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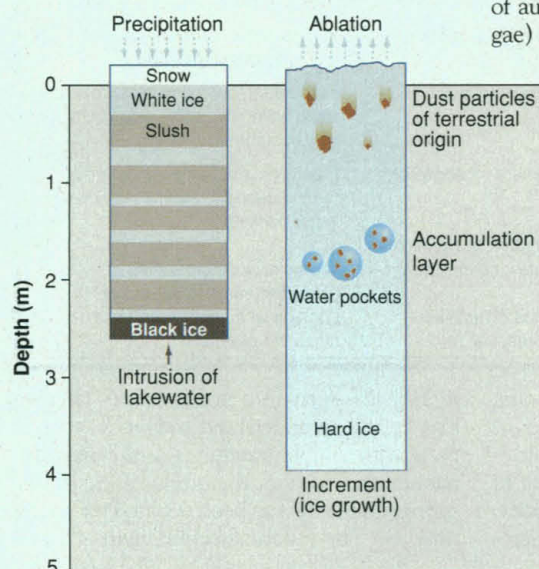
## MICROBIAL COMMUNITIES

# Life at the Freezing Point

Roland Psenner and Birgit Sattler

What are the chances that one could cultivate bacteria and algae in a deep freezer? The suggestion is not so outrageous, as Priscu and co-workers show on page 2095 of this issue (1), with their discovery of living organisms in surroundings that even in summer rarely exceed a chilling  $-20^{\circ}\text{C}$ . They describe a thriving microbial assemblage in the thick, hard, and permanent ice layer of lakes in the Antarctic McMurdo Dry Valleys. What at the first glance appears to be a contradiction in terms (being frozen and leading an active life at the same time) turns out to be an exciting example of the adaptation of microorganisms to environmental extremes.

How can there be life in the ice? A closer look at icy ecosystems demonstrates that ice comes in many forms, which are not always what we think of as ice. Sea ice, for instance, has been known for a long time to harbor algae and crustaceans because concentrated brine solutions remain liquid at temperatures well below zero. In contrast, ice layers on freshwater lakes have usually been seen as nothing but physical barriers to light transmission, heat flux, wind-induced turbulence, and gas and particle exchange. The sandwich-like structure of the winter cover on high mountain lakes in the Alps was described in great detail in the early 1950s, but it took a long time to recognize that the slush layers (see figure) host a rich and very productive assemblage of autotrophic and heterotrophic organisms, which we and our co-workers have termed LIMCO (lake ice microbial community) (2). Within the winter cover at  $0^{\circ}\text{C}$ , bacterial production was up to an order of magnitude higher than in the pelagic zone of the lake at a "warm"  $3^{\circ}$  to  $4^{\circ}\text{C}$ . It was Felip, Camarero, and Catalan (3) from the University of Barcelona in Spain who showed in a 2-year study that the composition of au-



**Cold communities.** Winter cover of high mountain lakes in the Alps and the Pyrenees (Left) and permanent ice cover of Antarctic lakes in the Dry Valleys (Right). The alpine lake cover consists of a sandwich-like structure of slush (a mixture of ice and snow crystals with lake water, rainwater, and meltwater) and white ice, covered by snow and separated from lake water by a thin layer of black ice, lasting for about 8 to 10 months. The Antarctic lakes in the Dry Valleys are covered by a permanent layer of hard ice containing pockets of liquid water during summer. These water pockets appear around clusters of terrestrial dust. They form a maximum at 2-m depth, where sinking speed and ice growth are in balance. Both habitats host only microorganisms—with some rare exceptions—and also the active period (the Austral summer in Antarctica and late winter, spring, and early summer in high alpine lakes) is reduced to about 6 to 8 months per year. In alpine lakes, slush has a constant temperature of  $0^{\circ}\text{C}$ ; in the water pockets of Antarctic lake ice, temperatures will not exceed  $0^{\circ}\text{C}$ .

trophic and heterotrophic microbial communities in lake ice clearly differed from that in the lake water, a fact that was also confirmed by Priscu *et al.* (1). Researchers from Innsbruck University have demonstrated that the genetic pattern—based on group-specific probes for ribosomal RNA—of communities of ice bacteria differed from that of lake water bacteria and also from that

of bacteria found in freshly fallen snow (4).

