The Vigor, Futility, and Application of Microbial Element Cycles in Alkaline Soda Lakes

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A beaker containing a microbial mat from an alkaline soda lake. Who resides within and to what future applications might they give rise?

Alkaline soda lakes are known as some of nature's most biologically productive ecosystems. **Vigorous production (photosynthetic conversion of inorganic carbon into biomass) is countered by incremental biomass degradation, which fuels and feeds a diverse microbial community. Learn here about key adaptations that help microbes survive and thrive in the extreme conditions of alkaline soda lakes. Dive into the interconnected microbial element cycles of alkaline soda lakes and discover how the geochemistry of these environments presents microbes with unique challenges and opportunities. Throughout this article, explore how the microbial inhabitants of alkaline soda lakes have been harnessed in biotechnological applications, including the production of protein-rich food, detergent enzymes, and the purification of biogas.**

INTRODUCTION

Despite their extreme chemistry, high salt concentrations, and high pH, alkaline soda ($Na–HCO_3–CO_3$) lakes are very active biological ecosystems. Alkaline soda lakes are home to many. On a microscopic scale, bacteria, archaea, viruses, and microbial eukaryotes thrive. Small brine shrimp and brine flies are common. In some lakes, dense populations of cyanobacteria feed large flocks of flamingos. Although plants are scarce, photosynthesis is in full force.

Vigorous oxygenic photosynthesis by cyanobacteria and microalgae lead to some of the world's highest rates of carbon fixation and growth (Melack and Kilham 1974). Yet, primary production fuels an active biological food chain. Thus, high gross productivity does not necessarily translate into high net productivity. Microbial element cycling in alkaline soda lakes is to some extent futile, a fascinating network of diverse metabolisms producing little permanent change.

The microbiology of alkaline soda lakes has been an intense and successful area of study. Alkaline soda lake microbes are implicated in the biogeochemical cycling of carbon, nitrogen, sulfur, iron, phosphorous, and other elements. Almost all microbial metabolisms known at neutral pH have been described in alkaline soda lakes, although their geochemistry appears to favour some metabolisms while hindering others. Alkaline soda lakes present unique challenges and opportunities to life. Understanding how microbes contend with high pH, carbonate alkalinity, and sodium concentrations drives interest from both fundamental and applied perspectives. This work explores biomass production and breakdown in alkaline soda lakes and features intriguing uses of their microbial inhabitants in society (packaged in 'BOXES' throughout this article).

KEY MICROBIAL ADAPTATIONS

High carbonate and sodium concentrations present unique challenges to life—challenges that have been overcome by alkaline soda lake microbes. Microbes adapted to high pH (9+) are dubbed 'alkaliphiles'. Those specifically accustomed to life in sodium carbonate brines are 'natronophiles' or 'soda-loving' (Sorokin 2017). To date, natronophile research has dealt almost exclusively with bacteria and archaea—thus they are the spotlight of this article.

Numerous microbes collected from alkaline soda lakes have been isolated, grown, characterised, and identified in the laboratory. These are collectively known as 'culture-dependent' approaches. DNA sequencing of entire alkaline soda lake microbial communities has revealed even more species. This is an example of a 'culture-independent' approach (Antony et al. 2013; Sorokin et al. 2014; Vavourakis et al. 2016; Zorz et al. 2019). Unsurprisingly, alkaline soda lake microbes differ from their freshwater and marine relatives.

Compared with pH-neutral microbes, natronophiles contend with different chemiosmotic gradients. All living cells have an ion gradient across their membrane that they use to drive molecule transport, cell mobility, and regeneration of the energy carrier adenosine triphosphate (ATP). At neutral pH, protons (H^+) are integral to this gradient with cells having a higher internal pH than their surroundings. Natronophiles have the same internal pH as microbes living at neutral pH, but this pH is *lower* than their surroundings. For natronophiles, the ion gradient instead consists mainly of sodium, which has a high external and low internal concentration (Sorokin 2017). From an evolutionary perspective, this requires changes or additional modules to many ion-transport enzymes. Adaptions to high sodium concentrations are also present in marine microbes. In both ecosystems, high ion concentrations require additional work for cells to balance osmotic forces across the cell membrane.

