15. An application of the fundamental theorem

In this lecture we apply the fundamental theorem to answer a question from nature.*

Small animals such as platyhelminths are able to "breathe" without the help of a vascular system. They obtain all the oxygen they need by diffusion across the surface of their bodies from the surrounding respiratory medium. Why can't large animals do this? The answer, of course, is that they are too large: they have too little surface area for oxygen to diffuse across compared to the volume of cells that must be supplied with oxygen. But how large is too large? Or to put it another way: How big can a flatworm be (and still survive without a vascular system)? That's our question from nature.

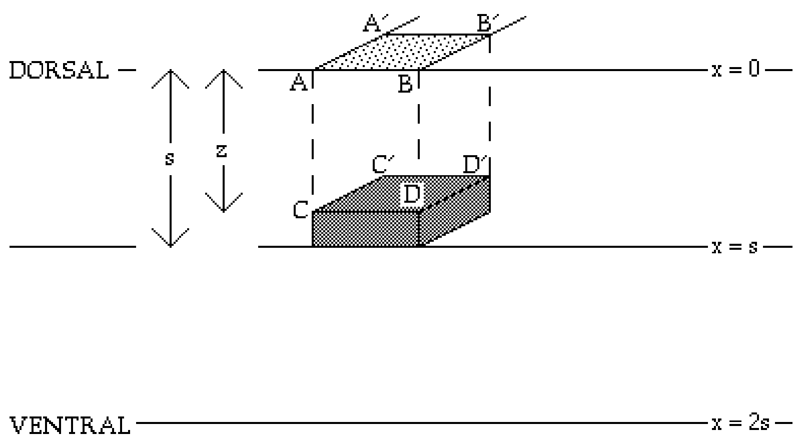

Figure 1: Section of a toy flatworm.

To simplify this question let us assume at the outset that flatworms are flat (in the sense that most of their surface area is on two opposite sides), so that as much of their cell tissue is as near to the surface as possible. Then instead of asking how big a flatworm can be, we ask more specifically: How wide can a flatworm be? For the sake of definiteness, let our flatworm have thickness $2s$ millimeters, and let x measure depth from its dorsal (upper) surface—see the figure above. Then we seek an upper bound on s.

Let $F(x)$ be the rate per unit area (mm^2) at which oxygen at depth x diffuses downward, perpendicular to the flatworm's dorsal surface. That is, $F(x)$ is the volume of oxygen transported downward per unit time (second) per unit area (mm^2) at depth x, and so $-F(x)$ is the rate per unit area at which oxygen at depth x diffuses upward. Now, diffusion of oxygen is simply flow of oxygen from regions of higher oxygen concentration to regions of lower oxygen concentration. The greater the imbalance between higher and lower concentration, the faster the flow. In other words, the steeper the concentration gradient, the faster the flow. By tradition, concentration of oxygen is expressed in terms of its partial pressure, which is the fraction of the total gas pressure attributable to oxygen; for example, the partial pressure of oxygen in air at atmospheric pressure is 0.21 atm

*Section 4.3 (pp. 119-122) of Alexander (1990) is the primary source for the remainder of this lecture. Note, however, some errors on p.121 of his discussion; in particular, he confuses dorsal and mid-section partial pressures in the mathematical analysis that leads to his equation (4.2).

(because air by volume is about 21% oxygen and 78% nitrogen, with 1% trace elements). Accordingly, let y be the partial pressure of oxygen at depth x; and let the partial pressure at the dorsal surface be atmospheric, hence equal to 0.21 atm. The higher the value of $\left|\frac{dy}{dx}\right|$, the faster the flow of oxygen, i.e., the higher the value of $|F|$. Moreover, if $\frac{dy}{dx} > 0$ then $F < 0$, because if oxygen concentration is higher at lower levels then oxygen diffuses upward; whereas if $\frac{dy}{dx} < 0$ then $F > 0$, because if concentration is higher at higher levels then oxygen diffuses downward. It is consistent with these observations to assume that downward flux of oxygen per unit area is a constant times the concentration gradient or

$$F \;=\; -q\,\frac{dy}{dx} \tag{1}$$

where q is called the diffusion coefficient. This proportional relationship between flux and concentration, satisfied remarkably well in practice, is commonly known as Fick's law.† Alexander (1990, pp. 120-121) suggests that a suitable value for flatworm tissue is $q = 2 \times 10^{-5}$ mm^2 atm^{-1} s^{-1}.

