

Introduction

A “Follow the Energy” Approach for Astrobiology

TORI M. HOEHLER,¹ JAN P. AMEND,² and EVERETT L. SHOCK³

A KEY CHALLENGE IN ASTROBIOLOGY is to comprehend life and its interaction with the environment at a level sufficiently fundamental to embrace the alternative biochemistries that may be encountered in a search for life elsewhere (Baross *et al.*, 2007). Life on Earth presents us with a single (albeit highly diversified) biochemical model around which to build this comprehension. This model is extremely valuable in providing an empirical starting point for understanding metabolic potential and environmental tolerance, and as a continuing “reality check” on whatever generalized concepts of life may be developed. Reference to this single example, however, also carries the risk of narrowing our sense of possibility—of leading us to define biochemistry, habitability, and biosignatures in terms so specific that they may exclude different forms of life.

The benefits and risks of reference to terrestrial life are both increasing as the current revolution in molecular biology unfolds. As our understanding of terrestrial biology rapidly expands, we are presented with an ever more complete and refined model to which we can refer. But this advance in understanding is fueled by tools, approaches, and insights that (appropriately) are increasingly and remarkably specific with respect to terrestrial biochemistry. Research in astrobiology has much to gain by harnessing these tools and approaches but must simultaneously strive for breadth and generality in understanding life.

The need for well-defined yet broadly applicable notions of habitability and biosignatures will become critical as astrobiological objectives are factored increasingly into space missions. The conception, parameterization, and instrumentation of these missions will require concrete determinations of where to look and what information to seek, and interpretation of the resultant data will require considerable plasticity in our conception of what constitutes evidence of life. Thus, we must not only pursue, in parallel, both a specific and general understanding of life and its functions, but also be continually prepared to unite these modes of understanding toward optimal development of astrobiological missions.

To unify the general and specific modes of understanding life requires a frame of reference that is applicable across a broad spectrum of alternative biological models yet capable of incisive insight into terrestrial biology. Consideration of the biological relationship with energy offers one such frame of reference.

ENERGY AS A UNIVERSAL IMPERATIVE FOR LIFE

A basic tenet of astrobiology is that life is shaped by, and shapes, its host environment. More than 60 years ago, Nobel laureate Erwin Schrödinger described this interaction at its most fundamental level: life consumes and transforms

¹Exobiology Branch, NASA Ames Research Center, Moffett Field, California.

²Department of Earth & Planetary Sciences, Washington University, St. Louis, Missouri.

³Department of Chemistry & Biochemistry and School of Earth & Space Exploration, Arizona State University, Tempe, Arizona.

the energy of its surroundings (Schrödinger, 1944). Life's dependence on energy is widely acknowledged (Conrad and Neelson, 2001; Neelson *et al.*, 2002; Benner *et al.*, 2004; Baross *et al.*, 2007) but seldom deeply considered in astrobiology, despite its central role in regard to habitability, the origin and evolution of life, and the nature of biosignatures. The understanding of energy metabolism in terrestrial biology, however, has progressed steadily over several decades—from conceptual to mechanistic, from qualitative to quantitative, and from petri dish to environment. Energetic considerations are increasingly utilized as incisive tools for understanding the distribution and activities of biological populations in nature (Lovley and Klug, 1983; Hoehler *et al.*, 1994; Rogers and Amend, 2005; Rogers *et al.*, 2007). In particular, the balance between biological energy demand and environmental energy availability represents a key determinant of activity in systems that represent some of the most active frontiers of environmental microbiology, *e.g.*, deep subsurface and extreme environments (Hoehler, 2004). Importantly, such environments are among the most relevant terrestrial analogs for possible abodes of life elsewhere in the solar system. The growing understanding of energy flow in terrestrial biology and ecology represents a firm foundation on which to develop an energy-based approach to a variety of astrobiological questions. The universal nature of biological energy demand ensures that such an approach will be applicable in the broadest possible sense. Simultaneously, the ability to consider energy flow in thermodynamic terms offers the ultimate potential for doing so with quantitative rigor.

Habitability

Life's universal need for energy represents a fundamental constraint on habitability. Although this fact is of little use as a purely qualitative statement—because energy is present almost ubiquitously throughout the universe—reference to energy metabolism in terrestrial biology offers a basis from which to develop a quantitative energy-based criterion for habitability. Theoretical and practical research on terrestrial life has demonstrated that (i) the need for energy includes a core set of applications that are conserved across all known organisms (Baross *et al.*, 2007), (ii) energy requirements consist of 2 components, one analogous to power (energy per unit