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Because of inorganic carbon speciation at high pH, natronophiles must also contend with extremely low CO_2 concentrations. Yet the primary productivity of alkaline soda lakes relies on photosynthesis—a process that requires CO_2. To combat this, alkaline soda lake cyanobacteria use a 'carbon-concentrating mechanism' (CCM). Bicarbonate is transported across the cell membrane and, once inside, is split by the enzyme carbonic anhydrase to yield CO_2. Carbon dioxide is concentrated in the vicinity of rubisco—the enzyme that creates the first organic carbon molecule. This CCM also occurs in marine cyanobacteria. At pH 8, seawater contains a greater relative proportion of CO_2 than alkaline soda lakes, but bicarbonate is still by far the most abundant form of inorganic carbon. Thus, both for marine and alkaline soda lake cyanobacteria, the CCM is critical in converting the large pool of available inorganic carbon into CO_2.

MICROBIAL ELEMENT CYCLING

Let us start our journey with an overview that explains how microbes behave in alkaline soda lakes—which elements do they use and for what? The microbial element cycles comprise a series of reactions that build and break down biomass. To build biomass, 'autotrophs' (organisms that produce their own food from sunlight, water, CO_2, or other chemicals) and 'heterotrophs' (organisms that eat other plants, animals, or microbes for energy and nutrients) use inorganic and organic carbon, respectively. To power cell growth and maintenance, microbes use sunlight and/or chemical energy. Chemical energy is acquired when microbes couple the oxidation of one molecule (the electron donor) to the reduction of another (the electron acceptor). A huge array of organic and inorganic electron donors are used by microbes. Most electron acceptors are inorganic.

Cyanobacteria and microalgae ('phototrophs'—organisms that use energy from sunlight to synthesize organic compounds for nutrition) feed and power a diverse community of microbes in alkaline soda lakes. Sunlight, water, and inorganic carbon are converted via photosynthesis to biomass and oxygen. While biomass sinks, oxygen bubbles rise. As we travel down the water column, oxygen availability wanes as a result of outgassing and the degradation of sinking biomass by aerobic respiration.

During aerobic respiration, oxygen is used as the electron acceptor. Once oxygen is depleted, microbes gain energy via anaerobic respiration by reducing other oxidised compounds like nitrate, ferric iron, and sulfate. When a single organic substrate serves both as the electron donor and acceptor, this is known as fermentation. Fermentation generates partially oxidised by-products like acetate and formate. Microbial activity creates chemical gradients in stagnant water, sediments, and microbial aggregates (like microbial mats and biofilms). Microbes occupy different locations along such gradients depending on their lifestyle. For example, oxygen may be toxic to microbe A but essential to microbe B. Microbes exhibit exceptional metabolic flexibility and can switch substrates based on availability.

Microbes use energy gained from oxidation and reduction to transport and assimilate elements from the environment into macromolecules including carbohydrates, proteins, lipids, and nucleic acid (DNA and RNA). These biomolecules contain carbon, nitrogen, phosphorus, sulfur, and a variety of transition metals like iron. In aquatic environments, the growth of primary producers is typically limited by the availability of nitrogen, phosphorous, or iron.

Microbially catalysed oxidation and reduction, as well as the uptake and release of inorganic and organic molecules, creates biologically mediated elemental cycles. Many related natronophilic microbes harbouring similar metabolisms have been found in alkaline soda lakes separated by large geographical distances (Antony et al. 2013; Sorokin 2017; Zorz et al. 2019). The microbes highlighted in this article are common inhabitants of alkaline soda lakes.

