

Be sure to write your name above. Read the three sub-questions carefully, think, then write your answers in the lined space (front and back of this page). When finished, please hand your answer in, separate from your exam booklet. **Be Sure to Show Units!**

QUESTION: Makarieva et al.¹ recently refined measurements of the *energetics of the smallest*, and conclude that bacteria normally exhibit a metabolic rate of about 8 Watts kg⁻¹ (a single bacterium weighs about 2 × 10⁻¹⁵ kg).



- Glucose is a common energy source for a bacteria and the Gibbs free energy change for conversion to H₂O and CO₂ is 2870 kJ mole⁻¹. If glucose is the only energy source available, what is the required flux (mole m⁻² s⁻¹) of glucose into a single bacterium to maintain a metabolic rate of 8 Watts kg⁻¹? Assume that the bacterium is spherical ($V = 4/3 \cdot \pi \cdot r^3$, $A = 4\pi r^2$) with a density of 10³ kg m⁻³.

$$\text{Bacterial Volume: } 2 \times 10^{-15} \text{ kg} \cdot \frac{1 \text{ m}^3}{10^3 \text{ kg}} = 2 \times 10^{-18} \text{ m}^3$$

$$\text{If a sphere, the radius is: } \sqrt[3]{\frac{V}{4/3 \pi}} = r$$

$$\sqrt[3]{\frac{2 \times 10^{-18} \text{ m}^3}{4/3 \pi}} = 7.816 \times 10^{-7} \text{ m} = r$$

$$\text{The bacterial area is } 4\pi r^2: 4\pi (7.816 \times 10^{-7} \text{ m})^2 = 7.677 \times 10^{-12} \text{ m}^2$$

$$\text{The glucose flux } \left(\frac{\text{Joule s}^{-1}}{\text{kg}} \right) (2 \times 10^{-15} \text{ kg}) \cdot \frac{1}{7.677 \times 10^{-12} \text{ m}^2}$$

$$= 7.262 \times 10^{-10} \text{ mole m}^{-2} \text{ s}^{-1} \text{ units check!}$$

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¹ Makarieva AM, Gorshkov VG, Li B-L (2005) Energetics of the smallest: do bacteria breathe at the same rate as whales? Proceedings of the Royal Society B (Biological Sciences) 272:2219–2224.

- If the diffusion coefficient of glucose is $7 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$ what is the external glucose concentration required to maintain the metabolic rate of 8 Watts kg^{-1} for a single bacterium?

Using the diffusive current: $J = -D \frac{dc}{dr}$

$$c_0 = \frac{(7.262 \times 10^{-10} \text{ mole m}^{-2} \text{ s}^{-1}) (7.677 \times 10^{-12} \text{ m}^2)}{(7 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}) (4\pi) (7.816 \times 10^{-7} \text{ m})}$$

(convert to moles s⁻¹)

$$= 1.117 \text{ mole m}^{-3} \quad \text{units check!}$$

convert to concentration $10^3 \text{ l} = 1 \text{ m}^3$

$$1.117 \left(\frac{\text{mole}}{\text{m}^3} \right) \left(\frac{1 \text{ m}^3}{10^3 \text{ l}} \right) = 1.117 \text{ mM} \left(\frac{\text{mMoles}}{\text{l}} \right)$$

- If the bacterium could swim, and did so at a velocity of $20 \mu\text{m s}^{-1}$, what is the minimum bacterium size at which swimming would provide more glucose than diffusion alone?

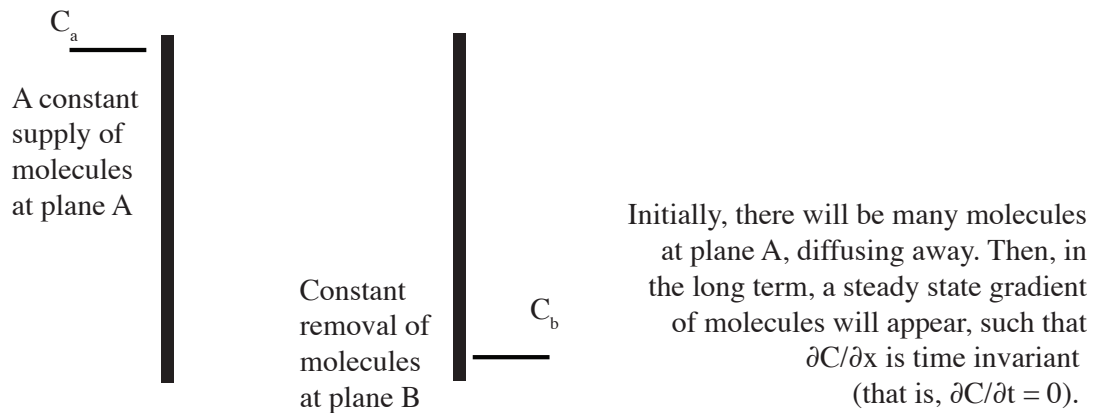
Set the Peclet number to 1 = $\frac{2 \cdot r \cdot v}{D}$

solve for r $r = \frac{D}{2v}$

$$\frac{7 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}}{2 (20 \times 10^{-6} \text{ m s}^{-1})} = 0.0175 \text{ m} \quad \text{units check!}$$

$$= 1.75 \text{ cm (quite large)}$$

Diffusion to capture can be explored using a simple model that assumes infinite absorptive capacity at the colony perimeter, so that we need consider only diffusive supply:

