

ICE ECOSYSTEMS AND BIODIVERSITY

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Summary

Since life as we know it needs liquid water to exist, a clear distinction between repository or storage sites for viable organisms and ice ecosystems (where organisms can not only survive but grow and reproduce) is given. Good knowledge exists about sea ice organisms and snow algae, but other habitats for living organisms, such as lake ice, glaciers and water in a supercooled state have been detected only recently.

Liquid water exists in many icy systems, however only as a thin film, as a highly concentrated salt solution or in a supercooled state. Although metabolism of microorganisms is lowered at zero or subzero temperatures, they do not inhibit the proliferation of microbial communities. Therefore, active and diverse assemblages of organisms develop in ice and snow covers of distinct geographical regions of the world, and even supercooled cloud droplets seem to be a suitable site for bacterial growth. This leads to the suggestion that life can be expected everywhere in the cold where liquid water can exist.

Ice and snow environments contribute to global biodiversity in at least two ways: first, by largely extending the area of habitats where active life exists formerly thought to be lifeless or just repositories of dormant cells; secondly by offering a site of interaction between organisms that are otherwise strictly separated into the terrestrial and aquatic sphere. We are still at the beginning of the exploration of snow and ice ecosystems, and we lack appropriate methodologies to measure activities and growth rates of organisms under *in situ* conditions and at the solid-liquid-gaseous boundaries of water. Extant knowledge on icy environments, however, let us suggest that, if life will be found on extraterrestrial bodies, there is a good chance that it will occur in association with ice.

1. Introduction

Life as we know it requires liquid water, carbon, energy and a supply of suitable inorganic compounds. Under high pressure and at high salinities, liquid water – and life – can exist far beyond 0°C. In sea ice, for instance, concentrated brines harbor a variety of organisms thriving at temperatures below -10°C. The possibilities and peculiarities of life in freshwater ice, however, have still to be explored.

In the past, most aquatic ecologists have concentrated on warm seasons and temperate habitats. This preference was supported by the observation that metabolic processes are generally reduced or completely inhibited at freezing temperatures. Life and ice have thus often been considered a paradox. Consequently, one can still find studies where the cold season is not considered as relevant for the understanding of ecological processes in lakes. Another reason for the virtual neglect of cold sites and seasons is a problem inherent to field research. High altitude and high latitude sites are generally not easily accessible and conducting research at low temperatures is not trivial. However, methods for *in situ* measurements of microbial growth and production have been improved to a degree that allows the study of very oligotrophic systems at low temperatures. Furthermore, the construction of observatories and field stations has increased accessibility to alpine, Arctic and Antarctic ecosystems, which has largely extended our knowledge of life in ice environments.

Where does this recent interest in ice ecosystems come from? After several years of focus on hot sites, driven by the expectation of commercial applications and by the interest in the early evolution of life we now have a better understanding of the conditions for, and the constraints of, life at high temperatures (see chapter Thermophily). Recent considerations about the tree of life, however, suggested that a “hot start” may not be the only alternative for the origin of life (see 3.6 *Implications for the origin of life*). A closer look to the other extreme, i.e. ice and snow, may provide an alternative perspective on the role of cold conditions in the evolution of life. In addition, ice ecosystems are of global ecological importance (for instance in radiative heat flux, for the release of greenhouse gases and cloud condensation nuclei by sea ice algae, for the control of sea level change, for the nutrition of krill, fish, birds and large mammals etc.). Build-up, duration and breakdown of ice ecosystems can largely influence adjacent pelagic and terrestrial ecosystems, and the seasonal wax and wane of ice ecosystems not only results from but is possibly also driving global changes. Importantly, ice ecosystems are of increasing interest as examples of adaptations of organisms to extreme conditions and as natural laboratories for the study of ecological interactions. They can be test sites for the applicability of general ecosystem theories, e.g. about the structure of food webs under the conditions of low numbers of species, reduced metabolism and other morphological and structural constraints (small scale, patchiness, seasonality, periodicity).

1.1 Definitions and dimensions

While cold aquatic ecosystems comprise those between 0° (or -1.8°C in the ocean) and 4°C, ice ecosystems by our definition contain ice or snow crystals as a characteristic component in contact with liquid water, or liquid water in a supercooled state. Cold ecosystems comprise the majority of all ecosystems in the world, while ice ecosystems are found at altitudes and latitudes where snow and ice can exist permanently or seasonally. This means that they can have huge dimensions: during winter time, snow covers very large areas (up to 52 million km²) of the world, while during summer the snow coverage can extend for ca. 3.9 million km². The area of permanent snow and ice cover is ca. 20 million km². Sea ice can have an extension of up to 15 million km², and supercooled water droplets exist in clouds which cover ca. 60% of the earth surface.

