Microbial Habitability of Icy Worlds

As our exploration of space begins its sixth decade, we have new tools and techniques to probe questions of planetary habitability

John C. Priscu and Kevin P. Hand

For most of Earth's history, life was microscopic and, even today, microorganisms dominate the planet. Hence, we believe that, if life exists beyond Earth, it likely started as microorganisms and may remain at this stage. Much of contemporary astrobiological research focuses on the metabolic potential of microorganisms and their ability to inhabit extreme environments.

The search for life beyond Earth prioritizes the search for liquid water because water on Earth is closely associated with life. However, our understanding of where liquid water can be found is changing. Moons in the outer solar system, including Europa, Ganymede, and Enceladus that orbit either Jupiter or Saturn, although covered with ice, carry subsurface oceans containing many times the volume of liquid water on Earth and may provide the greatest volume of habitable space in our solar system. On many of these worlds, water is maintained as a liquid through radiogenic decay, tidal energy dissipation, and the mere fact that ice floats and serves as a good insulator. These oceans are there today and have likely persisted for much of the history of the solar system, providing key environments in which to search for extant life beyond Earth—life from a second, independent origin. The recent discoveries of metabolically active microorganisms in subglacial environments on Earth provide useful analogues in that search.

Of these worlds, Europa holds perhaps the greatest potential as a modern habitat for microbial life, and its relatively thin ice shell of about 5–15 km eases the technical challenges of trying to detect such life. Along with a liquid ocean, Europa also likely harbors a rocky seafloor that can supply energy and elements needed to drive metabolism (Fig. 1). With the goal of investigating the habitability of Europa, the National Aeronautical and Space Agency (NASA) has recently identified a mission to Europa as second only to a Mars sample-return mission. Here, we focus on the potential for microbial habitability on Europa, drawing on what we know about microbial life in Earth's sub-ice environments.

Summary

- Although covered with ice, several moons of the outer solar system carry subsurface oceans containing many times the volume of liquid water on Earth and may provide the greatest volume of habitable space in our solar system.
- Europa holds perhaps the greatest potential as a modern habitat for microbial life.
- We know of three key requirements for habitability—liquid water, a suite of biologically essential elements, and a source of energy.
- Functional subglacial ecosystems in Antarctica, in concert with what we know about the geochemistry of Europa, provide a compelling case that its sub-ice ocean could support microbial life.
- Discovering life on Europa or elsewhere in the outer solar system would have an enormous impact on science and society.

Assessing the Habitability of Ocean Worlds

We know of three key requirements for habitability—liquid water, a suite of biologically essential elements, and a source of energy (Fig. 2). The subsurface liquid water

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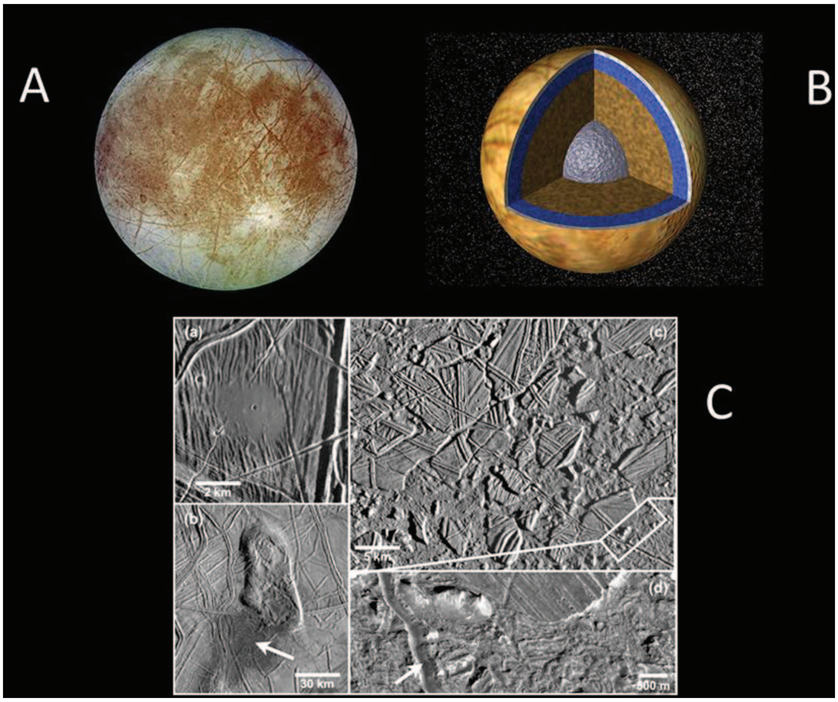
FIGURE 1



