CHAPTER 1

Two Ways to Move Material

Introducing a Variable

"No man is an island, entire of itself," said the English poet John Donne. Nor is any other organism, cell, tissue, or organ. We're open systems, continuously exchanging material with our surroundings as our parts do with their surroundings. In all of these exchanges, one physical process inevitably participates. In that process, diffusion, thermal agitation, and place-to-place concentration differences combine to produce net movements of molecules. On almost any biologically relevant scale, it can be described by exceedingly precise statistical statements, formulas that take advantage of the enormous numbers of individual entities moving around. Since it incurs no metabolic expenditure, it's at once dependable and free.

But except over microscopic distances, diffusion proceeds at a glacial pace. For most relevant geometries, doubling distance drops the rate of transport per unit time by a factor, not of two, but of four. Diffusive transport that would take a millisecond to cover a micrometer would require no less than a thousand seconds (17 minutes) to cover a millimeter and all of a billion (a thousand million seconds or 3 years) for a meter. Diffusion coefficient, the analog of conventional speed, has dimensions of length squared per time rather than length per time—it's not a rate in the ordinary sense.

Some organisms rely exclusively on diffusion to move material internally and to transfer it to and from their surroundings. Unsurprisingly, they're either very small or very thin or (as in many coelenterates and macroalgae) bulked up with metabolically inert cores. Diffusion coefficients in air run about 10,000 times higher than in water, which translates into a hundred-fold (the square root of 10,000) distance advantage. So under equivalent circumstances, those living in air or transferring gases (as do many arthropods) can get somewhat larger—perhaps one hundred-fold—but then still face that daunting size-dependence of diffusion. In response, one might say, macroscopic organisms inevitably augment diffusion with an additional physical agency, variously termed convection, advection, or just bulk flow, in any case fluid flow en masse. Circulatory systems as conventionally recognized represent only one version of this ubiquitous fix.

Indeed, the size scale at which life switches from reliance solely on diffusive exchange to convection supplementation—very roughly 10 micrometers—corresponds, roughly, to the switch from cellular to multicellular organization. While being essentially one- or two-dimensional does permit macroscopic size, it comes with obvious limitations. And while many plant cells, about which more shortly, do get comparatively large, they quietly practice intracellular bulk flow.

Solari et al. (2006) explore this transition point, using as material flagellated colonial green algae, mainly *Volvox*. In this genus, active cells populate the periphery of spherical colonies around 0.5 millimeters in diameter. The daughter colonies within (as in plate 1.1) depend on coordinated beating of the parental flagella on the outside of the colony to create enough external flow for adequate exchange of metabolites and wastes. Even at this relatively small size, flow plays an important role—in effect they have circulatory systems located around their external surfaces. Deflagellating colonies lowers photosynthetic productivity; providing forced external fluid motion (a bubbler in the suspension) restores normality.

One might expect good design to balance the two physical processes. Excessive reliance on diffusion would limit size, slow the pace of life, or require excessively surface-rich geometries. Excessive reliance on flow would impose an unnecessary cost of pumping (chapter 10) or require an unnecessarily large fraction of body volume for pipes, pumps, and fluid. So for biological systems a default ratio of convective transport to diffusive transport should be around one. As it happens, the chemical engineers provide us with just such a ratio. This so-called Péclet number, *Pe*, is a straightforward dimensionless expression:

$$Pe = \frac{vl}{D},\tag{1.1}$$

where v is flow speed, l is transport distance, and D is the diffusion coefficient. (Confusingly, a heat-transfer version of the Péclet number may be more common than this mass-transport form; it puts thermal diffusivity rather than the molecular diffusion coefficient in its denominator.)

Calculating values of the Péclet number can give us more than merely a way to check up on the performance of the evolutionary process. Often it can test hypotheses about the primary function of various features of organisms—"primary" in the sense of being most constraining on design. Perhaps that justification can be best put as a series of examples, which will follow after a few words about the origin of the ratio.

One can view the Péclet number several ways. The simplest sees it as the ratio of a convective or flow rate, v, to a diffusion rate, D/l. A slightly more formal version combines a simple numerator, mv, for flowing momentum, with a denominator that represents a simplified form of Fick's

first law for diffusive momentum transport, DSm/V, where S is cross-sectional area and V is volume. Taking l^2 as a crude proxy for area and l^3 for volume, one gets equation (1.1).

