Chapter 5
Energy Sources and Life

An external energy source is a necessary condition for life, because living systems require a flow of energy to organize materials and maintain a low state of entropy (Morowitz 1968). Energy is also needed to perform work. Life on Earth can be distinguished by the external energy source that it uses. Photoautotrophic life derives energy from sunlight and uses CO_2 as a carbon source. Chemolithotrophic life uses redox reactions involving abiological compounds and chemolithoautotrophic life uses CO_2 (or other small carbon compounds) as a carbon source. Chemoheterotrophic life uses high-energy organic molecules, produced in general by autotrophic life, as a source of energy and carbon. On other worlds, where other forms of energy may be more abundant, or where the primary sources for energy on Earth may be lacking, life may have evolved to depend on different forms of energy. In this chapter, we critically analyze the various forms of energy that are potentially available to living systems, consider other factors that bear on the evolution of energy harvesting mechanisms, and evaluate the apparent availability of different forms of energy at different sites in our Solar System.

5.1 Life as We Know It

The National Research Council (Baross et al. 2007) defined terran life as a form of life that (1) uses water as a solvent, (2) is built from cells and exploits a metabolism that focuses on the carbonyl group (C=O), (3) is thermodynamically dissipative, exploiting chemical-energy gradients, and (4) exploits a two-biopolymer architecture that uses nucleic acids to perform most genetic functions and proteins to perform most catalytic functions. Terran organisms store energy in two principle ways, either in a molecule that has a high free energy of reaction under the conditions that prevail inside the organism (e.g., ATP), or as a gradient of concentrations of chemical species across a physical structure (e.g., a biological membrane). The term "terran" was used to denote a particular set of biological and chemical characteristics that are

exhibited by all life on Earth. Thus, any alien life could be terran or nonterran depending on its characteristics. With regard to energy, terran life has evolved to use light, organic molecules, and oxidizable inorganic chemicals as abundant sources of energy on Earth, so living systems have evolved specialized adaptations to use these energy sources. As more organisms are discovered and described on our planet, the recognized "landscape" of terran life has expanded, and some theoretical possibilities previously considered only in science fiction have become reality. One example is the discovery of the first photosynthetic animal, a sea slug which has integrated a nuclear gene of oxygenic photosynthesis (*psb*O), derived from its algal food source, into its germ line (Rumpho et al. 2008). Another example is the discovery of the Loricifera, apparently actively metabolizing microscopic animals in the oxygen-free sediment on the bottom of the Mediterranean Sea (Danovaro et al. 2010), though whether they need no oxygen at all is still controversial.

5.1.1   Oxidation-Reduction Chemistry as an Energy Source for Life

Energetically favorable redox-reactions are the basis for life on Earth. The best known and most common types of metabolism are based on hydrogen oxidation and methanogenesis, sulfur reduction and oxidation, iron and manganese reduction, denitrification, and aerobic respiration. However, many other energy-yielding redox-reactions are known that involve the reduction or oxidation of relatively rare elements such as arsenic, selenium, copper, lead and uranium. Thus, there does not appear to be a basic limitation on which elements or redox-reactions can be used. Rather, the reactions that occur will likely be dictated by the abundance, availability and suitability of a specific element in a certain type of environment. The diversity of arsenic and selenium respiring bacteria thriving in playas (alkaline salt lakes) and mining tailings is a good example (Stolz and Oremland 1999). Another intriguing example is provided by co-cultured iron-reducing and iron-oxidizing bacteria that both use magnetite as a source medium. Magnetite contains both Fe(II) and Fe(III). Fe(II) was shown to be oxidized by *Rhodopseudomonas palustris TIE-1* using light energy, while the co-cultured bacterium *Geobacter sulfurreducens* reduced Fe(III) under anaerobic conditions, thus effectively using the mineral magnetite under varying environmental conditions as a naturally occurring battery (Byrne et al. 2015).

As pointed out in Chap. 3, the oxidation of hydrogen may be one of the most ancient and basic metabolic pathways for life on Earth, and possibly elsewhere. The oxidation of the most common element in the Universe yields an appreciable amount of energy, 2.5 eV per reaction (or 237.14 kJ/mole, 56.68 kcal/mole) assuming standard conditions (25 °C, 1 atm)

$$H_2 + \frac{1}{2}O_2 \rightarrow H_2O \tag{5.1}$$
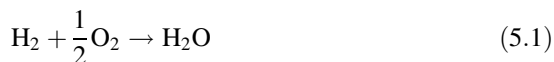
The metabolic pathway is called methanogenesis if the oxidation of hydrogen is coupled with the reduction of carbon dioxide to methane.

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O \tag{5.2}$$
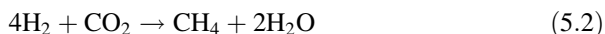
Methanogenesis as defined here does not imply that the hydrogen has to be supplied in molecular form, but it may also derive from an organic source. The reduction of carbon dioxide to methane requires the expenditure of energy, but due to the production of two water molecules the reaction is energy-yielding (1.4 eV energy yield at standard conditions, 474.28 kJ/mol). This reaction powers autotrophic life at hydrothermal vents and also some of the endolithic life present in the cracks and pores of the basaltic ocean floor. Seismogenic hydrogen gas, produced in rocks by brittle fracturing on fault planes, has also been suggested as a potential microbial energy source on Earth and Mars (McMahon et al. 2016). In addition to providing energy for metabolism, the methanogenesis pathway has the advantage of fixing carbon dioxide that can further be used for organic synthesis reactions. Another important redox reaction is the oxidation of molecular hydrogen coupled to the reduction of iron.

$$H_2 + 2Fe(III) \rightarrow 2H^+ + 2Fe(II) \tag{5.3}$$
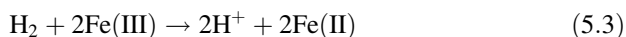
The energy yield from this reaction is 1.6 eV (148.6 kJ/mol). Examples of terrestrial organisms that use this reaction are *Pseudomonas* sp. (Balashova and Zavarzin 1980) and *Shewanella putrefaciens* (Lovley et al. 1989). There are many other compounds that can be coupled to the oxidation of hydrogen. One intriguing example is the reaction of hydrogen peroxide (H_2O_2) with molecular hydrogen to water, which is performed by *Acetobacter peroxidans* (Doelle 1969; Tanenbaum 1956). This can serve as a model pathway for highly oxidized environments not commonly found on Earth.

Sulfur metabolism appears to be very ancient, as many terrestrial microbes are thermophilic and are associated with expressions of volcanic activity such as hot springs. One of the reasons that sulfur is so widely used is that it occurs in a wide variety of oxidation states including fractional nominal oxidation states. Oxidation states for sulfur of $+7, +5, +4, +3\frac{1}{3}, +3, +2.5, +2, -0.4, -0.5, -\frac{2}{3}, -1$ are known, leading to a complex inorganic sulfur cycle, much of which is mediated by microbes (Amend and Shock 2001). Sulfur reducing bacteria are quite commonly observed to populate anoxic sediments of bottom fresh waters, and marine and hypersaline aquatic environments including submarine hydrothermal vents. Many sulfate reducers prefer molecular hydrogen or hydrogen from an organic source such as acetate or lactate, which is used as an electron donor. Some of the sulfur reducing bacteria live symbiotically with green sulfur bacteria that photooxidize hydrogen sulfide to elemental sulfur (early photosystem). Other sulfur bacteria such as

Desulfobulbus are capable of organizing themselves into long, insulating cables made up of several thousand individual cells and connecting the bottom bacteria, living in low oxygen concentrations, to those in high oxygen concentrations, shuttling electrons from one to another (Pfeffer et al. 2012). Sulfur oxidizing microbes are common in oxygen-rich aquatic ecosystems and ground-water systems, often in close proximity to sulfur reducing microbes (Schulze-Makuch 2003). Sulfur oxidation may be coupled to the reduction of iron as in the case of *Thiobacillus thiooxidans* or the thermophilic microbe *Sulfolobus acidocaldarus* (Brock and Gustafson 1976; Lovley 1991).

$$S^o + 6\,Fe(III) + 4\,H_2O \rightarrow HSO_4^- + 6\,Fe(II) + 7H^+ \tag{5.4}$$
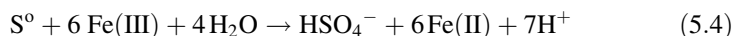
This reaction yields a high amount of energy, 2.6 eV per reaction under standard conditions and occurs in acidic environments.