Carbon Cycling

For phototrophs, like cyanobacteria and microalgae, light availability is paramount. Depending on lake conditions (particularly the depth of light penetration), phototrophs may form biofilms on the surface, be suspended in the water column, or reside at the sediment–water interface (FIG. 1A). Phototrophs uptake bicarbonate and create a locally oxic zone. In alkaline soda lakes, cyanobacteria (FIG. 2) are responsible for most productivity. *Arthospira*, *Spirulina* (BOX 1), Nostocales, *Phormidium*, and *Nodosilinea* are common, as are the microalgae *Dunaliella*, which can bloom when the salinity (g/L) increases (FIG. 1B) (Sorokin et al. 2014; Zorz et al. 2019). To fulfil their energy needs in the dark, oxygenic phototrophs catabolise internal energy storage compounds via aerobic respiration if oxygen is available or via fermentation in the absence of oxygen.
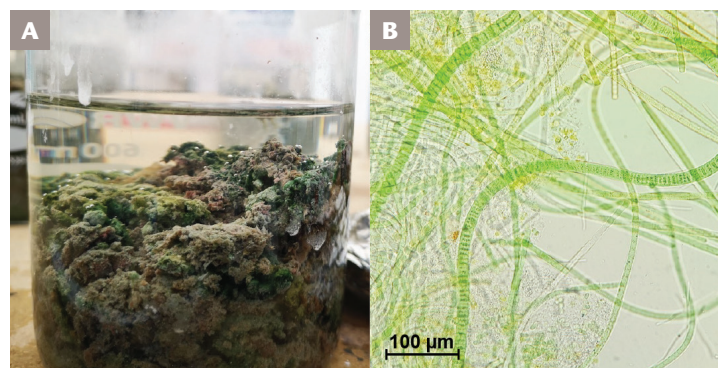

FIGURE 1 Microbial communities of alkaline soda lakes. (A) Phototrophic microbial mat collected from alkaline soda lakes on the Cariboo Plateau, Canada. PHOTO COURTESY OF YIHUA LIU. (B) Micrograph of oxygenic phototrophs, primarily filamentous cyanobacteria, from Goodenough Lake, Canada. PHOTO: MARIANNE HAINES.

BOX 1   **SPIRULINA**

For many, alkaline soda lakes are a food source. In African countries, *Spirulina* are collected from natural lakes and dried into cakes called dihé (Habib et al. 2008). *Spirulina* are nutritious and protein-rich (60%–70% of dry weight) (Habib et al. 2008). Their large-scale commercial production as a food and nutritional supplement began in the 1970s. Today, many companies produce *Spirulina* outdoors in warm climates in open hectare-scale raceway ponds (Habib et al. 2008; Lu et al. 2011). The chemistry of these ponds is important to their commercial success. At production facilities, *Spirulina* are typically grown around pH 9 with an alkalinity of 150 mEq, conferred by sodium bicarbonate (Habib et al. 2008). These conditions resemble those of alkaline soda lakes and help exclude predators (which might eat the cyanobacteria) and competitors (which might replace the cyanobacteria). *Spirulina* are harvested, dewatered, and sold in many forms—intact cells are sold fresh, dried to powder/cake, or compacted into pills.
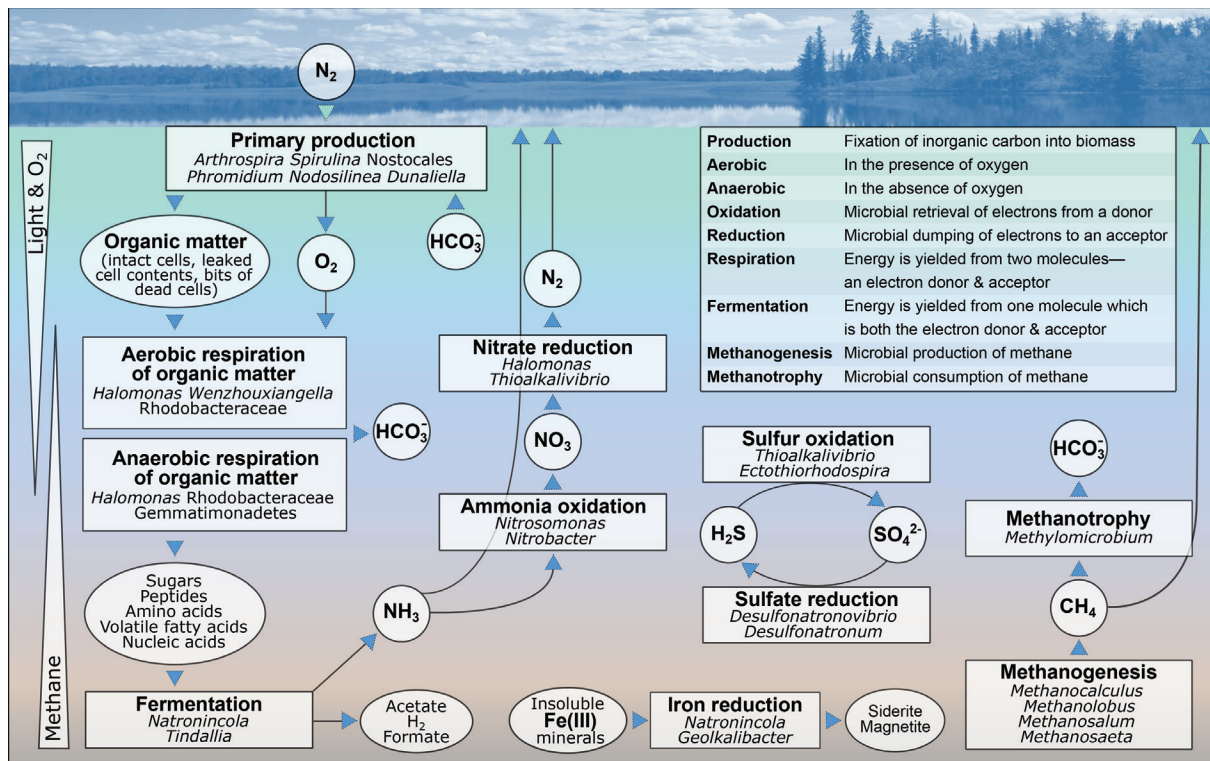
FIGURE 2 Microbial element cycling in alkaline soda lakes. A simplified overview of microbial element cycling in alkaline soda lakes with example taxa. Chemical gradients can change at the millimetre scale, influenced by, for example, water column mixing and the action of microbial metabolism. Microbial element cycling is extremely interconnected. Depending on availability, a single microbe may (or may not) use sunlight, switch between electron donors and acceptors, or partake in fermentation when required.

