary examination of the isotope record[4], estimates of the air-hydrate crystal growth rates[19] and ice flow modelling[20] provide evidence that the basal glacier ice could be as old as 1,000,000 years. This marks the maximum possible age of the youngest lake water. This also effectively marks the date at which Lake Vostok was last in direct contact with the biotic and chemical constituents of the Earth's atmosphere. The mean age of water within Lake Vostok is a function of the residence time of the water and how well the meltwater mixes with existing lake water. We speculate 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 (ref. 21). Hence the mean age of Lake Vostok's water is most probably of the order of 1 million years old.

Ice flows onto Lake Vostok from the ridge B ice divide, located approximately 200 km from the lake's western margin[8,13,22]. Surface ice motion across Lake Vostok has been measured using repeat-pass synthetic aperture radar interferometry (InSAR) from the ERS-1 satellite[22] (Fig. 2). At Vostok station, the surface ice velocity is measured at 4.2 m yr^{-1}. The distance along the ice flowline between the western shoreline of Lake Vostok and Vostok station is about 15 km (Fig. 3). Thus surface ice will take about 5,000 years to cross the lake to the station. However, it may take longer for basal ice to make this journey because grounding lines and mid-lake 'islands' (Fig. 3) may inhibit flow.

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[17,23]. The mean basal temperature gradient is about 0.02 °C m^{-1}, which relates to an outward heat flux through the ice from the lake ceiling of 46 mW m^{-2}, indicating that rates of subglacial freezing beneath the Vostok ice core site are probably around 4 mm yr^{-1}. In the extreme case that basal ice at −10 °C flows over the western lake margin, the rates of freezing beneath Vostok station will probably not be higher than about 11 mm yr^{-1}.

The spatial distribution of subglacial melting and freezing can theoretically be estimated 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 and freezing takes place in the south[11].

Lake salinity and water circulation

The pattern of density-induced water circulation within Lake Vostok may be influenced significantly by lake salinity. It is highly likely that the salinity of Lake Vostok varies vertically and horizontally. In order to understand the circulation in Lake Vostok, we must