When studying the ecology of ice the following question must be addressed: Can all icy sites containing organisms be considered ecosystems? While we try to give a better definition in the chapter „Barriers versus connectivity“, we will use the term „ecosystem“ for only those sites where organisms do not only survive in a frozen state but do actively grow and replicate within the described habitat and under the conditions of zero or subzero temperatures. The finding of viable organisms in polar ice or permafrost is important to document the long-term survival of organisms at very low temperatures, but Price has recently discussed the possibility that Antarctic ice sheets are not only storage sites for microorganisms but provide a functional ecosystem that supports microbial metabolism. Ice in temperate glaciers can, under certain circumstances, be considered a conveyor for freeze-resistant organisms down to the ice bed where liquid water and other suitable conditions exist to support growth. Glacier beds have stable temperatures and when they reach the pressure melting point, water is present in the subglacial sediments or it may form larger water pockets. Basal and

surface melting provides the input of nutrients, dissolved gases and organic matter. Under some circumstances, for instance in alpine glaciers during summer, the inputs and fluxes can be rather high, so one could compare these habitats with benthic or pelagic conditions of aquatic ecosystems. Whether or not these conditions can be regarded as proxies for subglacial lakes in Antarctica depends on the basin morphology, the rate of water, gas and nutrient exchange across or beneath the ice along the glacier bed.

The description of a „deep cold biosphere“ of permafrost soils in the Siberian and Canadian Arctic as well as in Antarctica where several million years old but still cultivable bacteria have been found raises again the question of what we really describe, a repository or an active system. Although the organisms found grew only on very rich media they could be cultured at temperatures below 0°C. *In situ* growth has not been observed, thus these types of environments are regarded as potential and actual reservoirs of biogeochemical activity and a deposit of palaeo-life. Therefore, permafrost soils can be regarded as repositories of once viable cells, but for active growth these cells would need an interface where temperatures are close to 0°C and a liquid water film exists, for instance by geothermal heat. It is actually difficult to envisage a process which may provide input of nutrients, redox couples, dissolved gases etc. because – according to our knowledge – vertical or lateral inputs, as observed in temperate glaciers, do not exist in permafrost soils. Therefore, it is not clear how a redox gradient can be sustained in such environments (see also 3.5 *Can ice ecosystems exist without solar radiation?*). The sole presence of (viable) organisms in an environment does not warrant the term „ecosystem“. It must be shown that organisms can (at least for a certain period of time) metabolize and reproduce in this environment and interact with other organisms. The discovery of different life forms in fossil glacier ice supports the view that these are huge reservoirs of organisms, many of them possibly adapted to cold conditions and cultivable if the ice reservoir turns into a liquid and, thus, living system. So, by definition, ice ecosystems must sustain - at least for some time - the growth and proliferation of populations, communities and eventually also the existence of food webs, although at rates, with species diversities and in configurations which may not resemble known pelagic or terrestrial environments.

1.2 Physico-chemical constraints

Ice ecosystems do not exceed 0°C. At or below this temperature, liquid water can exist in a supercooled state, as a thin film on ice crystals, or as a saline solution. Beside brines in sea ice or saline lake ice which may cool down to -15°C without freezing, liquid fresh water can exist down to ca. -30°C under specific conditions. One example is the occurrence of supercooled cloud droplets in the absence of suitable crystallization grains. The second example is firn and non-temperate glaciers where ice crystals at subzero temperatures are surrounded by a water film in the nm (in thermodynamic equilibrium) to µm range. The measurement is rather complicated but water films of several µm thickness can exist in veins, little cavities and on non-temperate glacier ice. The water content of firn at 0°C can be up to 0.5% (v/v), suggesting a thickness of several µm. Lower snow temperatures do not necessarily mean that the water film becomes thinner, but -37°C seems to be the limit of both liquid water films on ice crystals and the existence of supercooled cloud droplets. The presence of dust particles,

ions and organisms can alter the consistence, composition and thickness of the water film on snow crystals. Generally, during each warming-freezing cycle (i.e. during each daily cycle in snow packs and glaciers) a reorganization of the liquid and solid phase occurs which will finally produce an ion-rich layer of water on eventually round-shaped, large ice crystals.

