OC523 Ocean Ecological Dynamics
Homework #1 - Winter, 2019

Mathematical calculation: Diffusive transport of a nutrient to the surface of a cell

Based on molecular diffusion of nutrients toward the cell surface, mathematical calculations suggest that a small cell should be able to sustain high growth rates (2 – 3 d^{-1}), even at the low-nanomolar nutrient concentrations that characterize much of the tropical and subtropical open ocean. How do those calculations work? What assumptions do we have to make to do a calculation like that?

Let's work this problem by considering a small spherical cyanobacterium with a diameter of 1.0 µm, growing in seawater at a temperature of 20°C. Let's assume that NH_4^+ is the only source of N available for growth, and that the cell has a minimum cell quota (Q_0) for N of 10 fmol N $cell^{-1}$ (1 femtomole (fmol) = 1 x 10^{-15} mol). Assuming that:

— each cell is surrounded by a microzone through which NH_4^+ can move toward the cell only by molecular diffusion,

— the cell's surface behaves as a theoretically perfect sink for ammonium (*i.e.* that it takes up every NH_4^+ ion instantly as soon as it reaches the cell surface, thus maintaining a [NH_4^+] of zero within an infinitesimal distance of the cell surface), and

— the molecular diffusion coefficient for NH_4^+ in seawater at 20°C is 6.0 x 10^{-5} cm^2 s^{-1},

let's plot the relationship between [NH_4^+] and distance from the cell surface that is required to support growth of this cyanobacterium at a specific growth rate of 2.0 d^{-1} (equivalent to ~2.9 divisions d^{-1} – a very high growth rate to try and sustain at low [NH_4^+]).

The minimum rate of N uptake (in mol N $cell^{-1}$ $time^{-1}$) that must be sustained to support any growth rate (µ, in $time^{-1}$) is equal to the product of that growth rate times the minimum cell quota for N (Q_0, in mol N $cell^{-1}$). To keep our units straight let's consider all NH_4^+ concentrations in (mol N cm^{-3}), all distances in cm and all time intervals in seconds. So, at the growth rate we're considering (2.0 d^{-1}, which is equal to ~2.32 x 10^{-5} s^{-1}) and a minimum cell quota (Q_0) of 10 fmol N $cell^{-1}$ (1.0 x 10^{-14} mol N $cell^{-1}$) the minimum uptake rate is:

$$\mathbf{2.32 \times 10^{-5}\ s^{-1} \times 1.0 \times 10^{-14}\ mol\ N\ cell^{-1} = 2.32 \times 10^{-19}\ mol\ N\ cell^{-1}\ s^{-1}}$$

(It isn't necessary for the diffusion calculation, but it may help you understand nutrient uptake rates at the cellular level to note that the uptake rate we just calculated is equivalent to ~140,000 atoms of N taken up per cell per second.)

Next we want to calculate the rate at which NH_4^+ must move toward the cell by molecular diffusion in order to support that rate of uptake by the cell. To do this calculation we can think of the space surrounding each cell as a series of concentric spheres. To make everyone's calculations comparable, let's let the smallest of these spheres be 0.2 µm from the cell surface, the largest 15 µm from the cell surface, and consider one sphere at every 0.2 µm distance from the cell. At steady state (which becomes established very quickly in the small volume of water surrounding the cell) the diffusive flux of NH_4^+ into each of these concentric spheres must be equal to that into each of the others, and also equal to the rate of NH_4^+ uptake by the cell (which we just calculated). Diffusion of NH_4^+ toward the cell surface follows Fick's first law:

$$\mathbf{F = D\ (d[NH_4^+]/dX)}$$

where:

F	=	the diffusive flux (mol N cm^{-2} s^{-1})
$[NH_4^+]$	=	the ammonium concentration (mol N cm^{-3})
X	=	the distance from the cell surface (cm)
D	=	the molecular diffusion coefficient (6.0 x 10^{-5} cm^2 s^{-1})

The surface area of the spherical cell is given by $4\ \pi\ r^2$ where r is the cell radius (in this case 0.5 µm, or 5.0 x 10^{-5} cm). So the cell's surface area is:

$$\mathbf{4\pi \times (5.0 \times 10^{-5}\ cm)^2 \approx 3.14 \times 10^{-8}\ cm^2}$$

Therefore the minimum rate of NH_4^+ diffusion to the cell surface per unit surface area (the F we can use to calculate the necessary $[NH_4^+]$ gradients according to Fick's first law) must be approximately:

$$\mathbf{2.32 \times 10^{-19}\ mol\ N\ cell^{-1}\ s^{-1} / 3.14 \times 10^{-8}\ cm^2\ cell^{-1} \approx 7.37 \times 10^{-12}\ mol\ N\ cm^{-2}\ s^{-1}}$$

