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**Diffusion Theory in Biology: A Relic of Mechanistic Materialism**

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Diffusion is a poor explanation for many examples of molecular motion in biological organisms. Simple models explain the movement of many molecules, but not all. Nor have we acknowledged the crucial effect of mass flow, a key aspect of molecular movement. The non-universality of diffusive properties has led to ideological attacks on biology. We need to explore mass flow and its relation to diffusive transport with due diligence.

**Abstract.** Diffusion theory explains in physical terms how materials move through a medium, e.g. water or a biological fluid. There are strong and widely acknowledged grounds for doubting the applicability of this theory in biology, although it continues to be accepted almost uncritically and taught as a basis of both biology and medicine. Our principal aim is to explore how this situation arose and has been allowed to continue seemingly unchallenged for more than 150 years. The main shortcomings of diffusion theory will be briefly reviewed to show that the entrenchment of this theory in the corpus of biological knowledge needs to be explained, especially as there are equally valid historical grounds for presuming that bulk fluid movement powered by the energy of cell metabolism plays a prominent note in the transport of molecules in the living body. First, the theory's evolution, notably from its origins in connection with the mechanistic materialist philosophy of mid nineteenth century physiology, is discussed. Following this, the entrenchment of the theory in twentieth century biology is analyzed in relation to three situations: the mechanism of oxygen transport between air and mammalian tissues; the structure and function of cell membranes; and the nature of the intermediary metabolism, with its implicit presumptions about the intracellular organization and the movement of molecules within it. In our final section, we consider several historically based alternatives to diffusion theory, all of which have their precursors in nineteenth and twentieth century philosophy of science.

**Keywords:** diffusion theory, Fick, 19th century physiology, mechanistic materialism, oxygen secretion, metabolic organization

Overview: The concept of transport by diffusion is encapsulated in Fick's First Law of Diffusion:

$$J = -D \frac{\partial c}{\partial x}$$

where flux,  $J$  (moles  $\text{cm}^{-2} \text{sec}^{-1}$ ) depends upon the concentration gradient  $(\partial c/\partial x)$  (moles  $\text{cm}^{-4}$ ) and the Diffusion coefficient  $D$  ( $\text{cm}^2 \text{sec}^{-1}$ ). This is a central description of flux, but misleading, because much of transport, especially at the multicellular level, relies on mass flow: the hydrodynamic movement of nutrients, etc., as a consequence of volume flow.

The term that is used to describe such mass transfer of matter (or heat) by the flow of a solution is ADVECTION.

The closely related term CONVECTION refers to the movement of fluid caused by the tendency of hot material to rise. That is, heat-induced flow.

The mathematics of advection are daunting, because in a three-dimensional space, the transport of material will rely on the velocity of the solvating medium (for example, water, the norm for biological systems) in three dimensions:

$$\nabla \mathbf{v} = u \frac{\partial}{\partial x} + v \frac{\partial}{\partial y} + w \frac{\partial}{\partial z}$$

velocity vector

with velocity components,  $u$ ,  $v$ , and  $w$ ,  
in the three dimensions,  $x$ ,  $y$ , and  $z$ .

The use of partial derivatives acknowledges that the velocity factors sum across the  $x$ ,  $y$ , and  $z$  coordinates, and each must be evaluated while the other two are held constant.

The meaning of the differential equation is clear: The rate of material transfer will depend upon the velocity and flow direction of the solvating medium.

Including mass flow in the flux equation, simplified to one (x) dimension:

$$J_x = -D \frac{\partial c}{\partial x} + v_x \cdot c$$

The relative contributions of diffusive flux and advective flow will depend upon the concentration gradient ( $\partial c/\partial x$ ) (and the Diffusion coefficient), and the velocity  $v_x$  (and concentration).

What will cause mass flow, such that  $v > 0$ ?

In a biological organisms, (and the environment in general), the primary driving force for mass flow is pressure. In its simplest form, mass flow  $J_v$  is proportional to the pressure gradient:

$$J_v \propto \frac{\partial P}{\partial x}$$

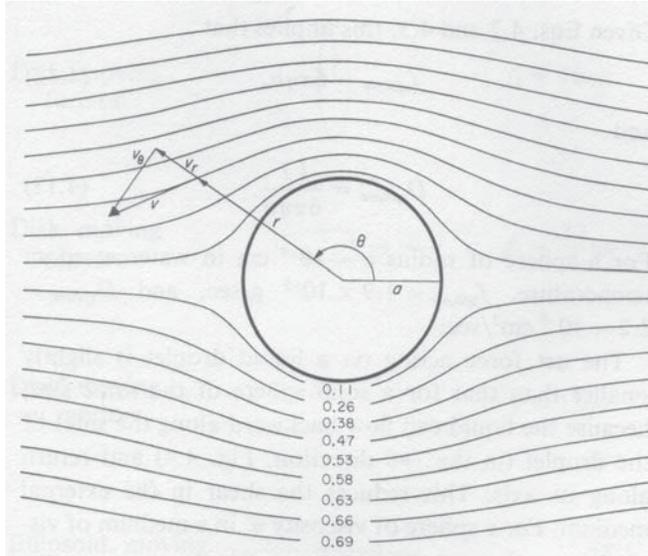
For flow through a pipe (a model for arterial/venal blood flow, or water flow through the xylem vessels of a vascular plant):

$$J_v = -\frac{r^2}{8 \cdot \eta} \cdot \frac{\partial P}{\partial x}$$

The  $r^2/8$  term refers to the cylindrical area of the 'pipe'. The term 'nu',  $\eta$ , is the viscosity of the solution.

