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# Life at low Reynolds number Re-visited: The efficiency of microbial propulsion

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ABSTRACT

It has for over 40 years been taken as a truth universally acknowledged that microbial swimming efficiency by flagellar propulsion is fixed by fluid mechanical limitations at 1–2%. And that the missing 98% dissipated as heat is inefficient or wasted. Estimates of such low swimming efficiency make no sense. Microbes have had billions of years to evolve highly efficient swimming; images of microbes in motion show movement with alacrity and maximum speeds of up to 10 body lengths per second, equivalent to the running and swimming speeds of far larger animals. This paradox can be resolved by taking into account the hydrogen-bonded nature of water and how efficient viscous flow over the surface of the animal is established. The minimal requirement for viscous flow is that the activation energy barrier be overcome. The activation energy for viscous flow in water and sea water is the amount of energy required to break 2 hydrogen bonds—breaking apart the dominant water pentamer into the single $H_2O$ species, thus greatly reducing the size of the molecular hole required for flow. Microbial swimming efficiency is made highly efficient by devoting some 95% of the energy expended (some must be lost to entropy) into the breaking of hydrogen bonds.

## 1. Introduction

In this paper we seek to resolve the paradox of the long-standing conflicts surrounding reports on the apparent swimming efficiency of microbial propulsion. We address the problem in light of recent work quantifying the hydrogen-bonded nature, and the activation energy of viscous flow, of water and sea water (Brewer et al., 2019, 2021). The vast majority of swimming microbes occur in the ocean. Yet papers on microbial swimming efficiency typically make no reference to sea water, or the influence of temperature, pressure and salinity. Here we look at the problem from the perspective of ocean scientists.

It was some 45 years ago that Purcell, in a brilliant and highly influential 1976 lecture (Purcell, 1977), first reported that the swimming efficiency of microbes driven by flagellar propulsion was extraordinarily low at about 1% based on a fluid dynamical analysis. This estimate has often been “confirmed” (Yates, 1986) and rarely challenged, although Guasto et al. (2012) comment: “How metabolically expensive microbial propulsion is remains unclear.” Direct measurement of the force required to hold a bacterium in an optical trap (Chattopadhyay et al., 2006) appears to confirm this estimate by yielding a carefully calculated value of 1.7% efficiency.

Yet this makes no sense in absolute terms for microbes are remarkably efficient in all other aspects and in quickly sensing their environment (Schultz and Ducklow, 2000; Brewer et al., 2014; Kondev, 2014). They have had over 1 billion years to evolve the most efficient mode of propulsion (Friedmann et al., 2001; Mitchell, 2002) and cannot be expected to squander their precious energy resources. If we assume some energy must be lost to entropy, this strongly suggests that the remaining 95% of the energy expended and not accounted for in the fluid dynamics analysis must be put to an as-yet-unspecified good use.

While Purcell (1977) voiced the opinion that “motion at low Reynolds number is very majestic, slow, and regular,” Yates (1986) noted that “single-celled organisms, typically between 2 and 1000 μm long, can sustain swimming speeds up to about 100 body lengths per second; ” this seems to be exaggerated and a ratio of about 10 body lengths per second is a more widely accepted upper limit. Nevertheless, the contrast between estimated efficiency and observed alacrity is stark. Video images of microbes engaged in lively and seemingly highly efficient swimming are now widely available (Deng et al., 2020). The careful analysis by Meyer-Vernet and Rospars (2016) covering a huge range of animal types and sizes reports that “bacteria perform as fast as ostriches.” These reports clearly indicate high efficiency of propulsion.

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Here we examine the differing assumptions behind these conflicting views and provide a possible way towards resolution. We point out that the underlying fluid dynamics assumption is that water is a simple Newtonian fluid with no complex hydrogen-bonded structure and constant molar volume. Purcell (1977) was apparently aware of this as a potential pitfall noting that "the reason viscosity changes is that it's got one of these activation energy things" but, displaying no relish for delving into the admittedly difficult activation energy problem (Eyring, 1936; Ewell and Eyring, 1937), he simply ignored it with long lasting consequences.

It has been known for over 80 years that water must be considered as an "abnormal" or "associated" liquid due to hydrogen bond formation (Ewell and Eyring, 1937) and modern spectroscopic techniques (Brewer et al., 2019) clearly reveal and quantify this molecular structure. Water has no fixed molecular weight: the mean molecular weight of pure water over the range 0–40 °C is 86.1-80.7 and 89.4–84.5 for sea water (Brewer and Peltzer, 2019).