Iron and manganese reduction occur in those environments associated with hydrothermal vents in the oceanic basalt crust as well. Iron reduction is coupled to the oxidation of hydrogen (see Eq. 5.3) or the oxidation of organic sources such as glucose, lactate, formate and organic acids. Under oxygen-rich conditions the energetically favorable reaction is the oxidation of iron, which can already occur under slightly oxidizing conditions.

$$Fe(II) + \frac{1}{4}O_2 + H^+ \rightarrow Fe(III) + \frac{1}{2}H_2O \tag{5.5}$$
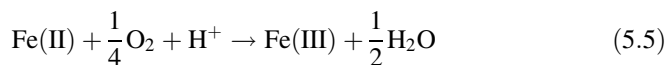
This kind of reaction is performed on Earth, for example, by *Gallionella* and *Thiobacillus ferrooxidans* (note that *T. ferrooxidans* can grow by oxidizing sulfur as well as iron). The net gain of energy is 0.5 eV for each Fe^{2+} that is oxidized. While metal-oxidizing bacteria are difficult to study under conventional culture conditions, Summers et al. (2013) used an electrode as the sole energy source for a laboratory culture of the iron-oxidizing, lithotrophic bacterium, *Mariprofundus ferrooxydans PV-1*. Schulze-Makuch and Irwin (2002a) suggested an iron cycle between anaerobic ocean bottom water and oxidized upper ocean water for ice-covered planetary oceans (such as the one suspected on Europa) as a possibility for a primitive microbial ecosystem.

Denitrification and metabolism using molecular oxygen are metabolic pathways that likely developed later as the Earth's atmosphere became enriched in nitrogen and oxygen. Thus, they don't relate directly to the primordial stages of life. However, denitrification and metabolism using molecular oxygen are among the highest energy-yielding metabolic pathways, and thus are extremely important for the later evolution of life. Heterotrophic organisms that use pre-existing, energetically rich organic macromolecules are usually considered to have evolved later as well. However, speculation has long held that the very earliest organisms on Earth were heterotrophic rather than autotrophic (Fox and Dose 1977; Haldane 1929; Oparin 1938), based on the assumption that energetically rich organic macromolecules may have been supplied on the early Earth in abundance by prebiotic synthesis (Miller and Orgel 1974) and/or by comet delivery (Chyba et al. 1990).

5.1.2   Light as an Energy Source for Life

Probably one of the most important factors in the success of life on Earth is the use of a narrow band of electromagnetic radiation (visible light) emitted from the Sun at a high intensity. The evolution of photosynthesis allowed life to tap into a practically unlimited source of energy. Sometime early in the history of the Earth, photosynthesis developed as a favorable energy capture mechanism.

The free energy that can be provided by photoautotrophy can be calculated by multiplying the frequency (f) of the light that is used by Planck's constant (h).

$$W = h f \tag{5.6}$$

The frequency varies inversely with wavelength, and somewhat different wavelengths are used by different organisms. For example, bacterial chlorophyll uses a wavelength of 800–1000 nm, while carotenoids in plants absorb wavelengths ranging from 400 to 550 nm. The average energy gain across the visible spectrum is about 2 eV (190 kJ/mol, 45 kcal/mol). It is interesting to note that this value is very similar to the free energy provided by hydrogen-oxidizing prokaryotes thought to represent early chemoautotrophic organisms. Thus, from a purely energetic viewpoint, light energy and chemical energy are equally competitive.

5.2   Life as We Don't Know It

Light, organic molecules, and oxidizable inorganic chemicals are abundant sources of energy on Earth. Thus, living systems on our planet have evolved to use these forms of energy. However, living cells make biological use of other forms of energy as well. Organisms can sense heat (Viswanath et al. 2003), pressure, stretch, movement of air and fluids, gravity, and electric and magnetic fields (Blakemore 1982; Schmidt-Nielsen 1990). All these stimuli generate responses through membrane transductions, either by altering the gating of ions that change transmembrane potentials, or by initiating metabolic changes through secondary messenger systems. Thus, they indicate the capacity of living systems to use energy in a variety of forms to affect biological processes.

The accumulation of high-energy intermediates such as adenosine triphosphate (ATP) depends on the generation of proton gradients across membranes. Since the molecular machinery of cell membranes mediates most sensory transductions, it is reasonable to assume that natural selection could have favored the evolution of membrane mechanisms that transform heat, pressure, stress, magnetic fields, or kinetic energy into high-energy covalent bonds, either directly or indirectly by coupling to ion or proton pumps. Perhaps these mechanisms have failed to evolve in living systems on Earth only because of the lack of a need for them. On other worlds where light is unavailable, natural selection would be expected to favor the

evolution of alternative energy harvesting mechanisms (Schulze-Makuch and Irwin 2002a).

How much energy is needed to power a living system? We do not know, but we can get a rough idea by calculating the amount of energy used by living organisms on Earth. First, as mentioned before, both light energy (in the visible spectrum) and chemical energy (hydrogen oxidation) provide about the same amount of energy (2 eV per photon or hydrogen molecule oxidized). Second, we know how much energy is required to assemble energy-storing compounds used on Earth. For example, an energy of about 7 kcal/mol or 0.304 eV per molecule (4.86×10^{-23} kJ or 1.16×10^{-23} kcal) is required to form the terminal phosphate bond in ATP. While the chemical storage form of energy used by another form of life would not necessarily be ATP or anything like it, the amounts of energy required for ATP phosphorylation on Earth provide a known benchmark. Given the required bonding energy of 0.304 eV, it follows that a photon of light or the oxidation of a molecule of hydrogen to water provides in theory sufficient energy to convert 6–8 molecules of ADP to ATP, if the conversion is close to 100% efficient. With this benchmark in mind, we can speculate whether other energy sources could be as efficient as chemical energy or light on Earth to provide sufficient energy for a living organism under a different set of environmental conditions.

5.2.1 Electromagnetic Waves (Other than Visible Light)

The wavelength of light used by phototrophic organisms lies in the visible and near-infrared spectrum. The fact that these specific frequencies are used may merely reflect adaptation by Earth organisms to the most prevalent wavelengths of electromagnetic radiation emitted from the Sun. These wavelengths are also transmitted through our atmosphere well, making them readily available to life on the surface of our planet. On other worlds the same may be true, even though many habitable worlds could be associated with other types of stars such as F, K or M dwarf stars. Kiang et al. (2007a, b) suggested that photosynthetic organisms on a planet surrounding an F2V star would likely exhibit peak absorbances in the blue, on a K2V star in the red-orange, and on an M star in the near infrared. Most atmospheres would absorb far less UV radiation, and absorb wavelengths below near-infrared to a great extent. However, in principle other wavelengths could be harvested. The problem with more energy-rich radiation such as that in the ultraviolet range, is its detrimental effect on many biogenic molecules such as proteins and DNA (Rettberg and Rothschild 2002). Thus, any organism using UV or more energy-rich radiation would need some kind of protection to harvest this type of electromagnetic wavelength, or would have to be based on a very different type of biochemistry. Alternatively, organisms may be able to take up a greater amount of less energy-rich radiation from near-infrared wavelengths. This radiation is plentiful in the Universe, as any body or substance above 0° K will radiate infrared light. A prime example is hydrothermal vents on the ocean floor of Earth that emanate infrared light

at a depth where photons from the Sun cannot reach (Van Dover et al. 1994; White et al. 2002). Analysis of a green sulfur bacterium from a deep-sea hydrothermal vent indicated that geothermal radiation and associated reduced sulfur compounds are sufficient to at least enhance the survival of green sulfur bacteria in the otherwise dark oceanic depths (Beatty et al. 2005). This organism, which was not found to be present in the surrounding water, thus expands the range of possible environments that could harbor life dependent on electromagnetic energy to drive endergonic biochemical reactions. In a quantitative assessment for the potential of photosynthesis at hydrothermal vents, Perez et al. (2013) found that organisms could theoretically use infrared photons up to a wavelength of 1300 nm if a high efficiency is maintained. However, more photons of infrared radiation than of visible light would have to be harvested to obtain a comparable energy gain. Nevertheless, this may be an option for life at hydrothermal vents in subsurface oceans, as speculated to exist at the water-mantle boundary of Europa. Experimental evidence has also been provided by Gusev and Schulze-Makuch (2005) that microbes may be capable of converting radio waves into chemical energy to supplement their energy needs. They hypothesized that protons in liquid water could be excited at their natural resonance frequencies by the Sun's and Earth's natural magnetic field through Langmuir oscillations, generating enough kinetic energy to charge the transmembrane potential of a cell. Even less energy would be available from this source. The hypothesis is very controversial, however, and has not yet been independently confirmed by other research groups.