From a slightly different viewpoint, the Péclet number represents the product of the Reynolds number (Re) and the Schmidt number (Sc). The first,

$$Re = \frac{\rho l v}{\mu},\qquad (1.2)$$

where ρ and μ are fluid density and viscosity respectively, gives the ratio of inertial to viscous forces in a flow. At high values, bits of fluid retain a lot of individuality, milling turbulently as in a disorderly crowd; at low values, bits of fluid have common aspirations and tend to march in lock-step formation. In short, Reynolds number characterizes the flow. The Schmidt number,

$$Sc = \frac{\mu}{\rho D},\qquad (1.3)$$

is the ratio of the fluid's kinematic viscosity (viscosity over density, a kind of relative viscosity) to the diffusion coefficient of the material diffusing through it. It gives the relative magnitudes of the mobilities of bulk momentum (solution flow) and molecular mass (solute diffusion). In short, it characterizes the material combination, solute with solvent, that does the flowing and diffusing.

Of course the way we've swept aside all geometrical details puts severe limits on what we can reasonably expect of numerical values of Pe and should be kept in mind. Only for comparisons among geometrically similar systems can we have real confidence in specific numbers. Furthermore, we'll ignore the tacit requirement that, strictly speaking, diffusion and flow should be in the same direction. Still, because living systems vary so widely in size, even order-of-magnitude values should be instructive.

As a quick illustration of the way a value of the Péclet number can shed light on a problem, consider the way we all-too-often demonstrate diffusion for students. One drops a crystal of some soluble material whose solution is intensely colored into a container of water, and the class watches the spread of colorant through the container. Some years ago I wrote a short diatribe about the scheme in response to a published recommendation for its use (Vogel 1994a). I claimed that such demonstrations were fraudulent, that they relied on convection rather than diffusion for material transport, and in part based my case on Péclet number. Here's the argument, put more pointedly in the present context:

Imagine that one can notice diffusion in a liquid when it has transported something about a millimeter. Assume a diffusion coefficient of

10^{-10} meters squared per second, corresponding to a non-electrolyte with a molecular weight of about 100. In that case a flow speed of a mere 1 micrometer per second yields a Péclet number of 1.0 (eq. 1.1). So at any higher speed, convection will be a greater transport agent than diffusion. 1 micrometer per second—8.6 centimeters per day—that's a glacial rate in an unusually literal sense. Under no easily contrived circumstances can water in a fully liquid state be kept still enough to meet such a criterion!

Now for a few more biological cases where calculating a Péclet number might prove instructive.

Inside Jobs

The Sizes of Our Capillaries and Kidney Tubules

Consider our circulatory systems, in particular the size of the ultimate vessels, capillaries, where function depends both on diffusion and on flow. Do we make capillaries of the proper size—or, to be less judgmental, can we rationalize their remarkably invariant size? Efficient operation ought to be important. After all, we devote about 6.5 percent of our body volume to blood and expend about 11 percent of our resting metabolic power pushing it around. Apparently we do size them properly. A capillary radius of 3 micrometers, a flow of 0.7 millimeters per second, and a diffusion coefficient (assuming oxygen matters most) of 18×10^{-10} meters squared per second yield a Péclet number of 1.2. If anything, the value turns out a bit closer to 1.0 than one expects, considering its underlying approximations (Middleman 1972).

Of course nature might pick different combinations of radius and flow speed without offending Péclet. (We'll ignore the issue of the fit of red blood cells to capillaries by tacitly assuming an evolutionarily negotiable RBC size.) Smaller vessels would permit faster flow and lower blood volume, but the combination would (following the Hagen-Poiseuille equation) disproportionately increase pumping cost. Larger vessels would entail greater blood volume, the latter already fairly high, and slower flow, which would make the system less responsive to changes in demand. One suspects something other than coincidence behind the similarity of our relative blood volume, 6.5 percent, to that of an octopus, 5.8 percent (Martin et al. 1958).

