



The Sand Lake Observer – Volume 6, Number 1, July 2026

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Summer Microbial Dynamics: Intraterrestrials in the Sediments and Phototrophic Helpers in the Clear Water

Big Sand Lake is at its clearest and most inviting in July. Water temperatures reach the low 70s in the shallows, Secchi depths often exceed 30 feet, and light penetrates well into the weed beds and the deeper spots. This clarity, long a hallmark of our oligotrophic system, is maintained in part by the very microbes that previous issues of the *Observer* have highlighted through flow-cytometry counts, nutrient-uptake kinetics, and seasonal phytoplankton records. Two recent publications—one a compelling book on life deep beneath the Earth's surface and the other a laboratory study of light-driven energy in planktonic bacteria—offer fresh ways to understand what is happening in the water of our lake and in the dark detritus of the west bay.

Intraterrestrials Beneath the Sand

Karen Lloyd's *Intraterrestrials: Discovering the Strangest Life on Earth* (Princeton University Press, 2025) takes readers into the subsurface biosphere—the vast microbial communities living hundreds of meters below land or lake bottom in conditions once thought incompatible with life. High pressure, near-zero nutrients, temperatures that would cook most surface organisms, extreme acidity, extreme base, and complete darkness define these habitats. Yet the microbes persist, often at extraordinarily low metabolic rates, by tapping geochemical energy sources or slowly recycling the organic detritus that settles from above.

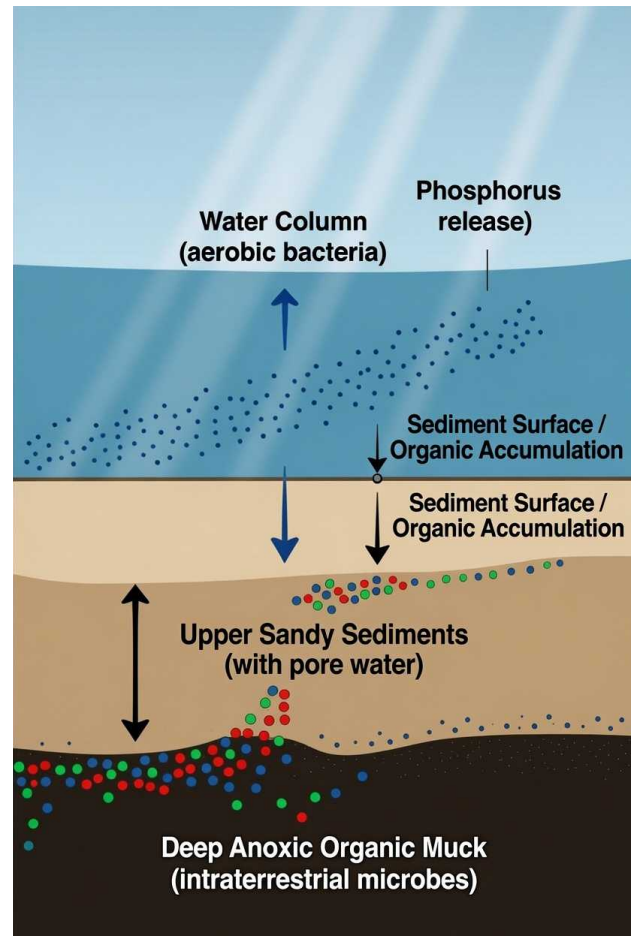
Big Sand's sediments are a toned-down version of that world. Mean lake depth is only nine feet, but the deep holes reach 55 feet and the west-bay muck is locally more than 18 feet thick. In July the bottom waters and especially the sediment pore waters are frequently devoid of oxygen (anoxic).

Sediment pore waters (also called interstitial water or porewater) refers to the thin film of water that fills the tiny spaces (pores) between sediment particles at the bottom of the lake (Figure 1)

Figure 1: Simplified stacked-layer cross-section of an oligotrophic lake. Layers show: sunlit water column → sediment surface → upper sandy sediments (with pore water) → deep anoxic organic muck hosting intraterrestrial microbes. Arrows indicate detritus settling and nutrient (phosphorus) cycling. (Image generated and edited with Grok Imagine by xAI).