This is known as Poiseuille's Law, and, importantly, assumes that there is no turbulent mixing of the fluid as it flows: no eddies or counterflow, only laminar flow.

It is easier to visualize laminar flow than to explain it:



Although the diagram shows a sphere moving through the solution, movement of solution around the sphere would be very similar (see below). Velocity ‘isovelocities’ are shown.  
 Source: Berg HC (1993) *Random Walks in Biology*. Princeton Univ. Press.

The image to the right documents laminar flow by photographing metal flakes as they flow around an anchored sphere. Source: Nelson P (2004) *Biological Physics*. WH Freeman.



The ‘test’ for laminar flow is the Reynolds number, the dimension-less ratio of inertial forces to viscosity:

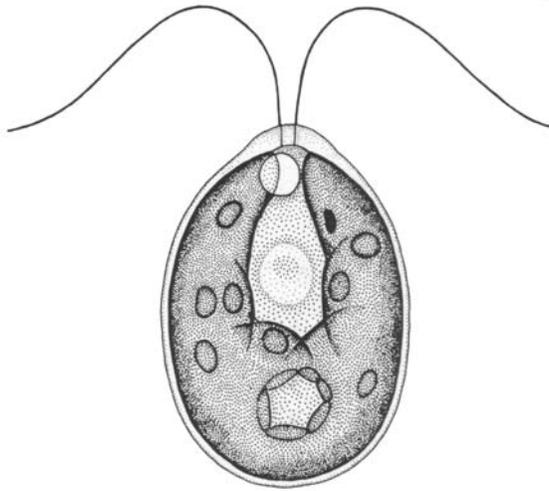
$$R_e = \frac{\rho \cdot v \cdot l}{\eta}$$

density (water =  $1 \text{ gm cm}^{-3}$ )  
 velocity ( $\text{cm sec}^{-1}$ )  
 tube diameter (cm)  
 viscosity (water =  $0.01 \text{ gm cm}^{-1} \text{ sec}^{-1}$ )

The cut-off for turbulent flow is normally considered to be about 2000<sup>[1]</sup>.

<sup>[1]</sup>Source: Nobel PS (1991) *Physicochemical and Environmental Plant Physiology*. Academic Press. pp.505–513.

Volvocalean algae are a model system in which the relative significance of diffusive and advective transport can be explored experimentally. The Volvocalean algae exist as either small unicellular algae (for example, *Chlamydomonas reinhardtii*); small (4–64 cells) multi-cellular colonies (for example *Gonium* and *Eudorina*)(in these groups, the cells do not differentiate); and large (1,000–50,000 cells) multi-cellular colonies in which cells are either reproductive (germ cells) or vegetative (“sterile” flagellated cells).

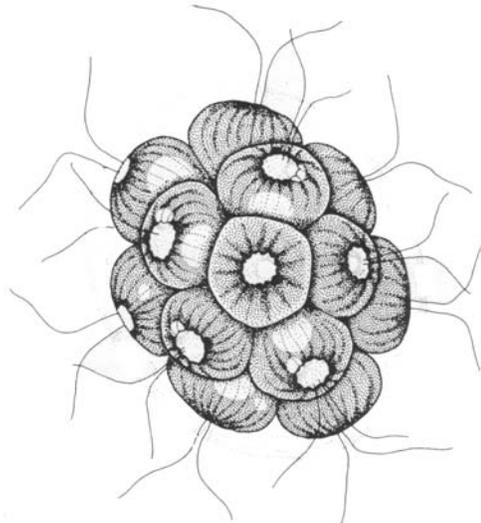
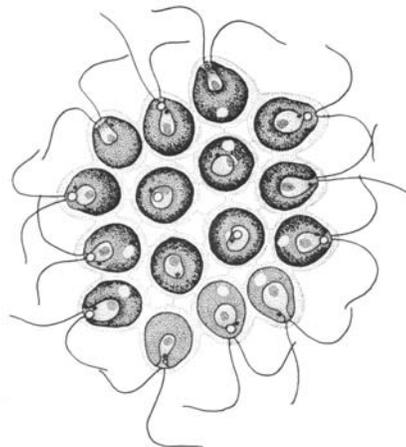


*Chlamydomonas*, a unicellular example of Volvocalean algae is a typical photosynthetic protist, with a cell length of 15 to 30  $\mu\text{m}$ .