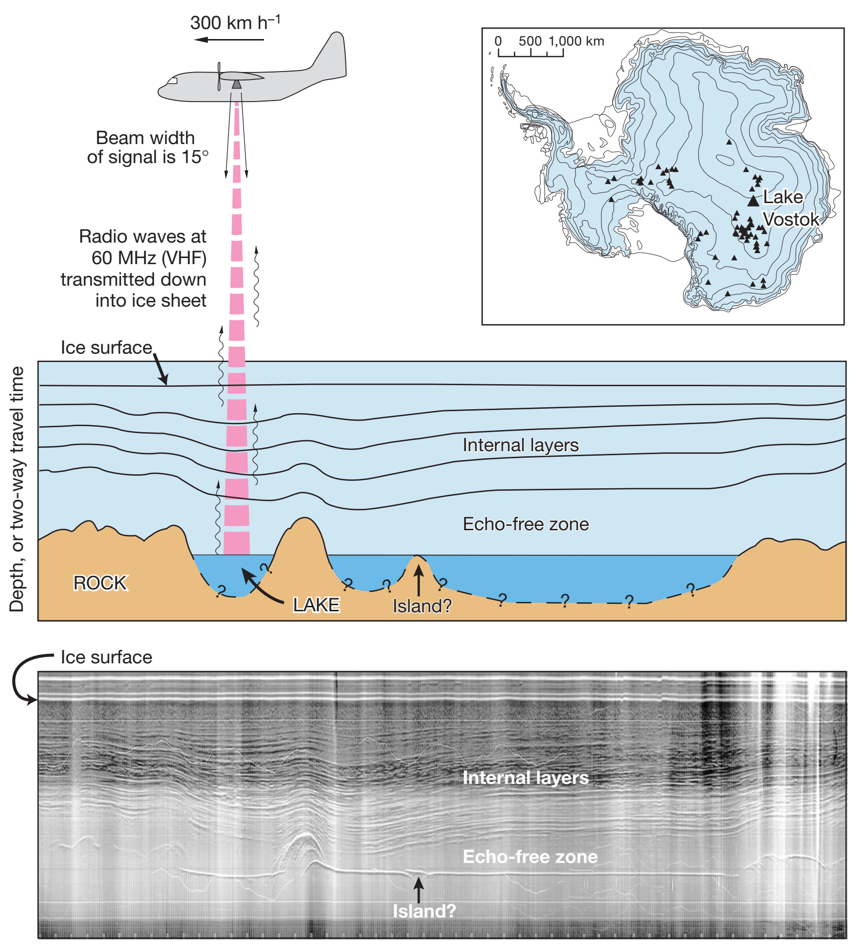

Figure 1 The technique of airborne radio-echo sounding, and its application to identifying Lake Vostok and other subglacial lakes. In the 1970s, airborne RES surveys were undertaken with a C130 Hercules transporter aircraft, with the wings mounted with the radar transmitter and receiver. Aircraft navigation was accurate to around 5 km in the centre of Antarctica. Today, most RES surveys use smaller aircraft and the global positioning system (GPS) to navigate. Subglacial lakes are easily identified on airborne RES records owing to their uniformly strong and flat appearance[2]. Bedrock perturbations are recorded as hyperbolae in radar data. The geographical location of known subglacial lakes (shown as triangles) is also provided[1].

evaluate how it would behave in the end-member scenarios of fresh and saline conditions. Evidence in support of saline water comes from the accreted ice from which an upper limit salinity of 0.4–1.2‰ has been estimated[7]. However, not all studies of the accreted ice agree with this, and some have argued that the accreted ice suggests that the lake waters are very pure[6]. Very high frequency (VHF) radio-wave penetration has been observed through up to 20 m of lake water in the north of Lake Vostok (where melting occurs), which could only be possible if the lake water is extremely pure[9].

The circulation of pure 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, resulting in an unstable water column[24]. This leads to vertical convective circulation in the lake, in which cold meltwater sinks down the water column and water warmed by geothermal heat ascends up the water column (Fig. 4a). However, in the south, where the ice sheet is thinner and subglacial freezing takes place, a pool of slightly warmer and stratified water may occur below the ice roof[24]. Here, the water would not be involved in the convective motion as heat is transferred from the ice towards the lake (that is, the temperature will decrease with depth).

There have been three numerical models from which the circulation of pure water in Lake Vostok can be evaluated[24–26] (Fig. 4a). The models indicate that in the northern area of Lake Vostok, where the ice is thickest, meltwater will be colder and denser 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. 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 (Fig. 4a).

In the case where the lake is saline to some extent[7], the fresh meltwater will be buoyant compared with the resident lake water (Fig. 4b). Because of this, the northern meltwater is likely to spread southwards and upwards travelling into regions of progressively lower pressure, 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) the vertical free convection driven by the geothermal heating of water at the lake bottom. If the heat flux from the basal water is not sufficiently high, the cold northern water will eventually enter a region where its temperature is at or below the pressure melting point. From this point on, the water will refreeze back onto the ice-sheet underside, some distance away from where it was first melted into the lake. In this case, a conveyor of fresh cool meltwater from north to south directly beneath the ice ceiling of Lake Vostok will be set up, which causes displacement of warmer dense lake water from south to north. Otherwise, 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[24]. The deep-water stratum will be subject to vertical thermohaline convection because, for any reasonable level of its salinity, the temperature at the lake bottom will be high enough to initiate convection.

Regardless of whether Lake Vostok is saline or fresh, meltwater from the north will be transferred towards the freezing zone in the south, and water will flow from the surface into the main body of the