## 2. Background

Although microbial activity is ubiquitous throughout the oceans and is responsible for the vastly greater part of the consumption of organic matter (Brewer and Peltzer, 2017), and in the decomposition of spilled oil (Weiman et al., 2021), there is little or no mention of the ocean in the papers on microbial swimming efficiency referenced above.

Purcell was influenced by the early analysis of this problem by Taylor (1951) who specifically addressed the challenge faced by swimming spermatozoa. His clear and succinct account of the very different modes of propulsion required for microscopic organisms in a viscous fluid can be re-stated here as an essential introduction to the problem:

"Large objects which propel themselves in air or water make use of inertia in the surrounding fluid. The propulsive organ pushes the fluid backwards, while the resistance of the body gives the fluid a forward momentum. The forward and backward momenta exactly balance, but the propulsive organ and the resistance can be thought about as acting separately. This conception cannot be transferred to problems of propulsion in microscopic bodies for which the stresses due to viscosity may be thousands of times as great as those due to inertia. No case of self-propulsion in a viscous fluid due to purely viscous forces seems to have been discussed."

Taylor analyzed the problem as the transmission of thin sheets driven in wave-like motions along the flagellum. We note here that this could be considered as the expenditure of mechanical energy as heat leading to the formation of a monomolecular layer—the thin sheets—at the flagellum-water interface, although Taylor drew no such inference. Taylor did not estimate the efficiency of propulsion by this mechanism.

The relevance to reproductive biology clearly did not escape the attention of Purcell who noted "It helps to imagine under what conditions a man would be swimming at, say, the same Reynolds number as his own sperm."

Papers describing the efficiency of microbial propulsion fall into two basic categories: the fluid dynamics approach and the allometric scaling law approach.

### 2.1. The fluid dynamics approach

Purcell (1977) analyzed flagella rotation in water in terms of the difference between the drag on a rigid helical wire moving perpendicular to its length and the drag on the wire moving parallel to its length as in: "The propulsion matrix must be diagonal. … The propulsion efficiency is more or less proportional to the square of the off-diagonal element of the matrix. The off-diagonal element depends on the difference between the drag on a wire moving perpendicular to its length and the drag on a wire moving parallel to its length. These are supposed to differ in a certain limit by a factor of 2. But for the models I've tested, that factor is more like 1.5. Since it's that factor minus 1 that counts, that's very bad for efficiency."

He noted that for such small animals swimming at Reynolds number of $10^{-4}$ or $10^{-5}$ "inertia is totally irrelevant", that "they could scarcely care less," and that "your intuitions about pushing water backwards are irrelevant."

This low efficiency was dismissed: "So they don't care whether they have a 1% efficient flagellum or a 2% efficient flagellum. It doesn't really make that much difference. They're driving a Datsun in Saudi Arabia."

These views have been broadly accepted. Mitchell (2002) provides a careful analysis noting the reported value of 1% as fixed by "mechanical limitations" citing Berg and Purcell (1977), Berg and Turner (1979) and Lowe et al. (1987). Yates (1986) provided a comprehensive history of this field and a careful review of the fluid dynamic processes. Purcell (1997) repeated his earlier dynamical analysis of propulsion as provided by the rotation of a rigid helical coil and reached the same conclusion of a 1% efficient process. The molecular properties of water, and the requirement for overcoming the activation energy of viscous flow were again ignored.

The swimming efficiency of the microbe *Escherichia coli* was recently evaluated by direct measurement of the force required to hold the bacterium in an optical trap (Chattopadhyay et al., 2006). The propulsive efficiency, defined as the ratio of the propulsive power output to the rotary power input provided by the motors, was found to be 1.7%, which again is consistent with the mechanical efficiency predicted theoretically for a rigid helical coil.

A review by Guasto et al. (2012) specifically on the fluid mechanics of planktonic microorganisms gave broad support to the fluid dynamics approach. In all these cases water is treated as a simple Newtonian fluid with no complex or varying molecular structure.