As the concentric spheres we're considering get farther from the cell surface the diffusive flux of NH_4^+ into each remains the same, and equal to the uptake rate that the cell must sustain (2.32 x 10^{-19} mol N s^{-1}). But the area of each sphere increases with the square of its distance from the center of the cell. Therefore the required diffusive flux of NH_4^+ <u>per unit surface area</u> (Fick's F) decreases as the spheres get farther from the cell surface (and thus larger). The first sphere we're considering, 0.2 µm (2.0 x 10^{-5} cm) from the cell surface has a radius of 0.5 µm + 0.2 µm = 0.7 µm (7.0 x 10^{-5} cm). Its surface area is thus:

$$\mathbf{4\pi \times (7.0 \times 10^{-5}\ cm)^2 \approx 6.16 \times 10^{-8}\ cm^2}$$

So the minimum N flux per unit surface area (Fick's F) into that sphere must be approximately:

$$\mathbf{2.32 \times 10^{-19}\ mol\ N\ cell^{-1}\ s^{-1} / 6.16 \times 10^{-8}\ cm^2\ cell^{-1} \approx 3.77 \times 10^{-12}\ mol\ N\ cm^{-2}\ s^{-1}}$$

or just over half of what it was right at the cell surface.

You can now calculate the diffusive flux (F) into each of the other concentric spheres, out to a distance of 15 µm from the cell surface. The repetitive parts of this calculation are best done on a spreadsheet.

Once you know F at each distance from the cell surface you're ready to calculate the $[NH_4^+]$ gradient necessary to support that inward diffusive flux, also as a function of distance from the cell surface. By rearranging Fick's first law (given above):

$$\mathbf{d[NH_4^+]/dX = F/D}$$

The molecular diffusion coefficient (D) for NH_4^+ is constant at 6.0 x 10^{-5} cm^2 s^{-1}, so the value (*i.e.* the steepness) of the $d[NH_4^+]/dX$ gradient is simply:

$$\mathbf{d[NH_4^+]/dX\ (mol\ N\ cm^{-4})\ (that\ is,\ mol\ N\ cm^{-3}\ cm^{-1}) = F\ (mol\ N\ cm^{-2}\ s^{-1})\ /\ 6.0\ x\ 10^{-5}\ cm^2\ s^{-1}}$$

Because you already know F at each 0.2 µm distance from the cell surface you can now calculate the necessary $[NH_4^+]$ gradient ($d[NH_4^+]/dX$) at each 0.2 µm step from the cell surface.

After you've done this you're ready to calculate $[NH_4^+]$ as a function of distance from the cell surface. Let $[NH_4^+] = 0$ at the cell surface (this is our assumption that the cell is acting as a 'perfect sink' for NH_4^+) and at each 0.2 µm step in distance from the cell, add the amount by which $[NH_4^+]$ must increase according to the $d[NH_4^+]/dX$ gradient your calculations require. (Remember that each step in distance is 0.2 µm, not 1 µm.) Plot the $[NH_4^+]$ you've calculated as a function of distance from the cell surface. If you do these calculations correctly your plot of the calculated minimum $[NH_4^+]$ *vs.* distance from the cell should approach an asymptotic $[NH_4^+]$ of ~7.5 nM. This shows that whenever the far-field $[NH_4^+]$ (the concentration you'd measure in a chemical analysis) is at least ~7.5 nM molecular diffusion should be able to support an NH_4^+ flux to cell surface that's high enough to support a growth rate of 2.0 d^{-1}. But if the far-field $[NH_4^+]$ were significantly lower than ~7.5 nM there would be no way for NH_4^+ to diffuse to the cell surface rapidly enough to support that growth rate.

OC523 Ocean Ecological Dynamics
Homework #1 - Winter, 2019

Continuing the diffusive transport calculation

Once you've set up a spreadsheet to calculate the minimum ammonium gradient in the vicinity of the 1 μm cell we considered in class, you should be able to calculate the minimum near-cell gradient of *any* nutrient required by a cell of *any* size to sustain *any* growth rate. To do this you need to know (or be able to assume) the size of the cell, its minimum cell quota (Q_0) for the nutrient in question, the growth rate you want the cell to sustain and the molecular diffusivity of the nutrient. But if you've set up the spreadsheet in a convenient way you should be able to plug in the new values you want to consider and let Excel take it from there.

As an example, let's consider a cell somewhat larger than the cyanobacterium you used in your first calculations. This larger cell has a diameter of 8 μm, but let's keep everything else the same. The minimum cell quota for any element should increase approximately in proportion to cell volume, which in turn increases with the cube of the cell's linear dimension. Since the larger cell we're considering has a diameter 8 times that of the small cyanobacterium we used in our first calculations (8 μm *vs.* 1 μm) we can estimate its minimum cell quota for N to be about:

$$\mathbf{1.0 \times 10^{-14}\ mol\ N\ cell^{-1} \times 8.0^{3} \approx 5.1 \times 10^{-12}\ mol\ N\ cell^{-1}}$$

or 5.1 picomoles N $cell^{-1}$. This, along with the calculation scheme we went through for the smaller cell, should give you all the information you need to calculate the minimum profile of $[NH_4^+]$ *vs.* distance from the cell surface that's necessary to support the growth of this larger species at a specific growth rate (μ) of 2.0 d^{-1}. I'd like you to give this a try. (One hint: You should probably have your spreadsheet carry these calculations out to a distance of at least 30 μm from the surface of the larger cell, rather than the 15 μm we used for the smaller one.)