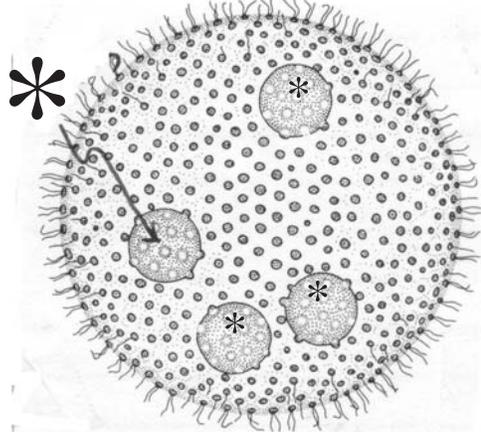
Multi-cellularity, implying coordinated development, represents an increase in complexity in an evolutionary context. It arose many times among the Volvocalean algal groups.

*Pandorina* is a simpler multi-cellular form. Each cell is about 20  $\mu\text{m}$  in diameter; eight or sixteen cells comprise a colony.

*Gonium* (below) is another example (5 to 15  $\mu\text{m}$  cells).

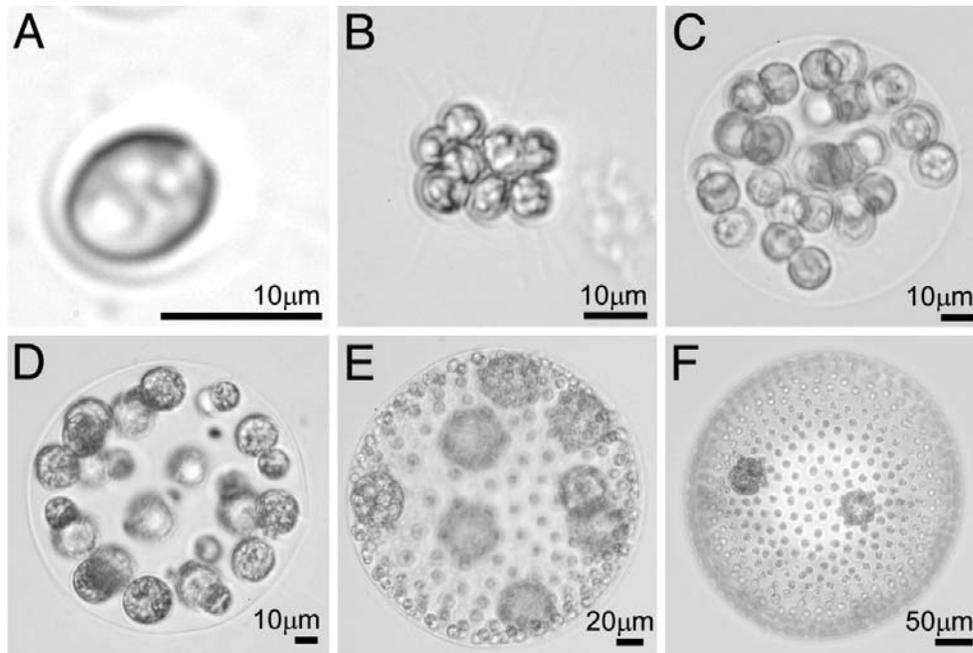


*Volvox* cells are relatively small (about 10  $\mu\text{m}$  in diameter), but the total number of cells is many (1,000–50,000 cells), creating a large multi-cellular colony up to 1000  $\mu\text{m}$  in diameter. Daughter colonies (\*) develop (from the germ/gonidial cells) within the parental colony.



In these large many-cell colonies, the cellular differentiation into germ (gonidial) and vegetative cells implies a ‘higher’ level of evolutionary complexity.

It is worthwhile to emphasize that multicellularity does not appear in a fixed phylogenetic sequence, but exists in divergent Volvocalean genera that are phylogenetically unrelated. Multi-cellular or not, all the species have survived a very long time.



“Species of volvocalean green algae spanning a large range in size. Shown are the single-cell *C. reinhardtii* (A), undifferentiated colonies *Gonium pectorale* (8 cells) (B) and *Eudorina elegans* (32 cells) (C), and those with germ-soma differentiation *Pleodorina californica* (64 cells) (D), *V. carteri* (ca. 1,000 cells) (E), and *Volvox aureus* (ca. 2,000 cells) (F).” Source: Solari CA, S Ganguly, JO Kessler, RE Michod, RE Goldstein (2006) Multicellularity and the functional interdependence of motility and molecular transport. Proc. Natl Acad. Sci USA 103(5):1353–1358.

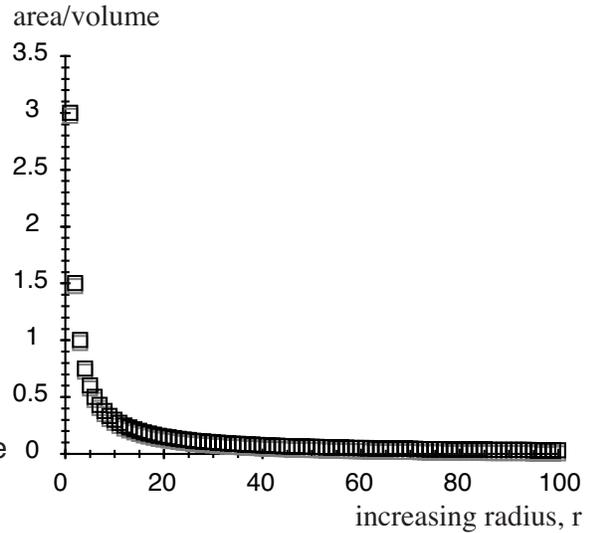
In the multi-cellular forms of the Volvocalean algae, a constraint on diffusive transport appears, because of a decline in surface area relative to the volume of the colony.