Views of Europa. (A) Enhanced composite image revealing the water-ice shell of Europa. The chemistry of the brown-red regions is largely unknown but oxidized sulfur species are known to be a key constituent. These areas may represent rocky material derived from the interior, implanted by impact, or from a combination of interior and exterior sources. The bright feature containing a central dark spot in the lower third of the image is a young impact crater ~50 km in diameter. (B) Cutaway view showing the internal structure of Europa. The interior characteristics are inferred from gravity field and magnetic field measurements by NASA's Galileo spacecraft. Europa's radius is 1,565 km, slightly smaller than our Moon. Europa has a metallic (iron, nickel) core (shown in gray). The core is surrounded by a silicate shell (shown in brown). The silicate layer of Europa is in turn surrounded by a shell of water in ice or liquid form (shown in blue and white). The surface layer of Europa is shown as brown to indicate that it may differ from the underlying layers. (C) Detail of surface units on Europa that may indicate transfer of material between the ocean and ice shell. Such areas would be prime targets for future lander missions designed to detect life. (a) the "Puddle" resulted from surface water that was once liquid and refroze. The crater in the middle of the frozen puddle is caused by a meteorite impact. The puddle might have formed as water melted from the heat of the impact or when water bubbled up from the subsurface ocean; (b) Castalia Macula consists of unusually dark and reddish material, most of which is confined to a broad topographic depression 350 m deep located between two large uplifted domes 900 and 750 m high, to the north and south, respectively. The preservation of topography at the bottom of Castalia Macula indicates that dark material initially filled the depression to a certain depth but was subsequently removed via drainage, resulting in a dark stain up to the original equipotential surface; (c) Conamara Chaos is a region of chaotic ice where rafts of ice have moved around and rotated; (d) high resolution of boxed inset in (c). Image credit: NASA/JPL.

reservoir of Europa has likely persisted for much of the moon's nearly 4.5 billion years. By virtue of its contact with a rocky floor, the 100-km deep ocean could be geochemically suitable for life. Though the ocean lies beneath several to many kilometers of ice, the global nature of the ocean implies that much of this world could be inhabited if the chemical conditions are appropriate.

In addition to those three key requirements, several other conditions should be considered, including water activity, temperature, radiation, pH, salinity, and temporal stability. In terms of energy, the environment should be in a state of energetic disequilibrium to power life either through chemical or photon-catalyzed reactions. The availability of free energy is a critical determinant of whether metabolism, repair, growth, and reproduction can occur. The mantra "follow the energy" has become a theme that constrains NASA's "follow the water" approach, which has driven the search for life beyond the Earth.

Europa as a Microbial Habitat

The ocean of Europa is not particularly extreme in terms of temperature and pressure. The temperature of the water may be suppressed to about −20°C by the dissolution of salts, but ultimately the temperature hovers near the freezing point. The pressures, despite the ocean being about 100 km deep, are not that great because the gravitational acceleration is less than one-seventh that of our more massive Earth. The 110 MPa pressure in the 11-km-deep Marinas Trench on Earth, which is known to support an active microbial assemblage, is comparable to the seafloor of a 100-km ice shell plus ocean on Europa.