Terran life is dominated by oxygenic photosynthesis, which is used by all plants and some bacteria (e.g., cyanobacteria). The more ancient anoxygenic photosynthesis also uses chlorophyll to capture light energy and build biomass, but does not make free oxygen. It is used by some bacteria such as green sulfur bacteria and purple bacteria. Other types of photosynthesis have been suggested that are not known to occur on Earth. Houtkooper and Schulze-Makuch (2007) suggested a type of oxygenic photosynthesis with hydrogen peroxide rather than molecular oxygen as a product; and Bains et al. (2014) wondered about methane-based photosynthesis, which they thought might be common in hydrogen-dominated atmospheres. Haas (2010) proposed chlorinic photosynthesis, the phototolytic oxidation of aqueous Cl^- by hypothetical organisms to form dihalogen and halocarbon products, coupled with the assimilation of carbon dioxide. O'Malley-James et al. (2012) speculated that Earth-like planets in binary and multiple star systems could not only host photoautotrophs, but also allow for more exotic forms of photosynthetic life.

5.2.2   Thermal Energy

Radiogenic elements decay in planetary interiors and produce heat that drives all major processes in the interior of planetary bodies. Examples for Earth include keeping the outer core liquid, establishing a protective magnetic field, and driving

plate tectonics. Tidal flexing can also cause heat to emanate as observed on Io, the volcanically most active planetary body in the Solar System. The tidal flexing is caused by the changes in gravitational attraction to Jupiter and to some minor degree to the other Galilean satellites. Heat released by tidal flexing is also observed in the Earth-Moon system, but to a lesser degree.

This geothermally produced heat results in thermal gradients on which thermotrophic organisms could feed. We have named these putative organisms "thermotrophs" by analogy with phototrophic and chemotrophic organisms that use light and chemical energy as basic energy sources, respectively (Schulze-Makuch and Irwin 2002a). A relatively straightforward possibility would be to harvest energy from the thermal gradients at hydrothermal vents. Thermotrophic life could harvest energy from the high heat capacity of water, which is about 4 kJ/kg K between 0 and 100 °C and 0 and 100 MPa pressure. If we assume a cell mass of 10^{-12} g comparable to that of microbes on Earth (Madigan et al. 2000), and further assume that one tenth of the cell mass is a vacuole of water from which the thermotrophic organism could extract energy, about 2.5×10^6 eV would be obtained from cooling the vacuole by 1 °C. If a microbe were able to use the Carnot cycle, the organism could extract about 9000 eV of usable energy for a temperature change from 5 °C to 4 °C (Schulze-Makuch and Irwin 2002a); upon larger decreases the potential free energy gain would increase proportionally. High-energy metabolites within the organism could be produced via conformational changes if a temperature gradient between vacuole and cell plasma were present. For a cell as large as the giant pantropical alga, *Valonia macrophysa* (Shihira-Ishikawa and Nawata 1992), containing a water vacuole of approximately 10 g, the potential energy yield could be close to 1 J.

Thermal gradients could also be harvested directly. In a series of papers Muller (1985, 1993, 1995, 2003) and Muller and Schulze-Makuch (2006a) suggested thermosynthesis as a plausible metabolic pathway. Thermosynthesis, just as a steam engine, would make use of a phase transition (Muller and Schulze-Makuch 2006b). Membranes undergoing the thermotropic phase transition would increase the mobility of the molecules within the membrane (Muller and Schulze-Makuch 2006a). Due to a change in dipole potential, such a transition would quite plausibly result in a change in potential across the membrane (Muller 1993). Although this potential change has not been measured directly, similar potential changes that undergo the thermotropic phase transition have been measured across monolayers of lipids at the water/air interface. The changes can easily reach 100 mV—high enough to drive ATP synthesis (Muller and Schulze-Makuch 2006a). Electrogenic ATP synthases might be capable of converting the electrical energy gained by thermosynthesis into ATP if their activity and stoichiometry were properly regulated (Muller 1993). If correct, thermosynthesis could be a plausible basic pathway of metabolism for early organisms on Earth, possibly a progenitor of bacterial photosynthesis (Muller 1985, 1995, 2003), and an option for possible life on many other worlds.

A potential drawback to the use of thermal energy is its inefficiency. The most efficient thermodynamic system known—the Carnot engine—is very inefficient,

especially for small temperature differences. Because of the low efficiency, most of the energy in a thermal gradient would be dissipated as heat without being captured by chemical bonds, and would readily degrade the thermal gradient itself. A possible solution to the problem would be a thermotrophic organism that could shuttle back and forth across fairly sharp environmental gradients, or a thermotrophic organism that possesses an elongated body and makes use of convection to dissipate the unusable entropy-related energy.

Based on these principles, Muller and Schulze-Makuch (2006a) visualized four different physiological versions of a possible thermotrophic organism (Fig. 5.1). In the first type, a water vacuole would be warmed when the thermotroph moved into the vicinity of a hydrothermal vent. It could then float into the colder ocean, using the buoyancy of the warm vacuole, and harvest the free energy released by heat flow down the internal thermal gradient between the vacuole and the surrounding cell.

The other three types of thermotrophs are envisioned as sessile, with one end remaining anchored to the surface of the hydrothermal vent. The second thermotroph is a filamentous-type of organism that spans the thermal gradient between the hot structure and the cold ocean. Near the structure it could take up hot water in a vacuole, and then gain free energy as the vacuole moves inside the cell to the cooler distal part. The third type of thermotroph would take up cold ocean water in a vacuole or cavity, and eject warm water from its base, not unlike the pattern of water flow seen in sponges, barnacles or mussels. While this process is used for filter feeding by these contemporary organisms, it may hint at an ancestral mechanism for the direct harvesting of energy from heat (Muller and Schulze-Makuch 2006a).
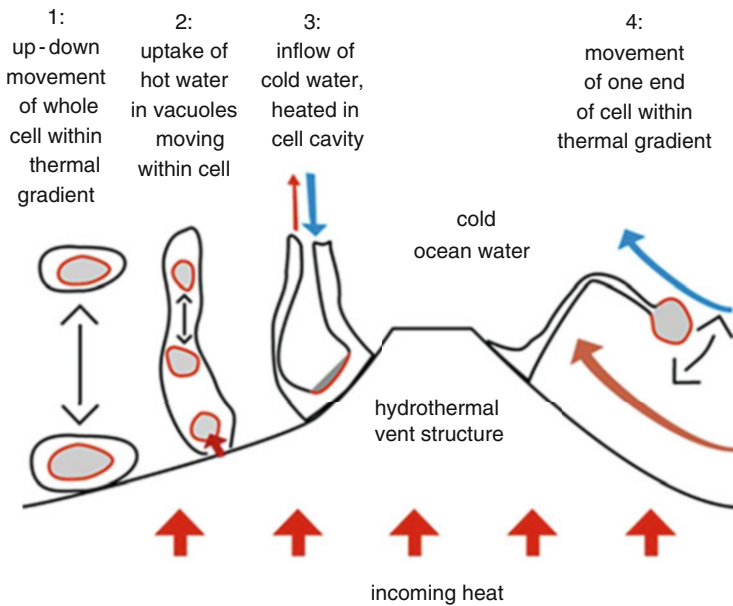

Fig. 5.1 Four types of thermotrophs that could be present near a hydrothermal vent. Areas within the organisms where the thermal gradient is tapped are marked in grey, hot water areas are red, and cold water areas are blue (modified from Muller and Schulze-Makuch 2006a)

Interestingly, mussels are still commonly found near vent structures today (Van Dover and Lutz 2004).