Liquid water films on snow crystals and cloud droplets are small, generally not larger than 10-100 μm . To produce larger volumes of liquid water in the presence of ice, a heat source is necessary. At or below 0°C air temperatures, ice can melt if enough solar radiation is absorbed by the ice itself or by dark particles of a certain dimension. The size of a black particle which allows melting of the surrounding ice or heating of the particle above the ambient temperature is ca. 1-10 μm under the conditions of high alpine or polar summer solar radiation. Good examples for the melt-down of particles into the ice are cryoconite holes on alpine glaciers and the ice ecosystem described by Priscu et al. in permanently frozen lakes of the Antarctic Dry Valleys. In the thick and permanent ice cover of Antarctic lakes, solar radiation during the Austral summer is strong enough to create large lenses of meltwater about 2 m beneath the ice surface where dark sediments accumulate. Therefore, a dark rock surface covered by ice not thicker than several meters, can be heated by solar radiation to produce a liquid water inclusion. This means that liquid water in ice covered ecosystems does not necessarily originate from the underlying liquid water body. If the ice cover grows thicker (and remains non-temperate), solar heating is reduced and the rock-ice interface will be permanently frozen to the bed rock. Colle Gnifetti, a cold glacier saddle at the Swiss Italian border at an altitude of 4500 m, seems to be an example of a palaeo-ice-ecosystem at around -12°C; actually buried under 120 m of ice, it still contains signals of former life at the bottom, for instance relatively high values of DOC and a clear excess of CO₂ shown to be of organic origin.

1.3 Effects on microorganisms

The effect of temperature on the growth rate of microorganisms is fairly well described by the Arrhenius equation, $k = A e^{-E_a/RT}$, where E_a is the activation energy (kJ mol^{-1}), R the gas constant (8.31 kJ mol^{-1}) and T the temperature in Kelvin. Thus the rate constant k depends strongly on the temperature if the activation energy is high. However, at temperatures near the upper or lower limits, such plots deviate from linearity, and below a minimum no growth occurs. A shift from a normal to a subnormal temperature results in a lag phase and a re-start of growth at a lower rate than the theoretical one. The terminology for microorganisms living under cold conditions is not completely convincing, but psychrophiles are those which do not grow at temperatures at 20°C and above, while psychrotrophs (more exactly: psychrotolerants) grow better at temperatures above 20°C. At low temperatures, the growth rate of psychrophiles and psychrotolerants remains higher than that of mesophiles, and there are observations that temperatures higher than those experienced in their natural environment (-2 to 4°C) led to faster growth rates in bacteria isolated from various Antarctic environments. At the same time, however, viability of the strains decreased. The enzymatic activity of living cells measured *in vivo* depends on protein synthesis and its regulation, enzyme maturation and stability, enzyme secretion (for exoenzymes) or substrate uptake (for endoenzymes). The thermal effects on all these processes include both proteins and

lipids. The fluidity of the membrane depends on the chemistry of the fatty acids. Unsaturation, cis double bond (instead of trans double) and chain shortening increase the fluidity of the membrane. The stability of proteins in aqueous solutions depends mainly on internal hydrophobic interactions and on polar and ionic interactions at the interior and at the surface. When the temperature is lowered, the polar/ionic interactions are favoured, while that of hydrophobic interactions decreases which may result in the unfolding or/and dissociation of protein subunits and, consequently, in the denaturation of the enzyme. Each of the three actions of an enzyme (recognition and binding of substrate; conformational stress and formation of product; release of the product) involves weak bonding interactions sensitive to temperature changes. Purified enzymes from cold-adapted bacteria are more active at low temperatures but may become deactivated at temperatures of 30-40°C. Cold-adaptation generally results in heat-sensitivity, e.g. blocking of protein synthesis or leakage of intracellular substances. There is no single obvious explanation for the molecular determinants of psychrophily, but the overall increased flexibility of proteins depends on a larger number of small changes throughout the protein structure. Enzymes produced by psychrophiles have a lower stability than their mesophilic counterpart. The improved plasticity is supposed to provide the appropriate flexibility of crucial regions involved in substrate binding and catalysis.

