Theoretical constraints imposed by gradient detection and dispersal on microbial size in astrobiological environments

Manasvi Lingam*

Department of Aerospace, Physics and Space Science, Florida Institute of Technology, Melbourne, FL 32901, USA

Institute for Theory and Computation, Harvard University, Cambridge, MA 02138, USA

Abstract

The capacity to sense gradients efficiently and acquire information about the ambient environment confers many advantages like facilitating movement toward nutrient sources or away from toxic chemicals. The amplified dispersal evinced by organisms endowed with motility is possibly beneficial in related contexts. Hence, the connections between information acquisition, motility, and microbial size are explored from an explicitly astrobiological standpoint. By using prior theoretical models, the constraints on organism size imposed by gradient detection and motility are elucidated in the form of simple heuristic scaling relations. It is argued that environments such as alkaline hydrothermal vents, which are distinguished by the presence of steep gradients, might be conducive to the existence of “small” microbes (with radii of $\gtrsim 0.1 \mu$m) in principle, when only the above two factors are considered; other biological functions (e.g., metabolism and genetic exchange) could, however, regulate the lower bound on microbial size and elevate it. The derived expressions are potentially applicable to a diverse array of settings, including those entailing solvents other than water; for example, the lakes and seas of Titan. The paper concludes with a brief exposition of how this formalism may be of practical and theoretical value to astrobiology.

1 Introduction

The ability to precisely sense physical and chemical gradients is a ubiquitous feature of the microbial world, which is not surprising in light of the many desirable outcomes that are documented to result from this ability (Alexandre et al., 2004; Mann and Lazier, 2006; Hu and Tu, 2014; Bi and Sourjik, 2018). For instance, the ability to sense gradients in the chemical concentration enables organisms to move either toward or away from these compounds (Phillips et al., 2013, pp. 159-161); see also Wadhams and Armitage (2004). In the former case, one of the chief advantages is the ability to reach nutrient sources and thereby benefit from enhanced uptake (Lauro et al., 2009; Stocker, 2012; Kirchman, 2018), while other positives include range expansion, biofilm formation and the onset of symbiosis (Porter et al., 2011; Cremer et al., 2019; Wong-Ng et al., 2018; Raina et al., 2019). In the latter (i.e., movement away from the sources), microbes can endeavor to avoid toxic chemicals.

*Electronic address: mlingam@fit.edu
by travelling in the direction with lower concentration, or they could come up ways to mitigate the damage (Kirchman, 2018).

This mechanism, which constitutes a response to chemical stimuli and gradients, is known as chemotaxis. It has a long and distinguished history spanning myriad disciplines of science dating back to the nineteenth century (Engelmann, 1881; Pfeffer, 1884; Bonner, 1947; Adler, 1966; Keller and Segel, 1971; Berg and Brown, 1972; Berg and Purcell, 1977; Hazelbauer, 2012; Tu, 2013; Camley, 2018; Painter, 2019). Chemotaxis in bacteria, with the well-known model organism \textit{Escherichia coli} being one example, exhibits many remarkable features including high sensitivity, flexibility and robustness vis-à-vis chemical stimuli (Alon et al., 1999; Bialek and Setayeshgar, 2005; Sourjik and Wingreen, 2012; Micali and Endres, 2016; Waite et al., 2018; Figueroa-Morales et al., 2020).

Aside from chemotaxis, the likes of phototaxis and thermodaxis—which are reliant on identifying light and thermal gradients, respectively—have also been widely investigated in model organisms and via theoretical modelling (Armitage, 1999; Mori, 1999; Jékely, 2009; Demir and Salman, 2012; Hu and Tu, 2014; Lozano et al., 2016; Wilde and Mullineaux, 2017; Yang et al., 2018). In each of these mechanisms, the key common point that deserves to be appreciated is: organisms sense information about their environments. While this information can be put to many uses, one of the key aspects that we shall focus on herein is targeted locomotion (Webster and Weissburg, 2009)—that is to say, movement along some preferred direction. Thus, if microbes are not efficient at acquiring information about their habitats, their capacity for meaningful motility could be stymied, although there are latent subtleties at play (Celani and Vergassola, 2010; Taktikos et al., 2013). This process of detecting gradients and gaining information is reliant on accurately measuring the “intensity” of the stimulant at multiple points in space or time (Berg and Purcell, 1977; Berg, 1993).

As the preceding sentence indicates, there exist two basic modes of sensing, namely, the spatial and the temporal (Dusenbery, 2009). In the former, microbes use the data garnered from receptors at different spatial locations to determine the direction of locomotion. In the latter, measurements from the receptors are collected at various moments in time to regulate the direction. The upshot of the prior discussion is that gradient sensitivity is generally expected to play a crucial role in modulating the efficacy of motility (Fenchel, 2002). This statement yields a vital corollary: if the organism is too small to sense gradients efficiently, this bottleneck would pose difficulties for meaningful locomotion. In other words, the constraints imposed by information specify a minimum cell radius ($R_{\text{min}}$) for microbes that are efficient at gradient sensing and dispersal. Naturally, this does not represent the only limiting factor, and we will touch upon other controls later in the paper.

It is worth highlighting that motility is regarded a viable biosignature candidate for \textit{in situ} life-detection missions (Nadeau et al., 2016, 2018; Neveu et al., 2018, 2020; Riekeles et al., 2021). In fact, the spatial resolution required to identify motile organisms is lower when compared to their non-motile counterparts (Nadeau et al., 2016, pg. 755). The ability to pin down the minimum cell size, and the cell density of motile lifeforms thence (Lingam and Loeb, 2021b), is valuable therefore from the practical goal of gauging and designing suitable instruments for future missions. However, we emphasize that the \textit{raison d’être} of this paper is not to solely assess the feasibility of motility as such. Our major objective is, instead, to unveil the constraints on gradient sensing imposed by size; to put it differently, the chief purpose is to explore how size conditions the efficiency and efficacy of organisms to acquire information about their environment, which in turn permits them to act in a number of ways delineated above. It is essential to recognize that this is \textit{not} the only bottleneck on size because factors like energy, nutrients, cell structure and physiology also play a role (LaRowe and Amend, 2015; Lever et al., 2015; Kempes et al., 2019; Lopatkin and Collins, 2020). As stated earlier, our goal is to explicate some of the inherent connections between gradient detection and organism dispersal on the one hand and microbial size on the other.

For the purposes of this paper, we will adopt the heuristic framework explicated in Dusenbery.
(1997) due to its comparative simplicity and broad scope. To reiterate, the objective is to develop uncomplicated scaling relations that may pave the way toward understanding how the sizes of microbes in variegated astrobiological environments might be constrained by the capacity to promote dispersal as well as resolve gradients and obtain information about the neighborhood. The importance of studying the physical, chemical and biological constraints on size and its attendant evolutionary and ecological consequences has a rich history, dating back to at least the pioneering essay by Haldane (1926). While this topic has been commonly explored at the level of macroscopic organisms (Went, 1968; Denny, 1993; Blanckenhorn, 2000; Angilletta, 2009; Ginzberg et al., 2015), size constraints at the microscopic level have also been investigated (Morowitz, 1967; Koch, 1996; Knoll et al., 1999; Andersen et al., 2016; Cockell, 2018).

There are certain aspects, however, whereby our treatment diverges from that of Dusenbery (1997). First, one of the principal purposes of the aforementioned publication is to estimate the signal-to-noise ratio (S/N), the metric used for measuring the efficacy of gradient detection, as a function of the cell size. Here, we tackle the converse problem, in which we employ the condition $S/N = 1$ to deduce the corresponding $R_{min}$. Second, we modify some of the fiducial values employed in Dusenbery (1997) in light of current developments; the pertinent references are cited when we deviate from the canonical estimates. Third, and most importantly, we frame our analysis in an astrobiological context by focusing on domains and worlds that are perceived as promising from this standpoint.

The outline of the paper is as follows. We begin by presenting the salient equations and model parameters in Section 2. We explore the predictions of this framework for two distinct environments in Section 3—to wit, submarine hydrothermal vents on Earth (and elsewhere), and generic lakes and seas of Titan. Finally, we conclude with a summary of our findings along with a brief exposition of their practical and theoretical implications in Section 4.

### 2 Model description and results

Given that our analysis mirrors that of Dusenbery (1997), we begin with a brief summary of the caveats and simplifications involved in constructing the heuristic model for surface and subsurface habitats. For starters, the organisms are taken to have spherical symmetry; changing the shape to ellipsoidal or cylindrical is anticipated to yield noteworthy benefits but also incur concomitant costs, as elucidated in Kiarboe (2008, pp. 31-32) and Schuech et al. (2019). Second, the power per unit volume accessible by an organism for swimming is held roughly constant (cf. Makarieva et al., 2008; DeLong et al., 2010). Third, the effect of noise (the S/N to be more precise) is taken to directly impact the capability of organisms to obtain information about stimuli and it is consequently pressed into service as a proxy. Fourth, the temporal duration over which an organism can undertake rectilinear motion or ascertain the direction of stimuli is governed by rotational Brownian motion.

Fifth, the scaling relations expounded herein are applicable at low Reynolds number (Purcell, 1977; Lauga, 2016). Turbulence could lead to sizable quantitative changes, such as through the effects of turbulent diffusion (Weissburg, 2000; Okubo and Levin, 2001). Sixth, the methodology is apropos only for single microbes and is therefore not applicable to collective behavior, which is characterized by much richer dynamics (Brenner et al., 1998; Vicsek and Zafeiris, 2012; Hakim and Silberzan, 2017; Fu et al., 2018). When microbes form consortia, which is particularly pertinent in harsh environmental conditions, it might be feasible for these aggregates to perform gradient sensing beyond the limits of single-cell chemotaxis analyzed herein (Varennes et al., 2016; Camley, 2018). Lastly, it is assumed that the gradients in question are maintained continuously (with spatiotemporal variations) by virtue of geological, chemical, and physical activity and are consequently not dissipated by metabolism and other biological processes. Certain environments on Earth (e.g., submarine hydrothermal vents) are
known to sustain long-lived chemical and thermal gradients (Russell et al., 2014; Meadows et al., 2020).

In spite of these limitations, we note that the results have proven to be fairly accurate for prokaryotes (e.g., Martens et al., 2015; Kirchman, 2018; Beeby et al., 2020); similar considerations could apply to eukaryotes in differentiating between motile and non-motile species (Wan and Jékely, 2021).

2.1 Expressions for the minimal cell size

The first point to note is that motility, by definition, can facilitate faster dispersal. In the absence of motility, the behavior of microbes can be described by the classical diffusion coefficient $D_0$, whereas its inclusion leads to an “effective” diffusion coefficient $D_M$ (Berg, 1993). The ratio of these two diffusion coefficients is $\zeta = D_M / D_0$. We can solve for $R_{\text{min}}$ by demanding that this ratio must exceed the minimum threshold of $\zeta = 1$ in order for dispersal to start becoming effective. By implementing this procedure, we end up with

$$R_{\text{min}} \approx 0.36 \mu m \left( \frac{U}{U_{\oplus}} \right)^{-1/3} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-1/3} \left( \frac{T}{T_{\oplus}} \right)^{1/3},$$

where the subscript ‘⊕’ hereafter is taken to signify representative values on Earth, chosen based on Dusenbery (1997, Table 1) and other sources, with the explicit proviso understanding that Earth-based organisms and habitats display a substantial degree of heterogeneity. In the above equation, $\eta$ denotes the dynamic viscosity of the environment and $U$ embodies the speed of swimming relative to the organism’s size. The reason behind introducing $U$ (units of s$^{-1}$) has to do with the empirical linear scaling discerned between the speeds and sizes of organisms (Bonner, 2006, Figure 34), which is supported by theoretical arguments (Vogel, 2008; Dusenbery, 2009; Meyer-Vernet and Rospars, 2016). We have adopted $T_{\oplus} = 293 \, K \, (20 ^\circ C)$, $\eta_{\oplus} = 10^{-3} \, N \, s \, m^{-2}$, and $U_{\oplus} = 10 \, s^{-1}$; note that the latter parameter is close to the median value for swimming microbes (Meyer-Vernet and Rospars, 2016) and to $Escherichia coli$ in particular (Milo and Phillips, 2016, pg. 270). With that said, some species of Archaea evince fast swimming speeds that are more than one order of magnitude higher than $E. coli$ (Herzog and Wirth, 2012). Our understanding of archaeal motility remains incomplete despite the available data (Albers and Jarrell, 2018), partly due to the variety of propulsion methods accessible in theory (Bechinger et al., 2016).

Next, we turn our attention to the various constraints imposed by garnering information from gradients in stimuli via spatial and temporal methods. The rest of the formulae are derived by taking the corresponding equations from Dusenbery (1997, Table 2) for the signal-to-noise ratio (S/N), and deploying the criterion $S/N = 1$ to solve for $R_{\text{min}}$. The first example from this category are chemical gradients. For the spatial mode, the relevant scaling is given by

$$R_{\text{min}} \approx 0.32 \mu m \left( \frac{D_0}{D_{\oplus}} \right)^{-1/6} \left( \frac{C}{C_{\oplus}} \right)^{-1/6} \left( \frac{\mathcal{L}_c}{\mathcal{L}_{c,\oplus}} \right)^{1/3} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-1/6} \left( \frac{T}{T_{\oplus}} \right)^{1/6},$$

where $C$ represents the average concentration of the appropriate chemical in the environment, $D$ denotes the diffusion coefficient corresponding to that chemical in the given solvent, and $\mathcal{L}_c \approx \mathcal{L} (dC/dz)^{-1}$ embodies the characteristic length scale associated with the chemical gradients. The
fiducial values chosen are \( D_{\oplus} = 10^{-9} \text{ m}^2 \text{ s}^{-1} \), \( L_{c,\oplus} = 10^{-3} \text{ m} \), and \( C_{\oplus} \approx 10 \mu \text{M} \); note that the latter is commensurate with the concentrations of nutrients and other chemicals observed in marine environments (Sarmiento and Gruber, 2006; Schlesinger and Bernhardt, 2013).

In the same vein, we tackle the second category—to wit, thermal gradients. For the spatial mode of obtaining information, the minimum cell size is

\[
R_{\text{min}} \approx 0.46 \mu \text{m} \left( \frac{\kappa}{\kappa_{\oplus}} \right)^{-3/13} \left( \frac{\mathcal{H}_{\oplus}}{\mathcal{H}} \right)^{1/13} \left( \frac{L_t}{L_{t,\oplus}} \right)^{4/13} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-3/13} \left( \frac{T}{T_{\oplus}} \right)^{3/13},
\]

while this quantity under the temporal mode is estimated to be

\[
R_{\text{min}} \approx 0.43 \mu \text{m} \left( \frac{U_{\oplus}}{U} \right)^{-4/25} \left( \frac{\kappa}{\kappa_{\oplus}} \right)^{-3/25} \left( \frac{\mathcal{H}_{\oplus}}{\mathcal{H}} \right)^{1/25} \left( \frac{L_t}{L_{t,\oplus}} \right)^{4/25} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-7/25} \left( \frac{T}{T_{\oplus}} \right)^{7/25},
\]

where \( \kappa \) constitutes the thermal conductivity of the organism and the ambient solvent, \( \mathcal{H} \) represents the volumetric heat capacity of this system, and \( L_t \approx T (dT/dz)^{-1} \) encapsulates the characteristic length scale linked with the thermal gradient. The normalization factors for these parameters are \( \kappa_{\oplus} = 0.6 \text{ W m}^{-1} \text{ K}^{-1}, \mathcal{H}_{\oplus} = 4.2 \times 10^6 \text{ J K}^{-1} \text{ m}^{-3} \), and \( L_{t,\oplus} = 10^4 \text{ m} \); the last relation follows from the above definition of \( L_t \) along with an average thermal gradient of 30 K/km and temperature of 288 K for Earth (Chiasson, 2016, pg. 65).