Assuming a spherical shape:  $\text{area} = 4 \cdot \pi \cdot r^2$

The ratio of area/volume:

$$\frac{4 \cdot \pi \cdot r^2}{\frac{4}{3} \cdot \pi \cdot r^3} = \frac{3}{r}$$

$$\text{volume} = \frac{4}{3} \cdot \pi \cdot r^3$$

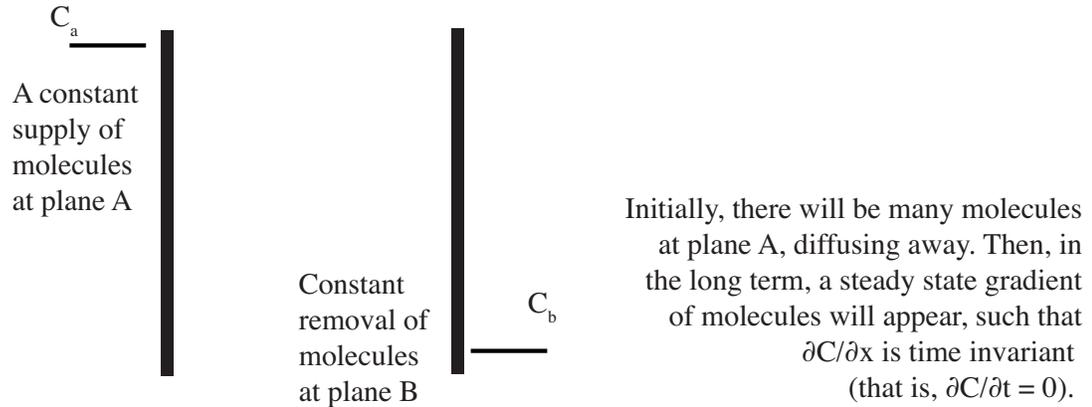


As colony size increases, the surface area available to supply the increasing volume declines precipitously..

Put another way, the metabolic requirements of the cell(s) scales with volume,  $r^3$ , but the surface available to supply metabolic requirements only scales as  $r^2$ .

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

To explore the contributions of diffusive and advective transport into a Volvoclean algal colony, we need to explore “diffusion to capture”, a model for diffusive uptake. As a simple example:

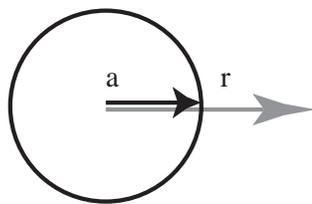


The time dependence (Fick's Second Law) is:

Under steady state conditions,  $\frac{\partial C}{\partial t}$  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  $\frac{\partial C}{\partial x}$ , but instead  $\frac{\partial C}{\partial r}$ , where  $r$  is the radial distance from the spherical cell.

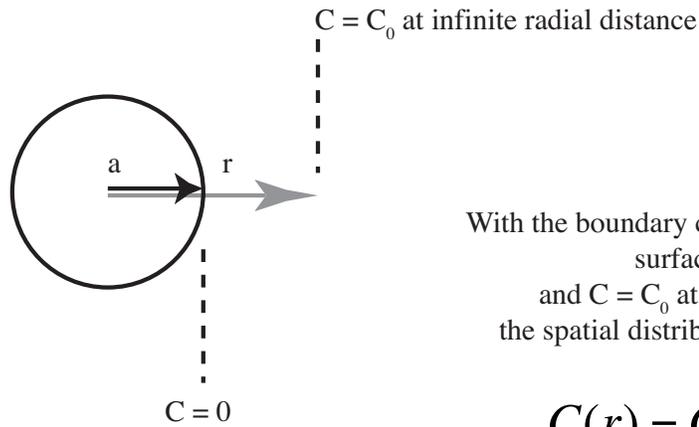


Fick's First law :  $J_r = -D \frac{\partial C}{\partial r}$

Fick's Second Law :  $\frac{\partial C}{\partial t} = D \frac{1}{r^2} \frac{\partial}{\partial r} \left( r^2 \frac{\partial C}{\partial r} \right) = 0$

(steady state)

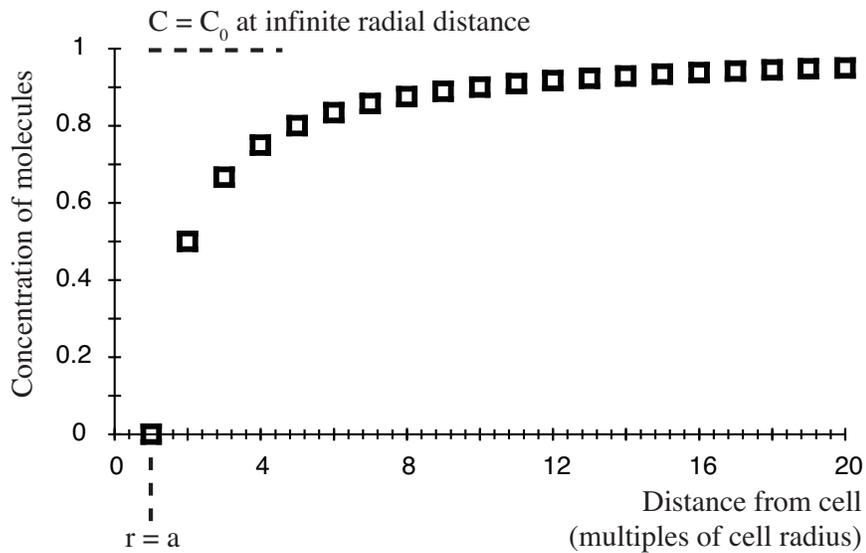
For a spherical (colony) “absorber” of radius  $a$ :