The formation of heat-shock-proteins (Hsps) in cells of animals, plants and microorganisms exposed to temperatures above their normal growth has been observed in a large number of organisms. Hsps mediate the correct folding of polypeptides (chaperones) or/and the removal of heat-denatured mature proteins. In psychrotolerant bacteria, Hsps may be induced already at temperatures around 30°C. While Hsps are induced also by other environmental factors such as heavy metals, ethanol and other surfactants, sudden exposure of bacteria to low temperatures can also induce the heat-shock response as well as a group of cold-shock proteins (Csps) which seem to function mainly at the transcriptional level and can also act as RNA chaperones for efficient translation (see chapter Cold-Shock Response in Microorganisms). In their natural habitat, cold-adapted bacteria generally encounter freezing temperatures and are subjected to freezing and thawing cycles. Therefore, an important trait of microorganisms is not only the potential to grow at low temperatures but also their resistance to freezing and thawing. Some bacterial species were found to be more resistant to freezing when pre-incubated at low temperatures, but others were not. Csps do not act as an antifreeze agent and antifreeze proteins found in eukaryotes have not been detected in bacteria. Ice nucleation, on the other hand, is well known in bacteria, caused by a protein with highly repetitive sequences of amino acids in the outer membrane that serves as a template for ice crystallization (see also 2.4 *Supercooled cloud droplets*). This process may provide protection from desiccation but also prevent intracellular ice formation. While Antarctic yeasts and algae may avoid freezing by the accumulation of sugars, bacteria tend to accumulate a number of amino acids. There is no evidence, however, of their role in the freeze tolerance of bacteria.

2. Known and unknown ice ecosystems

Recent interest in ice ecosystems has been stimulated by the recognition that global climate change will strongly influence these systems, and by the notion that ice

dynamics in the oceans and inland waters can largely influence the emission of greenhouse gases. The study of lake ice microbial communities, although their contribution to climate change is likely to be marginal, may foster the understanding of microbial communities in extreme environments, their functional role in the cycling of nutrients and organic matter, and their sensitivity to climate variations. With the exception of sea ice and cryoconites, known since the 19th century, ice ecosystems or ice communities are newcomers in the list of described ecosystems (Table 1) where we tried to use a classification based on the state of knowledge and the history of their exploration. Presumed ice ecosystems in need of confirmation are permafrost soils, ice wedges, bloc glaciers and Englacial lakes, e.g. Lake Vostok. Unknown Ice ecosystems may exist on the Jupiter moons Europa, Io and Ganymed, and on Mars.

Ice ecosystem	Observation
Snow fields, red or colored snow	Snow algae, 1819
Polar Region	Ice diatoms, 1841
Sea Ice - Antarctica	Ice coloration by algae, 1847
Sea Ice - Arctic	Ice flora (mainly diatoms) and fauna, 1852
Cryoconite holes on alpine glaciers	19 th century
Frozen Antarctic ponds	Algal community, 1979
Ice cover of Alpine Lakes	Microbial community, 1995
Ice cover of Antarctic Lakes	Microbial community, 1998
Basal layer of glaciers	Microbial activity, 1999
Supercooled cloud droplets	Microbial activity, 2001

Table 1. Ice ecosystems which have been described – at least partially – in historical order.

Thriving sea ice microbial and multicellular communities have been known since the early observations of Nansen about 100 years ago. Also cryoconite holes on the surface of alpine glaciers are known since long time, while Alpine and Antarctic lake ice microbial communities (LIMCOs) have been described only recently. In the 60s, bubbles filled with algae were described in surface ice of frozen Antarctic ponds but have received little mention since that time. The role of snow and freshwater ice as habitat for algae have been summarized by Hoham and Duval, but these studies considered primarily the late „warm“ phase of snowpacks soaked with meltwater, mostly under the specific conditions of sites rich in organic matter and inorganic nutrients. The phylogenetic composition of bacteria in freshly fallen snow were described first in 1996, and Sattler et al. studied growth rates of bacteria in snow collected within a snow cloud and in supercooled cloud droplets from a high altitude station in the central Alps. Carpenter et al. recently described microbes similar to the genus *Deinococcus* in surface snow at the South Pole where the annual temperature averages -55°C . With the exception of Sharp et al. who suggested that bacteria may contribute to weathering processes in glacial meltwater, the liquid water at the base of glaciers has not been described as an ice ecosystem yet, but there are strong indications

of the existence of a former ice ecosystem in a cold glacier (i.e. englacial temperature well below freezing point) in the western Alps (Wagenbach et al., unpublished). Cold ground waters in contact with ice crystals may also form an ice ecosystem. In the accretion zone of the ice cover on Lake Vostok, organisms have been recently described, though confirmation of an ice ecosystem deep within the Antarctic ice sheet is still lacking, Price has recently suggested that a metabolically active microbial assemblage may exist in the veins between ice crystals.