### 2.2. The allometric scaling law approach

The allometric scaling laws are based on the correlation between organism mass and quantity of work done in motion. They have been found to apply across an enormous range of animal mass and can be related to fundamental properties of energy and matter, although temperature dependence is typically not considered. The review of microbial motility by Mitchell (2002) deals in detail with the remarkably effective use of the available 1%—the fraction not "fixed by mechanics"—of the total energy. And in summing the fixed and available energy for microbes of different size found that the energy expenditure required to swim fell exactly in line with the classic allometric relationship scaling over a range of body mass spanning some 20 orders of magnitude.

A comprehensive look at this was provided by Meyer-Vernet and Rospars (2016). They supported the allometric model approach and in examining body size ranging from bacteria to the largest running and swimming animals on Earth found a maximum relative speed of the order of magnitude of ten body lengths per second. This relationship held over a $10^{20}$-fold mass range of both running and swimming animals. The vast majority of living organisms could not survive working at only 1% efficiency and bacteria are no different—they are governed by the same laws.

## 3. Analysis

Neither the fluid dynamics approach nor application of the allometric scaling law make any reference to the fact that water is a hydrogen-bonded fluid with both large and small (single $H_2O$) molecular species existing in temperature dependent dynamic equilibrium. The essential requirement for successful propulsion is to create viscous flow over the surface of the animal. The minimal requirement is to do enough work to overcome the activation energy of viscous flow (Brewer et al., 2021). The early work of Einstein (1906) developed a theory of viscosity based on his work on Brownian motion, and reference to this is still used today

(Breki and Nosonovsky, 2018). But Einstein was not able to derive the molecular basis for viscous flow due to the limited knowledge of molecular processes and intermolecular forces at that time. Thirty years later the general molecular theory of viscous flow was described by Eyring (1936) and the specific example for the viscosity of liquids was described by Ewell and Eyring (1937).

The unique contribution of Eyring was to move beyond the particle theory of Einstein and recognize that in order for molecular flow in a liquid to occur a vacancy in the fluid must be created and this requires overcoming an activation energy barrier. Here too size matters. **Eyring's** theory has long been established and is described in textbooks (Tabor, 1991) but has rarely been cited within the context of the ocean sciences so a brief summary is provided here. The general concept (Ewell and Eyring, 1937) "considers viscous flow as a chemical reaction in which the elementary process is the passing of a single molecule from one equilibrium position to another over a potential energy barrier."

The original equation describing this process was given as:

$$\eta = \frac{\lambda_1 h}{\kappa \lambda^2 \lambda_2 \lambda_3} \ \frac{F_n}{F_a{}^*} \ \exp \frac{\Delta E_{\mathrm{act}}}{kT}$$

where, η = viscosity.

$\lambda$ = distance between equilibrium positions in the direction of flow,

$\lambda_1$ = perpendicular distance between adjacent layers of molecules,

$\lambda_2$ = distance between adjacent molecules in the direction of flow,

$\lambda_3$ = distance between molecules in the plane of flow and normal to the direction of flow,

$\kappa$ = transmission coefficient.

$F_n$ = partition function of normal molecule.

$F_a{}^*$ = partition function of the activated molecule, omitting the degree of freedom corresponding to flow.

$\Delta E_{\mathrm{act}}$ = activation energy for the flow process,

$h$ = Planck's constant,

$k$ = Boltzmann's constant.

$T$ = absolute temperature in Kelvins.

The distance between molecules is defined by the Lennard-Jones potential (Lennard-Jones, 1925). For water at maximum density, the L-J potential minimum occurs at 3.48 Å with an energy minimum of 0.316 kJ/mol (Stillinger and Rahman, 1974; Brewer et al., 2021).

Ewell and Eyring (1937) note that "for a molecule to flow it must have a hole to flow into but this need not necessarily be a hole the full size of the molecule." They go on to model the viscosity of a large number of simple organic liquids (carbon tetrachloride, chloroform, etc) and liquid gases based upon the molal volume and the energy of vaporization.

This model and its modifications has found wide applicability for a great many fluids. But while it is often noted (Tabor, 1991) that this model does not appear to work well in predicting the viscosity for polar molecules such as water, this comment is somewhat misleading. Ewell and Eyring (1937) did tackle the problem of the viscosity of water and made specific mention that in order for viscous flow to occur both the weaker non-directional Lennard-Jones forces and the far stronger directed force of the hydrogen bond must be overcome. But it is not correct to state that these forces are purely additive; work done below the activation energy threshold simply leads to wasted energy or increased entropy. Work done that exceeds the activation energy threshold can be considered as useful in creating viscous flow.