Heterotrophic bacteria are bacteria that obtain their carbon and energy by consuming organic matter produced by other organisms (as opposed to making it themselves from inorganic sources like CO_2).

In the anoxic waters, heterotrophic bacteria continue the work described in earlier *Observer* issues: they oxidize the settling detritus, release phosphate and other minerals, and, when oxygen is absent, shift to anaerobic pathways that can dissolve iron-bound phosphorus. These “intraterrestrial” populations are not the flashy cyanobacteria or the proteorhodopsin-bearing cells of the water column; they are the slow, patient recyclers whose activity ultimately controls how much new plant growth the lake can support each summer.



Lloyd emphasizes that subsurface life challenges our assumptions about what organisms “need.” Many intraterrestrials operate with genomes streamlined for extreme efficiency, using every available electron acceptor and leaking minimal waste.

In Big Sand’s sediments the same principle applies. The black, gelatinous detritus that accumulates where currents are weak is not inert; it is a living reactor whose bacterial inhabitants help keep the overlying water clear by locking phosphorus into new biomass or burying it. When

beaver dams or road culverts reduce flushing, these sediment communities can tip the balance toward internal nutrient loading; the process that once produced the fish kill observed in the west bay.

In these deep, energy-poor environments, life is constrained by fundamental thermodynamics. The key quantity is the Gibbs free energy change (ΔG) of a chemical reaction, which tells us how much usable energy is actually available under real conditions. The full equation is: $\Delta G = \Delta G^\circ + RT \ln(Q)$.

- ΔG° is the standard free energy change (the energy yield under > standardized laboratory conditions),
- R is the gas constant,
- T is the absolute temperature (in Kelvin),
- $\ln(Q)$ is the natural logarithm of the reaction quotient — a term > that reflects the actual concentrations of the reactants and > products present in the environment.

When Q is much smaller than the equilibrium constant (i.e., the reaction is far from equilibrium), ΔG becomes more negative and more energy is available. As a reaction proceeds and approaches equilibrium, ΔG approaches zero and the energy yield drops toward nothing.

Professor (of Microbiology) Lloyd explains that microbes in the deep subsurface often live on reactions whose ΔG is only slightly negative — sometimes just a few kilojoules per mole, barely enough to support the minimum energy needed to maintain a cell and make ATP¹. These organisms have evolved extraordinary efficiencies: streamlined genomes, minimal maintenance costs, and the ability to harvest energy from an enormous variety of redox reactions (electron transfers) that surface life largely ignores. They operate at the thermodynamic “edge” where the energy return is minuscule compared with the oxygen respiration most familiar surface organisms use.

Big Sand’s sediments provide a milder window into the same principle. In the black, organic-rich muck of the west bay and deeper holes, oxygen is rapidly consumed. The remaining chemical reactions that heterotrophic bacteria use to slowly break down detritus have relatively small (less negative) ΔG values. The bacteria living there must therefore function close to these thermodynamic limits, recycling phosphorus and other nutrients while operating on very low energy fluxes. The gelatinous black layers are not inert mud — they are active, low-power

¹ ATP (adenosine triphosphate) is the main energy currency of all living cells. Think of it as a small, rechargeable battery that cells use to power almost everything.

biogeochemical reactors running under the same fundamental energetic constraints that govern life kilometers underground.

Proteorhodopsin Phototrophy in the Water Column

While the sediments host the deep, dark life, the sunlit water column hosts a different microbial strategy. Phototrophs—organisms that harvest light energy—come in three principal kinds. Oxygenic phototrophs (cyanobacteria, algae, and plants) use chlorophyll-based photosystems to split water, release oxygen, and fix carbon dioxide. Anoxygenic phototrophs (purple and green sulfur and nonsulfur bacteria) rely on bacteriochlorophyll and alternative electron donors such as hydrogen sulfide or organic compounds, producing no oxygen. The third kind employs retinal-based pigments such as proteorhodopsin: these single-protein pumps use light to move protons across the membrane, generating a proton-motive force for ATP synthesis without complex reaction centers or carbon-fixation machinery. Roughly half of all marine bacterioplankton carry proteorhodopsin (PR), which supplements cellular energy much like a tiny solar panel.