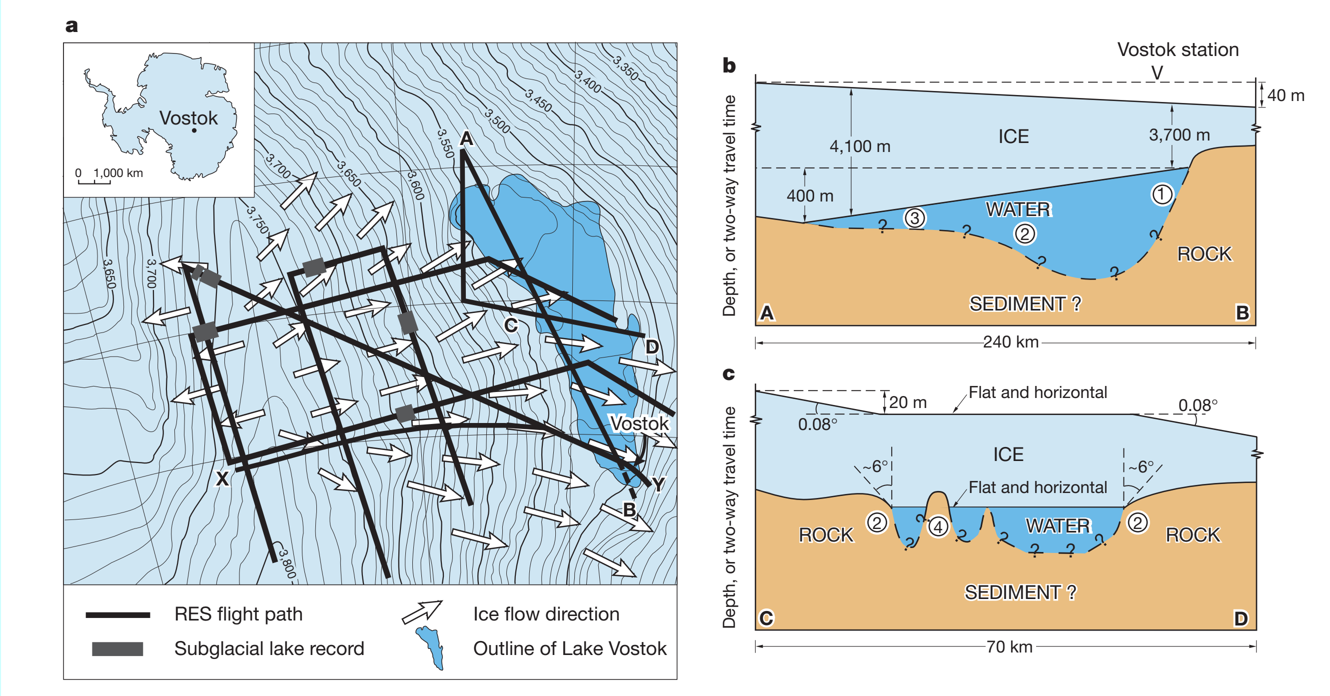

Figure 2 The dimensions and topographic setting of Lake Vostok. **a**, ERS-1 altimetry of the Antarctic ice sheet between ridge B and dome C. The location of Lake Vostok can be identified from the anomalous flat ice-surface region. The contour interval is 10 m. SPRI (Scott Polar Research Institute) RES flight lines and the location of all known subglacial lakes around Lake Vostok (shown as black squares) are provided. Arrows denote the direction of surface flow of ice over Lake Vostok calculated from InSAR[11,12]. **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[15], which has revealed a water depth of over 500 m beneath Vostok station and ~1000 m to the north of the station; (2) a 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) radiowave 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 RES.

lake before it returns to the north. This process is critical to evaluating the chemical and biological information stored within the accreted ice beneath Vostok station.

Lake water chemistry and life-supporting nutrients

Solutes are added to the water in Lake Vostok during ice melt and via chemical weathering of debris in and around the base of the lake.