Europa is composed of chondritic material, that is, space rocks rich in biologically essential elements. The surface chemistry is dominated by sulfur and water, making the cycling of sulfur on Europa important for its potential habitability. Spectra from the Galileo Near Infrared Mapping Spectrometer (NIMS) indicate regions where hydrated sulfate constitutes up to 90% of the numerical molecular surface abundance. Moreover, radiolysis (chemistry driven by radiation processing) likely drives a sulfur cycle, forming surface reservoirs of hydrated sulfate, sulfur dioxide, elemental and polymerized sulfur, and possibly traces of hydrogen sulfide. Some sulfur on Europa comes from volcanoes on the nearby satellite of Jupiter, Io. As such, volcanism on Io is influencing the habitability of Europa.

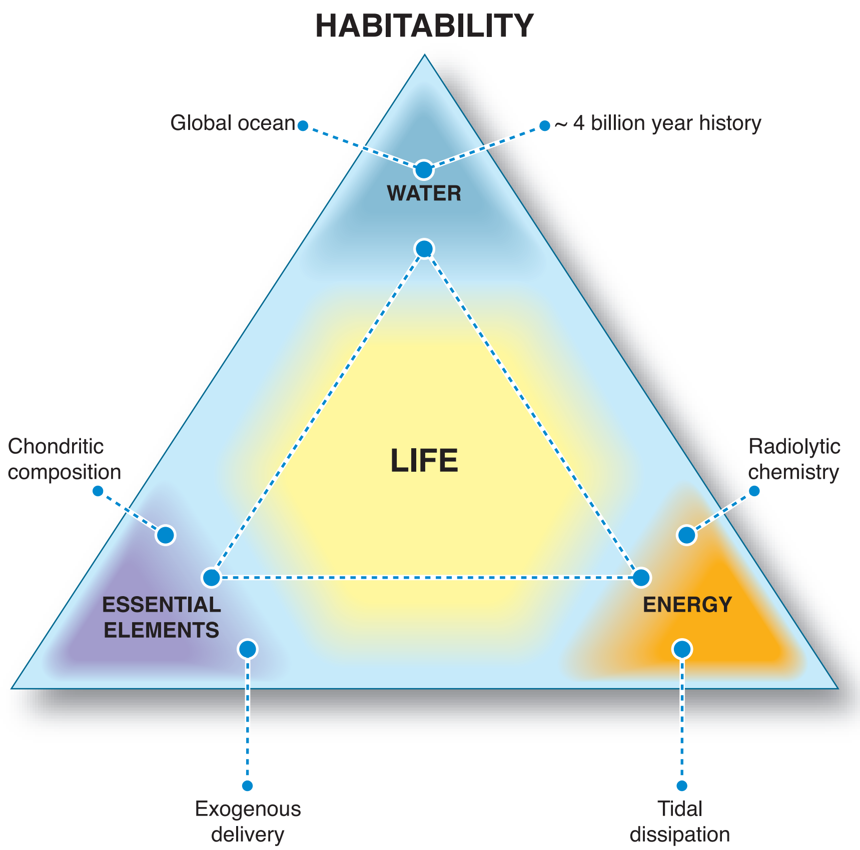
From a bioenergetics standpoint, the coupling of surface oxidants with hydrothermal seafloor reductants could be key for Europa's habitability (Fig. 3). Whether Europa is geologically active today and cycles surface oxidants like sulfate into the ocean remains an open question. Based on the paucity of impact craters, Europa's ice shell is considered geologically young, making it reasonable to expect exchanges between the ice shell and ocean.

When Europa formed, quenched hydrothermal fluids rich in hydrogen, methane, and organic compounds likely coupled with dissolved sulfate, yielding energy like that found in sulfate-reducing microbial ecosystems in anoxic environments on Earth:

$$SO_4^{2-} + 2H^+ + 4H_2(aq) \rightarrow H_2S(aq) + 4H_2O(l)$$

From estimates based on known microbes, these reactions would be capable of producing about 10^{16} kg of total biomass throughout the Europan ocean over its history. This total is small compared to what happens on Earth, where photosynthesis dominates and produces about 10^{14} kg of biomass per year. A sulfate and carbon flux from the ice shell would serve to maintain a cycle of sulfate reduction on a hydrothermally active Europa.