The third, and last, category of interest is gradients in photon flux (i.e., intensity). As before, one can proceed to determine the minimum cell sizes for the spatial and temporal pathways. After simplification, they are respectively given by

\[
R_{\text{min}} \approx 0.64 \mu \text{m} \left( \frac{\delta}{\delta_{\oplus}} \right)^{-1/7} \left( \frac{\Phi}{\Phi_{\oplus}} \right)^{-1/7} \left( \frac{L_t}{L_{t,\oplus}} \right)^{2/7} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-1/7} \left( \frac{T}{T_{\oplus}} \right)^{1/7},
\]

\[
R_{\text{min}} \approx 0.49 \mu \text{m} \left( \frac{U_{\oplus}}{U} \right)^{-2/13} \left( \frac{\delta}{\delta_{\oplus}} \right)^{-1/13} \left( \frac{\Phi}{\Phi_{\oplus}} \right)^{-1/13} \left( \frac{L_t}{L_{t,\oplus}} \right)^{2/13} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-3/13} \left( \frac{T}{T_{\oplus}} \right)^{3/13},
\]

where \( \delta \) quantifies the fraction of photons that are absorbed by a single layer composed of photoreceptors (taken to be rhodopsins), \( \Phi \) is the flux of photons in a suitable wavelength range, and \( L_t \approx \Phi (d\Phi/dz)^{-1} \) represents the characteristic length scale associated with light gradients. The fiducial value of \( \delta_{\oplus} = 3 \times 10^{-4} \) is constructed from the absorption coefficient of photoreceptors (Warrant and Nilsson, 1998, Table 1) and the thickness of an individual rhodopsin molecule (Hargrave, 2001). As the longest dimension of rhodopsin is \( \sim 7.5 \text{ nm} \) (Palczewski, 2006, pg. 748), it should not be an issue in principle to fit these molecules into a cell of radius \( \geq 0.1 \mu \text{m} \); the exact number of such molecules will depend on the undetermined packing fraction. We choose the normalization \( \Phi_{\oplus} = 10^{21} \text{ photons m}^{-2} \text{ s}^{-1} \), as it corresponds to the maximal flux of 400-700 nm photons incident on the Earth’s surface.\(^1\)

Lastly, in order to maintain consistency with Dusenbery (1997, Table 1), we have chosen \( L_{t,\oplus} = 10^{-3} \text{ m} \).

Apart from the spatial and temporal modes of information sensing, microbes are also capable of detecting the orientation of the light source, i.e., discerning the direction in which light is propagating. This process is, however, feasible only when the radiation passing across the organism is subject to substantial attenuation. The minimum cell size required in order to determine the positioning of the light source is expressible as

\[
R_{\text{min}} \approx 0.45 \mu \text{m} \left( \frac{\delta}{\delta_{\oplus}} \right)^{-1/7} \left( \frac{\Phi}{\Phi_{\oplus}} \right)^{-1/7} \left( \frac{K}{K_{\oplus}} \right)^{-2/7} \left( \frac{\eta}{\eta_{\oplus}} \right)^{-1/7} \left( \frac{T}{T_{\oplus}} \right)^{1/7},
\]

\(^1\)https://www.nrel.gov/grid/solar-resource/spectra.html
The signal-to-noise ratio (S/N) as a function of the cell size $R$ (in $\mu$m) for Earth-analogs. The curves reflect the various ambient gradients and attendant pathways for perceiving them. Red, green and blue are used to demarcate chemical, thermal and light gradients, respectively. The dotted and dashed lines (for all colours) indicate the spatial and temporal means for identifying gradients. The solid blue line represents the S/N for detecting the direction of the light source via gradient sensing. All results were obtained by combining (9) with (2)-(8).

where $K$ denotes the attenuation coefficient for photoreceptors, and the nominal value of $K_0 = 10^4$ $m^{-1}$ is taken from Warrant and Nilsson (1998, Table 1).

For the sake of completeness, the consolidated expression for the signal-to-noise ratio for arbitrary cell radius $R$ is furnished below:

$$S/N = \left( \frac{R}{R_{\min}} \right)^{\beta},$$

where the values of $R_{\min}$ and $\beta$ are dependent on the type and modality of gradient detection.

- Chemical gradients: for the spatial mode, $R_{\min}$ is calculated using (2) and $\beta = 3$, whereas for the temporal mode $R_{\min}$ is determined by (3) and $\beta = 6$.

- Thermal gradients: for the spatial mode, $R_{\min}$ is computed from (4) and $\beta = 13/4$, whereas for the temporal mode $R_{\min}$ is estimated using (5) and $\beta = 25/4$.

- Light gradients: for the spatial mode, $R_{\min}$ is evaluated via (6) and $\beta = 7/2$, whereas for the temporal mode $R_{\min}$ is ascertained using (7) and $\beta = 13/2$. When it comes to sensing the
direction of the light source, \( R_{\min} \) is set by (8) and \( \beta = 7/2 \).

From this list, we see that even a modest increase in \( R \) would result in a significant gain in the signal-to-noise ratio. To illustrate our point, let us choose \( R \approx 3R_{\min} \), which translates to \( S/N \approx 30-1260 \) depending on the modality of gradient sensing. We have plotted \( S/N \) as a function of \( R \) in Figure 1, where the expressions for \( R_{\min} \) in (9) were held fixed at their normalization factors in (2)-(8). In all models, we see that \( S/N \) grows rapidly with the size, along expected lines.

Finally, as we had remarked at the beginning of Section 2.1, larger cell size permits effective dispersal. The latter is measured in terms of \( \zeta \), the ratio of the two motile and non-motile diffusion coefficients, and obeys the relationship:

\[
\zeta = \left( \frac{R}{R_{\min}} \right)^6,
\]

where \( R_{\min} \) is given by (1). If we adopt \( R \approx 3R_{\min} \), as we did in the preceding paragraph, we obtain \( \zeta \approx 730 \). Thus, even when the cell size is elevated by a modest amount, the accompanying boost in the dispersal is strikingly high.

### 2.2 On the categories of parameters in the equations

Our final results for the minimal cell size are exemplified by (1)-(8). It is instructive to define \( R_{\min} \), which is the global minimum of these equations, namely, it refers to the \( R_{\min} \) that is smaller than all the other expressions; it goes without saying, the exact form of \( R_{\min} \) will vary based on the parameters of the system under consideration. The mathematical significance of \( R_{\min} \) can be understood as follows. If \( R < R_{\min} \), it would imply that the organism is incapable of efficient dispersal and gradient sensing. Hence, at least insofar as these issues are concerned, \( R_{\min} \) would comprise a viable lower bound for the radius of microbes.

At this stage, it is helpful to carry out a meticulous scrutiny of the parameters involved in our formulae prior to applying them to specific astrobiological settings. The first group is composed of variables that are chiefly dictated by the nature of the environment(s), which includes the solvent(s). The likes of \( \eta, \mathcal{H}, \kappa, \) and \( T \) are straightforward examples, since they can be predicted from basic properties, e.g., solvent, temperature and pressure. On a more subtle level, \( \Phi, D_c, C, \) and the gradient length scales (collectively denoted by \( L \)) also fall under this umbrella. It is harder to quantify them precisely, but one could at least draw upon either physical principles or analogues on Earth (see Section 3) to estimate them. For instance, calculating the photon flux (\( \Phi \)) in underwater environments is quite straightforward if the depth, temperature and solvent are provided (Lingam and Loeb, 2020a).

The second group is composed of \( \delta \) and \( \mathcal{K} \), both of which are intimately connected to the molecular properties of photoreceptors. It is certainly conceivable that extraterrestrial life may use macromolecules other than rhodopsins. Yet, the ubiquity and diversity of rhodopsins warrants further explication. Rhodopsins are widespread in photoreceptors in plants, animals and unicellular eukaryotes (Foster et al., 1984; Hegemann, 2008; Möglich et al., 2010). Looking beyond eukaryotes, the so-called microbial rhodopsins are known to play myriad roles in phototaxis, intracellular signalling and harvesting electromagnetic energy (Gordeliy et al., 2002; Ernst et al., 2014). Recent studies indicate that microbial rhodopsins constitute the dominant source of light harvesting in Earth’s oceans (Gómez-Consarnau et al., 2019). Despite their multifarious functions, rhodopsins across taxa share many core structural features in common (Birge, 1990; Bryant and Frigaard, 2006). It has been conjectured that rhodopsins might have been widespread on the young Earth and exoplanets (DasSarma and Schwierterman, 2018). In view of these details, it does not seem unreasonable to utilize fiducial values derived from Earth as proxies for \( \delta \) and \( \mathcal{K} \).
The remaining parameter, which is also the one subject to the most ambiguity, is $U$. The reason is that $U$ is dictated by physiology and not by the properties of the medium or individual macromolecules as in the former two categories. A careful inspection of Milo and Phillips (2016, pg. 270) and Bechinger et al. (2016, Table 1) reveals that $U$ deviates from our choice of $U_\oplus$ by roughly an order of magnitude only for certain microbes. Due to the relatively weak dependence of $R_{\text{min}}$ on $U$—as evident from (1), (3), (5) and (7)—our results are likely to change by a factor of $\lesssim 2$. However, these results pertain solely to Earth-based organisms, which leads us to the question: what about extraterrestrial organisms? Although there is admittedly no clear answer, it has been conjectured by Meyer-Vernet and Rospars (2016, Section 4.4) that the magnitude of $U$ has a strong mechanistic basis and is therefore constrained to a somewhat narrow interval.

3 Applications of the formalism

Before we tackle a couple of specific environments, a few general trends are discernible from Section 2.1, which are adumbrated below.

1. $R_{\text{min}}$ decreases when the swimming velocity measured in units of body size is increased.

2. In all of the formulae, $R_{\text{min}}$ is proportional to $(T/\eta)^\gamma$, where $\gamma > 0$ although the exact values varies from one expression to another.

3. $R_{\text{min}}$ displays monotonically increasing behaviour with respect to the gradient length scales ($\mathcal{L}$). To put it differently, sharper gradients (i.e., smaller values of $\mathcal{L}$) are predicted to bring about a reduction in $R_{\text{min}}$.

4. Broadly speaking, $R_{\text{min}}$ decreases monotonically with many environmental parameters such as $D_c$, $C$, $\kappa$ and $\Phi$, although exceptions can and do exist. For such variables, increasing their magnitude would result in lowered $R_{\text{min}}$ and vice versa.

5. If $U$ is held fixed, we perceive that $R_{\text{min}}$ evinces a stronger algebraic dependence on the appropriate parameters for the spatial mode as opposed to the temporal mode.

Even though it is tempting to dismiss the above points because they are qualitative, there are several important trends and consequences that emerge from them. We will illustrate this statement with one notable example by focusing on point #3.

In habitats with sharp gradients—whether it be chemical, thermal, or photon flux—we find that the corresponding $R_{\text{min}}$ can decrease significantly, and so could $R_{\text{opt}}$. A microbe with smaller cell size, but equipped with similar gradient detection capabilities, would entail a lower metabolic cost ceteris paribus, as per current allometric models and empirical data (Brown et al., 2004; DeLong et al., 2010). Moreover, theoretical models indicate that the total energetic costs incurred for protein and nucleic acid repair are reduced for smaller cells because they are posited to have a lower inventory of biomolecules (Kempes et al., 2017, Figures 2 and 3). Last, if we make the ostensibly reasonable assumption that the first living organisms were on the smaller side, this premise suggests that environments with sharp gradients might have been conducive to the origin of life in this regard.

It is intriguing, therefore, that both past and recent research has emphasized thermodynamic disequilibria as a sine qua non for abiogenesis (Schrödinger, 1944; Prigogine and Nicolis, 1971; Russell et al., 1994; Fry, 2000; Smith and Morowitz, 2016; Barge et al., 2017; Branscomb et al., 2017; Lingam and Loeb, 2019b; Spitzer, 2021), and several geological settings have been proposed as viable candidates (Westall et al., 2018; Sleep, 2018; Kitadai and Maruyama, 2018; Camprubi et al., 2019; Meadows et al., 2020; Altair et al., 2020). We will explore one of the leading contenders—to wit, submarine
alkaline hydrothermal vents—from this standpoint in more detail shortly hereafter. Geothermal fields in subaerial locations (e.g., hot springs), which have a long history in origins-of-life research (Harvey, 1924), exhibit marked gradients in inorganic substances, temperature and redox chemistry (Brock and Brock, 1968; Swingley et al., 2012; Mulkidjanian et al., 2012; Deamer et al., 2019; Des Marais and Walter, 2019; Damer and Deamer, 2020; Boyer et al., 2020). Beaches represent another crucial environment that have been relatively underappreciated in origins-of-life research, despite the presence of strong gradients in salinity, temperature and light intensity (Lathe, 2004; Bywater and Conde-Frieboes, 2005; Stüeken et al., 2013; Lingam and Loeb, 2018a). In the event that life emerged in one (or more) of these domains, it is conceivable that the concomitant existence of steep gradients may have permitted (proto)cells to efficiently acquire information via chemotaxis, phototaxis or thermotaxis among other avenues.

It is worth taking a brief detour at this juncture, and highlighting that the aforementioned variants of taxis are by no means the only ones that abound on Earth. Magnetotactic bacteria are capable of magnetotaxis, whereby these bacteria orient themselves along Earth’s magnetic field (Blakemore, 1975; Bazylinski and Frankel, 2004; Schüler, 2007; Lefèvre and Bazylinski, 2013). Magnetotactic microbes are not tackled in this study for two principal reasons: (i) important questions pertaining to their evolution, ecological distribution, physiology and mechanistic basis are not yet unambiguously settled (Erglis et al., 2007; Fairen and Schuler, 2008; Lefèvre and Bazylinski, 2013; Uebe and Schuler, 2016); and (ii) not all worlds possess strong magnetic fields (Christensen, 2010; de Pater and Lissauer, 2015); the likes of Titan, Venus and Mars are either weakly magnetized or unmagnetized (Stevenson, 2010; Brain et al., 2016; Horner et al., 2020) and the same might hold true for tidally locked terrestrial exoplanets around M-dwarfs (Dong et al., 2017, 2018; McIntyre et al., 2019). In spite of these caveats, further research along these lines is clearly warranted.

With this essential qualitative discussion out of the way, we will now outline how our formalism could be harnessed to arrive at quantitative predictions by concentrating on two representative locales of relevance to astrobiology.

3.1 Submarine alkaline hydrothermal vents

Submarine hydrothermal vents have been recognized as promising sites for abiogenesis ever since the 1980s at the minimum (Corliss et al., 1981; Baross and Hoffman, 1985), with alkaline hydrothermal vents (AHVs) garnering the lion’s share of attention. Reviews and analyses of this rapidly developing field were expounded in Russell et al. (1994); Russell and Hall (1997); Martin et al. (2008); Russell et al. (2014); Sojo et al. (2016); Weiss et al. (2018); Cartwright and Russell (2019); Russell and Ponce (2020), whereas dissenting viewpoints and critiques of the underlying principles have been laid out in Bada (2004); Orgel (2008); Cleaves et al. (2009); Jackson (2016); Sutherland (2017); Deamer and Damer (2017). In recent experiments, the availability of mineral and metal catalysts has been shown to facilitate the emergence of protometabolic networks under roughly hydrothermal conditions, with close connections to the reverse tricarboxylic acid cycle and the Wood–Ljungdahl pathway (Kitadai et al., 2019; Preiner et al., 2020; Muchowska et al., 2020; Hudson et al., 2020). From a different perspective, the synthesis of prebiotic monomers (e.g., amino acids) and their oligomerization has been documented in AHV-like laboratory conditions (Burcar et al., 2015; Harrison and Lane, 2018; Barge et al., 2019). Lastly, both theoretical modelling and laboratory experiments have revealed that hydrothermal pores are propitious to the synthesis and efficient accumulation of prebiotic compounds, and could initiate their oligomerization in turn (Baaske et al., 2007; Kreysing et al., 2015; Niether et al., 2016; Salditt et al., 2020).

Several reasons can be identified in favor of our decision to focus on AHVs. First, as explained in the preceding paragraph, there are compelling (although not definitive) grounds to contend that
they may represent the sites where the origin of life occurred on Earth. Second, AHVs are viewed as promising candidates for enabling abiogenesis on icy worlds in our Solar system such as Europa and Enceladus (Vance et al., 2007; Russell et al., 2014). Last, and perhaps most importantly, the existence of ongoing hydrothermal processes has been indirectly confirmed on Enceladus by analyzing the data from its plume collected by the Cassini spacecraft (Waite et al., 2017; Postberg et al., 2018) and there is broad evidence for past hydrothermal activity on Mars (Oskinii et al., 2013; Westall et al., 2015; Michalski et al., 2018; Farley et al., 2020). On a related note, Triton exhibits clear signatures of geysers (Soderblom et al., 1990; Hand et al., 2020), and two independent lines of evidence suggest that Europa has plumes and perhaps hydrothermal activity (Sparks et al., 2017; Jia et al., 2018). Hence, when viewed collectively, there are robust reasons to apply the model to hydrothermal vents.