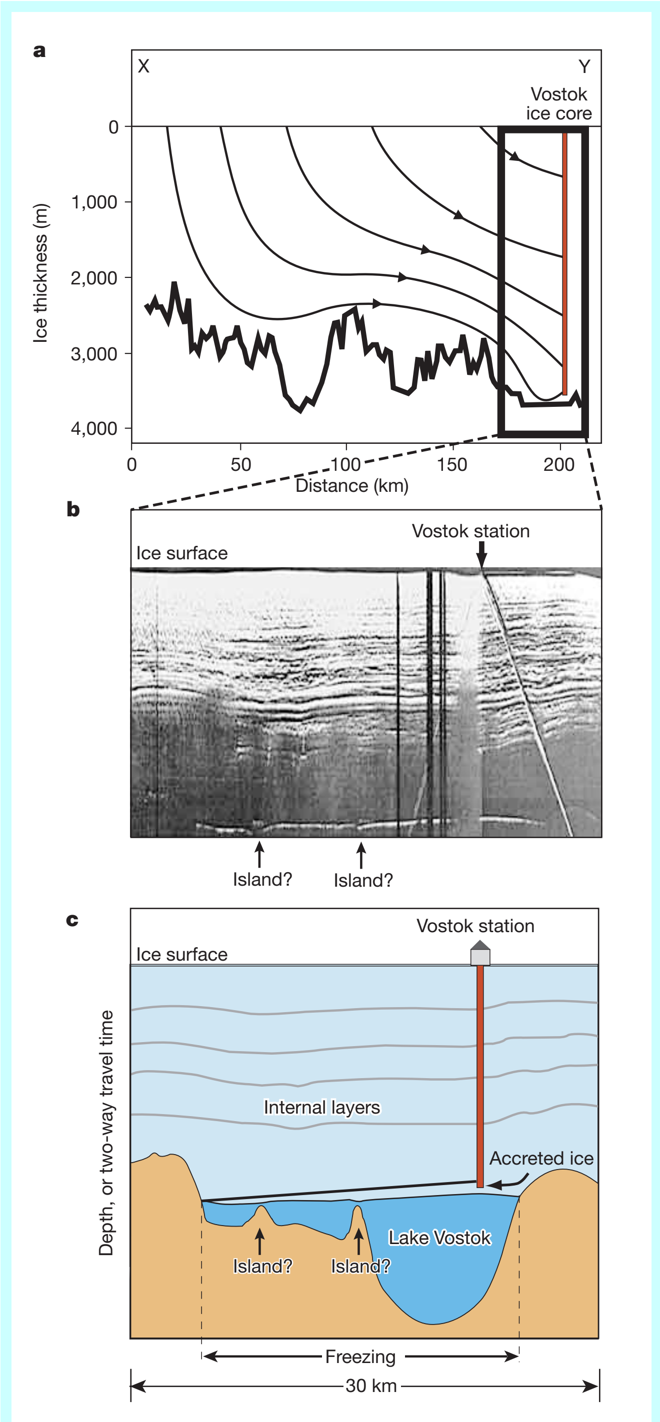

Figure 3 Ice sheet cross-sections along the line of ice flow from the ice divide, across Lake Vostok, to the Vostok ice core. **a**, Suggested ice particle flowpaths between ridge B and the southern end of Lake Vostok (Fig. 1a). The bedrock elevation has been measured from airborne RES[2]. **b**, Raw records along an ice surface 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**, Interpretation of the RES data provided in **b**.

Solute is rejected from the ice lattice during freezing[27], and hence there should be an accumulation of solute in the lake water over time. The isotopic and major ion composition of Lake Vostok can be inferred from the composition of the accreted ice, provided assumptions are made about the percentage of lake water entombed within growing ice crystals and the partitioning of solute between lake water and ice[6,7]. Geochemical investigations of the accreted ice indicate that near-surface water at the southern end of Lake Vostok has a composition comparable with water sampled directly from subglacial environments[6,28] (Na^+, 200–700 microequivalents per litre ($\mu eq\ l^{-1}$); Ca^{2+}, 115–270 $\mu eq\ l^{-1}$; Mg^{2+}, 275–350 $\mu eq\ l^{-1}$; Cl^-, 54–461 $\mu eq\ l^{-1}$; SO_4^{2-}, 444–1,150 $\mu eq\ l^{-1}$; HCO_3, 300 $\mu eq\ l^{-1}$). This suggests that the principal reactions that supply solute to subglacial waters include silicate and carbonate hydrolysis, carbonation, sulphide oxidation and oxidation of organic carbon.

Gas hydrates (or clathrates; crystal lattices formed by water molecules around gas molecules under conditions of low temperatures and high pressures[29]) have the potential to store significant quantities of gas in Lake Vostok. Hydrates are known to be present in the glacial ice above the lake[30,31] and have also been observed in the accreted ice (Fig. 5). Thus, gas hydrates should be present in Lake Vostok. If, as seems probable, the rate of hydrate supply to the lake through melting of glacial ice exceeds their loss through freezing within accreted ice, they will accumulate in the lake over time. Experimental studies of a range of gas hydrates suggest they may be stable within an environment such as Lake Vostok[32,33], in which the pressure is about 350 atm and the temperature is about −3 °C. Some hydrates may have a lower density than the surrounding melt water and could therefore migrate beneath the sloping ice–water interface and accumulate in certain regions. Dissolved oxygen is expected in Lake Vostok's water owing to continuous equilibration with gas hydrates[33], making certain areas of the lake more oxic/suboxic than anoxic. This oxygenation will probably occur near the surface of the lake, proximal to the supply of hydrates from the melting ice sheet base. Water circulation (Fig. 4) will then allow the transfer of oxygenated water to other parts of the lake, including the southern side, where subglacial freezing occurs, and deeper regions.