Their comments were prescient; but knowledge of the hydrogen-bonded structure of water was in its infancy at that time and it was not until some 24 years later that the dominant tetrahedral pentamer molecule was identified (Walrafen, 1964, 1967) as the most stable (longest lived) hydrogen-bonded form of water. Nonetheless the essential process requiring formation of a molecular hole with an associated activation energy to achieve this remains as a fundamental step in achieving flow.

An experimental determination of the activation energy of viscous flow in water and sea water has been reported by Stanley and Batten (1969). Yet no interpretation of the meaning of this was offered. They made no acknowledgement of the fundamental theory derived by Eyring (1936) or the report by Ewell and Eyring (1937) specifically on the activation energy of flow in water.

In Brewer et al. (2021), we showed that the observed activation energy was driven primarily by the work required to break two hydrogen bonds, thereby breaking apart the dominant large water pentamer (Walrafen, 1964) into individual $H_2O$ molecules. We also provided a careful review and analysis of the strength of the intermolecular (Lennard-Jones) forces. Overcoming these forces greatly facilitates hole formation and thereby eases viscous flow by creating a monomolecular layer rich in the single $H_2O$ species.

This process of the breaking of hydrogen bonds is a fundamental requirement for efficient microbial swimming. Any inefficient work done in simply re-ordering the local intermolecular structures held together solely by the far weaker Lennard-Jones forces will result only in increased disorder - the classic description of entropy. In this we echo the finding of Ewell and Eyring (1937) that "the single $H_2O$ molecule is the unit of flow at all temperatures."

The matter of a possible temperature dependence of the activation energy of viscous flow must be discussed. The activation energy of a chemical reaction (Arrhenius, 1889; Eyring, 1935) is properly independent of temperature—that is its purpose. But when Ewell and Eyring (1937) evaluated the temperature dependence of water viscosity they reported that a plot of "log η *versus* 1/T is not a straight line for $H_2O$, but that $\Delta E_{vis}$ (the activation energy of viscous flow) decreases rapidly as the temperature increases."

We point out here that this finding was based on the viscosity data available at that time. It would be another 11–32 years before new higher quality results were reported (Miyake and Koizumi, 1948; Stanley and Batten, 1969). Our analysis of these results (Brewer et al., 2021) contradicted this finding that $\Delta E_{vis}$ decreases with increasing temperature and we could detect no non-linearity in the plot of log η versus 1/T. Thus we suggest that—as with any standard chemical reaction—there is no detectable temperature dependence of the activation energy of viscous flow in water.

The strength of the hydrogen bond varies to some degree with the molecular environment; the range of values reported by Silverstein et al. (2000) is from 1.5 to 2.9 kcal/mol. The original estimate by Walrafen (1964) yielded a value of −12.5 kcal/mol for the process in which 5 single $H_2O$ molecules are combined into the water tetrahedral pentamer. This process forms 4 hydrogen bonds (between the central water molecule and the 4 apical water molecules) thus giving a single hydrogen bond enthalpy of 3.1 kcal/mol for the single O–H…O bond.

Recent field observations of the H-bond enthalpy in sea water (appendix 1, Brewer et al., 2019) find a value of 2.624 kcal/mol so the value for water and sea water at 1 atm pressure may now be regarded as well-constrained. Walrafen (1964) noted that "two hydrogen bonds are broken when one $H_2O$ molecule is liberated in the complete breakdown of a tetrahedral network. This is reasonably consistent with the 1 atm pressure activation energy of flow of ~4.3 kcal/mol reported by Stanley and Batten (1969) and reanalyzed in Brewer et al. (2021).

The work done by microbes in swimming must produce heat, and this heat must be sufficient to overcome the strength of the intermolecular forces and break hydrogen bonds. We can find no mention of this in the literature on the efficiency of microbial propulsion—the entire 98–99% fraction of the energy expended has been regarded as "inefficient" without mention of the fundamental linkage of work and heat.

## 4. How many hydrogen bonds must be broken?

It has long been established that the work done in swimming is a function of the mass of the animal. Mitchell (2002) provides a very careful analysis of the total microbial energy expenditure as a function of size. Here we use these data to calculate how many hydrogen bonds are broken to create viscous flow by increasing the population of individual $H_2O$ molecules within the monomolecular layer surrounding the microbe. We note that it is not necessary for 100% of the H-bonded water molecules in the boundary layer to be broken—just a sufficient number to allow flow to proceed with efficiency, and that fraction can be very small. We note also that the estimate necessarily includes the contribution made by work done in overcoming the far smaller intermolecular forces.