FIGURE 2

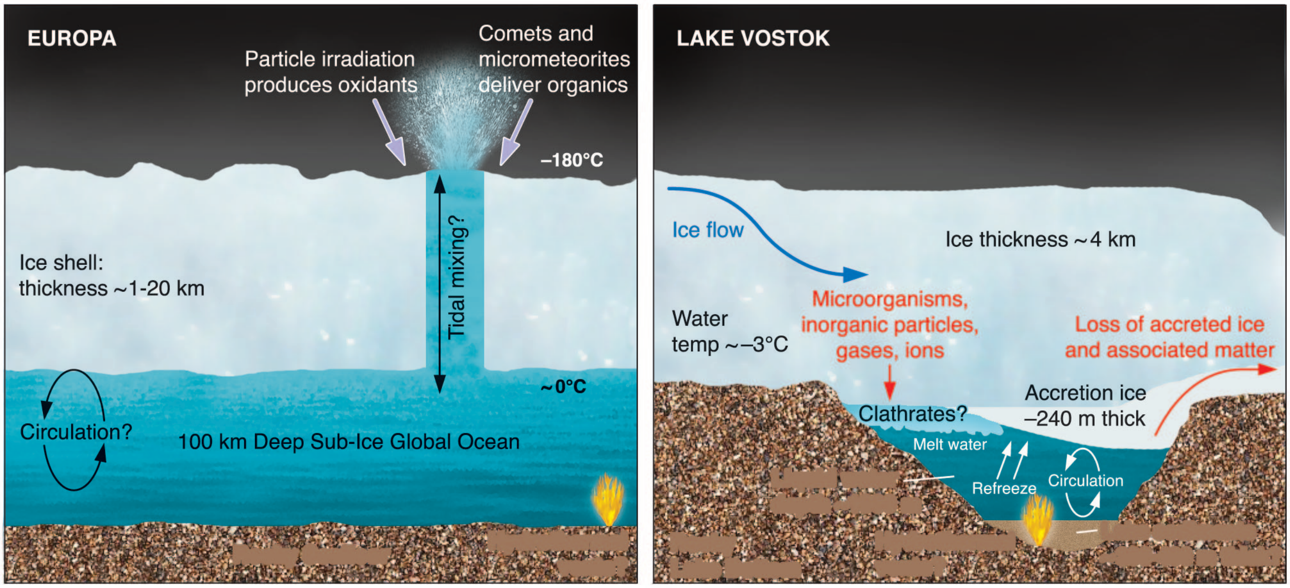


The habitability of Europa. At present, our understanding of the conditions necessary for life can be distilled down to three broad requirements: (1) a sustained liquid water environment, (2) a suite of elements critical for building life (e.g., C, H, N, O, P, S), and (3) a source of energy that can be utilized by life. Here we show how these "pillars of habitability" intersect with our current understanding of the conditions on, and within, Europa.

Polar Sub-Ice Habitats

The 200 or more Antarctic subglacial lakes, estimated to collectively contain about 7% of all lake water on Earth, provide examples of how life adapted to cold, dark environments comparable to Europa. Many of these lakes lie beneath more than 3 km of ice and have had no direct contact with the atmosphere for more than 15 million years. The largest is Lake Vostok, which is about 1,000 m deep and holds about 5,400 km^3 of water, making it the third deepest lake on our planet and the sixth largest in terms of volume (Fig. 3). Water remains liquid in the lake owing to background geothermal heating, the insulating properties of the overlying ice sheet, and pressure-induced lowering of the freezing point. Data from Vostok accretion ice, lake water frozen to the underside of the Antarctic ice sheet above the lake, reveal an active microbial consortium within the surface waters of the lakes with cell abundance ranging from 150 to 460 cell ml^{-1}. Sequence data from DNA encoding for small-subunit ribosomal RNA (16S rRNA) reveal phylotypes related to the α-, β-, and γ-Proteobacteria, Firmicutes, Bacteroidetes, and Actinobacteria. If those microbes are typical of the lake microbiota, the microorganisms within Lake Vostok are not evolutionarily distinct. The phylotypes from Vostok are related to aerobic