Recent investigations into microbially mediated chemical weathering in subglacial environments have shown that such places, out of free contact with the atmosphere, can become progressively anoxic over time[28,34]. This is because chemical oxidation and microbial respiration of organic matter deplete the original dissolved oxygen. The anion stoichiometry of the accreted ice is consistent with sulphide oxidation and carbonate dissolution being important chemical reactions in Lake Vostok. Further, the presence of dissolved organic carbon (DOC) in the accreted ice and therefore the lake water[6] implies that biological oxidation of organic matter may occur within the lake, consuming the dissolved oxygen. This suggests that the concentration of dissolved oxygen will decrease with distance from the hydrate supply as the water flows around the lake. Bottom waters may therefore be suboxic compared with the surface and sediments would probably be anoxic. When the water eventually returns to the surface of the lake in the north, the dissolved oxygen would be replenished from the gas hydrate supplied by the melting ice sheet.

Thus, subglacial melting and refreezing above Lake Vostok leaves the water enriched with modest quantities of solute, maintains a reservoir of gas in hydrate form from which dissolved oxygen (and other gases) may be transferred to the water, and supplies sediment that will accumulate at the floor of the lake[11].

Life in Lake Vostok and other subglacial lakes

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[35,36]. In its absence, microorganisms in subglacial lakes must use chemical