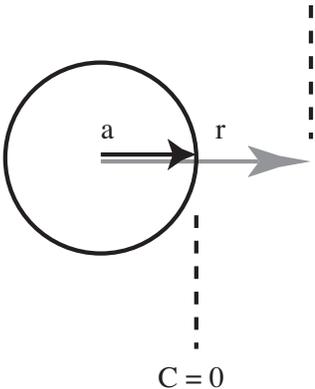
With the boundary conditions that  $C = 0$  at the surface of the colony of radius  $a$ , and  $C = C_0$  at an ‘infinite’ distance away, the spatial distribution of molecules,  $C(r)$  is:

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

Graphically:



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  $\frac{\partial}{\partial r} C_0 \cdot a \cdot r^{-1} = C_0 \cdot a \cdot r^{-2}$

On an area basis, from the sphere area equal to  $4 \cdot \pi \cdot a^2$ :

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

The metabolic demand of the cell is dependent on the metabolic rate per unit area of the cell (beta):

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

Setting the two equations for diffusive and metabolic currents equal reveals the critical size of the cell, where diffusive currents cannot fulfill the colony's metabolic requirements:

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

$$a_{critical} = \frac{D \cdot C_0}{\beta}$$

Concentration, diffusion and metabolic rate will all affect the critical size of the colony

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

To the basic 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:

$$P_e = \frac{2 \cdot a \cdot u}{D}$$

where  $a$  is the cell radius,  $u$  the velocity, and  $D$  is the Diffusion coefficient.

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

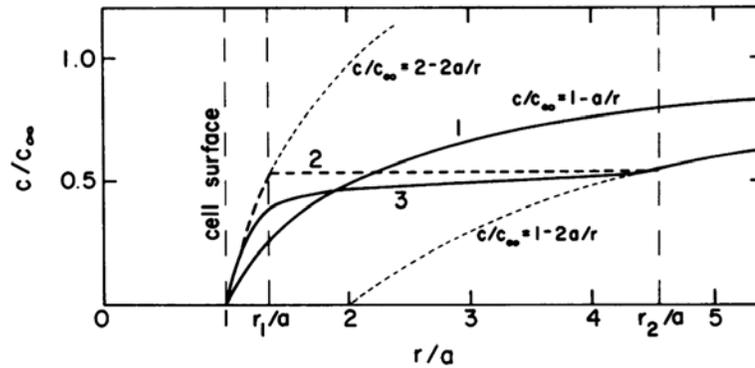
$$u \cdot \frac{\partial C}{\partial r} \cdot C \text{ becomes } \frac{U \cdot C}{L}$$

$$\text{and } D \frac{\partial^2 C}{\partial r^2} \text{ becomes } \frac{D \cdot C}{L^2}$$

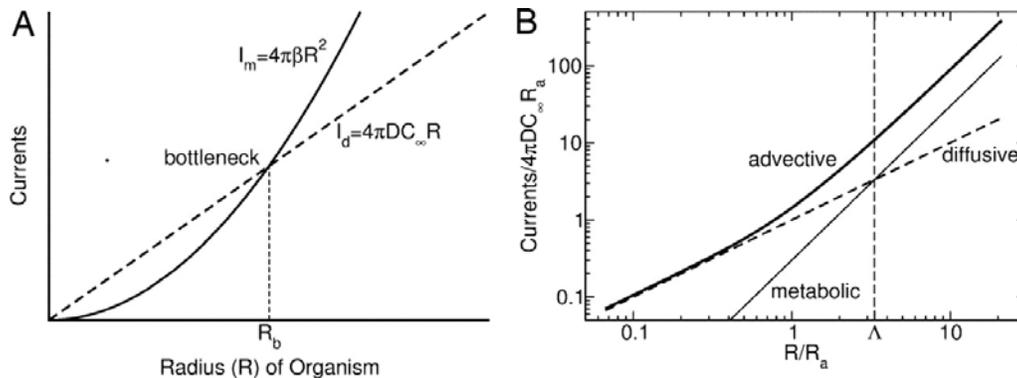
This leads to a ratio of advective to diffusive fluxes:  $U \cdot L/D$ , which, for the colony becomes  $2 \cdot a \cdot (L) \cdot u (U) / D$ .

where  $U$  is the characteristic velocity (average fluid velocity), and  $L$  is the characteristic length (for example, the diameter of the cell).