Quite likely this choice of capillary size, based on Péclet number and some compromise of volume versus cost, sets the sizes of the other vessels of our circulatory systems in a cascade of consequences. According to Murray's law (LaBarbera 1990), the costs of construction and operation set the relative diameters of all vessels. Thus, a factor that sets vessel diameter at one level in their hierarchy ends up determining the diameters of all the rest.
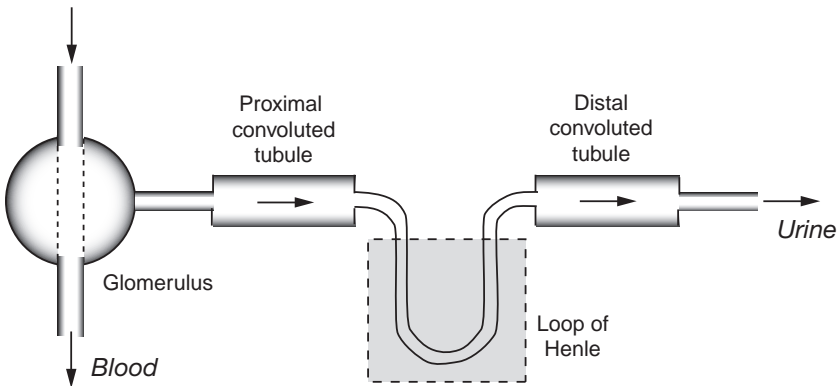
Figure 1.1. An unusually diagrammatic view of the filtration and reabsorption stages of most vertebrate kidneys.

The rule is a simple one—branching conserves the cubes of the radii of vessels, so the cube of the radius of a given vessel equals the sum of the cubes of the vessels at some finer level of branching that it supplies or drains.

What about the reabsorptive tubules of our kidneys, in particular those just downstream from the glomerular ultrafiltration apparatus (the "proximal convoluted tubules"), as in figure 1.1. We're again looking at a system that represents a far-from-insignificant aspect of our personal economies. Twenty to 25 percent of the output of the heart passes through this one pair of organs. About 20 percent of the plasma volume squeezes out of the blood in a pass, in absolute terms around 60 milliliters per minute per kidney. Each kidney consists of about 2 million individual units, the nephrons, operating in parallel. Thus each glomerulus sends on for selective reabsorption about 0.5×10^{-12} cubic meters per second.

The sites of the initial phase of reabsorption are these proximal tubules, each about 40 micrometers in inside diameter. Combined with the earlier figure for volume flow, that determines a flow speed of 0.40 millimeters per second. So we have speed and size. Diffusion coefficient can be assigned no single number, since the tubules reabsorb molecules from small organic molecules and ions to small proteins with molecular weights of around 40,000. Coefficients most likely range from about 0.75×10^{-10} to 40×10^{-10} meters squared per second. That produces Péclet numbers from 2 to 100.

At first glance these seem a bit high, but the story has another part. The calculation uses the velocity of the filtrate as it enters the tubules from the glomeruli. The tubules, though, reabsorb at least 80 percent of the volume of the filtrate, so by the time fluid leaves them, its speed has dropped by

at least a factor of 5. That gives exit Péclet numbers a range of 0.4 to 20, with an average in between—quite reasonable values, indicative (to be presumptuous) of good design. The cost of pushing flow through the tubules is low, at least relative to the power requirements of filtration and of the kidney's chemical activities. So one might speculate that the system is contrived to bias its Péclet numbers so they exceed one, albeit not by much, for most molecules over most of the lengths of the tubules.

The Sizes of Plant Cells and Algal Colonies

One can argue that the boundary between the cellular and the super- (or multi-) cellular world reflects the upper size limit of practical, diffusion-based systems. In short, for anything but exceedingly leisurely large-scale life to get above the typical cell size requires some kind of convective augmentation for moving material. That makes the cellular world a diffusion-based one and the supercellular world a convection-augmented one. I like the view because it tickles my particular bias toward physical determinants.

But I have to admit that it won't work for plant cells. On average, the cells of vascular plants run about ten times the size of animal cells, taking "size" as typical length. They are of the order of 100 micrometers in length if somewhat less in width, so 25 micrometers should be typical of the distance from cell wall to center. That increased size might have devastating consequences for transport were it not for the internal convection common to such cells. Put another way, in plants the size scale at which convective transport comes into play doesn't correspond to the sizes of plant cells.