Let us assume that oxygen is supplied to the upper half of our flatworm's body by diffusion across its dorsal surface, and to its lower half by diffusion across its ventral (lower) surface. Then the cuboid shaded in the figure must receive its oxygen across its upper surface CC′D′D (and hence ultimately across speckled area AA′B′B of the dorsal surface). Let CC′D′D (and hence AA′B′B) have area ϵ mm^2. Then the cuboid's volume is just ϵ times its height, or $\epsilon(s-x)$. Thus if m is the rate per unit volume at which oxygen is consumed by flatworm tissue (in mm^3/sec), then $m\epsilon(s-x)$ mm^3 of oxygen must be supplied across CC′D′D every second. But the rate of oxygen supply across unit surface area is ϵF. Hence, from above (Fick's law):

$$\epsilon\left(-q\,\frac{dy}{dx}\right) \;=\; \epsilon m(s-x) \tag{2}$$

or

$$\frac{dy}{dx} \;=\; \frac{m}{q}(x-s). \tag{3}$$

Note that, because $x \le s$ inside the cuboid, $\frac{dy}{dx} \le 0$.

We have shown that $\frac{m}{q}(x-s)$ is the derivative of y. So y must be an anti-derivative of $\frac{m}{q}(x-s)$. But we know from the chain rule that

$$\frac{d}{dx}\left\{\frac{m}{2q}(x-s)^2\right\} \;=\; \frac{m}{2q}\cdot 2(x-s)\cdot 1 \;=\; \frac{m}{q}(x-s). \tag{4}$$

Thus we already know *one* anti-derivative of $\frac{m}{q}(x-s)$ . . . and if you've seen one, you've seen them all! So we can write

$$y \;=\; \int \frac{m}{q}(x-s)\,dx \;=\; \frac{m}{2q}(x-s)^2 + C \tag{5}$$

† After Adolf Fick, a 19th-century professor of physiology at Wurzburg

where at this stage C is an arbitrary constant. However, the partial pressure at the surface must be atmospheric, i.e., when $x = 0$, y must be 0.21 (atm). Hence

$$0.21 \;=\; \frac{m}{2q}(0 - s)^2 + C \tag{6}$$

or $C = 0.21 - \frac{m}{2q}s^2$, implying

$$y \;=\; \frac{m}{2q}(x - s)^2 + 0.21 - \frac{m}{2q}s^2 \;=\; 0.21 + \frac{m}{2q}x(x - 2s). \tag{7}$$

Thus the partial pressure of oxygen at the flatworm's midsection is

$$0.21 + \frac{m}{2q}s(s - 2s) \;=\; 0.21 - \frac{ms^2}{2q}. \tag{8}$$

But partial pressure cannot be negative; hence $0.21 \geq ms^2/2q$, or $s^2 \leq 0.42q/m$. This means that $4s^2 \leq 1.68q/m$, or

$$2s \;\leq\; \sqrt{\frac{1.68q}{m}}. \tag{9}$$

The right-hand side of this inequality is an upper bound on the thickness of the flatworm.

According to Alexander (1990, p.119), flatworms consume oxygen at a rate in excess of 0.1 cm^3 per hour per gram of body tissue. Since the density of flatworm tissue is about 1 gram per cm^3 and an hour is 3600 seconds, the volume rate of consumption exceeds 0.1 cm^3 of oxygen per 3600 seconds per cm^3 of flatworm; or, which of course is the same thing, 0.1 mm^3 of oxygen per 3600 seconds per mm^3 of flatworm. Thus $m > 0.1/3600$, implying that $1/m < 3600/0.1 = 3.6 \times 10^4$. We have already seen that $q = 2 \times 10^{-5}$. So $1.68q = 3.36 \times 10^{-5}$, implying $1.68q/m < 3.36 \times 10^{-5} \times 3.6 \times 10^4 = 1.2096$. Hence, from above, $2s < \sqrt{1.2096} = 1.1$ mm. Thus, according to our analysis, a flatworm couldn't possibly be more than 1.1 millimeters thick.

In practice, a flatworm's thickness is never more than about 0.5 mm, less than half of our upper bound. Note, however, that if our flatworm could receive oxygen only through its dorsal surface, then our analysis would predict an upper bound of 0.55 mm on thickness instead, because in that case the ventral surface in the figure would be at $x = s$ (and the worm would have thickness s, instead of $2s$).

Suitable problems from standard calculus texts

Stewart (2003): pp. 358-359, ## 1-31, 33-46.

References

Alexander, R. M. 1990 *Animals*. Cambridge: Cambridge University Press.

Stewart, J. 2003 *Calculus: early transcendentals*. Belmont, California: Brooks/Cole, 5th edn.