The fourth type of anchored thermotroph would have a distal end that moves freely in the cold ocean water, similar to the large sulfur bacteria (Gundersen et al. 1992) and giant tubeworms (Van Dover and Lutz 2004) present in the deep ocean environment today. Since the heat flux would vary on time scales as short as minutes (Tivey et al. 2002), water flow would be turbulent, and significant thermal fluctuations near the surface would therefore be expected, which could be harvested by the organisms, especially at summits of microscopic roughness that stick out above the boundary layer. Similar thermal fluctuations have been observed on top of bacterial mats in these environments (Gundersen et al. 1992). This type of thermotroph, can be compared to an organism that 'filters' temperature fluctuations from water, possibly sharing important characteristics of a direct progenitor of water filtering organisms such as the sessile protist ciliate *Vorticella*, with its long, quickly contractable stalk (Moriyama et al. 1998; Muller and Schulze-Makuch 2006a). It has to be emphasized that there are no known contemporary organisms that use thermal gradients as an energy source for metabolism, though such organisms conceivably could have existed on the early Earth, to be later outcompeted by phototrophic and chemotrophic organisms. But they could exist on an alien world. One possible example would be within the likely subsurface ocean of Europa, where light as an energy source is not readily available, but thermal gradients are likely to exist.

5.2.3 Kinetic Energy

The kinetic energy of convection cells or tidal currents could be harvested directly and used to sustain life. Organisms could contain pili or cilia much like ciliated bacteria or protozoa and adhere to a substrate at the ocean bottom or on the underside of an ice ceiling, where they are exposed to currents of moving water that cause the cilia to oscillate through bend and flex cycles that extract energy from the convection current (Fig. 5.2). The cells could enclose protein-like macromolecules that induce an electrical polarity across the membrane through a Donnan equilibrium. The hair cells could be surrounded by Na^+ channels whose permeability is proportional to the deflection of the hairs, with properties like those of sensory hair cells in the vestibular membrane of vertebrates or lateral line organs of fish (Fig. 5.3).

By bending the cilia, the convection currents could open the ion channels, allowing ions to flow into the cell passively down their concentration gradients. This thermodynamically favored process could be coupled to the direct formation of high-energy phosphate bonds or to a H^+ transporter across another internal membrane, by analogy with mitochondrial membranes (Schulze-Makuch and Irwin 2001). The ionic gradient would be maintained by extrusion of the ions via exocytosis. The ions could bind, for example, to intracellular macromolecules whose tendency to fuse with the external membrane and disgorge their ionic ligands is
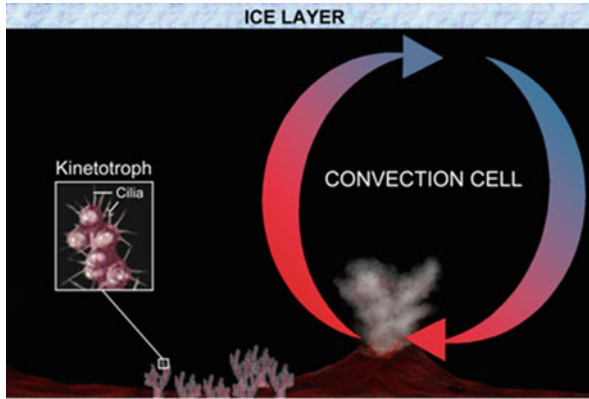
Fig. 5.2 Kinetotrophic organism in an oceanic environment, schematic. Convection currents can bend cilia leading to the opening of Na^+ channels, allowing Na^+ to flow into the cell passively down its concentration gradient. Art provided by Chris D'Arcy, Dragon Wine Illustrations, El Paso, Texas
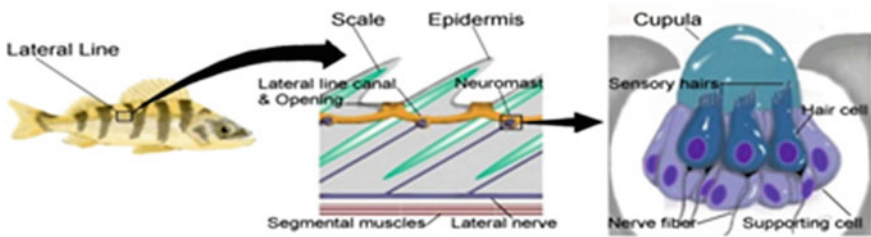

Fig. 5.3 Lateral line organ in fish, illustrating the role of cilia in transducing fluid movement into electrogenic signals. Cilia bend from the movement of fluid, allowing ions to move through the open channels. Art provided by Chris D'Arcy, Dragon Wine Illustrations, El Paso, Texas

thermodynamically favored, once the number of ions bound to the carrier reaches a concentration greater than the concentration of the ions outside the cell (Schulze-Makuch and Irwin 2002a). Alternatively, the ions could simply be precipitated as salts. A steady convection current with a velocity in the mm/s range would certainly be able to provide the requisite molecular distortion. Since this system works essentially like a battery that is charged over time, all that is needed is a minimal ionic gradient and enough time to charge the system high enough to form energy-storing chemical compounds.

5.2.4 Osmotic or Ionic Gradients

Osmotic gradients can be an enormously powerful source of energy. The osmotic pressure can be calculated by the van't Hoff formula.

$$\prod = c\,R\,T \tag{5.7}$$

where $\prod$ is osmotic pressure (atm), c is the molar solute concentration (mol/L), R is the universal gas constant (0.08206 L atm/mol K), and T is the absolute temperature (K). Some halophilic strains of cyanobacteria are known to tolerate salt concentrations of up to 2.7 M NaCl (Hagemann et al. 1999). Marine teleosts (bony fishes) retain a strong osmotic differential of roughly 0.7 osmoles between their intercellular fluids and their surrounding environment (Wilmer et al. 2000), where 1 osmole is 1 mole of osmotically active particles. Using this conservative figure as a first estimate at a temperature of 25° C (298 K), the osmotic pressure would be 16.9 atm (1.7×10^6 Pa). The force that acts on one water molecule along its concentration gradient is then

$$F = \prod A \tag{5.8}$$

where A is the cross-sectional area of one water molecule. This force is about 10^{-13} N. Further, assuming this force moves the water molecule through a membrane channel that couples the movement to the formation of a high-energy covalent bond, the energy available for bond formation is given by

$$W = F\,s \tag{5.9}$$

where s is the distance the water molecule moves down its density gradient (assumed to be 10^{-8} m for a biomembrane). Using the above figures, the calculated potential energy yield is 10^{-21} J, or 0.007 eV. Thus, one ATP could be phosphorylated from ADP for about every 45 water molecules entering the cell by osmosis. This is about two orders of magnitude below the energy yield for chemoautotrophs or photoautotrophs on Earth. The 0.007 eV may be a conservative estimate, because the osmotic differential calculated here is based on those of fish that have adapted from their freshwater origin to their marine environment rather than microbes adapted to use osmotic gradients. Halophilic microbes as described above, if adapted not only to tolerate but to use osmotic gradients, might easily be able to more than quadruple this energy yield.

The direct coupling of water movement to phosphorylation reactions is not known for living systems on Earth. However, evolution could have favored the origin of membranes in which water movement yields energy, where osmotic gradients were readily available and other forms of energy were not. A plausible mechanism would involve tertiary structural changes in a channel-associated protein that catalyzes formation of high energy bonds, much as ligand-induced conformational changes in membrane receptors lead to a series of steps culminating in the synthesis of high-energy cyclic AMP (Schulze-Makuch and Irwin 2002a). As in the case of thermal gradients, degradation of the osmotic gradient is a potential drawback to their use for generating free energy. The influx of many water molecules would either significantly increase the cell volume, or increase counteracting

pressure in rigid cells that cannot expand in volume. This could be mitigated, however, by a compensatory loss of solutes, such as efflux of Na^+ (and Cl^- for electrical balance) powered by the rise in intracellular pressure. Either the extrusion of solutes, or the pressure itself, could be coupled to conformational changes that could catalyze high energy bond formation. Alternatively, cell volume could be reduced by reverse osmosis upon movement of the organism to a more hypertonic level of the liquid medium. The zone close to the ocean bottom would be expected to be high in total dissolved solids due to persistent dissolution of the mantle and a higher density of salt water compared to fresh water. Solute gradients would be present both at the ocean bottom and in higher regions, but in opposite directions if not much water circulation is occurring. For example, a membrane water channel could be coupled to a reaction that forms a high-energy bond inside the cell as the water moves inward from hypotonic surroundings, while a similar channel oriented in the opposite direction could harvest energy when water leaves the cell in hypertonic surroundings. The hypothetical organism could thus move between two layers of different salinity, using both to harvest energy (Fig. 5.4).