The relation between advective and diffusive flow are summarized below by considering the effect of flow rate on the concentration gradient ( $C(r)$ ) near the spherical colony and the concept of a bottleneck where diffusive current becomes limiting:



“Relative concentration in the vicinity of a spherical absorber for three cases: (1) No stirring: the current absorbed is  $J_0 = 4 \cdot \pi \cdot a \cdot D \cdot C_0$ . (2) Volume between  $r_1$  and  $r_2$  stirred infinitely rapidly, fluid stationary elsewhere; current absorbed is  $2 \cdot J_0$ . (3) Finite stirring speed; region inside  $r_1$  still dominated by diffusion; current absorbed is  $2 \cdot J_0$ .”  
 Source: Berg HC and EM Purcell (1977) Physics of chemoreception. Biophysical Journal 20:193–219.

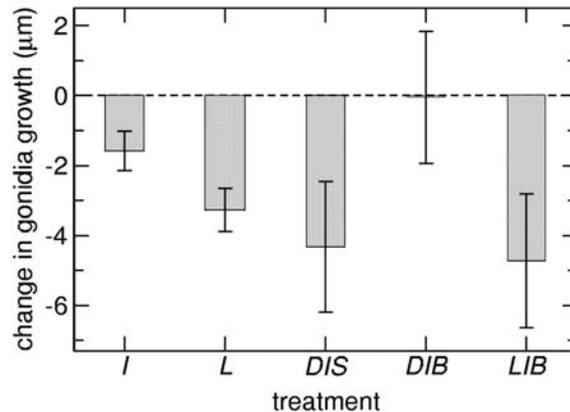


“Molecular currents (molecules per second) and requirements. (A) A schematic diagram illustrating the existence of the diffusive bottleneck  $R_b$ . When the metabolic demand current (solid line), which is quadratic in organism radius  $R$ , exceeds the diffusive current (dashed line), which is only linear in  $R$ , the metabolism is constrained by diffusion. (B) Log–log plot showing how the advective current (thick solid line) circumvents the diffusive bottleneck for the choice  $\{\Lambda\} \{\equiv\} R_b/R_a = 3.3$ . At radii greater than the advective radius  $R_a$  (Eq. 7), the advective current grows quadratically with  $R$ , allowing metabolic needs to be satisfied for any arbitrary size.”

Source: Short MB, CA Solari, S Ganguly, TR Powers, JO Kessler, RE Goldstein (2006) Flows driven by flagella of multicellular organisms enhance long-range molecular transport. Proc. Natl. Acad. Sci. USA 103:8315–8319.

To explore the role of advective flow generated by coordinated flagellar beating, Solari et al. (2006)<sup>[1]</sup> monitored germ cell growth relative to the control, normal flagellated colonies in a standard medium.

“Summary of germ cell growth experiments. Data show treatments that significantly affected the growth rate of germ cells compared with those of normal flagellated colonies in standard medium. I, inhibitor treatment; L, broken colonies treatment; DIS, deflagellated colonies with inhibitor in still medium; DIB, deflagellated colonies with inhibitor in bubbling medium; LIS, broken colonies with inhibitor in still medium; LIB, broken colonies with inhibitor in bubbling medium. DIB results illustrate the restoration of normal growth with artificial bubbling.”<sup>[1]</sup>



Growth of germ (gonidial) cells was unaffected in normal colonies with or without mixing. Inhibiting flagellar beating inhibited gonidial growth somewhat ( $-1.6 \pm 0.6 \mu\text{m}$ ) (the flagellar beating-induced flow can be observed under a microscope with the appropriate optical conditions). De-flagellating the colonies and inhibiting regeneration inhibited growth a great deal ( $-4.3 \pm 1.8 \mu\text{m}$ ), but recovery was complete if the colonies were artificially mixed ( $-0.0 \pm 2.0 \mu\text{m}$ ) (by ‘sparging’ the cells, that is bubbling air through the solution). Thus, advective flow enhances nutrient supply, enhancing gonidial cell growth.

A cautionary note is in order: Many organisms (some unicellular, most multicellular) exceed the critical size limit derived by Short et al. (2006)<sup>[2]</sup> of about 50-200  $\mu\text{m}$  where diffusive transport becomes limiting. They lack flagellar-induced flow, or any other mechanisms for creating flow around themselves. Even so, they have survived for a long time, 1,500 million years or so. Transport constraints are not a universal constraint on biological form and function.

<sup>[1]</sup>Solari CA, S Ganguly, JO Kessler, RE Michod, RE Goldstein (2006) Multicellularity and the functional interdependence of motility and molecular transport. Proc. Natl. Acad. Sci. USA 103:1353–1358.

<sup>[2]</sup>Short MB, CA Solari, S Ganguly, TR Powers, JO Kessler, RE Goldstein (2006) Flows driven by flagella of multicellular organisms enhance long-range molecular transport. Proc. Natl. Acad. Sci. USA 103:8315–8319.