A landmark 2014 study by Palovaara, Pinhassi and colleagues (doi:10.1073/pnas.1402617111) showed exactly how this works in the model marine flavobacterium *Dokdonia* sp. MED134.

The tricarboxylic acid (TCA) cycle — also known as the Krebs or citric acid cycle — is the central metabolic hub of the cell. It generates energy and supplies carbon skeletons for biosynthesis. When bacteria grow on sparse or single compounds such as the amino acid alanine, they withdraw intermediates from the cycle for growth. Anaplerotic² CO₂ fixation pathways act as “refilling” reactions that replenish those intermediates by incorporating inorganic carbon (CO₂ or bicarbonate). In the light, proteorhodopsin supplies extra energy that powers these anaplerotic enzymes (e.g., pyruvate carboxylase and PEP carboxykinase). In the experiments, this allowed 24 and 31% of the carbon atoms in new biomass to come directly from bicarbonate rather than from the supplied organic matter.

When dissolved organic carbon (DOC) is scarce or of poor quality (for example, single amino acids rather than a rich mixture), light dramatically stimulates growth—up to 2.4-fold higher specific growth rate and 4.2-fold higher cell yield. Even more striking, expression of the glyoxylate-shunt genes (isocitrate lyase and malate synthase) increased more than 300-fold in light under the most carbon-limited conditions. This shunt lets the bacteria use organic carbon more efficiently for biosynthesis instead of burning it all for energy (Figure. 2). The net result is a highly efficient facultative mixotroph (an organism that can obtain energy and carbon from more than one source) well suited to the nutrient-poor, sunlit conditions of Big Sand Lake.

² Anaplerotic reactions (from the Greek word meaning “to fill up”) are metabolic processes that replenish intermediates in the TCA cycle.

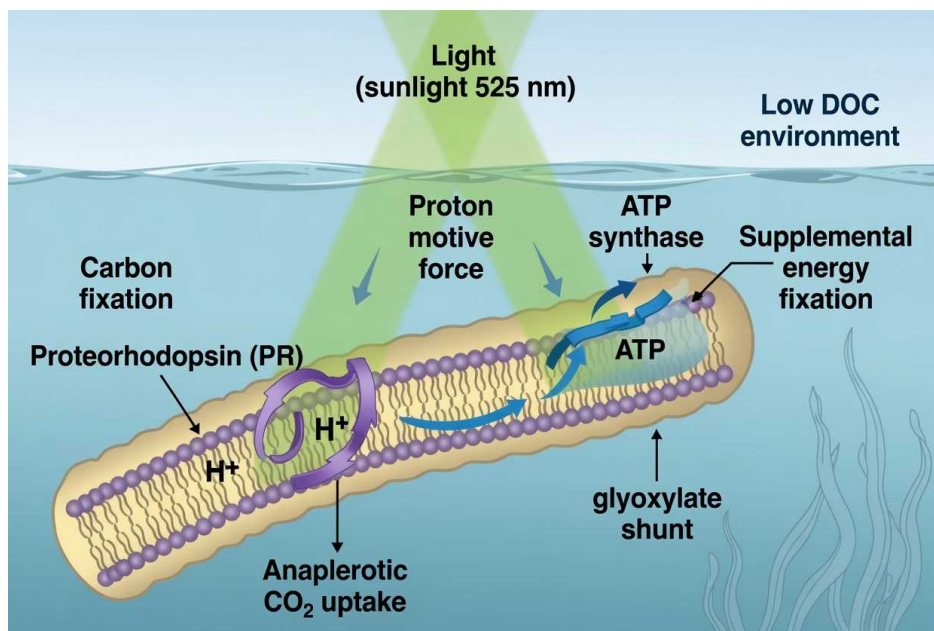


Figure 2: Proteorhodopsin-mediated phototrophy in a marine/freshwater bacterium. Cutaway view of a rod-shaped cell in a clear lake water column, showing proteorhodopsin (PR, purple) embedded in the plasma membrane. Green sunlight (525 nm) drives proton (H⁺) pumping, generating a proton motive force that powers ATP synthesis. Supplemental ATP supports anaplerotic CO₂ uptake (carbon fixation) and the glyoxylate shunt for efficient organic carbon assimilation in low dissolved organic carbon (DOC) environments. This light-driven mechanism supplements heterotrophic metabolism in nutrient-poor aquatic habitats. (Image created and edited with Grok Imagine by xAI).