Ionic gradients and H^+ gradients conceivably could also provide energy. For a 100-fold ionic gradient between the cytoplasm of an organism and its external environment—a differential observed in halobacteria on Earth (Madigan et al. 2000)—the amount of potential energy can be calculated from the Nernst equation

Fig. 5.4 A hypothetical osmotroph that harvests energy from osmotic gradients. Movement of water would be coupled to a reaction that forms a high-energy covalent bond through variants of a membrane molecular complex that are energized by the entrance or exit of water, depending on the direction of the osmotic gradient (P_i = inorganic phosphate, ATP formation is used as an example, not necessarily implying that ATP would be used by a hypothetical osmotroph). Redrawn from Schulze-Makuch and Irwin (2002a)
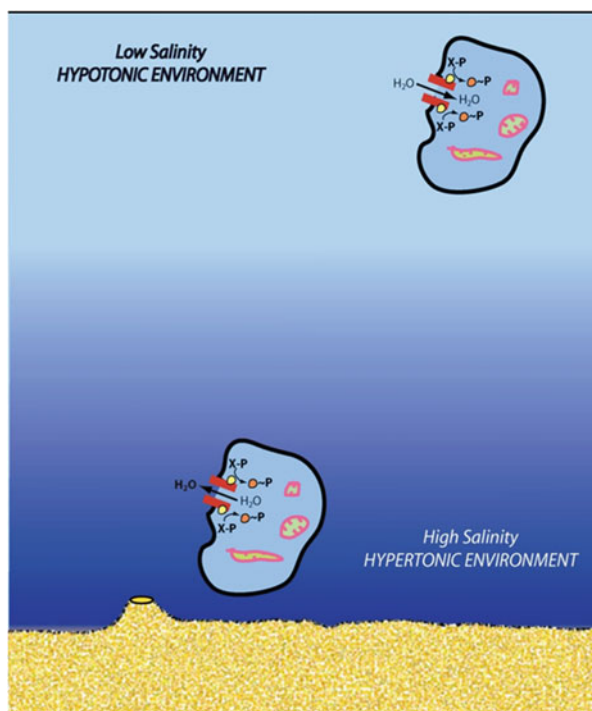
$$E = (RT/nF) \ln \left([ion]_{ext}/[ion]_{int}\right) \tag{5.10}$$

where n equals the number of charges transferred in the reaction, F the Faraday constant (J/mV mol) and R and T as above. The potential energy yield, $\Delta G = -nFE$, equals 0.12 eV, when $[ion]_{ext} = 100 \times [ion]_{int}$ at 298 K. This could drive the diffusion of about 3 ions, which could provide the energy for the phosphorylation of one ATP molecule. This might well be an underestimate of the potential energy yield since some bacteria achieve ionic distribution ratios as high as 10^6 across their membranes (Neidhardt et al. 1990).

Thus, the harvesting of osmotic or ionic gradients for bioenergetic purposes appears to be feasible in principle. Both types of gradients would often coexist, allowing for the possibility of reciprocal cycling between the two. On other planetary bodies where strong chemical concentration gradients are likely present, as in the putative liquid ocean on Europa (Kargel et al. 2000) and possibly other icy satellites, the use of osmotic or ionic gradients as bioenergetic sources must be considered a reasonable possibility, especially where other energy-yielding strategies may not be feasible. Irwin and Schulze-Makuch (2003) have modeled a putative multilevel ecosystem, based on the assumption of a hypertonic ocean bottom and a hypotonic ocean ceiling on Europa. Their calculations indicate that organisms the size of brine shrimp could be supported at a density of several hundred per cubic meter at the ocean bottom. While such an ecosystem is purely hypothetical at this point, their calculations point to the theoretical feasibility of an ecosystem in which the producer level is powered purely by osmotic or ionic gradients.

5.2.5 Magnetic Fields

Charge separation and extractable free energy can be generated from magnetic fields in theory. Magnetic fields can yield energy based on the Lorentz force, the movement of a charge within a magnetic field, or by induction from a periodically changing magnetic field. The Lorentz force can be expressed by

$$F_L = q(E + v \times B) \tag{5.11}$$

where E is the electric field acting on the charge (Newton/Coulomb; N/C), v is the velocity (m/s) of the charge in the magnetic field, and B (T) is the magnetic field strength. The cross product $v \times B$ is reduced to vB in the special case of a perpendicular movement of the charge with respect to the direction of the magnetic field B. If the movement of the charge occurs parallel to the direction of the magnetic field, the cross product is zero, and thus in the absence of an electric field no force acts on the charge q. A somewhat analogous directional dependence is observed for induction. In the absence of a magnetic field (B = 0), a charge is accelerated parallel to the electric field such that

$$F = qE \tag{5.12}$$

with E being the magnitude of the electrical field (N/C).

5.2.5.1   Possible Biogenic Use of the Lorentz Force

The amount of energy that can be extracted via the Lorentz force depends on the strength of the magnetic field of the particular planetary body. The strength of Earth's magnetic field at the surface is about 0.3 gauss, or 3×10^{-5} Tesla (T). There are planetary bodies that have a far larger magnetic field strength than Earth, such as Jupiter (4.3 gauss at the equator) and Saturn. Earth's magnetic field can be described in a first approximation as a magnetic dipole. Any charged particle moving in a conducting liquid at a direction perpendicular to the magnetic field line would experience the Lorentz force. Protons inside of organisms are charged and Earth's oceans consist of salt water, which is a conducting liquid. But would the Lorentz force be sufficiently strong to yield a significant amount of energy? Let us assume a hypothetical organism the size of an Earth microbe that is transported by the current of the convection cell at a rate of 1 m/s perpendicular to the magnetic field lines. Then the potential energy yield can be calculated from

$$W = F_L \ s \tag{5.13}$$

where W is the energy yield (J or eV), F_L is the Lorentz force as given above, and s is the distance where charge separation can occur. If it is assumed that the total length of the microbe (10^{-6} m) can be used for charge separation, then the Lorentz force that can act on a unit charge (electron or proton, $q = 1.6 \times 10^{-19}$ C) is about 5×10^{-24} N. This charge separation can be imposed if the magnetic field is perpendicular to the line of movement of the charge and released if the magnetic field is oriented parallel to the movement of the charge. It follows that the energy obtained from the Lorentz force is 3×10^{-11} eV, 11 orders of magnitude lower than the energy that could be obtained by chemoautotrophy (assuming hydrogen-oxidizing metabolism) or photoautotrophy. However, there is no conceptual reason why charge separation of only one electron or proton can be harvested at one time; several or thousands of reactions could occur in parallel. Also, the available energy yield could be increased by many orders of magnitude, if the microbe is an analog to hair cells on Earth with lengths in the millimeter or centimeter range instead of being ball- or pancake-shaped in the micrometer range. A plausible energy-harvesting mechanism could be that H^+-ions are driven across a one-way channel against their concentration gradient into an internal organelle, where they accumulate to a higher concentration gradient than on the outside of the organelle. Then, the H^+-ions can diffuse back out of the organelle through a different channel coupled to a phosphorylation reaction that produces a high-energy organic phosphate (similar to how mitochondria work). A more elaborate scheme would be if the Lorentz force is used to separate one electron and one

Fig. 5.5 Scheme for
magnetotrophic organism to
obtain energy, (**a**) Lorentz
force separates protons and
electrons, (**b**) magnetic field
lines are oriented parallel to
long axis of microbe, and
protons and electrons form
molecular hydrogen
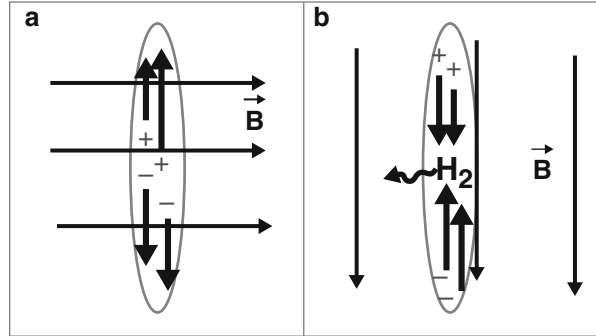
proton from the center of the cell in opposite directions toward the respective ends of
the hair cell. When the magnetic field lines are oriented parallel to the hair cell, the
energy could be released and the proton and electron would move toward each other
producing H_2 (Fig. 5.5). The efficiency of both types of model organisms could be
increased if its cells would contain magnetite crystals orienting themselves to the
external magnetic field to optimize the harvest of magnetic energy (Schulze-Makuch
and Irwin 2001).