The dynamic environment of AHVs is distinguished by the manifestation of steep gradients in chemical compounds, temperature, pH, and redox chemistry inter alia (Russell and Martin, 2004; Stüeken et al., 2013; Cartwright and Russell, 2019; Meadows et al., 2020; Barge et al., 2020a). We caution, however, that this very spatial and temporal dynamism makes it challenging to identify average values for the gradient length scales. Bearing this caveat in mind, we remark that the presence of strong gradients ensures that point #3 comes into play. In other words, due to the prominent role of gradients, it seems likely that the expression for $R_{\text{min}}$ would involve $L$ in one of its three forms. Next, provided that $U$ does not diverge significantly from $U_{\oplus}$, we invoke point #5 delineated previously, which implies that the spatial mode is likely to have a greater impact when the environmental variables are modified. Thus, by combining these two postulates, $R_{\text{min}}$ is given by one of either (2), (4) or (6).

Let us begin by scrutinizing the last equation of this trio. Field studies have established that bacteria from the family Chlorobiaceae are capable of photosynthesis at hydrothermal vents (Beatty et al., 2005; Raven and Donnelly, 2013; Björn, 2015). Furthermore, both empirical evidence and biophysical considerations indicate that photosynthesis at photon fluxes $\sim 5$ orders of magnitude smaller than $\Phi_{\oplus}$ is feasible (Raven et al., 2000; Beatty et al., 2005; Manske et al., 2005). In fact, Nisbet et al. (1995); Nisbet and Fowler (1996) hypothesized that photosynthesis evolved in organisms dwelling near hydrothermal vents as a means of initially detecting infrared radiation via thermotaxis. Thus, there are no compelling a priori reasons for ruling out the prospects for phototaxis near hydrothermal vents, all the more so given that non-thermal radiation at these locations dominates its thermal counterpart by more than an order of magnitude in select wavelength bands (Van Dover et al., 1996; White et al., 2000). However, upon carefully inspecting (6), we notice that $R_{\text{min}} \propto \Phi^{-1/7}$. Given that $\Phi$ is many orders of magnitude smaller than $\Phi_{\oplus}$ (White et al., 2002), it follows that $R_{\text{min}}$ in (6) may increase by nearly an order of magnitude unless the light gradients are unusually steep. Hence, we will direct our attention toward (2) and (4) instead.

The remaining step is to motivate characteristic values for the parameters in the formulae. We begin by adopting $T = 323$ K (50 °C), which is lower than the temperature of hydrothermal fluids in AHVs by a few tens of K (Sojo et al., 2016). This temperature has been employed in hydrothermal pore experiments (Mast et al., 2013), and higher temperatures could lead to the swift degradation of biomolecules. At this temperature and selecting a pressure of $\sim 25$ MPa, we use Schmelzer et al. (2005, Table 1) to obtain $\eta \approx 0.55\eta_{\oplus}$. Next, we adopt $\kappa \approx \kappa_{\oplus}$ based on Caldwell (1974), in conjunction with $H \approx H_{\oplus}$. On-site investigations suggest that the thermal gradients function over length scales of $\sim 0.01$-1 m (Kelley et al., 2002; Bates et al., 2010; Priye et al., 2017), which is also consistent with some of the microfluidic experiments simulating hydrothermal pores (Baaske et al., 2007; Mast et al., 2013).

---

2We point out that our ensuing results are only weakly dependent on the temperature, and are thus accurate for temperature changes of $< 10\%$ (measured in K).

3https://www.engineeringtoolbox.com/water-liquid-gas-thermal-conductivity-temperature-pressure-d_2012.html

4https://www.engineeringtoolbox.com/specific-heat-capacity-water-d_660.html
2013; Priye et al., 2017; Wang and Steinbock, 2020); therefore, we adopt the conservative estimate of $L_t \approx 1$ m. By substituting these values into (4), we end up with $R_{\min} \approx 30$ nm.

Turning our attention to chemotaxis (chemical gradients), the average concentration $C$ is strongly dependent on the compounds under consideration. For instance, there is tentative (albeit equivocal) evidence for the abiotic synthesis of amino acids at nanomolar concentrations in the oceanic lithosphere (Ménez et al., 2018). If we turn our gaze to simpler molecules, however, the concentrations are much higher. To begin with, we choose $\text{CO}_2$ as the chemical of interest, due to its prevalence in oceans and the crucial fact that it constitutes the cornerstone of carbon fixation pathways (autotrophy) on Earth (Berg, 2011; Fuchs, 2011; Ward and Shih, 2019). RuBisCO, the primary enzyme in carbon fixation, has a characteristic radius of $\sim 6.5$ nm (Engel et al., 2015), which could make it theoretically possible for such molecules to exist within a cell of radius $\gtrsim 100$ nm (cf. Raven, 1994). The dynamic environments emblematic of AHVs induce extensive fluctuations in the $\text{CO}_2$ abundance, which ranges between $\sim 0.1$ $\mu$M to $\gtrsim 1$ mM (Goffredi et al., 1997; Minic and Thongbam, 2011; Lang and Brazelton, 2020); to offer a benchmark, the typical concentration of dissolved $\text{CO}_2$ in Earth’s oceans today is $\sim 10$ $\mu$M (Gornitz, 2009, pg. 125). At the lower end of the spectrum (i.e., when the abundance of bioavailable $\text{CO}_2$ is $\lesssim 1$ $\mu$M), it is conceivable that $\text{CO}_2$ may function as the limiting resource, which is bolstered by the analyses of the Lost City hydrothermal field (Lang and Brazelton, 2020).

We shall opt for an intermediate value of $C \approx 10$ $\mu$M, while the diffusion coefficient is chosen to be $D_c \approx 3.7 D_\oplus$ (Cadogan et al., 2014, Table 2). Lastly, experiments in microfluidic reactors have shown that pH gradients are generated over length scales of $\sim 10^{-4}$ m (Möller et al., 2017; Sojo et al., 2019; Barge et al., 2020b; Hudson et al., 2020), and we adopt this estimate for $L_c$ although it is probably on the optimistic side if AHVs are viewed in toto. By substituting the preceding choices into (2), we obtain $R_{\min} \approx 130$ nm. In contrast, if we consider dissolved inorganic carbon (DIC) as our chemical of interest and adopt a fiducial estimate of $\sim 2$ mM for DIC on the basis of data collected from Earth’s oceans (Hansen et al., 2007), we arrive at $R_{\min} \approx 55$ nm after invoking (2).

Instead of working with $\text{CO}_2$ as the chemical compound of relevance, it is feasible to repeat the analysis for a different species. The preceding emphasis on $\text{CO}_2$ was a direct consequence of focusing on carbon fixation (autotrophy), but it is necessary to tackle other chemical substances that are relevant for heterotrophs as well. One natural candidate that springs to mind is phosphorus, specifically in the form of phosphates, because it constitutes the ultimate limiting nutrient for the past and current Earth (Tyrrell, 1999; Laakso and Schrag, 2018; Hao et al., 2020), and potentially worlds with exclusively (sub)surface oceans (Wordsworth and Pierrehumbert, 2013; Lingam and Loeb, 2018b, 2019a,c; Olson et al., 2020). A noteworthy aspect of phosphate is that it represents a vital nutrient for both heterotrophs and autotrophs (Kirchman, 1994). When it comes to dissolved phosphate, we adopt $C \approx 2$ $\mu$M as per measurements in the vicinity of hydrothermal zones on Earth (Wheat et al., 1996; Paytan and McLaughlin, 2007). The diffusion coefficient for phosphate is taken to be $D_c \approx 0.4 D_\oplus$ (Krom and Berner, 1980; Cheng et al., 2014). By repeating the calculation using (2) in conjunction with the prior data, we end up with $R_{\min} \approx 25$ nm.

In light of the results until this stage, we infer that $R_{\min} \lesssim 0.1$ $\mu$m is theoretically feasible in the general proximity of AHVs; recall that $R_{\min}$ is the minimum of all values spanned by $R_{\min}$. However, this statement should not be misconstrued as implying that microbes with radii $\lesssim 0.1$ $\mu$m would exist in actuality. This limit has been derived via the application of a simple “high-level” mechanistic model that does not take into account the accompanying constraints imposed by the intricate molecular machinery associated with cells. For instance, cellular components such as receptor molecules (e.g., rhodopsins) are necessary for gradient sensing, whereas motility could enforce stringent requirements for motor molecules and ATP synthesis. Mechanical action based on the sensed information would

---

5 If one excludes these “sweet spots”, however, it is credible that $L_c$ may increase by an order of magnitude or more even in the neighbourhood of AHVs.
call for protein and messenger RNA synthesis (entailing RNA polymerases in turn), which militates against a cell radius of $\lesssim 100$ nm. Moreover, in the case of autotrophs, the necessity of large enzymes—such as RuBisCO, which was briefly introduced and analyzed a few paragraphs earlier—imposes an additional bottleneck on the minimal cell size. This issue is, however, likely to be less significant for heterotrophs because they ought not depend on these macromolecules.

There are several other factors that may collectively restrict the minimum radius of living organisms to $\gtrsim 100$ nm. In a classic study, Morowitz (1967, pg. 52) calculated that a radius of $\gtrsim 50$ nm is necessary for a minimal self-replicating unit on the basis of the desired genetic and metabolic complexity. Subsequent evidence from uncultured bacteria as well as additional theoretical constraints—imposed by cell wall, genome size, and nutrient uptake efficiency—suggests that lifeforms must have a minimum radius of $\sim 70$ nm (Koch, 1996; Maniloff et al., 1997; Velimirov, 2001; Raven et al., 2013; Luef et al., 2015; Andersen et al., 2016). Lastly, the full panoply of evolutionary processes involving the (ex)change of genetic material, such as harboring prophage (which influences the rate of lateral gene transfer), might be rendered untenable when the cell radius is $\lesssim 100$ nm.

It is instructive to compare the above threshold radius of $\sim 100$ nm against a few of the smallest microbes that have been unearthed to date. For starters, the lower limits for picoplankton are known to approach this threshold (Li et al., 1983; Schmidt et al., 1991; Jones, 1993). For instance, members of the ubiquitous free-living SAR11 bacterial clade attain an effective radius of $\sim 130-200$ nm (Rappé et al., 2002; Malmstrom et al., 2004). The parasitic bacterium *Mycoplasma genitalium* is characterized by a radius of 150 nm (Svenstrup et al., 2003) and certain species from the phylum *Nanoarchaeota*, such as the recently discovered symbiont *Nanopilus acidilobi* (Wurch et al., 2016), attain cell radii of $\gtrsim 50$ nm. But, it is essential to appreciate that some of these specific examples are either parasites or symbions and not free-living microbes. Hence, by the same token, if the smallest organisms capable of effective gradient sensing and dispersal are parasites on larger lifeforms (which is not the case tout court), discerning the latter would prove to be an easier task for life-detection missions. It goes without saying that the limits for viruses, which are, however, not living entities sensu stricto, are much smaller: the porcine circovirus and cowpea mosaic virus have radii of $\sim 10$ nm (Milo and Phillips, 2016, pg. 8).

We will explore the ramifications of our analysis in Section 4, but there are two points that merit highlighting before proceeding further. First, in order to calculate $R_{\text{min}}$, a number of variables intimately linked to the ambient environment (e.g., gradient length scales) came into play. Hence, in case other domains evince physico-chemical properties similar to AHVs, *mutatis mutandis*, it is plausible that the above results are broadly applicable to them. Geothermal fields might represent promising candidates in this respect, because they possess some attributes in common with AHVs (Deamer and Damer, 2017; Deamer, 2019; Lingam and Loeb, 2021a), while diverging from the latter environs in certain notable respects (e.g., wet-dry cycling).

Second, in the event that the Earth-based fiducial values chosen in our analysis of AHVs are applicable to similar environments in (sub)surface ocean worlds, most notably Europa and Enceladus, then the results obtained earlier could also be valid in such settings. In other words, it is conceivable that AHVs in subsurface oceans of certain icy worlds might be conducive to the existence of comparatively small microbes capable of effective gradient sensing and dispersal.

### 3.2 The role of the solvent: Titan as case study

Titan is one of the most intriguing and compelling astrobiological targets in our Solar system (Sagan, 1994; McKay, 2014; Nimmo and Pappalardo, 2016; Schulze-Makuch and Irwin, 2018; Cockell, 2020). As a sidenote, the composition of a minimal protocell is much more pared down relative to current microbes (Oró and Lazcano, 1984; Dyson, 1999), indicating that smaller sizes are conceivable for these entities.
Our understanding of this moon—such as its methane cycle, atmospheric composition, sand dunes and transport, lakes and seas—has advanced by leaps and bounds, primarily by virtue of the Cassini-Huygens mission (Brown et al., 2010; Hayes, 2016; Höst, 2017; Lorenz, 2019). One of the chief reasons as to why Titan is considered an exciting target stems from the possibility that it may harbour “weird life”, sensu being based on hydrocarbon solvents (Benner et al., 2004; McKay and Smith, 2005; Stevenson et al., 2015; McKay, 2016; Sandström and Rahm, 2020; Carrer et al., 2020); see also Sagan et al. (1992); Schulze-Makuch and Grinspoon (2005); Raulin et al. (2012); Irwin and Schulze-Makuch (2020). Moreover, Titan-like objects endowed with seas of methane or ethane might be among the most common type of habitable worlds (Bains, 2004; Gilliam and McKay, 2011; Ballesteros et al., 2019; Lingam and Loeb, 2020b), which increases the significance of Titan and its analogs in the context of gauging the frequency of life in the Universe (Lunine, 2009).

Due to Titan’s immanent potentiality for hosting life in non-polar solvents, we are free to take this opportunity to examine how the properties of the solvent influence $R_{\text{min}}$, that is, in what ways does the solvent alone influence the capacity for putative organisms to garner information and thereby take part in directed movement. Hence, we will proceed to modify only the solvent-related parameters like temperature, viscosity and heat conductivity, while leaving the other variables unaltered. We select $T \approx 90$ K and an atmospheric pressure of roughly 1 atm (Jennings et al., 2016; Hayes, 2016); our results remain virtually the same if these magnitudes are slightly altered. Next, we must determine what solvent should be utilized in our calculations. Liquid bodies on Titan are composed of both methane and ethane, but we select the former as the model solvent because the northern lakes are mostly composed of it (Höst, 2017, pp. 460-461).

We are now in a position to begin computing $R_{\text{min}}$ in its diverse forms. For the scenario investigated herein, we have $\eta \approx 0.19 \eta_{\oplus}$, and substituting these numbers into (1) yields

$$R_{\text{min}} \approx 0.42 \mu m \left( \frac{U}{U_{\oplus}} \right)^{-1/3}.$$ (11)

Next, we consider the prospects for chemotaxis; the respective expressions for the spatial and temporal modes can be simplified to obtain

$$R_{\text{min}} \approx 0.26 \mu m \left( \frac{D_c}{D_{\text{CH}_4}} \right)^{-1/6} \left( \frac{C}{C_{\oplus}} \right)^{-1/6} \left( \frac{L_c}{L_{c,\oplus}} \right)^{1/3},$$ (12)

$$R_{\text{min}} \approx 0.37 \mu m \left( \frac{U}{U_{\oplus}} \right)^{-1/6} \left( \frac{D_c}{D_{\text{CH}_4}} \right)^{-1/12} \left( \frac{C}{C_{\oplus}} \right)^{-1/12} \left( \frac{L_c}{L_{c,\oplus}} \right)^{1/6},$$ (13)

where we have chosen to normalize $D_c$ in terms of $D_{\text{CH}_4} \approx 5D_{\oplus} = 5 \times 10^{-9}$ m$^2$ s$^{-1}$ because it approximates the self-diffusivity of methane (Van Loef, 1978; Harris and Trappeniers, 1980). Moving on to thermal gradients, the spatial and temporal paths toward sensing information respectively impose the following constraints:

$$R_{\text{min}} \approx 0.67 \mu m \left( \frac{L_t}{L_{t,T}} \right)^{4/13},$$ (14)

$$R_{\text{min}} \approx 0.56 \mu m \left( \frac{U}{U_{\oplus}} \right)^{-4/25} \left( \frac{L_t}{L_{t,T}} \right)^{4/25}.$$ (15)
where we have made use of $\kappa \approx \kappa_\oplus / 3$ (Vargaftik et al., 1994, Table 10.39), and $\mathcal{H} \approx 0.2\mathcal{H}_\oplus$ (Youngev, 1974, Figure 4). We have normalized $\mathcal{L}_t$ in terms of $\mathcal{L}_{t,T} \approx 1.5\mathcal{L}_{t,\oplus}$, where $\mathcal{L}_{t,T}$ is the typical gradient at the surface of Titan; this normalization is chosen to make the results Titan-centric. It is the spatial and temporal pathways, respectively, are given by the following:

Finally, we turn our attention to the trio of equations associated with phototaxis. The formulae for $dT/dz$ing a few characteristics such as photon flux and temperature. The similarity is unexpected because these two classes are markedly different in terms of not only their solvents but also other characteristics such as photon flux and temperature.