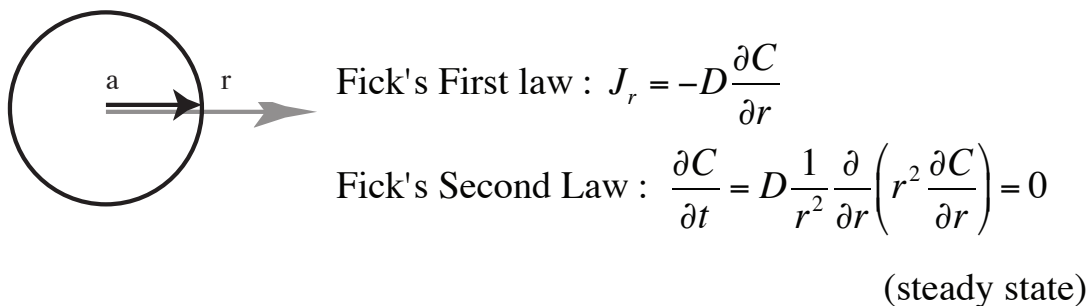


The time dependence (Fick's Second Law) is:

Under steady state conditions, $\partial C/\partial t$ is equal to 'zero', simplifying analysis.

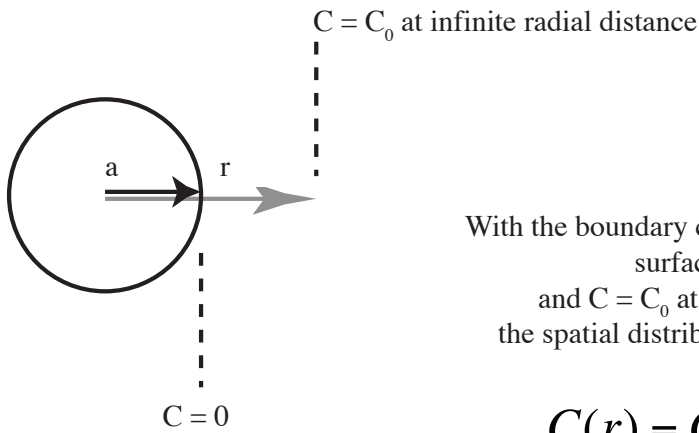
$$\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial x^2}$$

Since Volvox is spherical, we are not interested in $\partial C/\partial x$, but instead $\partial C/\partial r$, where r is the radial distance from the spherical cell.



^[1]Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp. 19–27.

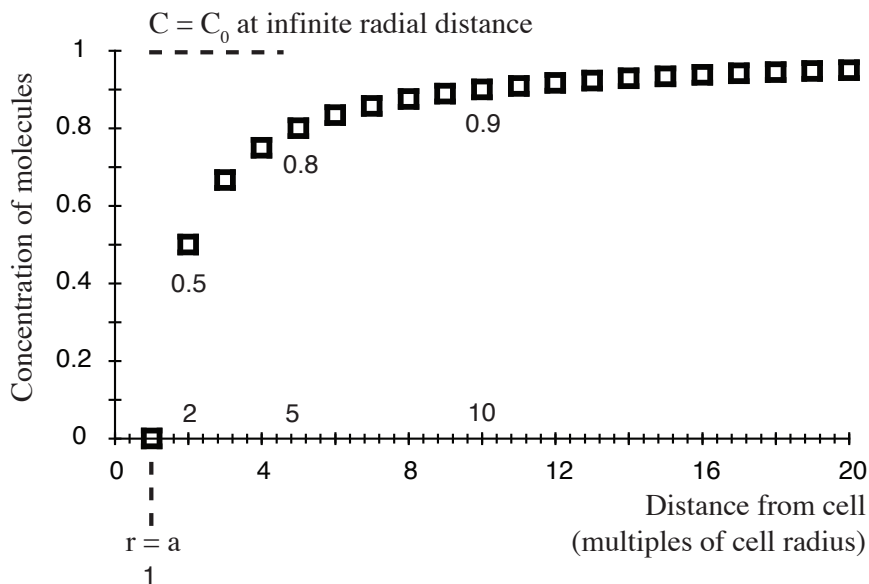
For a spherical (colony) “absorber” of radius a :



With the boundary conditions that $C = 0$ at the surface of the colony of radius a , and $C = C_0$ at an ‘infinite’ distance away, the spatial distribution of molecules, $C(r)$ is:

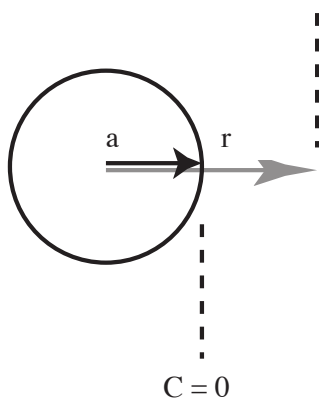
$$C(r) = C_0 \left(1 - \frac{a}{r} \right)$$

Graphically:



^[1]Berg, HC (1908) Random Walks in Biology. Princeton University Press. pp. 19–27.