In oxygen-depleted zones, a different flavour of photosynthesis occurs; 'anoxygenic' phototrophs use light and can fix CO_2 but use electron donors like sulfide and hydrogen (as H_2) for CO_2 reduction instead of water, and thus, do not produce oxygen. For example, 'purple sulfur bacteria' (visible to the naked eye as a purple layer in microbial mats) of the order Chromatiales gain electrons from sulfide oxidation for carbon fixation (Sorokin et al. 2014; Vavourakis et al. 2016). Other common phototrophic microbes include the family Rhodobacteraceae and members of the class Gemmatimonadetes (FIG. 2)—whose capacity to use light energy has only recently been discovered (Sorokin et al. 2015; Vavourakis et al. 2016; Zorz et al. 2019).

The death of phototrophs releases diverse lipids, sugars, proteins, and nucleic acids like DNA. These are taken up by heterotrophs and used both as energy sources and supplies of carbon, nitrogen, sulfur, etc. To break down large biomolecules into smaller moieties that can be imported into their cells, heterotrophs secrete various enzymes. These enzymes include proteases (digest proteins); lipases (deconstruct lipids); amylases, cellulases, and pectinases (depolymerise polysaccharides); and more. Because enzymes are secreted or exposed on the cell surface, they must be stable and active at high pH and in $Na-HCO_3-CO_3$ brines.

Laundry detergent used to be just soap. Today, a diversity of added enzymes enhance their cleaning performance (Contesini et al. 2018). Enzymes target different types of grime. Common additives include proteases (e.g., for blood), lipases (e.g., for animal fat), amylases (e.g., for starchy baby food), mannases (e.g., for gelling agents in mayonnaise), pectinases (e.g., for fruit jam), and cellulases (Bora et al. 2013). Cellulases degrade the cellulose in, for example, pilling cotton, releasing dirt and keeping clothing smooth. Laundry enzymes contend with three challenges: they must (1) function in the presence of other detergent ingredients like surfactants and chelating agents; (2) withstand the temperature of a wash cycle (hot or cold); and (3) be stable at high pH (laundry detergent pH ranges from 9 to 12) (Ibrahim et al. 2015). Proteases prospected from *Bacillus* species from Egyptian alkaline soda lakes were the first enzymes added to laundry detergents in the 1950s (Contesini et al. 2018). Given the high pH of laundry detergent, alkaline soda lakes are prime ecosystems to search for novel laundry enzymes. By most accounts, the laundry detergent market is the largest consumer of high-pH enzymes, especially proteases (Contesini et al. 2018).