That bulk flow system within plant cells goes by the name "cyclosis." We know quite a lot—but far from all—about how microfilaments of actin (a key component of muscle) power it, but here only its speed matters. That speed is around 5 micrometers per second (Vallee 1998). Focusing on oxygen penetration and using a penetration distance of 25 micrometers gives a Péclet number of 0.07. That tells us that the system remains diffusion dominated, that cyclosis doesn't reach a significant speed to make much difference to transport effectiveness. Looking at carbon dioxide penetration, with a diffusion coefficient of 0.14 meters squared per second, raises that number too little to change the conclusion. So why bother with cyclosis?

Perhaps we should take a different view. From size, speed, and a presumptive Péclet number around 1 we can calculate a diffusion coefficient of 1.25×10^{-10} meters squared per second. That corresponds to a non-ionized molecule with a molecular weight of about 6000. Thus plant cells appear diffusion dominated for dissolved gases, amino acids, sugars, and

the like. But they make significant use of (in effect, need) convection for moving proteins and other macromolecules, where molecular weights are in the thousands. In a sense, of course, that reliance on cyclosis bolsters the underlying argument about the practical size limit of diffusional systems.

Essentially the same picture emerges from a different (and much more sophisticated) analysis, one by Pickard (2006). The situation of an organelle provides the vantage point here. If stationary in the cytoplasm, diffusion limits its effective rates of absorption or secretion, but cyclosis even at 1 micrometer per second would produce sufficient convective augmentation to double transport rates. That point, $Pe = 1.0$, corresponds to an organelle size of 1 micrometer and a diffusion coefficient of 10^{-12} meters squared per second—a molecular weight of about 10,000,000. It establishes another transition point as well. For values below 1.0, flux increases with Pe^2, while for higher values, flux increases only with $Pe^{1/3}$. Pickard (2006) also provides an especially good entry into the nonbiological literature on Péclet number.

That boundary between cellular and multicellular worlds also receives scrutiny in the work on *Volvox* by Solari et al. (2006) that was mentioned earlier. Mature colonies apparently require flow for adequate growth of gonidia and the daughter colonies within their lumens. One might imagine that inverting each cell so flagella faced inward rather than outward would provide proper internal circulation—the equivalent of cyclosis. But the flagella also act as propulsive devices that move the colonies around, preventing sinking and enabling them to explore spatial variation in nutrient concentration. Still, putting them on the outside does help the situation. Augmenting flow around the outside assures minimal local depletion and gives internal diffusive transport a better starting point. The report gives Péclet numbers in the hundreds, but these take colony diameter as characteristic length. I think a more appropriate length for present purposes is that of the flagella, about 12 micrometers, the length over which convection and diffusion might well balance. Combining that with a swimming speed of 400 micrometers per second and a diffusion coefficient of 2×10^{-10} meters squared per second gives $Pe = 24$. So the system looks mildly convection-biased, which may offset the lack of internal flow and the resulting reliance of daughter colonies on diffusion within their parents.

Transport at External Surfaces

Sinking Speeds of Phytoplankton

Diatoms plus some other kinds of small algae account for nearly all the photosynthetic activity of open oceans. Paradoxically, most of these light-dependent phytoplankters are negatively buoyant most of the time.

Not that they sink rapidly; 4 micrometers per second (a foot a day, in antediluvian everyday units) is typical. According to one common explanation, such sinking improves access to carbon dioxide by minimizing the organism's own local depletion of dissolved gas. In effect, the cell walks away from its personal environmental degradation. Still better, it walks away without locomotory cost. Of course it (or its progeny) will eventually suffer, inasmuch as sinking takes it to depths at which respiratory demand exceeds photosynthetic rate. Somehow (and wave-induced water mixing comes into the picture) some organism-level cost-benefit analysis favors this slight negative buoyancy.

Calculating a Péclet number casts serious doubt on the notion of escape from local CO_2 depletion, doubt long ago raised (with an equivalent argument) by Munk and Riley (1952). From that sinking rate of 4 micrometers per second, the diffusion coefficient of CO_2, 14×10^{-10} meters squared per second, and as distance the 10-micrometer diameter of a typical diatom, we get a value of 0.03. So diffusion rules; convection, here due to sinking, will not significantly improve access to carbon dioxide. We might have chosen a larger distance over which CO_2 had to be transported to be available at an adequate concentration, but even a distance ten times greater would not raise *Pe* enough to pose a serious challenge to the conclusion.