time) and a second analogous to voltage (energy delivered per unit event), each exhibiting discrete minimum values below which biological function does not appear possible (Tempest and Neijssel, 1984; Tjihuis *et al.*, 1993; Schink and Stams, 2002; Hoehler, 2004), and (iii) the linkage of environmental energy source to biological application is almost universally accomplished by dedicated systems of energy transduction, which utilize a small number of biochemical schemes and molecules that are conserved across the entire spectrum of biology (Hill, 1977; Thauer *et al.*, 1977). The potential for development of a rigorous energy criterion for habitability that is applicable beyond terrestrial life depends, at a conceptual level, on identifying the set or subset of these characteristics that are dictated by general principles (those that underlie all life) rather than specific “choices” in the development of our biology. Quantification of an energetic habitability criterion—which represents the ultimate potential and would yield the greatest practical application of this endeavor—will develop through coupled work to determine the universal constraints on biological energy demand (*e.g.*, whether a “critical mass” of information content and, therefore, a certain energy to support it is required for life-like function) and “calibrate” the energy demand scale by quantifying the energy requirements of terrestrial biology.

Origin and evolution of life

The availability of energy in a system makes it possible—provided appropriate mechanisms exist—to yield, reproducibly, specific outcomes of otherwise very low probability. For example, the extremely low probabilities of generating polymers of specified sequence (as in protein or DNA synthesis), of net production of thermodynamically unfavorable species, or of the creation and maintenance of such locally ordered states as characterize the biological system can all be overcome by directed investment of energy. Life as we see it now, even in the simplest microorganisms, combines together great numbers of such low-probability processes. The full complement of these processes specifies an offsetting energy that is met by (and, at least in our biology, is wholly dependent on) dedicated mechanisms of energy transduction. Conversely, the full capability for energy transduction, as defined by both environmental energy availability and biological

processing capacity, places boundaries on the collection of low-probability events that can be supported and, thereby, on the overall complexity, order, information content, and thermodynamic disequilibrium that a given system can achieve. The spectrum of possibility in origin-of-life chemistry is thus constrained at any point by the extent to which energy can be delivered into the system. This consideration can be brought to bear in evaluating potential origin-of-life scenarios, both for Earth and elsewhere, particularly in relation to the emergence of complexity and the functionality that accompanies it. Because the capability for energy transduction is, itself, a function of the emerging complexity and functionality of the system, it must, in essence, represent a third component in the classic chicken-and-egg (information-and-function) problem that surrounds the origin of life.

Biosignatures

Our present understanding of biosignatures, which is dominated by specific reference to terrestrial biology, risks missing much of the spectrum of possibility. That is, certain lipids, nucleic or amino acid polymers, particular combinations of molecules, specific structures, etc., represent diagnostically biogenic features to us solely because we know that our sort of life happens to make them. If we are to rely on observational knowledge of the specific molecules and structures life is capable of creating, our potential for identifying life elsewhere is, by definition, limited to biochemistries that represent the same highly specific outcomes of protobiological chemistry and biological evolution as occurred in our own case—quite probably a small subset, indeed, of the full spectrum of possibility. Yet the features described above—or their counterparts in alternative biochemical models—can almost certainly serve as evidence of biological process even in the absence of direct evidence that life creates them. To understand such features in this non-specific frame of reference, and to develop a means by which to quantify their “degree” of biogenicity, will be crucial as space missions increasingly include components designed to search for evidence of life.

That all life harnesses energy from the environment and uses that energy to support low-probability outcomes represents the basis for an energetic frame of reference in which to assess

biogenicity in non-specific terms. Where the activities of energy harvesting or energy investment are (or can be) demonstrably distinct from equivalent abiotic processes of energy flow, biosignatures potentially exist.

The products or residuals of energy-harvesting may have somewhat limited utility as potential biosignatures, simply because available energy sources will always ultimately be dissipated, whether by abiotic or biotic means. Development of biogenic character in such cases depends on life imposing greater order, catalytic speed, or selectivity on the process than would be possible without life. The development of near-equilibrium in processes that would otherwise be sluggish, the expression of large kinetic isotope effects, or the absorption of light in sharply defined and highly wavelength-specific patterns, all represent biological imprints on energy dissipation and, therefore, potential energy-harvesting biosignatures.

Consideration of life’s capability to direct energy into specific processes, particularly via well-developed mechanisms of energy transduction, has great potential in developing a quantitative metric for biogenicity. The detectable products of such energy investment are thermodynamic disequilibrium (*e.g.*, high oxygen concentrations in an otherwise reducing system), high information content (*e.g.*, an over-representation of a polymer of specific sequence with respect to a landscape of alternative sequence possibilities), and physically or chemically ordered systems or structures. In principle (with development of appropriate means), such observations could be arrayed along a spectrum of inherent “energy content.” The basis for resolving any uniquely biogenic components of such an array will arise through characterization and quantification of the unique capabilities for energy transduction in biological versus abiotic systems.