Note that the former set is applicable to Earth as well as other worlds with water as the solvent (e.g., Europa and Enceladus), while the latter pertains to Titan and Titan-like worlds involving methane as the solvent. The former set is applicable to Earth as well as other worlds with water as the solvent (e.g., Europa and Enceladus), while the latter pertains to Titan and Titan-like worlds involving methane as the solvent. The similarity is unexpected because these two classes are markedly different in terms of not only their solvents but also other characteristics such as photon flux and temperature.

From a mathematical standpoint, the reason that the two groups yield closely matched results is because the equations for $R_{\text{min}}$ exhibit a fairly weak dependence on the environmental parameters; to
Figure 2: The signal-to-noise ratio (S/N) as a function of the cell size $R$ (in $\mu$m) for Titan-analogs. The curves reflect the various ambient gradients and attendant pathways for perceiving them. Red, green and blue are used to demarcate chemical, thermal and light gradients, respectively. The dotted and dashed lines (for all colours) indicate the spatial and temporal means for identifying gradients. The solid blue line represents the S/N for detecting the direction of the light source via gradient sensing. All results were obtained by combining (9) with (12)-(18).
put it differently, there is no single variable that distinctly stands out. The corollary of this statement is that the scalings for \( R_{\text{min}} \) possess a certain degree of universality, provided that the gradient length scales are held invariant. Thus, if we compare \( R_{\text{min}} \) for generic lakes and seas on Titan with those on Earth, the two will be close to each other in terms of their magnitudes. In contrast, if hydrothermal vents on Earth (or Enceladus and Europa) with their accompanying steep gradients are juxtaposed against the lakes and seas of Titan, the former will typically engender a lower value than the latter. To put it more simply, the first scenario is akin to comparing “apples with apples”, whereas the second is analogous to comparing “apples with oranges.”

The goal of this section was to demonstrate that the formalism might be suitably modified to tackle worlds with solvents other than water by taking Titan as our case study. Although we shall not delve into this subject further, another intriguing milieu that could merit theoretical analysis is the same vein as the lower and middle cloud decks of Venus, which are known to host liquid sulfuric acid with traces of liquid water (Schulze-Makuch and Irwin, 2018). This layer of the Venusian atmosphere has been long regarded as a promising astrobiological target for multiple reasons (Morowitz and Sagan, 1967; Schulze-Makuch et al., 2004; Grinspoon and Bullock, 2007; Linaye et al., 2018; Greaves et al., 2020; Seager et al., 2021; Lingam and Loeb, 2020c), but any putative lifeforms are likely to face substantive challenges in this region such as the extremely low water activity, regulation of the osmotic pressure, and high acidity (Cockell, 1999; Cockell et al., 2021).

From a more “exotic” standpoint, the formalism could be employed to study size constraints in crystalline and amorphous ices. There is growing awareness that glacial and sea ices harbor a diverse range of extremophiles (Boetius et al., 2015; Martin and McMinn, 2018). There are, however, several challenges that confront putative microbes in these environments insofar as our analysis is concerned. First, the sizes of veins and pores are a few millimeters at the maximum (Martin and McMinn, 2018, pg. 2), but at lower temperatures, the typical dimensions are much reduced and may become \( \lesssim 1 \mu m \) for subsurface ocean worlds in the outer Solar system (Price, 2007, pg. 218); this is expected to obstruct motility over extended intervals.

Second, in order for high concentrations of chemicals to exist in the ice—which would be partly responsible for lowering \( R_{\text{min}} \) on the basis of (2) and (3)—they must be incorporated in some fashion from the external environment. However, the diffusion through ice is many orders of magnitude smaller relative to water (Mispelaer et al., 2013; Cuppen et al., 2017), which is anticipated to impede the accumulation of reactants and nutrients to significant concentrations. Lastly, a number of the parameters inherent in (1)-(8) are poorly constrained in (extra)terrestrial ices, thereby rendering quantitative analyses difficult to undertake. On account of these reasons, we have not attempted to derive explicit estimates for \( R_{\text{min}} \) in the realm of saline and freshwater ices.

### 4 Conclusion

The ability of organisms to sense and act upon encountering physical and chemical gradients is of considerable importance. The capacity to garner such information efficiently would, inter alia, permit lifeforms to adapt and coexist with their environment, and to undertake locomotion in a directed fashion. Close connections exist between information retrieval and motility on the one hand and cell size on the other, since organisms below a certain size would become inefficient at undertaking the former. By drawing upon results derived by Dusenbery (1997, 2009), we recast them into formulae for the minimal cell size \( (R_{\text{min}}) \) that are more amenable to astrobiological analyses; we reiterate that these results should be viewed as heuristic criteria because they are not necessary and sufficient conditions. After deriving these expressions, we applied the framework to a couple of settings.

The first was submarine alkaline hydrothermal vents (AHVs) on Earth and other worlds where
they appear to exist (e.g., Enceladus). What we inferred is that, inasmuch as information acquisition via gradient sensing is concerned, AHVs are theoretically capable of harboring organisms with radii of $\gtrsim 0.1 \mu m$. It is worth reiterating that constraints from other biological functions (e.g., metabolism and replication) could come into play and thereby elevate $R_{\text{min}}$ above the values predicted in this work; some of the relevant caveats and additional factors in this context are delineated in Section 3.1. To offer one specific example from the section, autotrophs may require large enzymes for carbon fixation (e.g., RuBisCO) that accordingly elevate the magnitude of $R_{\text{min}}$, whereas this is anticipated to be less significant for heterotrophs. Our analysis does not imply, however, that such sub-$\mu m$ microbes originated in these environments or that they would necessarily manifest this size. Nonetheless, our results indicate at the minimum that information-centric arguments taken in isolation are insufficient to rule out the existence of organisms with these dimensions in the neighbourhood of AHVs.

One might, in fact, contemplate whether the steep gradients at AHVs, which facilitate the reduction in $R_{\text{min}}$, were accordingly amenable to the evolution of sub-$\mu m$ microbes in AHV habitats. Lastly, if the parameters we have adopted in the relevant formulae are roughly characteristic of AHVs on icy moons and planets in the outer Solar system like Enceladus and perhaps Europa (Nimmo and Pappalardo, 2016; Hand et al., 2020; Jebbar et al., 2020; Taubner et al., 2020), it is conceivable that those worlds could also support similar organisms. We caution that small microbes with radii $\gtrsim 0.1 \mu m$ delineated in the above paragraph might prove to be parasitic, in which case it is easier to search for their larger hosts when conducting life-detection experiments. However, on the basis of the simple mechanistic model developed herein, it is not possible to gauge a priori whether the smallest microbes with effective gradient sensing and dispersal abilities will always turn out to be obligate parasites or whether they may end up being symbionts or free-living cells. Further empirical research, allied to theoretical modeling, is needed to resolve this issue and come up with optimal search strategies in hunting for microorganisms on other worlds.

In the second instance, we chose to tackle Titan, largely because of its unique potential for hosting exotic life in non-aqueous solvents. By taking the properties of the new solvent (methane) into account as well as the astrophysical attributes of Titan (e.g., its size and location), we computed the constraints on the cell size and thereby deduced $R_{\text{min}}$. We found that, when all other traits such as the microenvironment and organismal physiology are held fixed, $R_{\text{min}}$ is virtually identical to its equivalent on Earth. In mathematical terms, this result was along expected lines because the various formulae for the microbial size exhibit a fairly weak dependence on the relevant physicochemical variables, thereby engendering some degree of universality, provided that the gradient length scales are held fixed. Hence, taken at face value, this result implies that organisms on Titan with the capacity to sense gradients efficiently may perhaps possess a similar lower bound on their size despite the dissimilarities between this world and present-day Earth.

Our work has a number of practical implications in the search for extraterrestrial life via in situ life-detection missions. The presence of sharp gradients drives down $R_{\text{min}}$ and might therefore have aided in the early evolution of life. Thus, the search for biomarkers may benefit from prioritizing environments where such gradients exist today or were prevalent in the past; the Gusev crater on Mars with its opaline silica deposits reminiscent of hot springs on Earth is an intriguing example (Ruff and Farmer, 2016; McMahon et al., 2018; Ruff et al., 2020). On the other hand, organisms dwelling in relatively homogeneous environments could require higher $R_{\text{min}}$ if they are to be effective at gradient sensing because of the joint requirements enforced by (2)-(9).

The detection of larger organisms is probably more feasible, as is their likelihood of undergoing fossilisation and possibly being unearthed by field studies. In either event, our framework offers a simple heuristic for predicting what are the smallest organisms with gradient sensing and motility in a given domain, and this tool can be gainfully employed in the selection and design of apposite instrumentation. The latter subject is being vigorously pursued vis-à-vis Mars, Venus, and the sub-
surface ocean worlds of the Solar system (Ball et al., 2007; Hays et al., 2017; Vago et al., 2017; Chan et al., 2019; Williford et al., 2018; Stamenković et al., 2019; Dachwald et al., 2020; Taubner et al., 2020; Carrier et al., 2020; Hein et al., 2020). It is not implausible, therefore, that the discovery of extraterrestrial life might progress a posse ad esse in the coming decades.

Naturally, theoretical consequences of some import emerge from this study as well. As noted above, a reduction in $R_{\text{min}}$ might prove amenable to the evolution of “minimalistic” lifeforms. Furthermore, due to the lowered constraints on information sensing and motility set by size in this case, the transition to more complex organisms may have encountered fewer hurdles. There are reasons to suppose that chemotaxis and movement are intertwined with the prospects for initiating symbiotic interactions and the emergence of complex spatio-temporal aggregates (Budrene and Berg, 1995; Harshey, 2003; Wadhams and Armitage, 2004; Kearns, 2010; Porter et al., 2011; Raina et al., 2019).

Among the critical steps, the advent of multicellularity stands out because it is distinguished by sophisticated intercellular signalling, coordination and specialization (Shapiro, 1998; Grosberg and Strathmann, 2007; Lyons and Kolter, 2015), each of which presumably entailed significant “motion” in both the physical and informational realms (Ben-Jacob et al., 2000; Kearns, 2010; Zhang et al., 2012; Alexandre, 2015). It is tempting to speculate that environments that are more conducive to information acquisition of the type analysed herein would have relatively higher likelihoods for the evolution of simple and complex multicellularity and the profound ecological and evolutionary changes that accompany these transitions (Smith and Szathmáry, 1995; Knoll, 2015; Lingam and Loeb, 2021a); needless to say, this conjecture remains unproven.

Acknowledgments

The author is grateful to Michael Russell, Chris McKay, and Charles Cockell for the valuable comments and references pertaining to certain facets of this work. The insightful and constructive feedback provided by the reviewers is also duly acknowledged. This research was supported by the Florida Institute of Technology and the resources provided by the Harvard Library system were of much use during the course of undertaking this study.

References

J. Adler. Chemotaxis in Bacteria. Science, 153(3737):708–716, Aug. 1966. doi: 10.1126/science.153.3737.708.

S.-V. Albers and K. F. Jarrell. The Archaellum: An Update on the Unique Archaeal Motility Structure. Trends Microbiol., 26(4):351–362, 2018. doi: 10.1016/j.tim.2018.01.004.

G. Alexandre. Chemotaxis Control of Transient Cell Aggregation. J. Bacteriol., 197(20):3230–3237, 2015. doi: 10.1128/JB.00121-15.

G. Alexandre, S. Greer-Phillips, and I. B. Zhulin. Ecological role of energy taxis in microorganisms. FEMS Microbiol. Rev., 28(1):113–126, 2004. doi: 10.1016/j.femsre.2003.10.003.

U. Alon, M. G. Surette, N. Barkai, and S. Leibler. Robustness in bacterial chemotaxis. Nature, 397 (6715):168–171, Jan. 1999. doi: 10.1038/16483.

T. Altair, L. M. Sartori, F. Rodrigues, M. G. B. de Avellar, and D. Galante. Natural Radioactive Environments as Sources of Local Disequilibrium for the Emergence of Life. Astrobiology, 20(12):1489–1497, Dec. 2020. doi: 10.1089/ast.2019.2133.
K. H. Andersen, T. Berge, R. J. Gonçalves, M. Hartvig, J. Heuschele, S. Hylander, N. S. Jacobsen, C. Lindemann, E. A. Martens, A. B. Neuheimer, K. Olsson, A. Palacz, A. E. F. Prove, J. Sainmont, S. J. Traving, A. W. Visser, N. Wadhwa, and T. Kiørboe. Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *Annu. Rev. Mar. Sci.*, 8:217–241, Jan. 2016. doi: 10.1146/annurev-marine-122414-034144.

M. J. Angilletta. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford: Oxford University Press, 2009.

J. P. Armitage. Bacterial Tactic Responses. *Adv. Microb. Physiol.*, 41:229–289, 1999. doi: 10.1016/S0065-2911(08)60168-X.

P. Baaske, F. M. Weinert, S. Duhr, K. H. Lemke, M. J. Russell, and D. Braun. Extreme accumulation of nucleotides in simulated hydrothermal pore systems. *Proc. Natl. Acad. Sci. USA*, 104(22):9346–9351, May 2007. doi: 10.1073/pnas.0609592104.

J. L. Bada. How life began on Earth: a status report. *Earth Planet. Sci. Lett.*, 226(1-2):1–15, Sept. 2004. doi: 10.1016/j.epsl.2004.07.036.

W. Bains. Many Chemistries Could Be Used to Build Living Systems. *Astrobiology*, 4(2):137–167, June 2004. doi: 10.1089/153110704323175124.

A. J. Ball, J. R. C. Garry, R. D. Lorenz, and V. V. Kerzhanovich. *Planetary Landers and Entry Probes*. Cambridge: Cambridge University Press, 2007.

F. J. Ballesteros, A. Fernandez-Soto, and V. J. Martínez. Diving into Exoplanets: Are Water Seas the Most Common? *Astrobiology*, 19(5):642–654, May 2019. doi: 10.1089/ast.2017.1720.

L. M. Barge, E. Branscomb, J. R. Brucato, S. S. Cardoso, J. H. E. Cartwright, S. O. Danielache, D. Galante, T. P. Kee, Y. Miguel, S. Mojzsis, K. J. Robinson, M. J. Russell, E. Simoncini, and P. Sobron. Thermodynamics, Disequilibrium, Evolution: Far-From-Equilibrium Geological and Chemical Considerations for Origin-Of-Life Research. *Orig. Life Evol. Biosph.*, 47(1):39–56, Mar. 2017. doi: 10.1007/s11084-016-9508-z.

L. M. Barge, E. Flores, M. M. Baum, D. G. VanderVelde, and M. J. Russell. Redox and pH gradients drive amino acid synthesis in iron oxyhydroxide mineral systems. *Proc. Natl. Acad. Sci. USA*, 116(11):4828–4833, Mar. 2019. doi: 10.1073/pnas.1812098116.

L. M. Barge, E. Flores, D. G. VanderVelde, J. M. Weber, M. M. Baum, and A. Castonguay. Effects of Geochemical and Environmental Parameters on Abiotic Organic Chemistry Driven by Iron Hydroxide Minerals. *J. Geophys. Res. Planets*, 125(11):e06423, Nov. 2020a. doi: 10.1029/2020JE006423.

L. M. Barge, J.-P. Jones, J. J. Pagano, E. Martinez, and J. Bescup. Three-Dimensional Analysis of a Simulated Prebiotic Hydrothermal Chimney. *ACS Earth Space Chem.*, 4(9):1663–1669, 2020b. doi: 10.1021/acsearthspacechem.0c00186.

J. A. Baross and S. E. Hoffman. Submarine hydrothermal vents and associated gradient environments as sites for the origin and evolution of life. *Orig. Life Evol. Biosph.*, 15(4):327–345, Dec. 1985. doi: 10.1007/BF01808177.

A. E. Bates, R. W. Lee, V. Tunnicliffe, and M. D. Lamare. Deep-sea hydrothermal vent animals seek cool fluids in a highly variable thermal environment. *Nat. Commun.*, 1(2):14, May 2010. doi: 10.1038/ncomms1014.
D. A. Bazylinski and R. B. Frankel. Magnetosome formation in prokaryotes. *Nat. Rev. Microbiol.*, 2(3):217–230, 2004. doi: 10.1038/nrmicro842.