In Table 1, we calculate the number of H-bonds broken by the heat generated by the productive swimming motion of microbes of various sizes. The microbe sizes (cell radii) were chosen to match the data range from Mitchell (2002). For simplicity we modeled “spherical microbes” that are neutrally buoyant in sea water ($S = 34.7$, $T = 16\ ^{\circ}C$, $P = 1$ dbar; density = 1.026). Their masses were calculated based upon their radii and their density. There are microbes with other shapes and sizes, of course, and different means of propulsion, and each will yield numerically different calculations, but the conclusions drawn from these alternate calculations will not be substantially different from the ones obtained here. For calculating the heat released, we choose 95% of the heat expended according to Fig. 11 in Mitchell (2002) regression ($E_{Total} = 7.38\ X^{-0.28}$, where X is the cell mass in grams and E has units of cal/g/km) with the rest of the energy being used for mechanical propulsion and lost due to an increase in entropy. We emphasize that this reflects the quantity useful for the creation of viscous flow. The unproductive energy expended (as entropy is increased) is also lost as heat.

Since the amount of energy expended is proportional to the distance traveled, we chose 10 times the cell diameter as our standard of reference. It is interesting to note, that although the cell radius varies by a factor of 100, the number of H-bonds broken by the heat released varies by a factor of 2 million.

There is no description present in the literature as how the flow cascade initiated by the breaking of a relatively small number of hydrogen bonds proceeds and we can offer only a simple qualitative sketch here. The mechanical force exerted by the flagellum acts on the surface area of the large water pentamer. This has nowhere to go (no vacancy to move to) until it is broken into smaller water molecule clusters and individual $H_2O$ molecules. Energy is used in this process. The small $H_2O$ molecules are thus set in directed motion in the boundary layer and can flow with ease. The energy used is carried along in the kinetic energy of the molecules and is only slowly dissipated by diffusion. Exactly how the transfer into the shedding of far larger quantity of water in the microbe boundary layer occurs cannot be stated at this time and it remains as a challenge in molecular fluid dynamics.

**Table 1**

Calculation of the number of hydrogen bonds broken by the energetics of microbial swimming. Table 1. The range of the cell radii was chosen to match the range of data found in Figure 11 within Mitchell (2002). Cell volume was estimated assuming the cells were spheres. Cell mass was calculated assuming that the cells were neutrally buoyant in sea water ($S = 34.7$, $T = 16\ ^{\circ}C$. $P = 1$ dbar; density = 1.026). Total energy expended by swimming was calculated using the allometric regression equation for microbes from Figure 11 in Mitchell (2002): $E_{Total} = 7.38\ X^{-0.28}$, where X is the cell mass in grams and E has units of cal/g/km). Multiplying the total energy expended by the mass per cell and the distance traveled (assumed to be 10 times the cell diameter) yields the amount of energy expended by each cell. Assuming 95% of this energy is released as heat, we can calculate the number of hydrogen bonds broken by dividing the heat released by the enthalpy (2.62 kcal/mol) and multiplying the result by Avogadro’s number.

| Microbe cell | | | Total energy | Calories per cell per 10 • Dcell | Number H-bonds broken |
|---|---|---|---|---|---|
| Radius | Volume | Mass | | | |
| µm | cc | g | cal/g/km | | |
| 10.0 | 4.19E-09 | 4.30E-09 | 1.62E+03 | 1.40E-12 | 3.04E+08 |
| 3.16 | 1.32E-10 | 1.36E-10 | 4.28E+03 | 3.66E-14 | 7.99E+06 |
| 1.00 | 4.19E-12 | 4.30E-12 | 1.12E+04 | 9.66E-16 | 2.11E+05 |
| 0.316 | 1.32E-13 | 1.36E-13 | 2.96E+04 | 2.53E-17 | 5.53E+03 |
| 0.100 | 4.19E-15 | 4.30E-15 | 7.78E+04 | 6.68E-19 | 1.46E+02 |