In addition to the model organisms discussed, there is another interesting possi-
bility: charge separation would not necessarily have to occur within the microbial
cell. Organisms of microbial dimensions could be envisioned that would cling to
strips of inanimate conducting material and harvest energy from the magnetically
induced electron flow in their substrates. That possibility would depend, in part, on
whether a suitable mineral or aggregate of conducting matter would be present under
the environmental conditions in question. Mineral assemblages including silicates,
zeolites, albite, sphene, and illites, plus the iron minerals pyrite and hematite, have
been identified at deep hydrothermal systems on Earth (Gonzalez-Partida et al. 2000)
and could constitute suitable materials. Although not impossible, it would take a
considerable effort to overcome a difference of 11 orders of magnitude in energy
gain. Thus, it is not surprising that we don't encounter magnetotrophic life on Earth.
However, sensitivity to magnetic fields, as in magnetotactic bacteria, is a well-
established phenomenon (Blakemore 1982; Frankel et al. 1979), and there is strong
evidence that some animals use magnetospheric orientation for navigation
(Aekesson et al. 2001; Ioale et al. 2001). This implies the presence of cellular
mechanisms for detecting magnetospheric energy. In the absence of more concen-
trated or effective sources of free energy, it seems plausible to assume that a cellular
mechanism for transducing magnetospheric energy into a biologically useful form
could evolve.

5.2.5.2   Possible Biogenic Use of Induction

The second physical option for harvesting energy from a magnetic field is by
induction. The possibilities and problems associated with that option will be

examined using Jupiter's moon Europa as an example (Schulze-Makuch and Irwin 2002a): It seems highly likely that Europa has a liquid subsurface ocean beneath its icy surface (Kivelson et al. 2000), which may be a suitable environment for microbial life. Jupiter's magnetospheric plasma corotates with Jupiter at a corotational velocity of 118 km/s at the orbit of Europa (Beatty and Chaikin 1990). Thus, Europa moves with respect to Jupiter's rotating field lines at a relative velocity of 102 km/s. However, the force exerted by this magnetic field cannot be used by an organism in the ocean. Europa's thick insulating layer of ice concentrates induced charges that produce an electric field that exactly cancels the Lorentz force. However, it was observed that Jupiter's magnetic field creates charge separation in a global conducting layer, which was interpreted as a shell of a salty ocean with a high electrical conductivity (Zimmer et al. 2000). Thus, the option remains that energy can be obtained from magnetic fields based on the induction from a periodically changing magnetic field (the Lorentz force, however, would still apply, as a charge can move perpendicular to the induced magnetic field, but it would be at a much lower magnitude). The alternating magnetic field that is experienced by Europa's ocean can be described as follows: Europa is subject to an oscillatory magnetic field

$$B = B_o \sin(w\,t) \qquad (5.14)$$

with an amplitude B_o of about 200 nT. Thus, the rate of change is

$$dB/dt = w\,B_o \cos(w\,t) \qquad (5.15)$$

with a maximum value of $2\pi\,B_o/10$ h, which corresponds approximately to 2 nT/min (Khurana et al. 1998). The work W performed on a charge q (e.g. an electron or proton) is then given by

$$W = U_{ind}\,q \qquad (5.16)$$

where $U_{ind} = A\,(dB/dt)$ with A being the microbial cross-sectional area (m^2), dB/dt the change of the magnetic field strength (T/s), W is work or energy (J), and q is a unit charge of 1.602×10^{-19} C per electron or proton.

Assuming a microbial diameter of 1 μm, and the above figure for a reasonable maximum temporal magnetic field change in Europa's ocean, the amount of energy per reaction that can be extracted via induction is about 4×10^{-42} J or 3×10^{-23} eV per electron, which is 23 orders of magnitude lower than the energy that can be harvested via chemosynthesis or photosynthesis on Earth. Even if many of those reactions would occur simultaneously, the energy gain is much too low. Thus, induction does not appear to be a feasible option for living systems to capture energy in Europa's ocean, and would only be very unlikely anywhere else.

5.2.5.3 Concluding Remarks on the Biogenic Use of Magnetic Energy

Life based on magnetic energy does not appear to be very promising in an Earth-type environment. However, magnetic field strengths much larger than on Earth would present certain possibilities. The gas giants Jupiter and Saturn have much larger magnetic field strengths, and neutron stars have magnetic field strengths millions of times stronger than the Sun or planets that surround a star like our Sun (Lattimer and Prakash 2004). Although life on gas giants or a neutron star itself would be very unlikely due to other considerations that are discussed in the following chapters, some moons that orbit the gas giants, and especially planets that orbit neutron stars, may provide an opportunity for organisms to harvest magnetic energy. For example, the neutron star SGR 1806-20, a magnetar, has been reported to have a magnetic field strength of about 10^{15} Gauss, or 10^9 T (Ibrahim et al. 2003). Energies from these huge fluctuating magnetic fields could become competitive for organisms on planets orbiting neutron stars, depending on the magnetic field strength of the particular star, distance of the planetary body from the neutron star, environmental conditions on the planet or moon, and the availability of suitable niches below the planetary surface for protection from radiation intensity, among other factors. Refined adaptive strategies by organisms that would have evolved in such an environment presumably would have increased the efficiency of magnetic energy to make it competitive with light and chemical energy, even under planetary conditions similar to our Solar System; but the strategies would have to be highly refined in a more efficient direction to make up for the generally low energy yield.

5.2.6 Gravitational Forces

Gravitational energy could be harvested in a direct fashion by the movement of protons or molecules through a gravitational field. The effects of gravity on a large scale are readily seen on Earth by the tidal amplitudes in the oceans caused by gravitational interactions between the Earth, Moon and Sun. Tidal flexing is more dramatic on Io, the volcanically most active planetary body in our Solar System, due to strong tidal interactions between Jupiter inside Io's orbit and the other three major moons beyond its orbit. But gravity is the weakest of the fundamental forces known in nature, and the free energy that it yields on a small scale is very slight. That value can be calculated by assuming a simple model in which a proton is moved a micrometer (assumed microbial diameter) against a defined gravitational attraction.

$$W = m_H + g\,h \tag{5.17}$$

On Earth, the energy would be about 10^{-13} eV and thus much smaller than the energy than can be harvested via chemotrophy and phototrophy. If large macromolecules (~10^6 atomic mass units) instead of protons were moved, the energy yield

could be as high as 10^{-7} eV. Even allowing for a planetary body the size of Jupiter, chemotrophy and phototrophy would still out-compete gravitational energy. Thus, gravitational forces seem unlikely as a useful direct basis for bioenergetics in our Solar System, because gravity is simply far too weak. However, the *indirect* effects of gravitational forces, such as convection currents in the oceans could be used to power living systems, as discussed before (see Sect. 5.2.3). It should also be pointed out that organisms are sensitive to gravity on Earth. Even single cell organisms can orient themselves in a gravitational field through the use of intracellular receptors located in the cell membrane (Bräucker et al. 2002).

5.2.7   Tectonic Stress

Meteorite impacts and fractures within a planetary crust release energy that could be used by organisms for obtaining energy. Meteorite impacts are common occurrences as can easily be observed on our Moon, Mercury and Mars. The meteorite's kinetic energy is converted upon impact into electrical potential, while the mechanical disruption of the impact causes the release of stress energy in the form of light, heat, electrical fields and magnetic fields (Borucki et al. 2002). While the impact only occurs in a short time period that can be measured in milliseconds, melted slurry pools under impact sites can persist for as much as a million years, depending on the size of the impact, as shown by Sagan et al. (1992) for Titan. Additional energy supplied from crustal stress to the subsurface regions after the impact could increase the lifetime of the melted impact zone and provide suitable conditions for microbial life. While the energy released from the immediate impact of the meteorite would dissipate relatively fast, energy provided by the piezoelectric effect could be provided for a very long time. Piezoelectric energy is a form of electricity generated when a pressure is applied to an ionic solid as a result of strain. A charge across the crystal is produced because a dipole moment is created by the deformation of the otherwise non-polar molecular structure. The polarization of the crystal faces parallel to the direction of strain converts the crystal into a capacitor, which temporarily stores an electrical charge. A good example for demonstrating this effect is a planar molecule of any ionic solid. Its structure has 3 electric dipoles at 120° to each other, which cancel and give a net dipole moment equal to 0. Applying a pressure or a voltage to this molecule will result in deformation of the molecule, and the generation of a dipole moment as a result of this deformation. The piezoelectric effect will immediately cease if the pressure or current is removed from the structure of the crystal. Piezoelectric energy, although somewhat "exotic," could thus provide a possible avenue for life. It could be associated not only with meteorite impacts but also with other geological events such as plate tectonics on Earth. However, it is restricted to 20 of the 32 crystal classes, ionic crystalline solids that lack a center of inversion such as quartz, perovskite, sodium chlorate, and Rochelle salt. Similar to the other alternative energy sources, no indication of its energetic use by microbial organisms has been observed on Earth. It is doubtful whether this process can

provide a sufficient or sufficiently constant amount of energy. At the very least, it does not appear to be competitive with chemical or light energy.