J. T. Beatty, J. Overmann, M. T. Lince, A. K. Manske, A. S. Lang, R. E. Blankenship, C. L. Van Dover, T. A. Martinson, and F. G. Plumley. An obligately photosynthetic bacterial anaerobe from a deep-sea hydrothermal vent. *Proc. Natl. Acad. Sci. USA*, 102(26):9306–9310, June 2005. doi: 10.1073/pnas.0503674102.

C. Bechinger, R. Di Leonardo, H. Löwen, C. Reichhardt, G. Volpe, and G. Volpe. Active particles in complex and crowded environments. *Rev. Mod. Phys.*, 88(4):045006, Nov. 2016. doi: 10.1103/RevModPhys.88.045006.

M. Beeby, J. L. Ferreira, P. Tripp, S.-V. Albers, and D. R. Mitchell. Propulsive nanomachines: the convergent evolution of archaella, flagella and cilia. *FEMS Microbiol. Rev.*, 44(3):253–304, 2020. doi: 10.1093/femsre/fuaa006.

E. Ben-Jacob, I. Cohen, and H. Levine. Cooperative self-organization of microorganisms. *Adv. Phys.*, 49(4):395–554, June 2000. doi: 10.1080/000187300405228.

S. A. Benner, A. Ricardo, and M. A. Carrigan. Is there a common chemical model for life in the universe? *Current opinion in chemical biology*, 8(6):672–689, 2004. doi: 10.1016/j.cbpa.2004.10.003.

H. C. Berg. *Random Walks in Biology*. Princeton: Princeton University Press, 2nd edition, 1993.

H. C. Berg and D. A. Brown. Chemotaxis in Escherichia coli analysed by Three-dimensional Tracking. *Nature*, 239(5374):500–504, Oct. 1972. doi: 10.1038/239500a0.

H. C. Berg and E. M. Purcell. Physics of chemoreception. *Biophys. J.*, 20(2):193–219, 1977. doi: 10.1016/S0006-3495(77)85544-6.

I. A. Berg. Ecological Aspects of the Distribution of Different Autotrophic CO₂ Fixation Pathways. *Appl. Environ. Microbiol.*, 77(6):1925–1936, 2011. doi: 10.1128/AEM.02473-10.

S. Bi and V. Sourjik. Stimulus sensing and signal processing in bacterial chemotaxis. *Curr. Opin. Microbiol.*, 45:22–29, 2018. doi: 10.1016/j.mib.2018.02.002.

W. Bialek and S. Setayeshgar. Physical limits to biochemical signaling. *Proc. Natl. Acad. Sci. USA*, 102(29):10040–10045, July 2005. doi: 10.1073/pnas.05043211102.

R. R. Birge. Photophysics and Molecular Electronic Applications of the Rhodopsins. *Annu. Rev. Phys. Chem.*, 41:683–733, Oct. 1990. doi: 10.1146/annurev.pc.41.100190.003343.

L. O. Björn. *Photobiology: The Science of Light and Life*. New York: Springer, 3rd edition, 2015.

R. Blakemore. Magnetotactic Bacteria. *Science*, 190(4212):377–379, Oct. 1975. doi: 10.1126/science.170679.

W. U. Blanckenhorn. The Evolution of Body Size: What Keeps Organisms Small? *Q. Rev. Biol.*, 75(4):385–407, 2000. doi: 10.1086/393620.

A. Boetius, A. M. Anesio, J. W. Deming, J. A. Mikucski, and J. Z. Rapp. Microbial ecology of the cryosphere: sea ice and glacial habitats. *Nat. Rev. Microbiol.*, 13(11):677–690, 2015. doi: 10.1038/nrmicro3522.
J. T. Bonner. Evidence for the formation of cell aggregates by chemotaxis in the development of the slime mold Dictyostelium discoideum. *J. Exp. Zool.*, 106(1):1–26, 1947. doi: 10.1002/jez.1401060102.

J. T. Bonner. *Why Size Matters: From Bacteria to Blue Whales*. Princeton: Princeton University Press, 2006.

G. M. Boyer, F. Schubotz, R. E. Summons, J. Woods, and E. L. Shock. Carbon Oxidation State in Microbial Polar Lipids Suggests Adaptation to Hot Spring Temperature and Redox Gradients. *Front. Microbiol.*, 11:229, 2020. doi: 10.3389/fmicb.2020.00229.

D. A. Brain, F. Bagenal, Y. J. Ma, H. Nilsson, and G. Stenberg Wieser. Atmospheric escape from unmagnetized bodies. *J. Geophys. Res. Planets*, 121(12):2364–2385, Dec. 2016. doi: 10.1002/2016JE005162.

E. Branscomb, T. Biancalani, N. Goldenfeld, and M. Russell. Escapement mechanisms and the conversion of disequilibria; the engines of creation. *Phys. Rep.*, 677:1–60, 2017. doi: 10.1016/j.physrep.2017.02.001.

M. Brenner, L. Levitov, and E. Budrene. Physical Mechanisms for Chemotactic Pattern Formation by Bacteria. *Biophys. J.*, 74(4):1677–1693, Apr. 1998. doi: 10.1016/S0006-3495(98)77880-4.

T. D. Brock and M. L. Brock. Relationship between Environmental Temperature and Optimum Temperature of Bacteria along a Hot Spring Thermal Gradient. *J. Appl. Bacteriol.*, 31(1):54–58, 1968. doi: 10.1111/j.1365-2672.1968.tb00340.x.

J. H. Brown, J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789, 2004. doi: 10.1890/03-9000.

R. H. Brown, J.-P. Lebreton, and J. H. Waite, editors. *Titan from Cassini-Huygens*. Dordrecht: Springer, 2010. doi: 10.1007/978-1-4020-9215-2.

D. A. Bryant and N.-U. Frigaard. Prokaryotic photosynthesis and phototrophy illuminated. *Trends Microbiol.*, 14(11):488–496, 2006. doi: 10.1016/j.tim.2006.09.001.

E. O. Budrene and H. C. Berg. Dynamics of formation of symmetrical patterns by chemotactic bacteria. *Nature*, 376(6535):49–53, July 1995. doi: 10.1038/376049a0.

B. T. Burcar, L. M. Barge, D. Trail, E. B. Watson, M. J. Russell, and L. B. McGown. RNA Oligomerization in Laboratory Analogues of Alkaline Hydrothermal Vent Systems. *Astrobiology*, 15(7):509–522, July 2015. doi: 10.1089/ast.2014.1280.

R. P. Bywater and K. Conde-Frieboes. Did Life Begin on the Beach? *Astrobiology*, 5(4):568–574, Aug. 2005. doi: 10.1089/ast.2005.5.568.

S. P. Cadogan, G. C. Maitland, and J. P. M. Trusler. Diffusion Coefficients of CO₂ and N₂ in Water at Temperatures between 298.15 K and 423.15 K at Pressures up to 45 MPa. *J. Chem. Eng. Data*, 59(2):519–525, 2014. doi: 10.1021/je401008s.

D. R. Caldwell. Thermal conductivity of sea water. *Deep-Sea Res. Oceanogr. Abstr.*, 21(2):131–137, Jan. 1974. doi: 10.1016/0011-7471(74)90070-9.

B. A. Camley. Collective gradient sensing and chemotaxis: modeling and recent developments. *J. Phys. Condens. Matter*, 30(22):223001, June 2018. doi: 10.1088/1361-648X/aabd9f.
E. Camprubi, J. W. de Leeuw, C. H. House, F. Raulin, M. J. Russell, A. Spang, M. R. Tirumalai, and F. Westall. The Emergence of Life. *Space Sci. Rev.*, 215(8):56, Dec. 2019. doi: 10.1007/s11214-019-0624-8.

M. Carrer, T. Skrbic, S. L. Bore, G. Milano, M. Cascella, and A. Giacometti. Can Polarity-Inverted Surfactants Self-Assemble in Nonpolar Solvents? *J. Phys. Chem. B*, 124(29):6448–6458, 2020. doi: 10.1021/acs.jpcb.0c04842.

B. L. Carrier, D. W. Beaty, M. A. Meyer, J. G. Blank, L. Chou, S. DasSarma, D. J. Des Marais, J. L. Eigenbrode, N. Grefenstette, N. L. Lanza, A. C. Schuerger, P. Schwendner, H. D. Smith, C. R. Stoker, J. D. Tarnas, K. D. Webster, C. Bakermans, B. K. Baxter, M. S. Bell, S. A. Benner, H. H. Bolivar Torres, P. J. Boston, R. Bruner, B. C. Clark, P. DasSarma, A. E. Engelhart, Z. E. Gallegos, Z. K. Garvin, P. J. Gasda, J. H. Green, R. L. Harris, M. E. Hoffman, T. Kieft, A. H. D. Koeppel, P. A. Lee, X. Li, K. L. Lynch, R. Mackelprang, P. R. Mahaffy, L. H. Matthies, M. A. Nelessen, H. E. Newsom, D. E. Northup, B. R. W. O’Connor, S. M. Perl, R. C. Quinn, L. A. Rowe, B. Sauterey, M. A. Schneegurt, D. Schulze-Makuch, L. A. Scuderi, M. N. Spilde, V. Stamenković, J. A. Torres Celis, D. Viola, B. D. Wade, C. J. Walker, R. C. Wiens, A. J. Williams, J. M. Williams, and J. Xu. Mars Extant Life: What’s Next? Conference Report. *Astrobiology*, 20(6):785–814, June 2020. doi: 10.1089/ast.2020.2237.

J. H. E. Cartwright and M. J. Russell. The origin of life: the submarine alkaline vent theory at 30. *Interface Focus*, 9(6):20190104, 2019. doi: 10.1098/rsfs.2019.0104.

A. Celani and M. Vergassola. Bacterial strategies for chemotaxis response. *Proc. Natl. Acad. Sci. USA*, 107(4):1391–1396, Jan. 2010. doi: 10.1073/pnas.0909673107.

M. A. Chan, N. W. Himman, S. L. Potter-McIntyre, K. E. Schubert, R. J. Gillams, S. M. Awramik, P. J. Boston, D. M. Bower, D. J. Des Marais, J. D. Farmer, T. Z. Jia, P. L. King, R. M. Hazen, R. J. Léveillé, D. Papineau, K. R. Rempfert, M. Sánchez-Román, J. R. Spear, G. Southam, J. C. Stern, and H. J. Cleaves. Deciphering Biosignatures in Planetary Contexts. *Astrobiology*, 19(9):1075–1102, Sept. 2019. doi: 10.1089/ast.2018.1903.

X. Cheng, Y. Zeng, Z. Guo, and L. Zhu. Diffusion of Nitrogen and Phosphorus Across the Sediment-Water Interface and In Seawater at Aquaculture Areas of Daya Bay, China. *Int. J. Environ. Res. Public Health*, 11(2):1557–1572, 2014. doi: 10.3390/ijerph11021557.

A. D. Chiasson. *Geothermal Heat Pump and Heat Engine Systems: Theory And Practice*. Chichester: John Wiley & Sons, 2016.

U. R. Christensen. Dynamo Scaling Laws and Applications to the Planets. *Space Sci. Rev.*, 152(1-4):565–590, May 2010. doi: 10.1007/s11214-009-9553-2.

H. J. Cleaves, A. D. Aubrey, and J. L. Bada. An Evaluation of the Critical Parameters for Abiotic Peptide Synthesis in Submarine Hydrothermal Systems. *Orig. Life Evol. Biosph.*, 39(2):109–126, Apr. 2009. doi: 10.1007/s11084-008-9154-1.

C. S. Cockell. Life on Venus. *Planet. Space Sci.*, 47(12):1487–1501, Dec. 1999. doi: 10.1016/S0032-0633(99)00036-7.

C. S. Cockell. *The Equations of Life: How Physics Shapes Evolution*. New York: Basic Books, 2018.

C. S. Cockell. *Astrobiology: Understanding Life in the Universe*. Hoboken: John Wiley & Sons, 2nd edition, 2020.

22
C. S. Cockell, S. McMahon, and J. F. Biddle. When Is Life a Viable Hypothesis? The Case of Venusian Phosphine. *Astrobiology*, 21(2), 2021. doi: 10.1089/ast.2020.2390.

J. B. Corliss, J. A. Baross, and S. E. Hoffman. An hypothesis concerning the relationship between submarine hot springs and the origin of life on Earth. *Oceanol. Acta Sp.*, 4:59–69, 1981. URL https://archimer.ifremer.fr/doc/00245/35661/34170.pdf.

J. Cremer, T. Honda, Y. Tang, J. Wong-Ng, M. Vergassola, and T. Hwa. Chemotaxis as a navigation strategy to boost range expansion. *Nature*, 575(7784):658–663, Nov. 2019. doi: 10.1038/s41586-019-1733-y.

H. M. Cuppen, C. Walsh, T. Lamberts, D. Semenov, R. T. Garrod, E. M. Penteado, and S. Ioppolo. Grain Surface Models and Data for Astrochemistry. *Space Sci. Rev.*, 212(1-2):1–58, Oct. 2017. doi: 10.1007/s11214-016-0319-3.

B. Dachwald, S. Ulamec, F. Postberg, F. Sohl, J.-P. de Vera, C. Waldmann, R. D. Lorenz, K. A.zacny, H. Hellard, J. Biele, and P. Rettberg. Key Technologies and Instrumentation for Subsurface Exploration of Ocean Worlds. *Space Sci. Rev.*, 216(5):83, June 2020. doi: 10.1007/s11214-020-00707-5.

B. Damer and D. Deamer. The Hot Spring Hypothesis for an Origin of Life. *Astrobiology*, 20(4):429–452, Apr. 2020. doi: 10.1089/ast.2019.2045.

S. DasSarma and E. W. Schwieterman. Early evolution of purple retinal pigments on Earth and implications for exoplanet biosignatures. *Int. J. Astrobiol.*, pages 1–10, 2018. doi: 10.1017/S1473550418000423.

I. de Pater and J. J. Lissauer. *Planetary Sciences*. Cambridge: Cambridge University Press, 2015.

D. Deamer and B. Damer. Can Life Begin on Enceladus? A Perspective from Hydrothermal Chemistry. *Astrobiology*, 17(9):834–839, Sept. 2017. doi: 10.1089/ast.2016.1610.

D. Deamer, B. Damer, and V. Kompanichenko. Hydrothermal Chemistry and the Origin of Cellular Life. *Astrobiology*, 19(12):1523–1537, Dec. 2019. doi: 10.1089/ast.2018.1979.

D. W. Deamer. *Assembling Life: How Can Life Begin on Earth and Other Habitable Planets?* Oxford: Oxford University Press, 2019.

J. P. DeLong, J. G. Okie, M. E. Moses, R. M. Sibly, and J. H. Brown. Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proc. Natl. Acad. Sci. USA*, 107(29):12941–12945, July 2010. doi: 10.1073/pnas.1007783107.

M. Demir and H. Salman. Bacterial Thermotaxis by Speed Modulation. *Biophys. J.*, 103(8):1683–1690, Oct. 2012. doi: 10.1016/j.bpj.2012.09.005.

M. Denny. *Air and Water: The Biology and Physics of Life’s Media*. Princeton: Princeton University Press, 1993.

D. J. Des Marais and M. R. Walter. Terrestrial Hot Spring Systems: Introduction. *Astrobiology*, 19(12):1419–1432, Dec. 2019. doi: 10.1089/ast.2018.1976.

C. Dong, M. Lingam, Y. Ma, and O. Cohen. Is Proxima Centauri b Habitable? A Study of Atmospheric Loss. *Astrophys. J. Lett.*, 837(2):L26, Mar. 2017. doi: 10.3847/2041-8213/aa6438.
C. Dong, M. Jin, M. Lingam, V. S. Airapetian, Y. Ma, and B. van der Holst. Atmospheric escape from the TRAPPIST-1 planets and implications for habitability. *Proc. Natl. Acad. Sci. USA*, 115(2):260–265, Jan. 2018. doi: 10.1073/pnas.1708010115.

D. B. Dusenbery. Minimum Size Limit for Useful Locomotion by Free-Swimming Microbes. *Proc. Natl. Acad. Sci. USA*, 94(20):10949–10954, Sept. 1997. doi: 10.1073/pnas.94.20.10949.

D. B. Dusenbery. *Living at Micro Scale: The Unexpected Physics of Being Small*. Cambridge: Harvard University Press, 2009.