FIGURE 3



Schematic showing the relationships among ice, water, and rock for Europa and Subglacial Lake Vostok. Microbial metabolism in both sub-ice systems can be driven by coupling surface oxidants with reductants associated with the rocky seafloor.

and anaerobic bacteria with metabolisms dedicated to iron and sulfur respiration or oxidation. This similarity implies that these elements play a key role in the bioenergetics of microorganisms in Lake Vostok, whose likely key chemoautotrophic metabolic pathways include:

$$4FeS_2 + 15O_2 + 14H_2O \leftrightarrow 16H^+ + 8SO_4^{2-} + 4Fe(OH)_3$$

Oxic

Anoxic

$$FeS_2 + 14Fe^{3+} + 8H_2O \leftrightarrow 15Fe^{2+} + 2SO_4^{2-} + 16H^+$$

These substrates can derive from physical glacial processes and do not require geothermal input. The pathways could supply organic carbon and support heterotrophic metabolisms that use O_2, NO_3^-, SO_4^{2-}, S_0, or Fe^{2+} as electron acceptors. The chemoautotrophic reactions fix carbon dioxide using iron and sulfur as both electron donors and electron acceptors. The pathways also indicate that these transformations may occur across an aerobic/anaerobic boundary. Organic carbon produced by chemoautotrophic metabolism could then fuel heterotrophic metabolism within the lake.

If similar microbial ecosystems exist throughout Antarctica's sub-ice environment, this unexplored habitat may contain a huge unexplored pool of bacterial carbon. Further, these subglacial bacteria might play an important role in mineral weathering beneath the Antarctic ice sheet. Direct sampling of these subglacial lakes will enable us to develop unequivocal conclusions about the phylogenetic and metabolic diversity in these ecosystems.

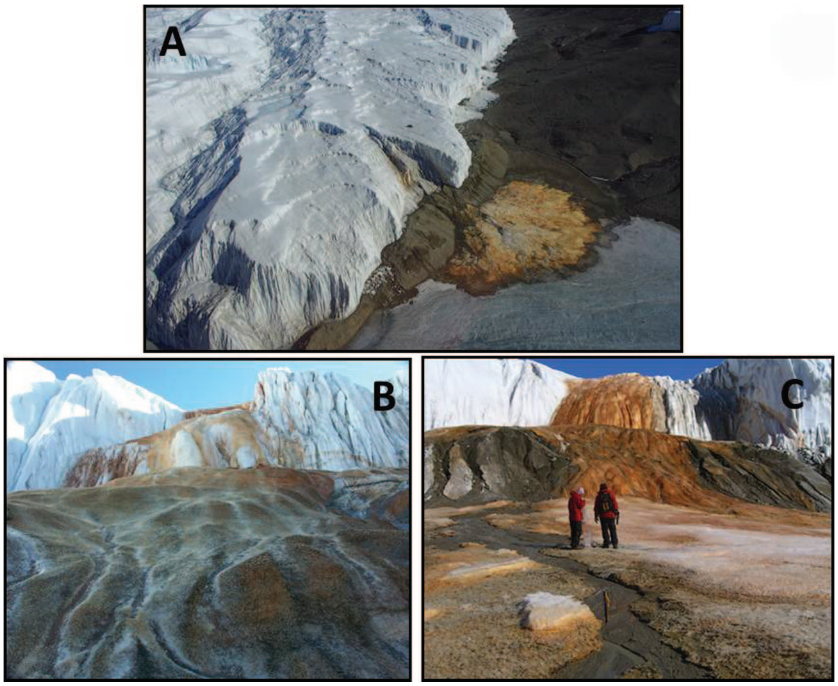
Blood Falls, Subglacial Outflow

Another example of a subglacial ecosystem involving sulfur and iron intermediates that drive microbial metabolism is Blood Falls, Antarctica, whose subglacial outflow originates beneath the Taylor Glacier in the McMurdo Dry Valleys (Fig. 4). A warming event during the Pliocene Epoch 3–5 million years ago enabled marine waters to enter the Taylor Valley. As the Taylor Glacier advanced during the late Pliocene or Pleistocene, those marine waters were sealed beneath the glacier, where cryoconcentration and chemical and biological weathering processes produced a suboxic subglacial brine three times saltier than seawater and rich in iron and sulfur. This environment has not been in direct contact with the atmosphere since it was sealed several million years ago.