A comparison of freshwater ice systems (see figure and table) suggests that the example described by Priscu *et al.* represents the most extreme community one can imagine, both regarding physico-chemical factors and organisms involved; namely, an assemblage of autotrophic cyanobacteria (blue-green algae) and heterotrophic bacteria, encapsulated in the permanent ice cover of lakes. The term "oasis" used by the authors (1) refers to the fact that pockets of liquid water form around dust particles and microorganisms blown in from a cold desert, allowing active growth and reproduction of predominantly prokaryotic organisms during the Austral summer. Some ecological properties are similar in high alpine and Dry Valleys lake ice habitats; for example, both systems seem to be closer to the benthic than the pelagic world. However, in the case of the Antarctic lake ice, the sediment derives from the terrestrial catchment, whereas in the alpine lakes the "sediment" consists of ice and snow crystals, surrounded by interstitial water that is a mixture of lake water, rainwater, and snow meltwater. Although Antarctic McMurdo Dry Valleys lakes are permanently ice covered, their microbial communities are active for only about 5 months, which is comparable to the active period of the microbial communities in the transient ice cover of alpine lakes. A major difference concerns the physical structure and the origin of organisms, which in the case of the alpine lakes do not arrive solely from the atmosphere but also from lake water and littoral sediments.

It has been held for some years that bacterial growth and respiratory rates in the ocean are unmeasurably low at  $0^{\circ}\text{C}$  (5), but Priscu *et al.*'s and our own findings clearly indicate that in some habitats bacteria may be quite active even at freezing point. Recently, active bacteria and their metabolic products have been found in supercool (around  $-5^{\circ}\text{C}$ ) cloud droplets collected at altitudes above 3000 m in the Alps (6). Thus, our knowledge about the number

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|                     | WINTER COVER OF ALPINE LAKES                                                                                                                                                                                                                                                                                      | ANTARCTIC LAKE ICE                                                                                                                                                                                                                                                                                          |
|---------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Where               | High mountain lakes (Alps, Pyrenees); annual precipitation: 1000 to >2000 mm                                                                                                                                                                                                                                      | Lakes in the Dry Valley, Antarctica; annual precipitation: <200 mm                                                                                                                                                                                                                                          |
| Duration            | 8–10 months: from November/December through June/July/August                                                                                                                                                                                                                                                      | Permanent; liquid water only in summer (5 months)                                                                                                                                                                                                                                                           |
| Thickness           | 1.5–3 m                                                                                                                                                                                                                                                                                                           | 3–6 m                                                                                                                                                                                                                                                                                                       |
| Formation           | Lake water penetrates through the ice cover, which is pushed downward by snow, forming slush and white ice layers; rain and melting water trickles down                                                                                                                                                           | Freeze-out of lake water: balance of ice formation from beneath and ablation to the atmosphere                                                                                                                                                                                                              |
| Liquid water        | 10–30%, consisting of lake water, snowmelt water and rain                                                                                                                                                                                                                                                         | Up to 40% during Austral summer, consisting of ice meltwater                                                                                                                                                                                                                                                |
| Temperature         | Constantly 0°C, from formation to melting                                                                                                                                                                                                                                                                         | 0°C in summer; <0°C during winter                                                                                                                                                                                                                                                                           |
| Radiation           | Strong light gradient, from nearly 100 to <0.1%; ultraviolet-B radiation ~50% higher than at sea level                                                                                                                                                                                                            | Strong light gradient; constant radiation in summer, low ultraviolet-B except during ozone hole events                                                                                                                                                                                                      |
| Origin of organisms | Lake water, airborne (snow and rain), littoral sediment                                                                                                                                                                                                                                                           | In-blown from surrounding soils, and long-range transport                                                                                                                                                                                                                                                   |
| Main feature        | Intermittent (~6 months) but constantly at 0°<br><br>Sandwich-like structure: "sediment" of snow-ice particles<br><br>Microbial world, LIMCO (prokaryotes and eukaryotes) origination from different sources; no metazoa<br><br>High bacterial production compared with lake water but reduced predation pressure | Permanent, but most times frozen: liquid water and microbial activity only in summer<br><br>Patchy distribution of sediment of terrestrial origin; activity restricted water pockets<br><br>Microbial world consisting of cyanobacteria and heterotrophic bacteria with some eukaryotic algae; no predation |