5.2.8   Pressure Gradients

Life based on energy harvested from a pressure gradient is another theoretical possibility. There are three principal opportunities. Energy could be harvested from atmospheric, fluid or subterranian pressure gradients.

Pressure gradients exist in the vertical column of any atmosphere held by gravity. However, the capacity of such a pressure gradient to be used as an autotrophic energy source is questionable. Atmospheric pressure is the sum of the forces of all the molecules striking a surface area, and thus a measure of the linear momentum of the gas molecules. A pressure gradient is established if the molecules do not move randomly, but in a preferred direction. It is difficult to see how a microbial organism suspended in the atmosphere could utilize the pressure gradient. The organism would just be carried along with the wind, unable to maintain a consistent orientation within the pressure gradient, which in any event would be miniscule over the linear dimensions of the organism. This does not exclude the atmosphere of planets and large moons as habitable environments, but other metabolic strategies such as chemoautotrophy or photoautotrophy would have to be employed, as suggested originally for the Jovian atmosphere (Sagan and Salpeter 1976) and more recently for the Venusian atmosphere (Grinspoon 1997; Schulze-Makuch and Irwin 2002b).

Large pressure gradients can also exist in fluids. For an organism suspended in the fluid, the same problem would be faced as that of an organism suspended in an atmosphere. If the organism were attached to a fixed substrate, it could at least maintain a consistent orientation within a localized pressure gradient. Such localized pressure gradients exist, for example, at hydrothermal vents on the ocean floor. However, the wide fluctuations in pressure likely arising at the vents would represent a practical problem. Furthermore, how an organism could stay attached to a substrate at these pressures and at the same time harvest the pressure gradient is unclear.

Tremendous pressures are present in the vertical rock column of a planetary body's lithosphere. Since microbial organisms are known on Earth to live at considerable subterranean depths, there is precedence for assuming that life on other worlds would occupy this habitat. Although the absolute pressure is high, the pressure gradient is not, especially with respect to microbial dimensions. Thus, life based on pressure gradients in the subsurface does not appear likely.

5.2.9   Spin Configurations

Atoms in molecules can revolve and rotate in various ways. For example, the two atoms of hydrogen gas, H_2, perform a vibrational motion in the direction of the line

Fig. 5.6 Motions of
o-hydrogen and p-hydrogen,
(**a**) o-hydrogen atoms
revolve around a common
center, while their nuclei
rotate around their own axis
at the same time, (**b**) In the
simplest version of
p-hydrogen the atoms do not
revolve and the nuclei rotate
in opposite directions.
Modified from Feinberg and
Shapiro (1980)
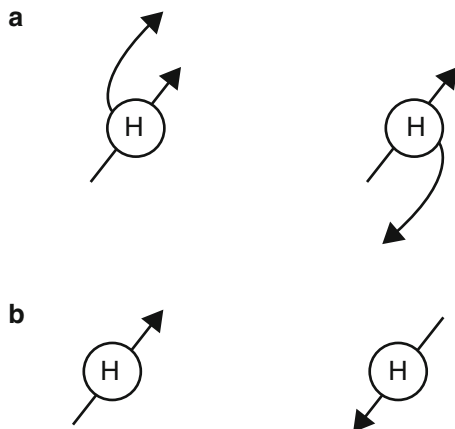
joining the nuclei, and a rotational motion around a direction perpendicular to the molecular axis in addition to the translational motion. The vibrational and rotational motions are in quantum states resulting in two different modifications of hydrogen, parahydrogen molecules that have antiparallel nuclear spins and even rotational quantum numbers, and orthohydrogen molecules that have parallel nuclear spins and odd rotational quantum numbers (Fig. 5.6). The two sets of molecules do not easily convert into each other but can be considered as two gases differing from each other in certain optical and thermal properties (Farkas 1935). The o-hydrogen is the higher energetic state but is relatively stable kinetically. For example, although at 20 K equilibrium hydrogen consists practically of pure parahydrogen, simply cooling the hydrogen to this temperature or transitory liquefaction or solidification does not cause equilibrium to be established.

The two states of hydrogen could provide a source of energy in very cold environments with abundant hydrogen. For example, one could envision a mechanism to retrieve energy by having o-hydrogens on a cell boundary collide with o-hydrogen molecules in the environment. Both o-hydrogens would convert to p-hydrogen and a relative high energy yield of about 700 J/g would be obtained. P-hydrogens could then be converted back to o-hydrogens by allowing rotating p-hydrogens to collide with magnetic impurity molecules (such as oxygen), which would catalyze the formation of o-hydrogens. The potential of spin configurations as an energy source was first realized by Feinberg and Shapiro (1980), who suggested the possibility of life based on spin configurations on a very cold and dark planet, just a few 10s of degrees above absolute zero. Although energy based on spin configurations represents an intriguing idea, it is doubtful that at these low temperatures energy could be transferred into chemical energy usable to organisms at a high enough rate. Energy from spin configurations may rather present an interesting engineering opportunity and challenge to obtain energy for space probes on cold and dark planetary bodies.

5.2.10 Radioactivity

Radioactivity is one of the most basic processes in our Universe. Radioactive nuclei of atoms decay with time and release particles and electromagnetic radiation. Forms of high-energy radiation include alpha (helium nuclei) and beta particles (electrons or positrons), gamma rays (short wavelength, high-energy photons), X-rays, neutrons, and heavy ions. This type of radiation is very destructive to life as we know it because it destroys biologically important molecules, especially the sensitive machinery for molecular replication. Biological effects depend on the spatial density of ionizations produced per unit absorbed dose in the irradiated tissue. For example, particles with high atomic numbers and high energy (HZE particles) cause the greatest damage for a given dose (Baumstark-Khan and Facius 2002). Nuclear processes are the ultimate source of energy for life on Earth, since the Sun emits photons as a byproduct of the fusion of hydrogen into helium at its core. And heating produced by radioactive decay in the Earth's core could serve as the energy source for possible thermoautotrophic organisms. The question remains, however, whether radioactivity can be tapped directly by living organisms. This may be too destructive for organic synthesis and reproduction. Due to the presence of many radioactive isotopes with short half-lives, radioactive material was much more common on the early Earth, when life originated or first became established. Yet, today high-energy radiation does not serve as an energy source for any form of life as far as we know. Gamma radiation and X-rays may have been too rich in energy and too difficult to control. Or, was the visible light of our Sun simply more accessible and easier to use? How about the alpha and beta particles? They possess ample amounts of kinetic energy over the short distance of cellular dimensions. From an energetic viewpoint they would be a preferential energy source. Yet, they are not used as far as we know either. Again, the basic problem may be control, as well as insufficient frequency, and inconsistency. Radiation and particle emissions occur in a random fashion from a decaying atom. The frequency, direction, and precise level of energy are all unpredictable. It is difficult to envision how any organism could control the decay in a way to obtain energy on a consistent basis. On Earth, organisms have developed mechanisms to avoid, tolerate, and repair damage caused by ionizing radiation. A prime example is *Deinococcus radiodurans*, which possesses a high redundancy of repair genes to cope with ionizing radiation and organic pigments to cope with UV radiation. However, ionic radiation has not only deleterious effects on life, but can also have beneficial consequences (Dartnell 2011). Radiolytic compounds created within Europa's crust by radiation and impact gardening are one example. Based on estimated delivery rates to the subsurface ocean, Greenberg (2010) concluded that oxygen levels could be high enough to support a substantial macrofauna.