2.1 Ice covers over liquid water

Ice covers on water can occur in many different forms, from hard, transparent („black“) ice under different layers of slush and white ice on top of alpine lakes to the thick, solid ice sheet on Antarctic lakes, or as platelet, pancake and solid ice in the sea. It plays a major role in determining the environmental properties of the pelagic world underneath by reducing or completely inhibiting heat and gas exchange and wind generated mixing of the water column. Consequently, the liquid water remains quiescent and is dominated by molecular processes, i.e. turbulent transport becomes less important. For these reasons, ice does not only influence the transfer of energy and matter between the atmosphere and the water, but within the pelagic system itself. Light transmission is severely limited especially by snow layers (by up to 99.9%).

Trapping of atmospheric gases in ice covered lakes can result in severe oxygen deficiency and strong oversaturation of CO₂ and other gases. Nutrient input from the atmosphere is also inhibited by the ice cover, and sedimentation fluxes can become very low. Thus, the formation of an ice cover is a major factor limiting the overall productivity in the pelagic zone and – if sufficiently thick and persisting – triggers a switch in a lake’s physico-chemical dynamics turning it into a heterotrophic system for long periods of time. In addition to their role as physical barriers and limiting factors for water column processes, ice covers add a new structural element where active and diverse microbial communities develop.

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Biographical Sketches

Roland Psenner is Professor of Limnology at the University of Innsbruck. He has worked on problems of eutrophication, especially on the phosphorus cycling in lakes and sediments, and, since 1990, on global change effects on alpine lakes, with special interest in acidification, dust deposition, UV radiation, and climate warming. He is leading a high altitude research station in the Alps where he focuses on the biogeochemistry and microbial ecology of aquatic environments including lakes, streams, snow fields, and glaciers. In addition, he has developed methods for the analyses of bacterial consortia in natural environments, including molecular biology, image analysis, and flow cytometry techniques.

Marisol Felip is an ecology teacher at the University of Barcelona. She was, together with Jordi Catalan, the first to detect lake ice microbial communities in Pyrenean lakes. During a postdoctoral stay at the University of Innsbruck, financed by a Marie Curie grant from the European Commission, she studied common patterns of lake ice physics and biology in alpine environments. She has published several

influential papers on lake ice microbial communities, phytoplankton dynamics, and UV effects on microbial assemblages.

John C. Priscu received his PhD in aquatic ecology from the University of California at Davis and has conducted research on the microbial ecology and biogeochemistry of desert, alpine, and polar aquatic systems for more than 20 years. He has been leading field expeditions into the Transantarctic Mountains of Antarctica since 1984 where his work has focused on the permanently ice-covered lakes in the region as well as life associated with sea ice in nearby McMurdo Sound. His team was the first to describe the microbial dynamics in the permanent ice covers of lakes in the McMurdo Dry Valleys and was among the first to define potential conditions in Lake Vostok, a large lake located under 4 km of ice in East Antarctica. He currently convenes an international group of specialists outlining the science and logistics plan to penetrate the East Antarctic Ice Sheet and sample Lake Vostok.

Dietmar Wagenbach is a senior research scientist and heading the paleoglaciological working group at the Institute of Environmental Physics Umweltphysik in Heidelberg, which he established in 1980. Since that time, he has pioneered ice-core studies in high Alpine glaciers and year-round aerosol-related observations in coastal Antarctica. In addition to the Alpine investigations, he has been involved in polar ice core studies and research on air/snow transfer processes, with special emphasis on stable isotopes, radio nuclides, and ice chemistry.

Anton Wille wrote his Master thesis on the chemistry, physics, and microbiology of the winter cover of a high mountain lake. His dissertation, due to be finished in 2003, deals with the structure and carbon flux through microbial assemblages of Gossenköllesee, an alpine lake in Tyrol, Austria. He participated in several research projects of the European Union and the Austrian Science Foundation on Mountain Lake Research (MOLAR) and Lake Ice Microbial communities (LIMCO).

Birgit Sattler is Research Assistant at the University of Innsbruck where she coordinates the working group "Microbiology in Snow and Ice." Together with Marisol Felip, Jordi Catalan, and Roland Psenner she described for the first time microbial communities in the winter cover of alpine lakes. She found also active bacteria living in supercooled cloud droplets and she did research in Antarctica to study the ice cover of the Dry Valley Lakes.