F. Dyson. *Origins of Life*. Cambridge: Cambridge University Press, 1999.

B. D. Engel, M. Schaffer, L. K. Cuellar, E. Villa, J. M. Plitzko, and W. Baumeister. Native architecture of the *Chlamydomonas* chloroplast revealed by in situ cryo-electron tomography. *eLife*, 4:e04889, 2015. doi: 10.7554/eLife.04889.

T. W. Engelmann. Neue Methode zur Untersuchung der Sauerstoffausscheidung pflanzlicher und thierischer Organismen. *Pflüger Arch. Gesamte Physiol. Menschen Tiere.*, 25(1):285–292, 1881. doi: 10.1007/BF01661982.

K. Erglis, Q. Wen, V. Ose, A. Zeltins, A. Sharipo, P. Janmey, and A. Cebers. Dynamics of Magnetotactic Bacteria in a Rotating Magnetic Field. *Biophys. J.*, 93(4):1402–1412, Aug. 2007. doi: 10.1529/biophysj.107.107474.

O. P. Ernst, D. T. Lodowski, M. Elstner, P. Hegemann, L. S. Brown, and H. Kandori. Microbial and Animal Rhodopsins: Structures, Functions, and Molecular Mechanisms. *Chem. Rev.*, 114(1):126–163, 2014. doi: 10.1021/cr4003769.

D. Faivre and D. Schuler. Magnetotactic Bacteria and Magnetosomes. *Chem. Rev.*, 108(11):4875–4898, 2008. doi: 10.1021/cr078258w.

K. A. Farley, K. H. Williford, K. M. Stack, R. Bhartia, A. Chen, M. de la Torre, K. Hand, Y. Goreva, C. D. K. Herd, R. Hueso, Y. Liu, J. N. Maki, G. Martinez, R. C. Moeller, A. Nelessen, C. E. Newman, D. Nunes, A. Ponce, N. Spanovich, P. A. Willis, L. W. Beegle, J. F. Bell, A. J. Brown, S.-E. Hamran, J. A. Hurowitz, S. Maurice, D. A. Paige, J. A. Rodriguez-Manfredi, M. Schulte, and R. C. Wiens. Mars 2020 Mission Overview. *Space Sci. Rev.*, 216(8):142, Dec. 2020. doi: 10.1007/s11214-020-00762-y.

T. Fenchel. Microbial Behavior in a Heterogeneous World. *Science*, 296(5570):1068–1071, May 2002. doi: 10.1126/science.1070118.

N. Figueroa-Morales, R. Soto, G. Junot, T. Darnige, C. Douarche, V. A. Martinez, A. Lindner, and É. Clément. 3D Spatial Exploration by *E. coli* Echoes Motor Temporal Variability. *Phys. Rev. X*, 10(2):021004, Apr. 2020. doi: 10.1103/PhysRevX.10.021004.

K. W. Foster, J. Saranak, N. Patel, G. Zarilli, M. Okabe, T. Kline, and K. Nakanishi. A rhodopsin is the functional photoreceptor for phototaxis in the unicellular eukaryote *Chlamydomonas*. *Nature*, 311(5988):756–759, Oct. 1984. doi: 10.1038/311756a0.

I. Fry. *The Emergence of Life on Earth: A Historical and Scientific Overview*. New Brunswick: Rutgers University Press, 2000.
X. Fu, S. Kato, J. Long, H. H. Mattingly, C. He, D. C. Vural, S. W. Zucker, and T. Emonet. Spatial self-organization resolves conflicts between individuality and collective migration. *Nat. Commun.*, 9:2177, June 2018. doi: 10.1038/s41467-018-04539-4.

G. Fuchs. Alternative Pathways of Carbon Dioxide Fixation: Insights into the Early Evolution of Life? *Annu. Rev. Microbiol.*, 65:631–658, 2011. doi: 10.1146/annurev-micro-090110-102801.

A. E. Gilliam and C. P. McKay. Titan under a red dwarf star and as a rogue planet: requirements for liquid methane. *Planet. Space Sci.*, 59(9):835–839, July 2011. doi: 10.1016/j.pss.2011.03.012.

M. B. Ginzberg, R. Kafri, and M. Kirschner. On being the right (cell) size. *Science*, 348(6236): 1245075, 2015. doi: 10.1126/science.1245075.

S. K. Goffredi, J. J. Childress, N. T. Desaulniers, R. W. Lee, F. H. Lallier, and D. Hammond. Inorganic carbon acquisition by the hydrothermal vent tubeworm *Riftia pachyptila* depends upon high external P$_{CO_2}$ and upon proton-equivalent ion transport by the worm. *J. Exp. Biol.*, 200(5): 883–896, 1997.

L. Gómez-Consarnau, J. A. Raven, N. M. Levine, L. S. Cutter, D. Wang, B. Seegers, J. Arístegui, J. A. Fuhrman, J. M. Gasol, and S. A. Sañudo-Wilhelmy. Microbial rhodopsins are major contributors to the solar energy captured in the sea. *Sci. Adv.*, 5(8):eaaw8855, Aug. 2019. doi: 10.1126/sciadv.aaw8855.

V. I. Gordeliy, J. Labahn, R. Moukhametzianov, R. Efremov, J. Granzin, R. Schlesinger, G. Büldt, T. Savopol, A. J. Scheidig, J. P. Klare, and M. Engelhard. Molecular basis of transmembrane signalling by sensory rhodopsin II-transducer complex. *Nature*, 419(6906):484–487, Oct. 2002. doi: 10.1038/nature01109.

V. Gornitz, editor. *Encyclopedia of Paleoclimatology and Ancient Environments*. Dordrecht: Springer, 2009.

J. S. Greaves, A. M. S. Richards, W. Bains, P. B. Rimmer, H. Sagawa, D. L. Clements, S. Seager, J. J. Petkowski, C. Sousa-Silva, S. Ranjan, E. Drabek-Maunder, H. J. Fraser, A. Cartwright, I. Mueller-Wodarg, Z. Zhan, P. Friberg, I. Coulsen, E. Lee, and J. Hoge. Phosphine gas in the cloud decks of Venus. *Nat. Astron.*, Sept. 2020. doi: 10.1038/s41550-020-1174-4.

D. H. Grinspoon and M. A. Bullock. Astrobiology and Venus exploration. *Geophys. Monogr. Ser.*, 176:191–206, Jan. 2007. doi: 10.1029/176GM12.

R. K. Grosberg and R. R. Strathmann. The Evolution of Multicellularity: A Minor Major Transition? *Annu. Rev. Ecol. Evol. Syst.*, 38:621–654, 2007. doi: 10.1146/annurev.ecolsys.36.102403.114735.

V. Hakim and P. Silberzan. Collective cell migration: a physics perspective. *Rep. Prog. Phys.*, 80(7): 076601, July 2017. doi: 10.1088/1361-6633/aa65ef.

J. B. S. Haldane. On being the right size. *Harper’s Magazine*, 152:424–427, 1926.

K. P. Hand, C. Sotin, A. Hayes, and A. Coustenis. On the Habitability and Future Exploration of Ocean Worlds. *Space Science Reviews*, 216(5):1–24, 2020. doi: 10.1007/s11214-020-00713-7.

P. J. Hansen, N. Lundholm, and B. Rost. Growth limitation in marine red-tide dinoflagellates: effects of pH versus inorganic carbon availability. *Mar. Ecol. Prog. Ser.*, 334:63–71, Mar. 2007. doi: 10.3354/meps334063.
J. Hao, A. H. Knoll, F. Huang, J. Schieber, R. M. Hazen, and I. Daniel. Cycling phosphorus on the Archean Earth: Part II. Phosphorus limitation on primary production in Archean ecosystems. *Geochim. Cosmochim. Acta*, 280:360–377, July 2020. doi: 10.1016/j.gca.2020.04.005.

P. A. Hargrave. Rhodopsin Structure, Function, and Topography The Friedenwald Lecture. *Investig. Ophthalmol. Vis. Sci.*, 42(1):3–9, 2001.

K. R. Harris and N. J. Trappeniers. The density dependence of the self-diffusion coefficient of liquid methane. *Physica A*, 104(1):262–280, Nov. 1980. doi: 10.1016/0378-4371(80)90087-4.

S. A. Harrison and N. Lane. Life as a guide to prebiotic nucleotide synthesis. *Nat. Commun.*, 9:5176, Dec. 2018. doi: 10.1038/s41467-018-07220-y.

R. M. Harshey. Bacterial Motility on a Surface: Many Ways to a Common Goal. *Annu. Rev. Microbiol.*, 57(1):249–273, 2003. doi: 10.1146/annurev.micro.57.030502.091014.

R. B. Harvey. Enzymes of Thermal Algae. *Science*, 60(1560):481–482, Nov. 1924. doi: 10.1126/science.60.1560.481.

A. G. Hayes. The Lakes and Seas of Titan. *Annu. Rev. Earth Planet. Sci.*, 44:57–83, June 2016. doi: 10.1146/annurev-earth-060115-012247.

L. E. Hays, H. V. Graham, D. J. Des Marais, E. M. Hausrath, B. Horgan, T. M. McCollom, M. N. Parenteau, S. L. Potter-McIntyre, A. J. Williams, and K. L. Lynch. Biosignature Preservation and Detection in Mars Analog Environments. *Astrobiology*, 17(4):363–400, Apr. 2017. doi: 10.1089/ast.2016.1627.

G. L. Hazelbauer. Bacterial Chemotaxis: The Early Years of Molecular Studies. *Annu. Rev. Microbiol.*, 66:285–303, 2012. doi: 10.1146/annurev-micro-092607.092847.

P. Hegemann. Algal Sensory Photoreceptors. *Annu. Rev. Plant Biol.*, 59:167–189, 2008. doi: 10.1146/annurev.arplant.59.032607.092847.

A. M. Hein, M. Lingam, T. Marshall Eubanks, A. Hibberd, D. Fries, and W. P. Blase. A Precursor Balloon Mission for Venusian Astrobiology. *Astrophys. J. Lett.*, 903(2):L36, Nov. 2020. doi: 10.3847/2041-8213/abc347.

B. Herzog and R. Wirth. Swimming Behavior of Selected Species of Archaea. *Appl. Environ. Microbiol.*, 78(6):1670–1674, 2012. doi: 10.1128/AEM.06723-11.

J. Horner, S. R. Kane, J. P. Marshall, P. A. Dalba, T. R. Holt, J. Wood, H. E. Maynard-Casely, R. Wittenmyer, P. S. Lykawka, M. Hill, R. Salmeron, J. Bailey, T. Löhne, M. Agnew, B. D. Carter, and C. C. E. Tylor. Solar System Physics for Exoplanet Research. *Publ. Astron. Soc. Pac.*, 132(1016):102001, Oct. 2020. doi: 10.1088/1538-3873/ab8eb9.

S. M. Hörst. Titan’s atmosphere and climate. *J. Geophys. Res. Planets*, 122(3):432–482, Mar. 2017. doi: 10.1002/2016JE005240.

B. Hu and Y. Tu. Behaviors and Strategies of Bacterial Navigation in Chemical and Nonchemical Gradients. *PLoS Comput. Biol.*, 10(6):e1003672, 2014. doi: 10.1371/journal.pcbi.1003672.

R. Hudson, R. de Graaf, M. S. Rodin, A. Ohno, N. Lane, S. E. McGlynn, Y. M. A. Yamada, R. Nakamura, L. M. Barge, D. Braun, and V. Sojo. CO₂ reduction driven by a pH gradient. *Proc. Natl. Acad. Sci. USA*, 117(37):22873–22879, 2020. doi: 10.1073/pnas.2002659117.
L. N. Irwin and D. Schulze-Makuch. The Astrobiology of Alien Worlds: Known and Unknown Forms of Life. *Universe*, 6(9):130, Aug. 2020. doi: 10.3390/universe6090130.

J. B. Jackson. Natural pH Gradients in Hydrothermal Alkali Vents Were Unlikely to Have Played a Role in the Origin of Life. *J. Mol. Evol.*, 83(1-2):1–11, Aug. 2016. doi: 10.1007/s00239-016-9756-6.

M. Jebbar, K. Hickman-Lewis, B. Cavalazzi, R.-S. Taubner, S. K. M. R. Rittmann, and A. Antunes. Microbial Diversity and Biosignatures: An Icy Moons Perspective. *Space Sci. Rev.*, 216(1):10, Jan. 2020. doi: 10.1007/s11214-019-0620-z.

G. Jékely. Evolution of phototaxis. *Phil. Trans. R. Soc. B*, 364(1531):2795–2808, 2009. doi: 10.1098/rstb.2009.0072.

D. E. Jennings, V. Cottini, C. A. Nixon, R. K. Achterberg, F. M. Flasar, V. G. Kunde, P. N. Romani, R. E. Samuelson, A. Mamoutkine, N. J. P. Gorius, A. Coustenis, and T. Tokano. Surface Temperatures on Titan during Northern Winter and Spring. *Astrophys. J. Lett.*, 816(1):L17, Jan. 2016. doi: 10.3847/2041-8205/816/1/L17.

X. Jia, M. G. Kivelson, K. K. Khurana, and W. S. Kurth. Evidence of a plume on Europa from Galileo magnetic and plasma wave signatures. *Nat. Astron.*, 2:459–464, May 2018. doi: 10.1038/s41550-018-0450-z.

J. G. Jones. *Advances in Microbial Ecology*, volume 13. New York: Springer, 1993. doi: 10.1007/978-1-4615-2858-6.

D. B. Kearns. A field guide to bacterial swarming motility. *Nat. Rev. Microbiol.*, 8(9):634–644, 2010. doi: 10.1038/nrmicro2405.

E. F. Keller and L. A. Segel. Model for chemotaxis. *J. Theor. Biol.*, 30(2):225–234, 1971. doi: 10.1016/0022-5193(71)90050-6.

D. S. Kelley, J. A. Baross, and J. R. Delaney. Volcanoes, Fluids, and Life at Mid-Ocean Ridge Spreading Centers. *Annu. Rev. Earth Planet. Sci.*, 30:385–491, Jan. 2002. doi: 10.1146/annurev.earth.30.091201.141331.

C. P. Kempes, P. M. van Bodegom, D. Wolpert, E. Libby, J. Amend, and T. Hoehler. Drivers of Bacterial Maintenance and Minimal Energy Requirements. *Front. Microbiol.*, 8:31, 2017. doi: 10.3389/fmicb.2017.00031.

C. P. Kempes, M. A. R. Koehl, and G. B. West. The Scales That Limit: The Physical Boundaries of Evolution. *Front. Ecol. Evol.*, 7:242, 2019. doi: 10.3389/fevo.2019.00242.

T. Kiørboe. *A Mechanistic Approach to Plankton Ecology*. Princeton: Princeton University Press, 2008.

D. L. Kirchman. The uptake of inorganic nutrients by heterotrophic bacteria. *Microb. Ecol.*, 28(2):255–271, 1994. doi: 10.1007/BF00166816.

D. L. Kirchman. *Processes in Microbial Ecology*. Oxford: Oxford University Press, 2nd edition, 2018.

N. Kitadai and S. Maruyama. Origins of building blocks of life: A review. *Geosci. Front.*, 9(4):1117–1153, 2018. doi: 10.1016/j.gsf.2017.07.007.
N. Kitadai, R. Nakamura, M. Yamamoto, K. Takai, N. Yoshida, and Y. Oono. Metals likely promoted protometabolism in early ocean alkaline hydrothermal systems. *Sci. Adv.*, 5(6):eaav7848, June 2019. doi: 10.1126/sciadv.aav7848.

A. Knoll, M. J. Osborn, J. Baross, H. C. Berg, N. R. Pace, and M. Sogin. *Size Limits of Very Small Microorganisms: Proceedings of a Workshop*. Washington, DC: National Academy Press, 1999.

A. H. Knoll. *Life on a Young Planet: The First Three Billion Years of Evolution on Earth*. Princeton Science Library. Princeton: Princeton University Press, 2015.

A. L. Koch. What size should a bacterium be? A question of scale. *Annu. Rev. Microbiol.*, 50(1):317–348, 1996. doi: 10.1146/annurev.micro.50.1.317.

M. Kreysing, L. Keil, S. Lanzmich, and D. Braun. Heat flux across an open pore enables the continuous replication and selection of oligonucleotides towards increasing length. *Nat. Chem.*, 7(3):203–208, Mar. 2015. doi: 10.1038/nchem.2155.

M. D. Krom and R. A. Berner. The diffusion coefficients of sulfate, ammonium, and phosphate ions in anoxic marine sedimentsI. *Limnol. Oceanogr.*, 25(2):327–337, Mar. 1980. doi: 10.4319/lo.1980.25.2.0327.