5.3   The Question of Entropy, Uniformity, and Origin

A qualitative and quantitative assessment of the various energy sources indicates the theoretical plausibility that several of them potentially could power living organisms on other worlds. From a purely energetic view, a thermotrophic organism appears to be most favored. Such an organism may have in fact developed on Earth, and may be the progenitor of the photoautotroph as suggested by Muller (1995). His proposed thermosynthesis scheme is certainly simpler than photosynthesis, and heat is a ubiquitous energy source. However, we do not observe the presence of thermotrophic life on Earth, even though it appears to be favored on the basis of theoretical energetic considerations. It may be present and yet undiscovered on Earth, but terran life definitely prefers chemical and light energy. What is the basic difference between thermal gradients on one hand, and chemical and light energy on the other hand that could account for this observation? Thermal energy has a high degree of entropy—it is highly disordered. Chemical and light energy are highly ordered forms of energy. According to the second Law of Thermodynamics, the degree of disorder in a system as a whole has to increase spontaneously with time. Any form of life is highly ordered and complex, and living processes increase the order of the system further. In order to maintain the highly ordered state of a living system, some free energy has to be expended to increase the degree of disorder, because the overall entropy of the system and its environment has to increase. In terran organisms this increase in entropy is achieved by giving off heat and waste products, which are highly disordered. Thus, using a highly disordered energy source to begin with is very inefficient. Much less of the total amount of energy obtained from a more highly ordered source has to be converted into the disorder required to obey the second Law of Thermodynamics. Clearly, then, entropy is a factor that needs to be considered when assessing whether alternative energy sources can be used to power an organism.

Another factor that needs to be considered is uniformity of intensity. An alternative energy source has to provide its energy in quanta suitable and manageable for the organism to use. High-energy particles as emitted from decaying atoms are inconsistent and unpredictable, for instance. It may be that living systems can evolve a capacity to harvest energy more easily when that energy comes in the specific and consistent quanta appropriate for the control of metabolic reactions in a reliable way.

One other factor that needs to be considered is the question of pre-biotic evolution. How difficult was it for the earliest organisms to develop a mechanism for harvesting a specific energy source? The molecular machinery that has survived in chemoautotrophs and photoautotrophs today is very complicated, hence highly unlikely to have been the earliest mechanism for energy extraction. At the origin of life, the mechanisms for harvesting energy must have been simpler, and quite possibly were dependent on sources other than those that are used today. Chemoautotrophy and photoautotrophy are now the dominant basis for life on Earth, presumably because of the abundance and efficiency of those sources of energy. However, there may have existed early bioenergetic mechanisms that possibly were outcompeted over evolutionary time by more efficient mechanisms.

5.4 Survey of Energy Sources in our Solar System

Energy sources are ubiquitous in our Solar System. Solar radiation providing light and thermal energy is one of the dominant energy sources for the interior terrestrial planets, and still significant for the Jovian and Saturnian systems. Heterogenous surface colorations such as on Venus and many of the icy outer satellites imply the presence of chemical energy. Geothermal energy is indicated by volcanism and a high-density interior that would imply radiogenic heating on planetary bodies such as Venus, Mars, Io, and Enceladus. Pressure is an energy source for planets with thick atmospheres such as the gas giants and Venus. Kinetic energy is a force on any planetary body with strong convection cells such as the gas giants, and possibly Europa. Tidal flexing is an energy source commonly found in the Solar System, for example at Io, Europa and Triton. Strong radiation and magnetic fields emanating from Jupiter and Saturn affect their satellites. Tectonic stress is definitely observable on Io, and osmotic gradients may be present on icy moons with a subsurface liquid ocean as proposed for Europa, Ganymede, and Titan. Observations indicating the presence of various energy sources on the major planetary bodies of our Solar System are listed in Table 5.1. This does not mean that the potentially available energy sources are actually used by putative organisms, but only that they are present based on our current knowledge. A discussion on the suitability of life on those planetary bodies based on energy sources plus other geoindicators is provided in Chap. 9.

Table 5.1 Energy sources in the Solar System that would be available in principle for other possible forms of life

Body	Observations	Energy source
Mercury	Thermal gradients pass through range for liquid water at slowly moving terminator. Possible water ice at poles. High density and electromagnetic field $\Rightarrow$ metallic core	Solar radiation, geothermal
Venus	Extensive resurfacing $\Rightarrow$ geological activity and chemical recycling. Very dense atmosphere $\Rightarrow$ pressure gradients	Solar radiation geothermal, chemical, pressure
Moon	Extensive cratering $\Rightarrow$ old surface. Evidence of past volcanism. High density $\Rightarrow$ metallic core. Strong sunlight. Minor amount of frozen water at poles	Geothermal, solar radiation
Mars	Daily to seasonal temperature fluctuations above melting point of water at some latitudes, volcanoes. High density and weak electromagnetic field $\Rightarrow$ metallic core. Surface erosion by flowing water. Likely aquifer beneath permafrost	Solar radiation, geothermal, chemical?
Jupiter, Saturn, Uranus, Neptune	Gas giants with indistinct high-pressure atmosphere/liquid transitions, extensive turbulence. Strong magnetospheres and radiation output	Pressure, convection, magnetism, radiation
Io	Volcanism, extensive resurfacing, large size, and density >3.5. Surface coloration $\Rightarrow$ complex chemistry. Strong Jovian radiation. Weak intrinsic electromagnetic field	Geothermal, tidal flexing, chemical, stress (tectonic), magnetic
Europa	Extensive resurfacing, density >3. Surface coloration $\Rightarrow$ complex chemistry and chemical recycling. Water ice surface, liquid subsurface water. Strong Jovian radiation. Projected high salt contents in subsurface liquids	Geothermal, tidal flexing, magnetic, chemical, convectional, radiation, osmotic gradients
Ganymede	Extensive resurfacing $\Rightarrow$ geological activity, subsurface liquid water. Rippled surface, low density, weak magnetic field. Surface coloration $\Rightarrow$ complex chemistry. Strong Jovian radiation	Geothermal, tidal flexing, chemical, radiation, magnetic
Callisto	Low density $\Rightarrow$ mostly water-ice. Strong Jovian radiation. Extensive cratering, lack of magnetic field $\Rightarrow$ little internal energy	Magnetic, radiation
Enceladus	Very low density and high albedo $\Rightarrow$ mostly water-ice. Strong Saturnian radiation. Heavily cratered but resurfaced in part, with evidence of a subsurface liquid water reservoir, ice geysers and volcanic activity $\Rightarrow$ internal energy	Geothermal, tidal flexing, radiation, magnetic, convectional

Table 5.1 (continued)

Body	Observations	Energy source
Iapetus	Low density and moderate albedo $\Rightarrow$ mostly water-ice. Dark leading edge $\Rightarrow$ possible hydrocarbon chemistry. Heavily cratered: Little internal energy	Chemical
Titan	Dense, colored atmosphere $\Rightarrow$ complex chemistry. Density $\simeq 1.8 \Rightarrow$ organic liquids and water-ice, with solid core. Atmospheric protection from radiation	Chemical, geothermal
Triton	Surface coloration $\Rightarrow$ complex chemistry, unusual surface features $\Rightarrow$ internal energy. Density $\simeq 2 \Rightarrow$ rocky core. Elliptical, retrograde orbit $\Rightarrow$ tidal flexing and seasonal temperature fluctuations; volcanism. Possible subsurface ocean	Chemical, geothermal, tidal flexing, stress (tectonic)
Pluto Charon	Density ~2.1 $\Rightarrow$ rock/ice mixture. Mix of light and dark features $\Rightarrow$ complex chemistry	Tidal flexing, chemical

5.5 Chapter Summary

We have used relatively straightforward evaluations and calculations to show that life does not need to be restricted to energy from chemical bonds and light as a basis for bioenergetics, as it apparently is on Earth. While light and chemistry do indeed represent cosmically abundant and efficient sources of energy, on many worlds other sources of energy may be more practical. Thermal, ionic, and osmotic gradients, as well as the kinetic energy of fluids in motion, appear to be the most promising alternatives to light and chemistry on worlds where the latter energy sources are not available. But in specialized circumstances, other exotic forms of energy could be favored. Life evolving under those alternative conditions would be pressured by natural selection to make use of the forms of energy available. The numerous alternative options that are plausible within our own Solar System are shown in Table 5.1. Even though life on Earth may not use any energy source other than chemistry and light, the sensitivity of terran organisms to many other forms of energy provides a hint of other bioenergetic possibilities elsewhere in the Universe.