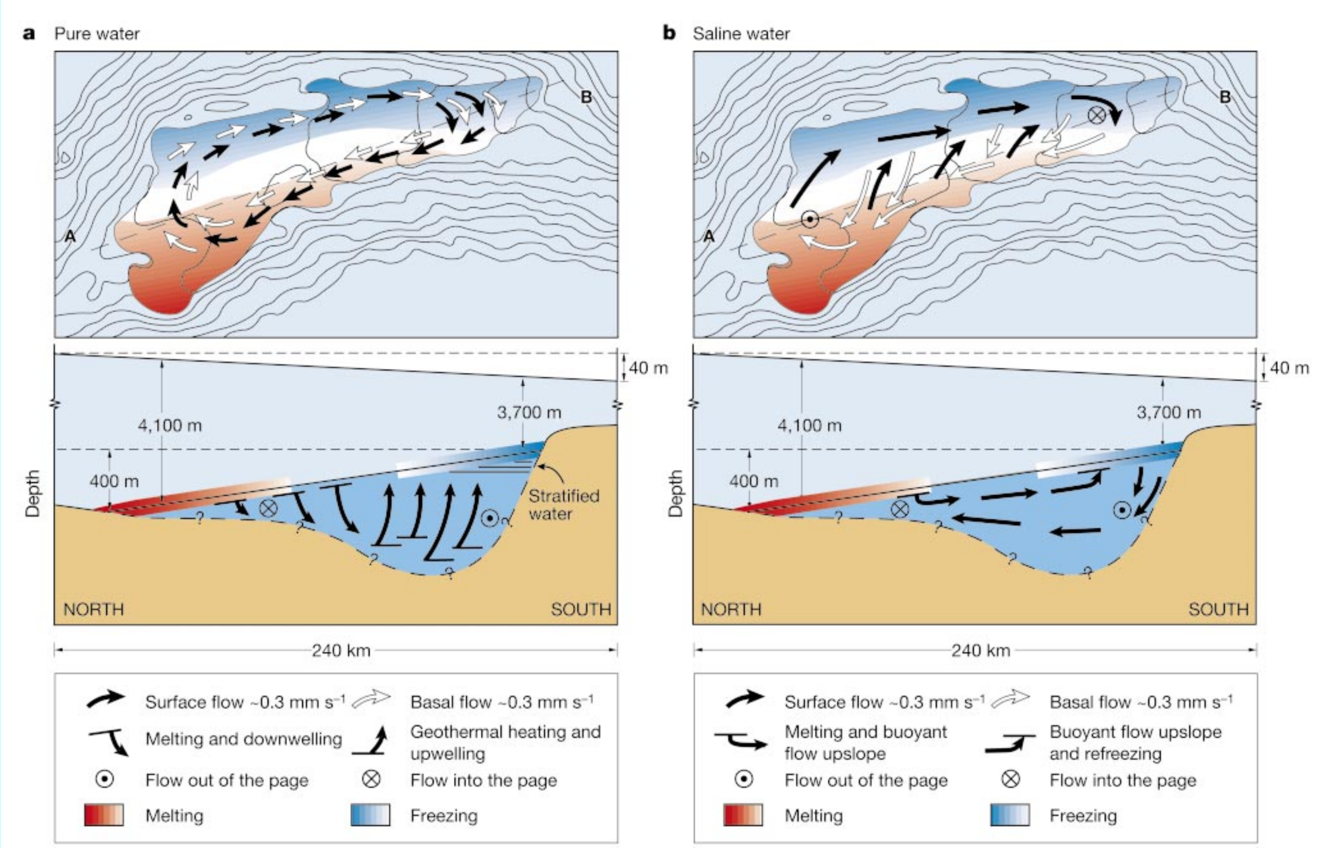

Figure 4 Water circulation patterns within Lake Vostok under fresh and saline conditions. **a**, Circulation calculated by numerical modelling, assuming that the water is pure[24–26]. The white arrows show the bottom water circulation and the black arrows denote the higher level circulation close to the ice base. 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 shading refers to predicted zones of subglacial freezing; red shading indicates subglacial melting. **b**, Circulation of Lake Vostok, thought to occur as a result of saline conditions[7] (that is, 1.2–0.4‰).

energy to power biological processes[37]. To this end, the dissolved oxygen supplied from gas hydrates is particularly important, as it will be utilized by microbes via oxidation of organic matter and sulphides as a source of energy.

The Vostok accreted ice offered the first opportunity for aquatic biologists to investigate material derived from a subglacial lake. Several studies have shown that the accreted ice contains bacteria (Fig. 6)[5,6] and low concentrations of inorganic and organic 'growth nutrients'[5]. Microbes released from melted ice cores of accretion ice are viable and have been shown to incorporate and respire ^{14}C-labelled organic substrates[5]. The accreted ice originates from Lake Vostok, so these microbes, if they are not contaminants, must have been present in the lake water at some point, and survived there before being incorporated into accreted ice[38].

Molecular profiling of accreted ice microbes using 16s rDNA techniques[6,38] 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[39], are transported towards the south of the lake after melting out at the north end, and consequently spend little time in the lake before refreezing. These biota may be unrepresentative of lake microbes that are more likely to originate from lake-floor sediments and rocks. In contrast to the accreted ice microbiota, if lake-floor biota exist, their period of isolation may be sufficient for significant evolutionary divergence to have occurred[40], particularly given the potential selection pressures that exist within the subglacial environment.

Knowledge of the physical and chemical environment of the lake

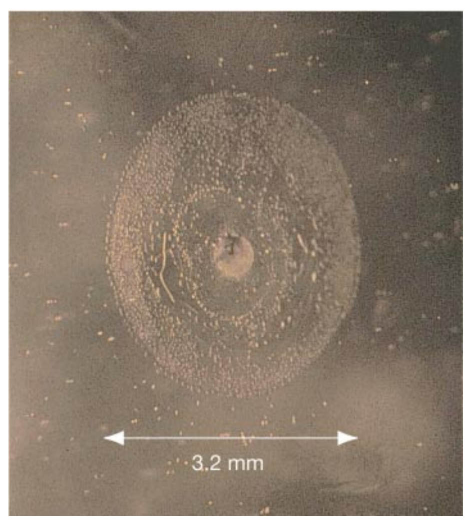

Figure 5 A microscope image of a gas hydrate (or clathrate) structure found in Lake Vostok's accreted ice 3,566 m below the ice-sheet surface, which is 174 m above the lake surface. Fifteen similar clathrate structures, between 3 and 5 mm in diameter, were identified within a 32-cm-long vertical section of the accreted ice. This structure is formed as the ice relaxes under normal atmospheric pressure, causing the hydrate to convert to gas and expand.