and diversity of freshwater systems hosting active organisms at or below 0°C may grow greater in the near future (7).

What is the attraction of studying life in the cold? It may be the beauty of simplicity, which—especially in the case of the Antarctic

lake ice—promises that sooner or later we may be able to understand and model ecosystems with simple structures and frozen dynamics. In addition, the origin of life in hot springs and vents has been debated for a long time (8). The vision of a cold origin of life—

supported for instance by prebiotic researchers such as Lazcano from the University of Mexico (9)—may lay the foundation for a model of past conditions on Mars and of present-day conditions on Europa.

There are still many unsolved questions regarding the buildup and the fate of microbial assemblages in the ice cover of freshwater lakes and the role they may play as inocula to the pelagic system during thawing or after migration through the ice column. Also, their role in nutrient cycling and element fluxes is still an open question, as well as their responses to climate warming or increased ultraviolet-B radiation. Whatever the answers to these questions may be, Priscu and co-workers have shown that the icy life is more diverse and more exciting than could have been imagined.

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#### SIGNAL TRANSDUCTION

## G Proteins and Small GTPases: Distant Relatives Keep in Touch

Alan Hall

Cells use all sorts of tricks to make the signal transduction pathways that tailor the cells' physiology to the changing environment. One feature used repeatedly is the protein switch, flicked on and off by the nucleotide guanosine 5'-triphosphate (GTP). When GTP is bound, two families of proteins—heterotrimeric guanine nucleotide-binding proteins (G proteins) and their distant relatives, the small molecular weight guanosine triphosphatases (GTPases)—are

"on" and can activate the element immediately downstream to send a signal further down the line. But each of these proteins is also a GTPase, containing within the molecule itself the ability to hydrolyze GTP to guanosine diphosphate (GDP) and so turn off the switch.

Small GTPases control fundamental cell properties—polarity, shape, and the commitment to divide or differentiate. The larger G proteins usually regulate more specialized signals—the production of second messengers like cyclic AMP and calcium. Two members of the G protein family, G<sub>12</sub> and G<sub>13</sub>, are unusual in that they promote cell cycle progression and reorganization of the actin

cytoskeleton, changes that are typically associated with the small GTPases. Now an impressive piece of detective work, described on pages 2109 and 2112 of this issue, unites the two distantly related families through these unique G proteins. Kozasa *et al.* and Hart *et al.* show that G<sub>13</sub> directly activates a guanine nucleotide exchange factor, which in turn promotes GDP dissociation from the small GTPase Rho, allowing it to be activated again by GTP (1, 2). At least in this instance, a G protein triggers action in its distant cousin, the small GTPase Rho.

Small, monomeric GTPases of the Rho-Rac family control the assembly of filamentous actin structures in response to signals from outside the cell (3). Rho, the founder member of this family, interacts with effector (downstream) proteins to cause the assembly of contractile actin-myosin filaments. Although the most clearly visible of these filaments are the stress fibers seen in fibroblasts adhering to a surface, actin-myosin structures actually play a fundamental role in all cell types. Consequently, Rho

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