Such enzymes are of industrial value (FIG. 3) because they perform specific reactions under 'extreme' conditions. High-pH enzymes are sold commercially for use in laundry detergents (BOX 2), the pulp and paper industry (BOX 3), and the leather making process (BOX 4). Enzymes can enhance the sustainability of these applications when they replace or reduce the use of aggressive chemicals (Wang et al. 2017; Khambhaty 2020). Additionally, the development of effective enzymatic cold water laundry detergents saves energy otherwise required for heating water (Contesini et al. 2018).

In their natural context, enzymes help release energy and nutrients bound up in biomolecules, profiting heterotrophs. Aerobic heterotrophs pair biomolecule degradation with oxygen reduction. This liberates chemical energy and organic material, which is used as cellular building blocks. In alkaline soda lakes, *Halomonas* and *Wenzhouxiangella* (Fig. 2) (Sorokin et al. 2014; Vavourakis et al. 2016; Zorz et al. 2019) live near cyanobacteria and microalgae, exploiting both the released organic carbon and the produced oxygen.

In the absence of oxygen, heterotrophs use other electron acceptors, discussed in subsequent sections of this text, including nitrate, ferric iron, and sulfate. These are used in a thermodynamically determined order. Fermentation of organic carbon also yields energy. For example, *Natronincola* and *Tindallia* species ferment remnants of proteins (Fig. 2) (Sorokin 2017).

Fermentation products, like acetate and H_2, are converted to methane by microbes in the sediment or within anoxic pockets of suspended particles (Nolla-Ardèvol et al. 2012; Porsch et al. 2015; Sorokin 2017; Fazi et al. 2021). This process is known as methanogenesis and is exploited industrially to produce biogas from waste by anaerobic digestion (Box 5). For microbes, there is more than one way to produce methane. In alkaline soda lakes, archaea like *Methanolobus* and *Methanosalsum* produce methane from methylated compounds like methanol (Nolla-Ardèvol et al. 2012; Sorokin et al. 2014; Sorokin 2017). *Methanocalculus* can generate methane by reducing CO_2 with H_2 or formate as electron donors (Sorokin 2017; Fazi et al. 2021). Alternatively, *Methanosaeta* ferments acetate to methane and CO_2 (Fig. 2) (Sorokin 2017; Fazi et al. 2021). When oxygen is available, methanotrophic bacteria like *Methylomicrobium* oxidise methane back to CO_2 (Fig. 2) (Antony et al. 2013; Sorokin et al. 2014). In Lake Sonachi in the East African Rift Valley, pelagic methanogenesis causes surface waters to accumulate high concentrations of biogenic methane (Fazi et al. 2021). It follows that lakes may emit what was once fixed organic carbon to the atmosphere as methane.