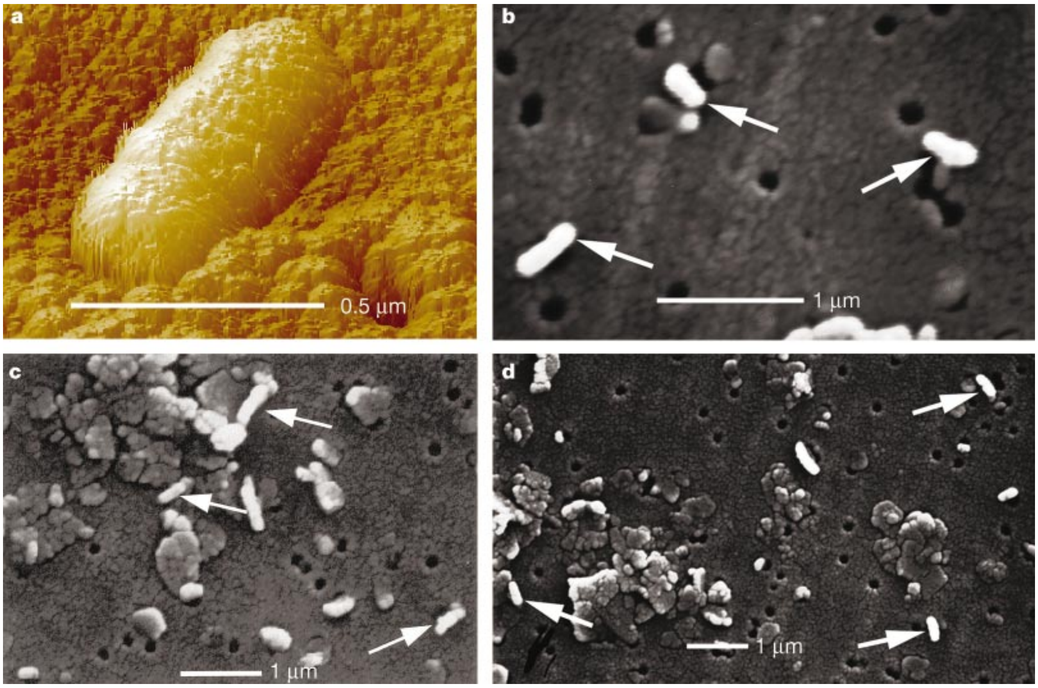

Figure 6 Images of bacteria frozen into Lake Vostok's accreted ice[6]. **a**, Atomic force microscope image of a single bacteria, illustrating how bacteria can be identified using this device. **b**–**d**, Scanning electron microscope images showing the occurrence of rod-shaped bacteria (noted by arrows) within the accreted ice. The ice was sampled from the Vostok ice core at a depth of 3,590 m, which is about 151 m above the lake surface and 60 m below the glacial accreted ice boundary.

provides an insight to community structure. For example, barotolerance is commonly encountered in microorganisms, so the pressure environment of Lake Vostok does not necessarily represent a significant obstacle. However, the lake's pressure environment is well below that associated with obligate barophiles[41], so this specialist group may not be present. The chemical composition of the lake water may provide adequate nutrients to support a heterotrophic microbial assemblage. DOC levels in accretion ice between 79 and 510 $\mu g\,l^{-1}$ (refs 5, 6) suggest that Lake Vostok itself may have a DOC level of up to 1,200 $\mu g\,l^{-1}$, which is adequate to support heterotrophic growth[6]. Inorganic nitrogen (nitrate plus nitrite) and total nitrogen levels ranging from 0.16 to 0.17 and 0.97 to 2.58 μM, respectively, have also been reported[5], which could support active biogeochemical cycling of essential nutrients within the lake.

The suite of biogeochemical reactions occurring in the water column and sediments are dependent on the supply of oxidants and reductants (such as oxygen, nitrate, organic carbon, sulphides and ammonium). These are ultimately provided only via melting of the glacial ice sheet and weathering of sediments, and their rates of supply will be critical for governing the rates of biological activity. It has been postulated that extreme oxidant depletion occurred on the 'snowball earth', where aquatic environments were secluded from solar radiation and the supply of oxidants by the persistence of a global ice sheet for millions of years[42]. This would eventually lead to the virtual annihilation of ecosystems on timescales of tens of millions of years. The possibility that Lake Vostok could have existed for a comparable timescale since the onset of Antarctic glaciation (~33 million years ago) has prompted comparison with the snowball earth[43]. However, the presence of microbes, dissolved oxygen and oxidants such as nitrate and sulphate, as well as the apparent utilization of nitrate in modern-day Lake Vostok[6], suggest that a state of chemical disequilibrium can persist for timescales of tens of millions of years, and that a range of biogeochemical processes based on chemical energy can likewise persist on these timescales.