## 5. Discussion

A clue towards resolving the large discrepancy between the fluid dynamics approach and the allometric scaling law approach is provided by Meyer-Vernet and Rospars (2016). They argue that the animal’s motor force should be weak enough not to break the motor’s internal 3-D structure held together by weak forces such as H-bonds, and cite Schliwa and Woehlke (2003). They also consider the thrust as acting on a water molecule of ~0.3 nm size—the size of the non-hydrogen-bonded $H_2O$ species. In doing so they echo the finding of Ewell and Eyring (1937) almost 80 years earlier that “the single $H_2O$ molecule is the unit of flow at all temperatures” as reported also in Brewer et al. (2021). Although Meyer-Vernet and Rospars (2016) reference the importance of hydrogen bonds in the animal’s internal structure the existence of hydrogen-bonded species in the external water is ignored.

These conflicting views of microbial swimming efficiency can be reconciled if we consider that ~95% of the work done by bacteria in swimming goes into the breaking of H-bonds in the monomolecular sheath surrounding the animal thereby disrupting the molecular structure and specifically the large hydrogen-bonded water molecules (of which the water pentamer is the most abundant form) and thus achieving far more efficient viscous flow. And that microbes have evolved a very carefully calculated mechano-sensory (Dunn and Price, 2015) motor structure to achieve this—strong enough to break the H-bonds in the external liquid water without destroying the H-bonded structures within their own “thrust bearing.”

Purcell (1977) noted that “The bug’s problem is not its energy supply; it’s its environment. At low Reynolds number you can’t shake off your environment. If you move you take it along; it only gradually falls behind.” We point out that a particular advantage to the microbe in breaking up the boundary layer water structure is to “shake off” the local environment as efficiently as possible.

There really is no mystery as to why the swimming efficiency of microbes has been misrepresented so often and for so long. The avoidance of dealing with the hydrogen-bonded nature of water and neglect of the rules established over 80 years ago governing the molecular basis for viscous flow is very clear.

Fluid mechanical analyses typically begin with a rhetorical statement such as “we consider water to be a simple Newtonian fluid ….” But while it is true that water fulfills the minimal definition that the viscous stresses and the strain rate are linearly correlated it is difficult to avoid the impression that this gives license to ignore the hydrogen-bonded nature of water. This has created much confusion: at a basic minimum, water must be treated as a bi-molecular fluid (Brewer, 2019).

This paper is primarily concerned with the molecular processes occurring at the flagellum-water interface and a fluid dynamical analysis of the operation of the flagella is not offered here. We do note that always there must be a resistance in the water to the mechanical force applied by the moving flagellum. At the molecular level this resistance results from the push-back from the Pauli wall (Brewer et al., 2021) as the flagellum attempts to compress the water. The heat generated must be sufficient to break the local hydrogen-bonded structures in order to achieve efficient flow.

We note here that the molecular consequences of Purcell’s description of the mechanical forces acting perpendicular and horizontal to the flagellum “wire” can be seen as the difference between compression and extension (shear) of the fluid: compression producing the basis for fluid resistance to thrust, and extension facilitating the formation of the molecular vacancies required for viscous flow. This hypothesis remains to be tested.

How multiple flagella combine their motions so that a neighbor can take advantage of the changed molecular structure resulting from the thrust of a partner is a problem that remains to be solved, although both Taylor (1951) and Purcell (1977) did address the advantages of coupled motion.

Microbial flagellar propulsion is made highly efficient by devoting some 95% of the effort to breaking apart the bulky $(H_2O)_5$ and other hydrogen-bonded molecular species into the single $H_2O$ form and thus greatly easing the challenge of creating viscous flow over their surface. Some losses due to entropy in simply rearranging the local water structures held together by weaker intermolecular forces must also occur.

Finally we should note, in keeping with the interests of both Taylor (1951) and Purcell (1977), that the microbial process of using sufficient energy to break apart the molecular structure of water in order to achieve viscous flow should apply equally to the swimming of sperm in semen. The viscosity of semen is some 10 times greater than that of sea water, but both fluids are ~96% water.

We are not aware of any experimental measurement of the activation energy of viscous flow in semen but it seems likely that this too will reflect the work required to break hydrogen bonds in order to achieve efficient swimming. If sperm were to swim with only 1% efficiency we would not have an efficient reproductive strategy and on this there is abundant evidence to the contrary.

## Author contributions

P. G. Brewer, concept and writing. E.T. Peltzer, calculations, table, and editing. K. Lage, literature searches and editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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