“FOLLOW THE ENERGY” AS A GUIDE TO EXPLORATION

The “Follow the Water” approach to astrobiology has guided a robust program of Mars exploration and has largely shaped our sense of priority for astrobiological exploration of other solar system bodies. Adopting a “Follow the Energy” approach to astrobiology offers potential to enhance this strategy in 2 main regards:

(i) *Follow the energy offers an additional layer of constraint to sharpen focus within an existing follow-the-water context.*

Follow the water has been useful because it serves to narrow the range of potential search-for-life targets. Our understanding of the chemical and physical behavior of water permits the application of powerful models to predict its distribution within an accreting solar system and (to a lesser extent) its trajectory on an evolving planet (Morbidelli *et al.*, 2000; Raymond *et al.*, 2005). And, as has been demonstrated by recent observational planetary science, water offers a robust signal of current or even long-past activity (Anderson *et al.*, 1998; Zimmer *et al.*, 2000; Squyres *et al.*, 2004; Carr, 2006). Thus, theoretical and observational approaches focused on mapping the activity of liquid water in the evolving solar system have illuminated high-priority targets for more intensive astrobiological exploration. Yet the landscape of possibilities is still daunting, and the presence or absence of a liquid water indicator at a given site offers little guidance on what sort of evidence for life might be expected there and how great the life-supporting potential may have been. The spectrum of attractive search targets can be further (perhaps dramatically) reduced by concentrating on sites in which liquid water coexisted with energy sources capable of meeting biological requirements. As with water, many such sources have the potential to leave long-lasting evidence of their presence through mineralogical and other features (Des Marais *et al.*, 2007). Although it is, of course, not possible to quantify with precision the energetic needs of as-yet unknown organisms, the simple notion that discrete energy requirements exist, and that sites offering higher levels and fluxes of energy have greater potential to support life, provides a valuable consideration in targeting future missions. Likewise, because the quantity of biomass that can be formed and supported within a system depends (universally and directly) on energy availability, sites that have greater energy flux offer greater potential magnitude in biomarker signals, both as biomass or structural remnants and as residuals of energy harvesting. (On this and the previous point, it must be borne in mind that the direct relationship between energy flux and habitability or biomarker potential breaks down at energy levels or fluxes that become destructive to biology or biological materials—see Hoehler, 2007). Lastly, consideration of available energy

sources offers to constrain the spectrum of biomarkers that may be present and should be sought, particularly in regard to residuals of energy harvesting, *e.g.*, metabolic end products and isotopic signatures. In this way, a follow-the-energy strategy offers an additional layer of discrimination and refinement in targeting future missions when considered in conjunction with a follow-the-water approach.

(ii) *Follow the energy is appropriate for all conceivable forms of life and offers a means by which to broaden the follow-the-water approach to habitability.*

Many qualities of water make it an excellent solvent for biochemistry and, clearly, one that is capable of supporting life. However, alternative solvents for biochemistry are at least conceivable (Bains, 2004; Benner *et al.*, 2004; Baross *et al.*, 2007), and the follow-the-water strategy has been adopted with the knowledge that it has the potential to exclude some forms of life from consideration. This potential for exclusion is acceptable in a practical sense, because follow the water provides useful mission constraints and a focal point for research in the near term. Arguably, too, we might be far less likely to recognize non-water-based life even if we did come across it. For the purposes of theoretical consideration of habitability, however, life should be defined so as to embrace as broad a range of alternative biochemical models as possible (Conrad and Nealson, 2001; Nealson *et al.*, 2002; Baross *et al.*, 2007). The need for energy is a universal common descriptor for life and, therefore, a universally applicable constraint on habitability. Thus, while follow the water should certainly be retained as the first guideline in a practical search for life, follow the energy unshackles our theoretical perception of habitability from the particulars of terrestrial life and may ultimately offer a broader basis on which to seek and assess life elsewhere.

ENERGY-THEMED RESEARCH IN ASTROBIOLOGY

Energetic and thermodynamic considerations have long been a key point of reference in many of the individual disciplines associated with astrobiology. Their rigorous application in many aspects of biological research, while historically less common, is gaining momentum. The papers in this

special issue reflect a cross-section of this growing area of research in astrobiology. Collectively, they consider the conceptual and quantitative aspects of the biological need for energy, and how it bears on habitability; the provision of energy to fuel the origins of life and to sustain biology in hydrothermal, deep-sea sediment, and rock-hosted systems; the relationships between energy flow and biological populations in natural and culture systems; and the implications of energetic considerations for life elsewhere in the Solar System. Although these papers represent but a subset of the ongoing energy-themed research in astrobiology, it is our hope that their collection into a single issue will represent a point of focus and coalescence for the broader community as it ponders a follow-the-energy approach to astrobiology.