Importantly, the benefit is strongest precisely when nutrients are limiting—the situation that prevails in Big Sand most of the year. Our own earlier flow-cytometry work showed bacterial populations stable at roughly 2-million per milliliter even in winter under the ice (The Sand Lake Observer, Volume 2, Number 3, June 2015).

In clear July water, light reaches deep enough that PR-containing cells (documented in many freshwater lakes, including members of the Flavobacteria and SAR11-like lineages) can harvest photons while they scavenge the trace DOC that leaks from phytoplankton or arrives with groundwater. The net result is tighter control of nutrients at the base of the food web: bacteria keep dissolved concentrations low, starve out excessive phytoplankton, and still pass carbon upward through the microbial loop to zooplankton and ultimately to fish.

Metagenomic surveys confirm that PR genes are widespread in freshwater systems worldwide, and metatranscriptomic data show their expression peaking with solar irradiance—exactly the pattern one would expect on a bright July afternoon on Big Sand.

Putting the Pieces Together for Lake Health

These two stories—one from the dark sediments, one from the sunlit water—converge on the same practical question we have asked for years: why does Big Sand remain clear and relatively unproductive even while phosphorus continues to enter from lawns, septic systems, and atmospheric deposition?

The intraterrestrial sediment community slowly buries or sequesters phosphorus, while the PR-equipped planktonic bacteria use light to extract maximum value from whatever sparse organic carbon is available, preventing runaway algal blooms. The result is the stable, clear-water state described in the alternate-stable-states diagram of earlier issues.

Yet both communities are sensitive to human choices. Reduced flushing (blocked culverts, beaver dams) favors sediment anoxia and internal phosphorus release—the very process that can tip a lake toward the weedy, turbid state. Excessive boat traffic or shoreline hardening³ disturbs the benthic habitat where many of these microbes live. Conversely, shoreline buffers and native plantings not only intercept runoff but also supply the leaf-litter carbon that supports a healthy microbial loop.

Practical Steps This Summer

1. **Observe and report microbial signs.** Watch for the metallic green sheen of buoyant cyanobacteria on calm mornings (still mostly *Anabaena* and occasional *Microcystis*). Note any unusual clarity or slight turbidity after heavy rain—the latter often signals a pulse of sediment bacteria or detritus.
2. **Support sediment health.** Keep woody debris and emergent vegetation along undeveloped shorelines; they stabilize the benthic habitat and provide refugia for both intraterrestrial microbes and the invertebrates they support.
3. **Minimize nutrient pulses.** Even small additions of phosphate can be rapidly taken up by the efficient bacterial community, but repeated inputs gradually

³ **Shoreline hardening** (also called shoreline armoring or hardscaping) refers to the practice of replacing natural, soft shorelines with artificial, rigid structures made of hard materials to control erosion or create easier access to the water.

enrich the sediments. Clover lawns and native buffers remain the simplest long-term fix.

4. **Continue monitoring.** The St. Croix Chippewa environmental program and volunteer Secchi readings already give us a baseline. Adding periodic bacterial counts or simple nutrient-uptake assays (building on the isotope methods developed here) would let us track whether the PR-equipped populations are maintaining their grip on the nutrient cycle.

Looking Ahead

The discoveries in *Intraterrestrials* and the Palovaara–Pinhassi experiments remind us that Big Sand is not just a body of water for swimming and fishing; it is a living biogeochemical engine whose smallest components—bacteria in the mud and in the sunlit water—set the stage for everything larger. By protecting the conditions that let both the “intraterrestrials” and the light-harvesting plankton do their work, we keep the lake clear, the fishery balanced, and the wild rice restoration efforts on a firmer footing.

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Bacterial counts and winter populations (including ~ 2 million cells ml^{-1} under ice): Volume 2, Number 3 (June 2015) — “Bacteria” and winter plankton sections.

Phosphorus limitation and wild rice experiments: Volume 1, Number 4 (May 2012) and Volume 2, Number 3a (June 2016).

Alternate stable states, trophic cascades, and lake regime shifts: Volume 1, Number 1 (July 2009) and Volume 1, Number 4 (May 2012).