A majority (74%) of clones and isolates from Blood Falls share high 16S rRNA gene sequence homology with phylotypes from marine systems. Bacterial 16S rRNA gene clone libraries are dominated by a phylotype with 99% sequence identity with *Thiomicrospira arctica*, a psychrophilic marine autotrophic sulfur oxidizer. The remainder of the library contains phylotypes related to the classes β-proteobacteria, δ-proteobacteria, and γ-proteobacteria and the division Bacteroidetes. The library includes clones whose closest cultured relatives metabolize iron and sulfur compounds.

These findings are consistent with the high iron and sulfate concentrations detected in Blood Falls, which are likely due to the interactions of the subglacial brine with the underlying iron-rich bedrock. That the majority of clones in the Blood Falls library are related to the obligate chemlithoautotroph *Thiomicrospira arctica* reveals the capacity for subglacial chemosynthetic primary production. *Thiomicrospira* may provide new organic carbon in the absence of sunlight and at permanently low temperatures.

FIGURE 4



Blood Falls, an iron-rich subglacial discharge from the Taylor Glacier, McMurdo Dry Valleys, Antarctica. Microorganisms in this subglacial system couple iron respiration to a catalytic sulfur cycle that creates no net sulfide. The result yields a subglacial ferrous-rich brine that becomes oxidized as it reacts with oxygen in the atmosphere as it is discharged.

Thus, the bacterial consortia below the Taylor Glacier grow chemoautotrophically or chemoorganotrophically by harvesting energy from bedrock minerals, or the assemblage may grow heterotrophically on ancient marine organics by respiring Fe(III) or SO_4^{2-}. Isotopic measurements of sulfate, water, carbonate, and ferrous iron in concert with functional gene analyses of adenosine 5′-phosphosulfate reductase imply that a microbial consortium facilitates a catalytic sulfur cycle resulting from a limited photosynthetic carbon supply, producing a system rich in electron acceptors relative to electron donors despite being anaerobic. This situation produces an environment that is reduced, but not sulfidic.

The discovery of functional microbial ecosystems in Lake Vostok and Blood Falls, once thought to be inhospitable, together with what we know about the geochemistry of Europa, provide a compelling case that Europa's sub-ice ocean might support microbial life. Thus, the phylogenetic and metabolic diversity here on Earth can guide our search for organisms on Europa and other ice-covered moons of the outer solar system.

Perhaps a Second Origin of Life

According to the rock record, Earth was inhabited within a billion years of being formed, and those early microorganisms were as complex and competent in their cellular and molecular functions as those of today. Although we know little of how fast life evolves, the temporal window of the Europan ocean offers ample time for complex cellular structure and biogeochemistry to develop. Without understanding how our own tree of life developed, we should not read too much into the chemistry of Europa and life's origins there. Nevertheless, such questions are precisely why Europa is such a prime astrobiological target—it poses a testing ground for a second, independent origin of life in our solar system. Informally, scientific wisdom suggests that:

Liquid water + Biologically essential elements + Energy + Catalytic surfaces + Time → Life

Even if microorganisms are absent from a Europa that fully satisfies the left-hand side of that expression, we could gain insight into the conditions that led to life on Earth. Similarly, if we discover life on Europa, we could then begin a rigorous cross-comparison to investigate the conditions leading to the emergence of life on both worlds. Such a discovery would have an enormous impact on science and society and would provide us with another world through which to advance our understanding of how microorganisms interact with their environment and how life evolves.

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