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REFERENCES

- Anderson, J.D., Schubert, G., Jacobson, R.A., Lau, E.L., Moore, W.B., and Sjogren, W.L. (1998) Europa's differentiated internal structure: inferences from four Galileo encounters. *Science* 281, 2019–2022.
- Bains, W. (2004) Many chemistries could be used to build living systems. *Astrobiology* 4, 137–167.
- Baross, J.A., et al. (2007) *The Limits of Organic Life in Planetary Systems*, National Academies Press, Washington, DC.
- Benner, S.A., Ricardo, A., and Carrigan, M.A. (2004) Is there a common chemical model for life in the universe? *Current Opinion in Chemical Biology* 8, 672–689.
- Carr, M.H. (2006) *The Surface of Mars*, Cambridge University Press, Cambridge.
- Conrad, P.G. and Nealson, K.H. (2001) A non-Earth centric approach to life detection. *Astrobiology* 1, 15–24.
- Des Marais, D.J., Jakosky, B.M., and Hynek, B.N. (2007) Astrobiological implications of Mars surface composition and properties. In *The Martian Surface: Composition, Mineralogy, and Physical Properties*, edited by J.A. Bell, Cambridge University Press, Cambridge (in press).
- Hill, T.L. (1977) *Free Energy Transduction in Biology*, Academic Press, New York.
- Hoehler, T.M. (2004) Biological energy requirements as quantitative boundary conditions for life in the subsurface. *Geobiology* 2, 205–215.
- Hoehler, T.M. (2007) An energy balance concept for habitability. *Astrobiology* 7(6), 824–838.
- Hoehler, T.M., Alperin, M.J., Albert, D.B., and Martens, C.S. (1994) Field and laboratory studies of methane oxidation in an anoxic marine sediment: evidence for a methanogen-sulfate reducer consortium. *Global Biogeochem. Cycles* 8, 451–463.
- Lovley, D.R. and Klug, M.J. (1983) Sulfate reducers can outcompete methanogens at freshwater sulfate concentrations. *Appl. Environ. Microbiol.* 45, 187–192.
- Morbidelli, A., Chambers, J., Lunine, J.I., Petit, J.M., Robert, F., Valsecchi, G.B., and Cyr, K.E. (2000) Source regions and timescales for the delivery of water to the Earth. *Meteorit. Planet. Sci.* 35, 1309–1320.
- Nealson, K.H., Tsapin, A., and Storrie-Lombardi, M. (2002) Searching for life in the universe: unconventional methods for an unconventional problem. *Int. Microbiol.* 5, 223–230.
- Raymond, S.N., Mandell, A., and Sigurdsson, S. (2005) Exotic Earths: forming habitable worlds with giant planet migration. *Science* 313, 1413–1416.
- Rogers, K.L. and Amend, J.P. (2005) Archaeal diversity and geochemical energy yields in a geothermal well on Vulcano Island, Italy. *Geobiology* 3, 319–332.
- Rogers, K.L., Amend, J.P., and Gurrieri, S. (2007) Temporal changes in fluid chemistry and energy profiles in the Vulcano Island hydrothermal system. *Astrobiology* 7(6), 905–932.
- Schink, B. and Stams, A.J.M. (2002) Syntrophism among prokaryotes. In *The Prokaryotes: An Evolving Electronic Resource for the Microbiological Community*, edited by M. Dworkin et al., Springer-Verlag, New York.
- Schrödinger, E. (1944) *What is Life? The Physical Aspect of the Living Cell*, Cambridge University Press, Cambridge.
- Squyres, S.W., Arvidson, R., et al. (2004) The Opportunity rover's Athena science investigation at Meridiani Planum, Mars. *Science* 306, 1698–1702.
- Tempest, D.W. and Neijssel, O.M. (1984) The status of Y_{atp} and maintenance energy as biologically interpretable phenomena. *Annu. Rev. Microbiol.* 38, 459–486.
- Thauer, R.K., Jungermann, K., and Decker, K. (1977) Energy conservation in chemotrophic anaerobic bacteria. *Bacteriol. Rev.* 41, 100–180.
- Tijhuis, L., van Loosdrecht, M.C.M., and Heijnen, J.J. (1993) A thermodynamically based correlation for maintenance Gibbs energy requirements in aerobic and anaerobic chemotrophic growth. *Biotechnol. Bioeng.* 42, 509–519.
- Zimmer, C., Khurana, K., and Kivelson, M.G. (2000) Sub-surface oceans on Europa and Callisto: constraints from Galileo magnetometer observations. *Icarus* 147, 329–347.

Address reprint requests to:
Tori M. Hoehler
NASA Ames Research Center
Mail Stop 239-4
Moffett Field, CA 94035, USA

E-mail: tori.m.hoehler@nasa.gov