# Diffusive and Advective Transport

## Multicellularity and the functional interdependence of motility and molecular transport

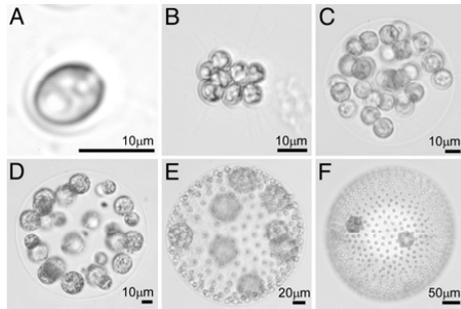
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Departments of \*Ecology and Evolutionary Biology and \*\*Physics, Program in Applied Mathematics, and BIOS Institute, University of Arizona,

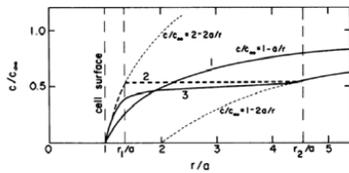
www.pnas.org/cgi/doi/10.1073/pnas.0528193102

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**Abstract.** Benefits, costs, and requirements accompany the transition from motile totipotent unicellular organisms to multicellular organisms having cells specialized into reproductive (germ) and vegetative (sterile soma) functions such as motility. In flagellated colonial organisms such as the volvoclean green algae, organized beating by the somatic cells' flagella yields propulsion important in phototaxis and chemotaxis. It has not been generally appreciated that for the larger colonies flagellar stirring of boundary layers and remote transport are fundamental for maintaining a sufficient rate of metabolite turnover, one not attainable by diffusive transport alone. Here, we describe experiments that quantify the role of advective dynamics in enhancing productivity in germ soma-differentiated colonies. First, experiments with suspended de-flagellated colonies of *Volvox carteri* show that forced advection improves productivity. Second, particle imaging velocimetry of fluid motion around colonies immobilized by micropipette aspiration reveals flow fields with very large characteristic velocities  $U$  extending to length scales exceeding the colony radius  $R$ . For a typical metabolite diffusion constant  $D$ , the associated Peclet number  $Pe = 2UR > 1$ , indicative of the dominance of advection over diffusion, with striking augmentation at the cell division stage. Near the colony surface, flows generated by flagella can be chaotic, exhibiting mixing due to stretching and folding. These results imply that hydrodynamic transport external to colonies provides a crucial boundary condition, a source for supplying internal diffusional dynamics.



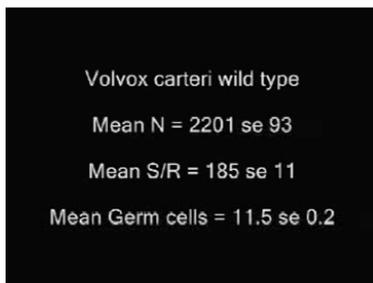
Species of volvoclean green algae spanning a large range in size. Shown are the single-cell *C. reinhardtii* (A), undifferentiated colonies *Gonium pectorale* (8 cells) (B) and *Eudorina oligocela* (32 cells) (C), and those with germ-soma differentiation *Pleodorina californica* (64 cells) (D), *Volvox carteri* (approx. 1,000 cells) (E), and *Volvox aureus* (approx. 2,000 cells) (F). Solari CA, Ganguly SJ, Kessler JO, Michod RE, Goldstein RE (2006) Multicellularity and the functional interdependence of motility and molecular transport. PNAS 103(5):1353–1358.



**FIGURE 2** Relative concentration in the vicinity of a spherical absorber, for three cases: (1) No stirring; the current absorbed is  $J_0 = 4\pi a D c_0$ . (2) Volume between  $r_1$  and  $r_2$  stirred infinitely rapidly, fluid stationary elsewhere; current absorbed is  $2J_0$ . (3) Finite stirring speed; region inside  $r_1$  still dominated by diffusion; current absorbed is  $2J_0$ .

## Diffusive and Advective Transport

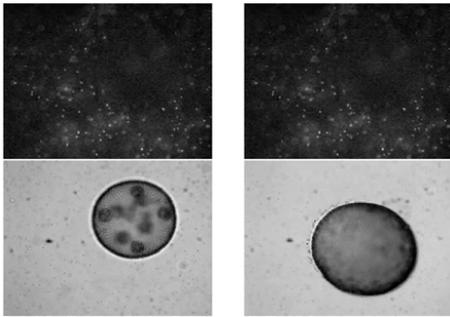
The concentration gradients are shown under conditions of no advective flow (1), infinitely fast advective flow (2) and finite advective flow. Note the strong effect of fluid flow on the concentration gradient ( $dc/dr$ ) near the cell surface. source: Berg and Purcell (1977) Physics of chemoreception. Biophys J. 20:193–219.



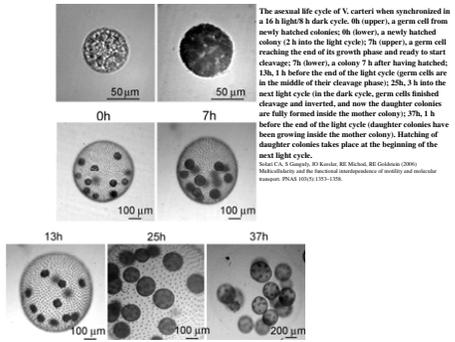
Movie file of *Volvox carteri* swimming and sinking for calculation of hydrodynamics model. Notice that mature large colonies starting cleavage (after 12 hours) can't swim upwards. (<http://webweb.arizona.edu/Michod/hydrodynamics.htm>) Solari CA, Ganguly SJ, Kessler JO, Michod RE, Goldstein RE (2006) Multicellularity and the functional interdependence of motility and molecular transport. PNAS 103(5):1353–1358.