Nitrogen Cycling

For every five carbon atoms assimilated, microbes need about one nitrogen atom. Nitrogen, as ammonia, nitrate, nitrite, or urea, is often a limiting nutrient in aqueous environments. Alkaline soda lakes contain variable, but mostly low, nitrogen concentrations. In alkaline soda lakes on the Cariboo Plateau, ammonia and nitrate are undetectable (Zorz et al. 2019). Melack et al. (1982) also reported low concentrations of inorganic nitrogen in alkaline soda lakes in the East African Rift Valley. Ammonia is detectable in lakes in the Russian Altai region, but nitrate remains
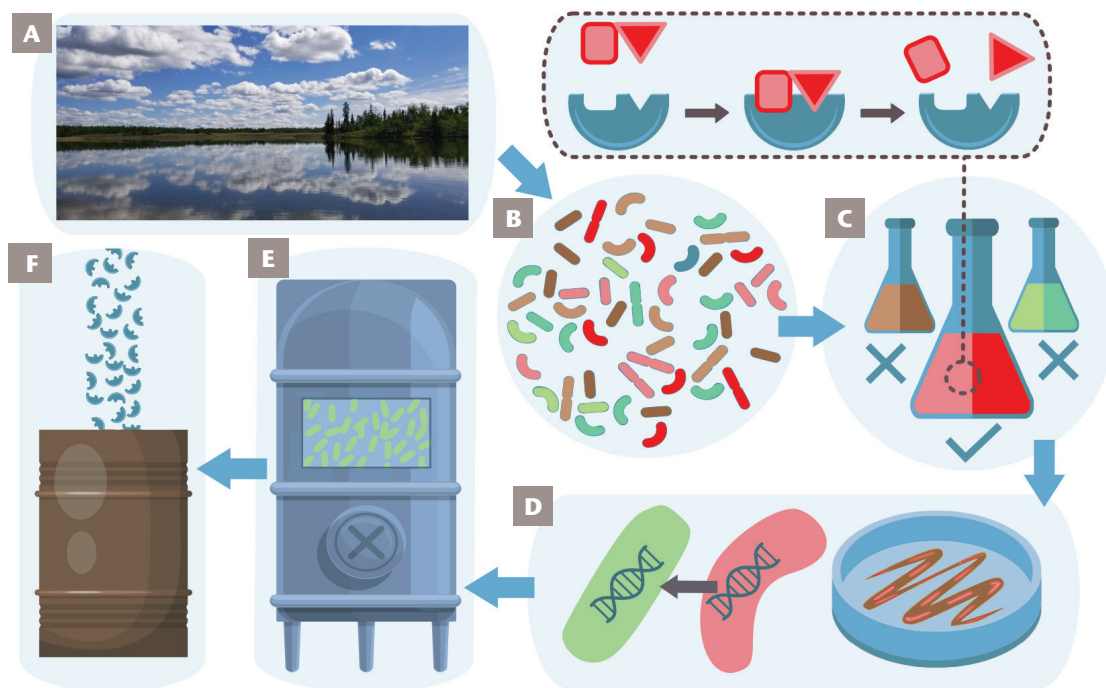
FIGURE 3 Path from enzyme discovery to production. **(A)** To discover a new enzyme that converts a target class of molecules, researchers 'bioprospect' an environment with chemistry as the target process. **(B)** The material collected contains a microbial community. **(C)** Typically, the community is exposed to the target substrate(s) in the lab. Microbes that naturally produce the desired enzyme are enriched. **(D)** Once microbes have been found that grow well on these molecules, the target enzymes may be separated from the cells for further tests. If successful, the gene responsible for encoding the novel high-performing enzyme may be transferred into different, fast-growing microbes. **(E)** Enzymes can be produced at scale by growing microbes in large bioreactors or 'fermenters'. **(F)** Finally, enzymes are sold as granules or in liquid form.

low (Samylina et al. 2019). Apparently, India's Lonar Lake is an outlier boasting a comparatively high (2.4 mg·L^{-1}) concentration of nitrate (Antony et al. 2013).

The presence and expression of genes involved in N$_2$ fixation in many natronophiles, as well as field and laboratory measurements of acetylene reduction rates (a proxy measurement for N$_2$ fixation), suggest some microbes can collect their own nitrogen from the atmosphere (Sorokin et al. 2014; Samylina et al. 2019; Zorz et al. 2019). Nitrogen-fixers in alkaline soda lakes include cyanobacteria, anoxygenic phototrophs, sulfate reducers, and fermentative Firmicutes (Sorokin et al. 2014; Zorz et al. 2019). Salinity (g·L^{-1}) appears to control which populations of N$_2$-fixers are active (Samylina et al. 2019). Nitrogen fixation is a bioenergetically costly process only used when other forms of nitrogen limit growth.

When heterotrophs break down nitrogen-rich organic matter, like amino acids, excess nitrogen is released to the environment as ammonia. This leads to a challenge at high pH as ammonium exists in part as toxic ammonia (NH$_3$) (Sorokin and Kuenen 2005a; Nolla-Ardèvol et al. 2012). Uncharged ammonia diffuses through cell membranes and, as a base, raises the cell's internal pH. Higher internal pH, an increase in maintenance energy, and enzyme inhibition are proposed mechanisms for ammonia toxicity. At high pH, nitrogen can be lost from lakes via ammonia volatilisation (Jellison et al. 1993).