The subglacial hydrology of the Antarctic ice sheet is not well known. However, the presence of subglacial lakes shows that large regions of the ice base are subject to melting[44]. It is possible that neighbouring subglacial lakes could have a hydrological connection, feeding water from one lake to another. By contrast, groups of lakes that are distant from each other (such as those in dome C compared with ridge B (ref. 1)) will be completely isolated. If the biota of subglacial lakes originate from the ice above, then it is probable that all lakes contain a similar biota that could be subject to adaptation dependent on the specific conditions in each lake. However, if there are extant biota from preglacial times in the basal sediments, there is potential for evolutionary processes to yield assemblages unique to groups of lakes.

Further research

Our understanding of subglacial lakes has improved through the identification of key physical and chemical processes in Lake Vostok. Subglacial melting occurs in the north and freezing occurs in the south, resulting in about 210 m of ice accreted to the ice-sheet base at Vostok station. The slope of the lake roof is much greater than the ice surface, causing spatial variation in the temperature and density of water near the ceiling of the lake, which drives water from north to south. Microbes found within the accreted ice have DNA profiles similar to those of contemporary microbes, suggesting that these originate from the relatively young (<1 Myr ago) glacial ice and were transported upslope to the freezing zone after melting out. These microbes may be unrepresentative of the biota deeper in the lake, or within the lake-floor sediments, which could be much older. The chemistry of the lake water has been inferred from analysis of the accreted ice. There is evidence that Lake Vostok's water contains dissolved oxygen, fed by a reservoir of oxygen in hydrate form from the ice above[33]. Dissolved oxygen allows the oxidation of sulphides and organic matter. As the lake biota must survive in an environment of permanent darkness, high pressure (350 atm) and low temperature (−3 °C), these reactions will, in the probable absence of hydrothermal activity[14], provide their only source of energy. Significant DOC and nitrogen have been found in the accreted ice, which is adequate to support heterotrophic growth, and a microbial assemblage within the lake itself. It is therefore anticipated that subglacial lakes house a variety of microorganisms potentially unique to subglacial Antarctica and, if they are isolated hydrologically, unique to each lake.

Future research on subglacial lakes will focus on three themes. The first concerns definition of Lake Vostok's physical environment and, to this end, airborne RES surveys have been performed to better define the lake physiography[45,46], and seismic experiments have taken place to measure Lake Vostok's depth and basal sediments[15]. RES surveys of lakes in ridge B and dome C are also planned for the next few years. The second theme involves the further analysis of accreted ice, which is taking place at a number of laboratories, and will result in a better understanding of the type and origins of microbes within the lake, and the water and gas chemistry of Lake Vostok. Comprehension of subglacial lake systems will also benefit from numerical modelling of water circulation and chemical processes, and this is under way at several institutes. The third theme relates to the exploration of subglacial lakes, and the sampling of water and sediments. Such activity appears to be some time away as there are technological hurdles and environmental concerns that need to be addressed. However, prototype machinery is being developed in several countries. Subglacial lake research is a new area of study and, to oversee its development and to ensure the environmental issues are upheld, the Scientific Committee on Antarctic Research has commissioned recommendations for future activities[47] and arranged for a group of specialists to develop science and implementation plans (scheduled to meet in November 2001). The investigation of subglacial lakes requires significant multinational cooperation and interdisciplinarity. The preliminary investigations above have helped to define the next generation of research objectives, and it is likely that several exciting bio-geochemical-physical systems will be documented during the next decade. □

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Acknowledgements

Many of the ideas developed in this review were formed during discussions at the International Conference on Antarctic Subglacial Lakes (1999), and two other international workshops: "Lake Vostok Study: Scientific Objectives and Technological Requirements" (1998); and "Lake Vostok: a curiosity or a focus for interdisciplinary study?" (1998). We thank the sponsors and organizers of these meetings (see http://salegos-scar.montana.edu).

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