T. A. Laakso and D. P. Schrag. Limitations on Limitation. *Global Biogeochem. Cy.*, 32(3):486–496, Mar. 2018. doi: 10.1002/2017GB005832.

S. Q. Lang and W. J. Brazelton. Habitability of the marine serpentinite subsurface: a case study of the Lost City hydrothermal field. *Phil. Trans. R. Soc. A*, 378(2165):20180429, 2020. doi: 10.1098/rsta.2018.0429.

D. E. LaRowe and J. P. Amend. Power limits for microbial life. *Front. Microbiol.*, 6:718, 2015. doi: 10.3389/fmicb.2015.00718.

R. Lathe. Fast tidal cycling and the origin of life. *Icarus*, 168(1):18–22, Mar. 2004. doi: 10.1016/j.icarus.2003.10.018.

E. Lauga. Bacterial Hydrodynamics. *Annu. Rev. Fluid Mech.*, 48(1):105–130, Jan. 2016. doi: 10.1146/annurev-fluid-122414-034606.

F. M. Lauro, D. McDougald, T. Thomas, T. J. Williams, S. Egan, S. Rice, M. Z. DeMaere, L. Ting, H. Ertan, J. Johnson, S. Ferriera, A. Lapidus, I. Anderson, N. Kyrpides, A. C. Munk, C. Detter, C. S. Han, M. V. Brown, F. T. Robb, S. Kjelleberg, and R. Cavicchioli. The genomic basis of trophic strategy in marine bacteria. *Proc. Natl. Acad. Sci. USA*, 106(37):15527–15533, Sept. 2009. doi: 10.1073/pnas.0903507106.

C. T. Lefevre and D. A. Baizlinski. Ecology, Diversity, and Evolution of Magnetotactic Bacteria. *Microbiol. Mol. Biol. Rev.*, 77(3):497–526, 2013. doi: 10.1128/MMBR.00021-13.

M. A. Lever, K. L. Rogers, K. G. Lloyd, J. Overmann, B. Schink, R. K. Thauer, T. M. Hoehler, and B. B. Jørgensen. Life under extreme energy limitation: a synthesis of laboratory- and field-based investigations. *FEMS Microbiol. Rev.*, 39(5):688–728, 2015. doi: 10.1093/femsre/fuv020.

W. K. W. Li, D. V. Subba Rao, W. G. Harrison, J. C. Smith, J. J. Cullen, B. Irwin, and T. Platt. Autotrophic Picoplankton in the Tropical Ocean. *Science*, 219(4582):292–295, Jan. 1983. doi: 10.1126/science.219.4582.292.
N. A. Lyons and R. Kolter. On the evolution of bacterial multicellularity. *Curr. Opin. Microbiol.*, 24: 21–28, 2015. doi: 10.1016/j.mib.2014.12.007.

A. M. Makarieva, V. G. Gorschkov, B.-L. Li, S. L. Chown, P. B. Reich, and V. M. Gavrilov. Mean mass-specific metabolic rates are strikingly similar across life’s major domains: Evidence for life’s metabolic optimum. *Proc. Natl. Acad. Sci. USA*, 105(44):16994–16999, Nov. 2008. doi: 10.1073/pnas.0802148105.

R. R. Malmstrom, R. P. Kiene, M. T. Cottrell, and D. L. Kirchman. Contribution of SAR11 Bacteria to Dissolved Dimethylsulfoniopropionate and Amino Acid Uptake in the North Atlantic Ocean. *Appl. Environ. Microbiol.*, 70(7):4129–4135, 2004. doi: 10.1128/AEM.70.7.4129-4135.2004.

J. Maniolf, K. H. Nealson, R. Psenner, M. Loferer, and R. L. Folk. Nannobacteria: size limits and evidence. *Science*, 276(5320):1773–1776, 1997. doi: 10.1126/science.276.5320.1773e.

K. H. Mann and J. R. N. Lazier. *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans*. Oxford: Blackwell Publishing, 3rd edition, 2006.

A. K. Manske, J. Glaeser, M. M. M. Kuypers, and J. Overmann. Physiology and Phylogeny of Green Sulfur Bacteria Forming a Monospecific Phototrophic Assemblage at a Depth of 100 Meters in the Black Sea. *Appl. Environ. Microbiol.*, 71(12):8049–8060, 2005. doi: 10.1128/AEM.71.12.8049-8060.2005.

E. A. Martens, N. Wadhwa, N. S. Jacobsen, C. Lindemann, K. H. Andersen, and A. Visser. Size structures sensory hierarchy in ocean life. *Proc. R. Soc. B*, 282(1815):20151346, 2015. doi: 10.1098/rspb.2015.1346.

A. Martin and A. McMinn. Sea ice, extremophiles and life on extra-terrestrial ocean worlds. *Int. J. Astrobio.*, 17(1):1–16, Jan. 2018. doi: 10.1017/S1473550416000483.

W. Martin, J. Baross, D. Kelley, and M. J. Russell. Hydrothermal vents and the origin of life. *Nat. Rev. Microbiol.*, 6(11):805–814, 2008. doi: 10.1038/nrmicro1991.

C. B. Mast, S. Schink, U. Gerland, and D. Braun. Escalation of polymerization in a thermal gradient. *Proc. Natl. Acad. Sci. USA*, 110(20):8030–8035, May 2013. doi: 10.1073/pnas.1303222110.

S. R. N. McIntyre, C. H. Lineweaver, and M. J. Ireland. Planetary magnetism as a parameter in exoplanet habitability. *Mon. Not. R. Astron. Soc.*, 485(3):3999–4012, May 2019. doi: 10.1093/mnras/stz667.

C. P. McKay. Requirements and limits for life in the context of exoplanets. *Proc. Natl. Acad. Sci. USA*, 111(35):12628–12633, Sept. 2014. doi: 10.1073/pnas.1304212111.

C. P. McKay. Titan as the Abode of Life. *Life*, 6(1):8, Feb. 2016. doi: 10.3390/life6010008.

C. P. McKay and H. D. Smith. Possibilities for methanogenic life in liquid methane on the surface of Titan. *Icarus*, 178(1):274–276, Nov. 2005. doi: 10.1016/j.icarus.2005.05.018.

S. McMahon, T. Bosak, J. P. Grotzinger, R. E. Milliken, R. E. Summons, M. Daye, S. A. Newman, A. Fraeman, K. H. Williford, and D. E. G. Briggs. A Field Guide to Finding Fossils on Mars. *J. Geophys. Res. Planets*, 123(5):1012–1040, May 2018. doi: 10.1029/2017JE005478.

V. S. Meadows, G. N. Arney, B. E. Schmidt, and D. J. Des Marais, editors. *Planetary Astrobiology*. Space Science Series. Tucson: University of Arizona Press, 2020.
B. Ménez, C. Pisapia, M. Andreani, F. Jamme, Q. P. Vanbellingen, A. Brunelle, L. Richard, P. Dumas, and M. Réfrégiers. Abiotic synthesis of amino acids in the recesses of the oceanic lithosphere. *Nature*, 564(7734):59–63, Nov. 2018. doi: 10.1038/s41586-018-0684-z.

N. Meyer-Vernet and J.-P. Rospars. Maximum relative speeds of living organisms: Why do bacteria perform as fast as ostriches? *Phys. Biol.*, 13(6):066006, Dec. 2016. doi: 10.1088/1478-3975/13/6/066006.

G. Micali and R. G. Endres. Bacterial chemotaxis: information processing, thermodynamics, and behavior. *Curr. Opin. Microbiol.*, 30:8–15, 2016. doi: 10.1016/j.mib.2015.12.001.

J. R. Michalski, T. C. Onstott, S. J. Mojzsis, J. Mustard, Q. H. S. Chan, P. B. Niles, and S. S. Johnson. The Martian subsurface as a potential window into the origin of life. *Nat. Geosci.*, 11(1):21–26, Dec. 2018. doi: 10.1038/s41561-017-0015-2.

R. Milo and R. Phillips. *Cell Biology by the Numbers*. New York: Garland Science, 2016.

Z. Minic and P. D. Thongbam. The Biological Deep Sea Hydrothermal Vent as a Model to Study Carbon Dioxide Capturing Enzymes. *Mar. Drugs*, 9(5):719–738, 2011. doi: 10.3390/md9050719.

F. Mispelaer, P. Thoué, H. Aoudidi, J. Noble, F. Duvernay, G. Danger, P. Roubin, O. Morata, T. Hasegawa, and T. Chiavassa. Diffusion measurements of CO, HNCO, H$_2$CO, and NH$_3$ in amorphous water ice. *Astron. Astrophys.*, 555:A13, July 2013. doi: 10.1051/0004-6361/201220691.

A. Möglich, X. Yang, R. A. Ayers, and K. Moffat. Structure and Function of Plant Photoreceptors. *Annu. Rev. Plant Biol.*, 61:21–47, 2010. doi: 10.1146/annurev-arplant-042809-042809.

F. M. Möller, F. Kriegel, M. Kieß, V. Sojo, and D. Braun. Steep pH Gradients and Directed Colloid Transport in a Microfluidic Alkaline Hydrothermal Pore. *Angew. Chem. Int. Ed.*, 56(9):2340–2344, 2017. doi: 10.1002/anie.201610781.

I. Mori. Genetics of Chemotaxis and Thermotaxis in the Nematode *Caenorhabditis Elegans*. *Annu. Rev. Genet.*, 33(1):399–422, 1999. doi: 10.1146/annurev.genet.33.1.399.

H. Morowitz and C. Sagan. Life in the Clouds of Venus? *Nature*, 215(5107):1259–1260, Sept. 1967. doi: 10.1038/2151259a0.

H. J. Morowitz. Biological self-replicating systems. *Prog. Theoret. Biol.*, 1:35–58, 1967.

K. B. Muchowska, S. J. Varma, and J. Moran. Nonenzymatic Metabolic Reactions and Life’s Origins. *Chem. Rev.*, 120(15):7708–7744, 2020. doi: 10.1021/acs.chemrev.0c00191.

A. Y. Malkidjianian, A. Y. Bychkov, D. V. Dibrova, M. Y. Galperin, and E. V. Koonin. PNAS Plus: Origin of first cells at terrestrial, anoxic geothermal fields. *Proc. Natl. Acad. Sci. USA*, 109(14):E821–E830, Apr. 2012. doi: 10.1073/pnas.1117774109.

J. Nadeau, C. Lindensmith, J. W. Deming, V. I. Fernandez, and R. Stocker. Microbial Morphology and Motility as Biosignatures for Outer Planet Missions. *Astrobiology*, 16(10):755–774, Oct. 2016. doi: 10.1089/ast.2015.1376.

J. L. Nadeau, M. Bedrossian, and C. A. Lindensmith. Imaging technologies and strategies for detection of extant extraterrestrial microorganisms. *Adv. Phys. X*, 3(1):1424032, 2018. doi: 10.1080/23746149.2018.1424032.
M. Neveu, L. E. Hays, M. A. Voytek, M. H. New, and M. D. Schulte. The Ladder of Life Detection. *Astrobiology*, 18(11):1375–1402, Nov. 2018. doi: 10.1089/ast.2017.1773.

M. Neveu, A. Anbar, A. F. Davila, D. P. Glavin, S. M. Mackenzie, C. Phillips-Lander, B. Sherwood, Y. Takano, P. Williams, and H. Yano. Returning Samples From Enceladus for Life Detection. *Front. Astron. Space Sci.*, 7:26, 2020. doi: 10.3389/fspas.2020.00026.

D. Niether, D. Afanasenkov, and J. K. G. Dhont. Accumulation of formamide in hydrothermal pores to form prebiotic nucleobases. *Proc. Natl. Acad. Sci. USA*, 113(16):4272–4277, Apr. 2016. doi: 10.1073/pnas.1600275113.

F. Nimmo and R. T. Pappalardo. Ocean worlds in the outer solar system. *J. Geophys. Res. Planets*, 121(8):1378–1399, Aug. 2016. doi: 10.1002/2016JE005081.

E. G. Nisbet and C. M. R. Fowler. The hydrothermal imprint on life: did heat-shock proteins, metalloproteins and photosynthesis begin around hydrothermal vents? *Geol. Soc. London Spec. Publ.*, 118(1):239–251, Jan. 1996. doi: 10.1144/GSL.SP.1996.118.01.15.

E. G. Nisbet, J. R. Cann, and C. L. Van Dover. Origins of photosynthesis. *Nature*, 373(6514):479–480, Feb. 1995. doi: 10.1038/373479a0.

A. Okubo and S. A. Levin. *Diffusion and Ecological Problems: Modern Perspectives*, volume 14 of *Interdisciplinary Applied Mathematics*. New York: Springer-Verlag, 2nd edition, 2001.

S. L. Olson, M. Jansen, and D. S. Abbot. Oceanographic Considerations for Exoplanet Life Detection. *Astrophys. J.*, 895(1):19, May 2020. doi: 10.3847/1538-4357/ab88c9.

L. E. Orgel. The Implausibility of Metabolic Cycles on the Prebiotic Earth. *PLoS Biol*, 6(1):e18, 2008. doi: 10.1371/journal.pbio.0060018.

J. Oró and A. Lazcano. A minimal living system and the origin of a protocell. *Adv. Space Res*, 4(12):167–176, Jan. 1984. doi: 10.1016/0273-1177(84)90559-3.

G. R. Osinski, L. L. Tornabene, N. R. Banerjee, C. S. Cockell, R. Flemming, M. R. M. Izawa, J. McCutcheon, J. Parnell, L. J. Preston, A. E. Pickersgill, A. Pontefract, H. M. Sapers, and G. Southam. Impact-generated hydrothermal systems on Earth and Mars. *Icarus*, 224(2):347–363, June 2013. doi: 10.1016/j.icarus.2012.08.030.

K. J. Painter. Mathematical models for chemotaxis and their applications in self-organisation phenomena. *J. Theor. Biol.*, 481:162–182, 2019. doi: 10.1016/j.jtbi.2018.06.019.

K. Palczewski. G protein–coupled receptor rhodopsin. *Annu. Rev. Biochem.*, 75:743–767, 2006. doi: 10.1146/annurev.biochem.75.103004.142743.

A. Paytan and K. McLaughlin. The Oceanic Phosphorus Cycle. *Chem. Rev.*, 107(2):563–576, 2007. doi: 10.1021/cr0503613.

W. Pfeffer. Locomotorische Richtungsbewegungen durch chemische Reize. *Untersuch. Botan. Inst. Tübingen*, 1:363–482, 1884.

R. Phillips, J. Kondev, J. Theriot, and H. G. Garcia. *Physical Biology of the Cell*. New York: Garland Science, 2nd edition, 2013.
S. L. Porter, G. H. Wadhams, and J. P. Armitage. Signal processing in complex chemotaxis pathways. *Nat. Rev. Microbiol.*, 9(3):153–165, 2011. doi: 10.1038/nrmicro2505.

F. Postberg, N. Khawaja, B. Abel, G. Choblet, C. R. Glein, M. S. Gudipati, B. L. Henderson, H.-W. Hsu, S. Kempf, F. Klenner, G. Moragas-Klostermeyer, B. Magee, L. Nolle, M. Perry, R. Reviol, J. Schmidt, R. Srama, F. Stolz, G. Tobie, M. Tricot, and J. H. Waite. Macromolecular organic compounds from the depths of Enceladus. *Nature*, 558(7711):564–568, June 2018. doi: 10.1038/s41586-018-0246-4.

M. Preiner, K. Igarashi, K. B. Muchowska, M. Yu, S. J. Varma, K. Kleinermanns, M. K. Nobu, Y. Kamagata, H. Tüysüz, J. Moran, and W. F. Martin. A hydrogen-dependent geochemical analogue of primordial carbon and energy metabolism. *Nat. Ecol. Evol.*, 4:534–542, 2020. doi: 10.1038/s41559-020-1125-6.

P. B. Price. Microbial life in glacial ice and implications for a cold origin of life. *FEMS Microbiol. Ecol.*, 59(2):217–231, 2007. doi: 10.1111/j.1574-6941.2006.00234.x.

I. Prigogine and G. Nicolis. Biological order, structure and instabilities. *Q. Rev. Biophys.*, 4(2-3):107–148, 1971. doi: 10.1017/S0033583500000615.

A. Priye, Y. Yu, Y. A. Hassan, and V. M. Ugaz. Synchronized chaotic targeting and acceleration of surface chemistry in prebiotic hydrothermal microenvironments. *Proc. Natl. Acad. Sci. USA*, 114(6):1275–1280, Feb. 2017. doi: 10.1073/pnas.1612924114.