Nitrification by aerobic microbes like *Nitrosomonas* and *Nitrobacter* (Fig. 2) (Sorokin and Kuenen 2005a) oxidises ammonia to nitrite, and subsequently nitrate, to yield energy. The first step, ammonia oxidation, has been detected in Mono Lake and Big Soda Lake in the US. However, the process may be inhibited at higher ammonia (>4 mM

NH$_3$) and sodium (>1 M Na$^+$) concentrations (Sorokin and Kuenen 2005a). The second step, nitrite oxidation, appears to be more robust—*Nitrobacter* species are easier to isolate from alkaline soda lakes. Nitrite oxidisers may be favoured by reduced nitrite toxicity at high pH. Under neutral pH conditions, nitrite exists partially as undissociated nitric acid, but at high pH, its concentration is low (Sorokin and Kuenen 2005a).

The produced nitrate can be used as an electron acceptor and reduced partially or fully to N$_2$ (denitrification) by, for example, heterotrophic *Halomonas* species or autotrophic *Thioalkalivibrio* (Fig. 2) (Sorokin et al. 2015). Nitrate may also be converted to ammonia in a process known as dissimilatory nitrate reduction to ammonia (DNRA) (Sorokin 2017). In a study of Canadian alkaline soda lakes, genes for denitrification were not found. DNRA genes were present but were not detected in the proteome and thus were apparently unused (Zorz et al. 2019). Laboratory studies have demonstrated active DRNA, but the extent to which this occurs in situ is unknown (Sorokin et al. 2015).

The nitrogen cycle in alkaline soda lakes is in part controlled by salinity. Salinity gradients influence which N$_2$-fixers are active, and high sodium concentrations appear to restrict nitrification (and thus perhaps the nitrogen cycle more generally) (Sorokin and Kuenen 2005a; Samylina et al. 2019). The nitrogen cycle of alkaline soda lakes remains an exciting topic for future research.

Sulfur Cycling

Microbes assimilate about 1 sulfur atom for every 20 carbon atoms. Sulfur is incorporated into cellular components, like the amino acids cysteine and methionine. Some microbes also rely heavily on sulfur compounds to acquire chemical

energy. Sulfur-metabolising microbes have been identified in numerous alkaline soda lakes and studied extensively (Sorokin and Kuenen 2005b; Sorokin et al. 2011). Likely, they are more active in Na–HCO$_3$–CO$_3$–SO$_4$ brines, e.g., Mono Lake (USA), as opposed to low-sulfate brines, e.g., Lonar Lake (India). In alkaline soda lakes, high pH creates distinctive sulfur chemistry.

At high pH, hydrogen sulfide dissociates to the non-volatile bisulfide ion (HS$^-$), reducing sulfide toxicity. At neutral pH, volatile hydrogen sulfide diffuses through the cell membrane and inhibits aerobic respiration. Hydrogen sulfide gas dissolves well at high pH and high carbonate alkalinity, enabling the successful development of desulfurisation biotechnology (Box 6). Elemental sulfur reacts abiotically with sulfide to form polysulfides (chains of sulfur atoms), which are stable only at high pH and represent a unique form of bioavailable sulfur in alkaline soda lakes (Sorokin and Kuenen 2005b). At neutral pH, microbial sulfide oxidation can acidify the environment, but in alkaline soda lakes, sulfuric acid is neutralised by the strong buffering capacity of the brine.

Aerobic or oxygen-tolerant microbes that oxidise sulfur compounds can be abundant in surface sediments, converting sulfide to thiosulfate (S$_2$O$_3{}^{2-}$) or sulfate (Sorokin et al. 2011). Members of the genus *Thioalkalivibrio* are apparently the most widespread with >100 different isolated variants (Fig. 2). Anaerobic phototrophic 'purple sulfur bacteria', including *Ectothiorhodospira*, are also very common (Driessen et al. 2011; Sorokin et al. 2014; Zorz et al. 2019).