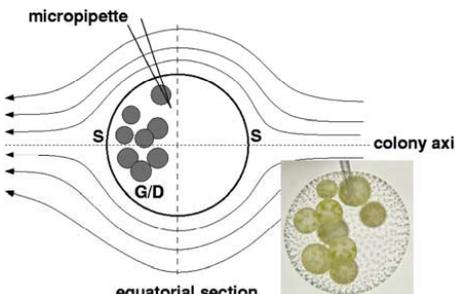
Movie file of *Pseudomonas fluorescens* (notice increasing flow rate into colony by flagellar beating) and *Haemotococcus* (a bi-flagellated unicellular alga). (<http://cehweb.uci.edu/MichaelHydrodynamics.html>)  
 Sabel CA, S Gopalay, D Kessler, RE Michael, RE Golestan (2006) Multicellularity and the functional interdependence of motility and molecular transport. PNAS 103(5):1353-1358.



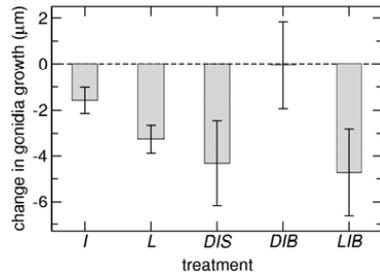
Flagellar feeding of *V. carterii* (narrow-band laser illumination, bright field) of *V. roussoletii*. (<http://cehweb.uci.edu/MichaelHydrodynamics.html>)  
 Sabel CA, S Gopalay, D Kessler, RE Michael, RE Golestan (2006) Multicellularity and the functional interdependence of motility and molecular transport. PNAS 103(5):1353-1358.



The asexual life cycle of *V. carterii* when synchronized in a 16-h light/8-h dark cycle. 0h (upper), a germ cell from newly hatched colonies; 0h (lower), a newly hatched colony (2 h into the light cycle); 7h (upper), a germ cell reaching the end of its growth phase and ready to start cleavage; 7h (lower), a colony 7 h after having hatched; 13h, 1 h before the end of the light cycle (germ cells are in the middle of their cleavage phase); 25h, 2 h into the next light cycle (in the dark cycle, germ cells linked cleavage and inverted, and now the daughter colonies are fully formed inside the mother colony); 27h, 1 h before the end of the light cycle (daughter colonies have been growing inside the mother colony). Hatching of daughter colonies takes place at the beginning of the next light cycle.  
 Sabel CA, S Gopalay, D Kessler, RE Michael, RE Golestan (2006) Multicellularity and the functional interdependence of motility and molecular transport. PNAS 103(5):1353-1358.



SMicropipette aspiration of *V. carterii* for PV studies. Schematic shows streamlines symmetric about the colony axis, on which are located the two stagnation points (S). Germ cells/daughter colonies (G/D) are located in posterior half of colony. Dashed line indicates equatorial section of PV flow field used to determine maximum fluid velocity.  
 Sabel CA, S Gopalay, D Kessler, RE Michael, RE Golestan (2006) Multicellularity and the functional interdependence of motility and molecular transport. PNAS 103(5):1353-1358.



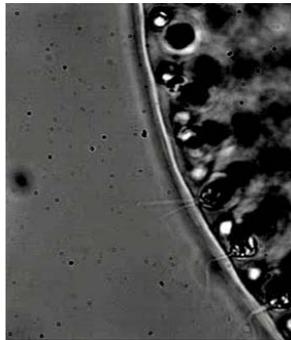
Summary of germ cell growth experiments. Data show treatments that significantly affected the growth rate of germ cells compared with those of normal flagellated colonies in standard medium. I, inhibitor treatment; L, broken colonies treatment; DIS, deflagellated colonies with inhibitor in still medium; DIB, deflagellated colonies with inhibitor in bubbling medium; LIB, broken colonies with inhibitor in still medium; LIB, broken colonies with inhibitor in bubbling medium. DIB results illustrate the restoration of normal growth with artificial bubbling.

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### High-speed movie (125 fps) showing flagella (brightfield)

University of Cambridge > DAMTP > Goldstein Lab > Pictures and Movies

<http://www.damtp.cam.ac.uk/user/gold/movies.html>



## Diffusive and Advective Transport

**Multicellular colonies of Volvocean algae have evolved multiple times. In the large colonies, flagellated cells on the outside function in colony motility, but, in addition, function to create advective flow to maximize supply of nutrients to the colony.**

### Multicellularity and the functional interdependence of motility and molecular transport

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Departments of \*Ecology and Evolutionary Biology and †Physics, ‡Program in Applied Mathematics, and §BIOS Institute, University of Arizona, www.pnas.org/cgi/doi/10.1073/pnas.0503181102 PNAS | January 21, 2006 | vol. 103 | no. 5 | 1333-1338