E. M. Purcell. Life at low Reynolds number. *Am. J. Phys.*, 45(1):3–11, Jan. 1977. doi: 10.1119/1.10903.

J.-B. Raina, V. Fernandez, B. Lambert, R. Stocker, and J. R. Seymour. The role of microbial motility and chemotaxis in symbiosis. *Nat. Rev. Microbiol.*, 17(5):284–294, 2019. doi: 10.1038/s41579-019-0182-9.

M. S. Rappé, S. A. Connon, K. L. Vergin, and S. J. Giovannoni. Cultivation of the ubiquitous SAR11 marine bacterioplankton clade. *Nature*, 418(6898):630–633, Aug. 2002. doi: 10.1038/nature00917.

F. Raulin, C. Brasse, O. Poch, and P. Coll. Prebiotic-like chemistry on Titan. *Chem. Soc. Rev.*, 41(16):5380–5393, 2012. doi: 10.1039/C2CS35014A.

J. A. Raven. Why are there no picoplanktonic O$_2$ evolvers with volumes less than $10^{-19}$ m$^3$? *J. Plankton Res.*, 16(5):565–580, 1994. doi: 10.1093/plankt/16.5.565.

J. A. Raven and S. Donnelly. Brown Dwarfs and Black Smokers: The Potential for Photosynthesis Using Radiation from Low-Temperature Black Bodies. In J.-P. de Vera and J. Seckbach, editors, *Habitability of Other Planets and Satellites*, pages 267–284. Springer, 2013. doi: 10.1007/978-94-007-6546-7_15.

J. A. Raven, J. E. Kübler, and J. Beardall. Put out the light, and then put out the light. *J. Mar. Biol. Assoc. UK*, 80(1):1–25, 2000. doi: 10.1017/s0025315499001526.

J. A. Raven, J. Beardall, A. W. D. Larkum, and P. Sánchez-Baracaldo. Interactions of photosynthesis with genome size and function. *Phil. Trans. R. Soc. B*, 368(1622):20120264, 2013. doi: 10.1098/rstb.2012.0264.

M. Riekeles, J. Schirmack, and D. Schulze-Makuch. Machine Learning Algorithms Applied to Identify Microbial Species by Their Motility. *Life*, 11(1):44, 2021. doi: 10.3390/life11010044.
S. W. Ruff and J. D. Farmer. Silica deposits on Mars with features resembling hot spring biosignatures at El Tatio in Chile. *Nat. Commun.*, 7:13554, Nov. 2016. doi: 10.1038/ncomms13554.

S. W. Ruff, K. A. Campbell, M. J. Van Kranendonk, M. S. Rice, and J. D. Farmer. The Case for Ancient Hot Springs in Gusev Crater, Mars. *Astrobiology*, 20(4):475–499, Apr. 2020. doi: 10.1089/ast.2019.2044.

M. J. Russell and A. J. Hall. The emergence of life from iron monosulphide bubbles at a submarine hydrothermal redox and pH front. *J. Geol. Soc.*, 154(3):377–402, 1997. doi: 10.1144/gsjgs.154.3.0377.

M. J. Russell and W. Martin. The rocky roots of the acetyl-CoA pathway. *Trends Biochem. Sci.*, 29(7):358–363, 2004. doi: 10.1016/j.tibs.2004.05.007.

M. J. Russell and A. Ponce. Six ‘must-have’ minerals for life’s emergence: Olivine, pyrrhotite, bridgmanite, serpentine, fougérite and mackinawite. *Life*, 10(11):291, 2020. doi: 10.3390/life10110291.

M. J. Russell, R. M. Daniel, A. J. Hall, and J. A. Sherringham. A hydrothermally precipitated catalytic iron sulphide membrane as a first step toward life. *J. Mol. Evol.*, 39(3):231–243, Sept. 1994. doi: 10.1007/BF00160147.

M. J. Russell, L. M. Barge, R. Bhartia, D. Bocanegra, P. J. Bracher, E. Branscomb, R. Kidd, S. McGlynn, D. H. Meier, W. Nitschke, T. Shibuya, S. Vance, L. White, and I. Kanik. The Drive to Life on Wet and Icy Worlds. *Astrobiology*, 14(4):308–343, Apr. 2014. doi: 10.1089/ast.2013.1110.

C. Sagan. The Search for Extraterrestrial Life. *Sci. Am.*, 271(4):92–99, Oct. 1994. doi: 10.1038/scientificamerican1094-92.

C. Sagan, W. R. Thompson, and B. N. Khare. Titan: a laboratory for prebiological organic chemistry. *Acc. Chem. Res.*, 25(7):286–292, 1992. doi: 10.1021/ar00019a003.

A. Salditt, L. M. R. Keil, D. P. Horning, C. B. Mast, G. F. Joyce, and D. Braun. Thermal Habitat for RNA Amplification and Accumulation. *Phys. Rev. Lett.*, 125(4):048104, July 2020. doi: 10.1103/PhysRevLett.125.048104.

H. Sandström and M. Rahm. Can polarity-inverted membranes self-assemble on Titan? *Sci. Adv.*, 6(4):eaax0272, Jan. 2020. doi: 10.1126/sciadv.aax0272.

J. L. Sarmiento and N. Gruber. *Ocean Biogeochemical Dynamics*. Princeton: Princeton University Press, 2006.

W. H. Schlesinger and E. S. Bernhardt. *Biogeochemistry: An Analysis of Global Change*. Waltham: Academic Press, 3rd edition, 2013.

J. W. P. Schmelzer, E. D. Zanotto, and V. M. Fokin. Pressure dependence of viscosity. *J. Chem. Phys.*, 122(7):074511–074511, Feb. 2005. doi: 10.1063/1.1851510.

T. M. Schmidt, E. F. DeLong, and N. R. Pace. Analysis of a marine picoplankton community by 16S rRNA gene cloning and sequencing. *J. Bacteriol.*, 173(14):4371–4378, 1991. doi: 10.1128/jb.173.14.4371-4378.1991.

E. Schrödinger. *What Is Life? The Physical Aspect of the Living Cell*. Cambridge: Cambridge University Press, 1944.
J. L. Vago, F. Westall, Pasteur Instrument Team, Pasteur Landing Team, A. J. Coates, R. Jaumann, O. Korablev, V. Ciarletti, I. Mitrofanov, J.-L. Josset, M. C. De Sanctis, J.-P. Bibring, F. Rull, F. Goesmann, H. Steininger, W. Goetz, W. Brinckerhoff, C. Szopa, F. Raulin, F. Westall, H. G. M. Edwards, L. G. Whyte, A. G. Fairén, J.-P. Bibring, J. Bridges, E. Hauber, G. G. Ori, S. Werner, D. Loizeau, R. O. Kuzmin, R. M. E. Williams, J. Flahaut, F. Forget, J. L. Vago, D. Rodionov, O. Korablev, H. Svedhem, E. Sefton-Nash, G. Kninek, L. Lorenzoni, L. Joudrier, V. Mikhailov, A. Zashchirinskiy, S. Alexashkin, F. Calantropio, A. Merlo, P. Poulakis, O. Vitasse, O. Bayle, S. Bayón, U. Meierhenrich, J. Carter, J. M. García-Ruiz, P. Baglioni, A. Haldemann, A. J. Ball, A. Debus, R. Lindner, F. Haessig, D. Monteiro, R. Trautner, C. Voland, P. Rebeyre, D. Goulty, F. Didot, S. Durrant, E. Zekri, D. Koschny, A. Toni, G. Visentin, M. Zwick, M. van Winnendael, M. Azkarate, C. Carreau, and ExoMars Project Team. Habitability on Early Mars and the Search for Biosignatures with the ExoMars Rover. Astrobiology, 17(6-7):471–510, July 2017. doi: 10.1089/ast.2016.1533.

C. L. Van Dover, G. T. Reynolds, A. D. Chave, and J. A. Tyson. Light at deep-sea hydrothermal vents. Geophys. Res. Lett., 23(16):2049–2052, Jan. 1996. doi: 10.1029/96GL02151.

J. J. Van Loef. Temperature and density dependence of the self-diffusion coefficient in compressed liquid methane. Physica B+C, 94(1):105–107, Apr. 1978. doi: 10.1016/0378-4363(78)90081-5.

S. Vance, J. Harnmeijer, J. Kimura, H. Hussmann, B. deMartin, and J. M. Brown. Hydrothermal Systems in Small Ocean Planets. Astrobiology, 7(6):987–1005, Dec. 2007. doi: 10.1089/ast.2007.0075.

J. Varennes, B. Han, and A. Mugler. Collective Chemotaxis through Noisy Multicellular Gradient Sensing. Biophys. J., 111(3):640–649, Aug. 2016. doi: 10.1016/j.bpj.2016.06.040.

N. B. Vargaftik, L. P. Filippov, A. A. Tarzimanov, and E. E. Totskii. Handbook of Thermal Conductivity of Liquids and Gases. Boca Raton: CRC Press, 1994.

B. Velimirov. Nanobacteria, Ultramicrobacteria and Starvation Forms: A Search for the Smallest Metabolizing Bacterium. Microbes Environ., 16(2):67–77, 2001. doi: 10.1264/jsme2.2001.67.

T. Vicsek and A. Zafeiris. Collective motion. Phys. Rep., 517(3-4):71–140, Aug. 2012. doi: 10.1016/j.physrep.2012.03.004.

S. Vogel. Modes and scaling in aquatic locomotion. Integr. Comp. Biol., 48(6):702–712, 2008. doi: 10.1093/icb/icn014.

G. H. Wadhams and J. P. Armitage. Making sense of it all: bacterial chemotaxis. Nat. Rev. Mol. Cell Biol., 5(12):1024–1037, 2004. doi: 10.1038/nrm1524.

A. J. Waite, N. W. Frankel, and T. Emonet. Behavioral Variability and Phenotypic Diversity in Bacterial Chemotaxis. Annu. Rev. Biophys., 47:595–616, 2018. doi: 10.1016/j.ribi.2014.12.007.

J. H. Waite, C. R. Glein, R. S. Perrymen, B. D. Teolis, B. A. Magee, G. Miller, J. Grimes, M. E. Perry, K. E. Miller, A. Bouquet, J. I. Lunine, T. Brockwell, and S. J. Bolton. Cassini finds molecular hydrogen in the Enceladus plume: Evidence for hydrothermal processes. Science, 356(6344):155–159, Apr. 2017. doi: 10.1126/science.aai8703.

K. Y. Wan and G. Jékely. Origins of eukaryotic excitability. Phil. Trans. R. Soc. B, 376(1820):20190758, Mar. 2021. doi: 10.1098/rstb.2019.0758.
Q. Wang and O. Steinbock. Materials Synthesis and Catalysis in Microfluidic Devices: Prebiotic Chemistry in Mineral Membranes. *ChemCatChem*, 12(1):63–74, 2020. doi: 10.1002/cctc.201901495.

L. M. Ward and P. M. Shih. The evolution and productivity of carbon fixation pathways in response to changes in oxygen concentration over geological time. *Free Radic. Biol. Med.*, 140:188–199, 2019. doi: 10.1016/j.freeradbiomed.2019.01.049.

E. J. Warrant and D.-E. Nilsson. Absorption of white light in photoreceptors. *Vision Res.*, 38(2):195–207, 1998. doi: 10.1016/S0042-6989(97)00151-X.

D. R. Webster and M. J. Weissburg. The Hydrodynamics of Chemical Cues Among Aquatic Organisms. *Annu. Rev. Fluid Mech.*, 41(1):73–90, Jan. 2009. doi: 10.1146/annurev.fluid.010908.165240.

M. C. Weiss, M. Preiner, J. C. Xavier, V. Zimorski, and W. F. Martin. The last universal common ancestor between ancient Earth chemistry and the onset of genetics. *PLoS Genet.*, 14(8):e1007518, 2018. doi: 10.1371/journal.pgen.1007518.

M. J. Weissburg. The fluid dynamical context of chemosensory behavior. *Biol. Bull.*, 198(2):188–202, 2000. doi: 10.2307/1542523.

F. W. Went. The size of man. *Am. Sci.*, 56(4):400–413, 1968.

F. Westall, F. Foucher, N. Bost, M. Bertrand, D. Loizeau, J. L. Vago, G. Kminek, F. Gaboyer, K. A. Campbell, J.-G. Bréhéret, P. Gautret, and C. S. Cockell. Biosignatures on Mars: What, Where, and How? Implications for the Search for Martian Life. *Astrobiology*, 15(11):998–1029, Nov. 2015. doi: 10.1089/ast.2015.1374.

F. Westall, K. Hickman-Lewis, N. Hinman, P. Gautret, K. A. Campbell, J. G. Bréhéret, F. Foucher, A. Hubert, S. Sorieul, A. V. Dass, T. P. Kee, T. Georgelin, and A. Brack. A Hydrothermal-Sedimentary Context for the Origin of Life. *Astrobiology*, 18(3):259–293, Mar. 2018. doi: 10.1089/ast.2017.1680.

C. G. Wheat, R. A. Feely, and M. J. Mottl. Phosphate removal by oceanic hydrothermal processes: An update of the phosphorus budget in the oceans. *Geochim. Cosmochim. Acta*, 60(19):3593–3608, Oct. 1996. doi: 10.1016/0016-7037(96)00189-5.

S. N. White, A. D. Chave, G. T. Reynolds, E. J. Gaidos, J. A. Tyson, and C. L. Van Dover. Variations in ambient light emission from black smokers and flange pools on the Juan De Fuca Ridge. *Geophys. Res. Lett.*, 27(8):1151–1154, Apr. 2000. doi: 10.1029/1999GL011074.

S. N. White, A. D. Chave, and G. T. Reynolds. Investigations of ambient light emission at deep-sea hydrothermal vents. *J. Geophys. Res. Solid Earth*, 107(B1):1.1–1.13, Jan. 2002. doi: 10.1029/2000JB000015.

A. Wilde and C. W. Mullineaux. Light-controlled motility in prokaryotes and the problem of directional light perception. *FEMS Microbiol. Rev.*, 41(6):900–922, 2017. doi: 10.1093/femsre/fux045.

K. H. Williford, K. A. Farley, K. M. Stack, A. C. Allwood, D. Beaty, L. W. Beegle, R. Bhartia, A. J. Brown, M. de la Torre Juarez, S.-E. Hamran, M. H. Hecht, J. A. Hurowitz, J. A. Rodriguez-Manfredi, S. Maurice, S. Milkovich, and R. C. Wiens. *The NASA Mars 2020 Rover Mission and the Search for Extraterrestrial Life*, pages 275–308. Amsterdam: Elsevier, 2018. doi: 10.1016/B978-0-12-809935-3.00010-4.
J. Wong-Ng, A. Celani, and M. Vergassola. Exploring the function of bacterial chemotaxis. *Curr. Opin. Microbiol.*, 45:16–21, 2018. doi: 10.1016/j.mib.2018.01.010.

R. D. Wordsworth and R. T. Pierrehumbert. Water Loss from Terrestrial Planets with CO₂-rich Atmospheres. *Astrophys. J.*, 778(2):154, Dec 2013. doi: 10.1088/0004-637X/778/2/154.

L. Wurch, R. J. Giannone, B. S. Belisle, C. Swift, S. Utturkar, R. L. Hettich, A.-L. Reysenbach, and M. Podar. Genomics-informed isolation and characterization of a symbiotic Nanoarchaeota system from a terrestrial geothermal environment. *Nat. Commun.*, 7:12115, July 2016. doi: 10.1038/ncomms12115.

Y. Yang, V. Lam, M. Adomako, R. Simkovsky, A. Jakob, N. C. Rockwell, S. E. Cohen, A. Taton, J. Wang, J. C. Lagarias, A. Wilde, D. R. Nobles, J. J. Brand, and S. S. Golden. Phototaxis in a wild isolate of the cyanobacterium *Synechococcus elongatus*. *Proc. Natl. Acad. Sci. USA*, 115(52): E12378–E12387, 2018. doi: 10.1126/science.1070118.

B. A. Younglove. The Specific Heats, $C_\sigma$, and $C_V$, of Compressed and Liquefied Methane. *J. Res. Natl. Bur. Stand. A Phys. Chem.*, 78(3):401, 1974. doi: 10.6028/jres.078a.023.

Y. Zhang, A. Ducret, J. Shaevitz, and T. Mignot. From individual cell motility to collective behaviors: insights from a prokaryote, *Myxococcus xanthus*. *FECS Microbiol. Rev.*, 36(1):149–164, 2012. doi: 10.1111/j.1574-6976.2011.00307.x.