The flux for the spherical (colony) is:



$$J_r = -D \left(\frac{\partial C}{\partial r} \right)$$

$$J(r) = -D \cdot C_0 \left(\frac{a}{r^2} \right)$$

from $\frac{\partial C}{\partial r}$ of $C_0 \left(1 - \frac{a}{r} \right) = \frac{\partial C}{\partial r}$ of $C_0 - \frac{C_0 \cdot a}{r}$
 $\frac{\partial}{\partial r} C_0 = 0$ and $\frac{\partial}{\partial r} C_0 \cdot a \cdot r^{-1} = C_0 \cdot a \cdot r^{-2}$

$C = 0$

On an area basis, from the sphere area equal to $4 \cdot \pi \cdot a^2$, setting $r = a$ and multiplying $J(r)$ by the area:

$J(r) = (D \cdot C_0 \cdot (a/a^2)) \cdot (4 \cdot \pi \cdot a^2)$. Simplifying:

$$J_r(a) = -D \cdot C_0 \cdot 4 \cdot \pi \cdot a = I_D \text{ (diffusive current)}$$

(units of mole sec⁻¹)

That is diffusive supply. We now need to consider the metabolic demand of the cell which is dependent on the metabolic rate per unit area of the cell (β):

(mole cm⁻² sec⁻¹)

$$I_m = 4 \cdot \pi \cdot a^2 \cdot \beta \text{ (metabolic current)}$$

(cm²) (units of mole sec⁻¹)

Setting the diffusive and metabolic current equation equal to each other reveals the critical size of the cell, where diffusive currents cannot fulfill the colony's metabolic requirements:

$$I_D = 4 \cdot \pi \cdot a \cdot D \cdot C_0 = 4 \cdot \pi \cdot a^2 \cdot \beta = I_m$$

(cm² sec⁻¹) (mole cm⁻³)

$$a_{critical} = \frac{D \cdot C_0}{\beta} \text{ (units of cm)}$$

(mole cm⁻² sec⁻¹)

Concentration and metabolic rate both affect the critical size of the colony, as does the diffusion coefficient for the nutrient molecule.

^[1]Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp. 19–27.

Now, in the Volvoclean multi-cellular colonies, the flagella extend out into the medium. With coordinated flagellar beating, the colonies are motile, moving either uni-directionally, or sometimes simply spinning in place. Are these advective flows generated by the flagellar beating important in nutrient supply?

To determine the constraints of advective supply on the colony is more complicated than the constraints of diffusive supply.

To the diffusive flux equation $\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial r^2}$

we need to add another term

$$\frac{\partial C}{\partial t} = u \cdot \frac{\partial C}{\partial r} \cdot C + D \frac{\partial^2 C}{\partial r^2}$$

flow velocity
concentration gradient
concentration

Note that this is not completely accurate, since the velocity is a vector that will vary both with distance from the colony and its polar location. Analogously, the concentration gradient may vary as a vector (that is, $\partial C/\partial x$, $\partial C/\partial y$, and $\partial C/\partial z$).

There is a test for the flow rate at which $u \cdot (\partial C/\partial r) \cdot C$ becomes more important (larger than) diffusive supply, the dimension-less Peclet Number:

where a is the cell radius, u the velocity, and D is the Diffusion coefficient. $P_e = \frac{2 \cdot a \cdot u}{D}$

The leap from the combination of diffusive and advective fluxes to the Peclet Number is not very intuitive.

The terms $u \cdot \frac{\partial C}{\partial r} \cdot C$ and $D \frac{\partial^2 C}{\partial r^2}$ are simplified by considering characteristic velocities and lengths, so that

where U is the characteristic velocity (average fluid velocity), and L is the characteristic length (for example, the diameter of the cell). $u \cdot \frac{\partial C}{\partial r} \cdot C$ becomes $\frac{U \cdot C}{L}$
and $D \frac{\partial^2 C}{\partial r^2}$ becomes $\frac{D \cdot C}{L^2}$

The ratio can be simplified $\frac{\frac{UC}{L}}{\frac{DC}{L^2}} = \frac{UL}{D} = \frac{2 \cdot a \cdot u}{D}$ For Volvox colonies, the Peclet number is about 100^[1]. Advective flow dominates.

^[1]Solari CA, Drescher K, Ganguly S, Kessler JO, Michod RE, Goldstein RE (2011) Flagellar phenotype plasticity in volvoclean algae correlates with Peclet number. J. R. Soc. Interface doi:10.1098/rsif.2011.0023