Alkaline soda lakes are also home to anaerobic microbes that reduce diverse sulfur compounds including sulfate, sulfite, thiosulfate, and polysulfides (Sorokin et al. 2014). Complete reduction, 'sulfidogenesis', produces hydrogen sulfide (H$_2$S). At neutral or acidic pH, sulfidogenesis can be restricted by product inhibition, e.g., when H$_2$S is not biologically/chemically oxidised or precipitated as FeS by ferric iron. At high pH, H$_2$S concentrations remain low, favouring sulfidogenesis (Sorokin 2017). *Desulfonatronum* and *Desulfonatrovibrio* are common alkaline soda lake residents with flexible sulfur-based metabolisms (Fig. 2; Sorokin 2017). Microbes that reduce sulfur compounds include autotrophic and heterotrophic species (Sorokin et al. 2011).

Iron Cycling

Some transition metals, such as iron and manganese, are used by microbes as electron sources and sinks to acquire energy. Many more, such as copper, nickel, and cobalt, are used as key components of enzymes. Although microbes use small amounts of transition metals relative to C, N, P, and S, they are essential to cell function. Here, we discuss the availability and uptake of one such transition metal used by almost all microbes: iron. Although iron is one of the most abundant metals in the Earth's crust, the unique geochemistry of alkaline soda lakes renders collecting and exploiting Fe a tricky microbial feat. At the high pH of alkaline soda lakes, iron exists primarily within insoluble Fe(III) minerals (Sorokin 2017). To access iron, some microbes produce extracellular iron-chelating 'siderophores', complex organic molecules that reversibly bind iron ions. Siderophore production has been reported for a *Halomonas* species isolated from Soap Lake in Washington State, USA (Figueroa et al. 2015). Microbes may also grow on the surfaces of iron minerals.

Iron-reducing microbes, like *Natronincola* species and *Geoalkalibacter ferrihydriticus,* capable of reducing chelated Fe(III) and amorphous Fe(III) hydroxide to minerals like

magnetite (an iron (II/III) oxide) and siderite (iron (II) carbonate), have been isolated from lakes in southern Siberia and Lake Magadi in Kenya (Sorokin 2017; Zavarzina et al. 2020). Recent work has shown that *G. ferrihydriticus* can also oxidise siderite while reducing carbonate to acetate (Zavarzina et al. 2020). Otherwise, Fe(II)-oxidising microbes, which are abundant in pH neutral and acidic anoxic environments, remain elusive.

Phosphorous Cycling

Microbes generally assimilate about 1 mole of phosphorous for every 100–200 moles of carbon. Phosphorous is an essential constituent of biomolecules (like DNA, lipids, and ATP). Dissolved inorganic phosphate is generally believed to be more bioavailable than dissolved organic phosphate (DOP)—an accumulation of DOP in the ocean indicates that recycling within the food chain is restricted. In marine and freshwaters, phosphate regularly limits growth.

In alkaline soda lakes, recent work has suggested that enhanced access to inorganic phosphate may contribute to the exceptional productivity of these lakes (Toner and Catling 2020). A positive relationship between dissolved inorganic carbon and the phosphorous concentration has been observed for carbonate-rich lakes. This phenomenon is explained by the sequestration of Ca^{2+} in carbonate minerals, thereby limiting the formation of apatite (calcium phosphate minerals) and enabling higher dissolved phosphate (Toner and Catling 2020). Extremely high (4 mM) phosphate concentrations are common in Last Chance Lake, Canada (Zorz et al. 2019; Toner and Catling 2020). Even so, many alkaline soda lakes have low phosphate concentrations, likely the result of spatial and temporal differences in biological uptake rates, precipitation, and source water supply. Early nutrient amendment studies in African alkaline soda lakes show that phosphate does limit productivity (Melack et al. 1982). To date, microbial phosphate cycling in these environments has not received much attention, leaving an interesting gap for future research.

CONCLUSIONS

Alkaline soda lakes display amazing effectiveness in transforming sunlight energy into electron and element flows. Phototrophs fix organic carbon into biomass, which in turn supports the growth and reproduction of diverse community members. During biomass degradation, fixed organic carbon is transformed back to inorganic carbon. Among microbes, natronophiles are uniquely suited to high pH and to high carbonate and sodium concentrations. In society, alkaline soda lake microbes can be harnessed to generate products and drive chemical transformations. Such microbes have already sparked many successful applications (see Boxes 1–6) as sources of protein-rich food, pools of robust enzymes, and reservoirs of metabolisms fit for industrial bioreactors. Likely, their contribution to the bioeconomy is only just beginning.

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