Why, then, should a phytoplankter sink at all? The argument tacitly assumed uniform concentration of dissolved gas except where affected by the organism's activity. It left open the possibility that a diatom might be seeking regions of greater concentration, even lowering its sinking rate wherever life went better, something mentioned earlier when considering the much larger *Volvox*. In a world mixed by the action of waves, that's uncertain, although patchiness isn't unknown and (as appears the case) buoyancy does in fact vary with the physiological state of a cell. Perhaps phytoplankters bias their buoyancy toward sinking so they won't rise in the water column and get trapped by surface tension at the surface. If perfect neutrality can't be assured, then sinking may be preferable, provided the speed of sinking can be kept quite low—as it is. Surface tension may be a minor matter for us, but it looms large for the small. In the millimeter to centimeter range a creature can walk on it since the Bond number, the ratio of gravitational force to surface tension force, is low. A smaller creature may not be able to get loose once gripped by it; specifically, the Weber number, the ratio of inertial force to surface tension force may drop too far (Vogel 1994b). But risky surface entrapment presumes that the surfaces of these diatoms and other small organisms are fairly hydrophobic, which, I'm told, may not be the case. So another hypothesis would be handy—plus some experimental work on interactions of individuals with interfaces. Calculating Péclet, Bond,

and Weber numbers certainly raises a possibility that at least ought to be ruled out.

I should note that a somewhat different version of the Péclet number has come into use in studies of natural populations of phytoplankton. Instead of molecular diffusivity, it uses so-called eddy diffusivity, an effective diffusivity set by a combination of turbulent mixing (mainly) and molecular diffusivity (additionally). Values of D run around 10^{-5} to 10^{-3} (MacIntyre 1993) rather than the 2×10^{-9} and down for molecular diffusion in water. A useful paper with copious references is O'Brien et al. (2003).

Swimming by Microorganisms and Growing by Roots

We most often think of movement by active swimming rather than by passive sinking. Some years ago, Edward Purcell (1977), a physicist, wrote a stimulating essay about the physical world of the small and the slow, looking in particular at bacteria. Among other things, he asked whether swimming, by, say, *Escherichia coli*, would improve access to nutrients. (Yes, that's the full name of *E. coli*.) By his calculation, a bacterium 1 micrometer long, by swimming at 20 micrometers per second (see Berg 1993) would only negligibly increase its food supply, assuming it to be dissolved sugar. To augment its supply by a mere 10 percent, it would have to go no less than 700 micrometers per second. That's well above the fastest swimming speed I've encountered for a bacterium—about 140 micrometers per second for a free-living marine species, *Vibrio harveyi* (Mitchell et al. 1995).

Purcell's answer to the question of why swim at all turned on the heterogeneity of ordinary environments and the advantage of seeking the bacterial equivalent of greener pastures, as suggested above for diatoms. That rationalization, incidentally, receives support from a recent literature on a sort of micro-patchiness within macroscopically uniform liquid environments. Otherwise the bacterium resembles a cow that eats the surrounding grass and then finds it most efficient, not to walk, but to stand and wait for the grass to grow again.

The Péclet number permits us to cast the issue in more general terms. Sucrose has a diffusion coefficient of 5.2×10^{-10} meters squared per second; together with the data above we get a Péclet number of about 0.04. Swimming, as Purcell said, should make no significant difference. But the conclusion should not be general for microorganisms. Consider a ciliated protozoan, say *Tetrahymena*, which is 40 micrometers long and can swim at 450 micrometers per second. If oxygen access is at issue, the Péclet number comes to 10, indicating that swimming helps a lot. Indeed it might just be going unnecessarily fast, prompting the thought that it might swim for yet another reason—or reasons.

Growing roots provide a case just as counterintuitive as that of swimming bacteria but in the opposite direction (Kim et al. 1999). A root can affect nutrient uptake by altering local soil pH. Root elongation speeds run (perhaps an inappropriate word) around 0.5 micrometers per second, again down in the range of a glacier not yet goaded by global warming. But it turns out to constitute a significant velocity, enough so that (at least in sandy soil) the Péclet number gets well above 1. Taking root diameter as length, *Pe* values for rapidly diffusing H^+ ions may exceed 30. Thus motion most likely affects the pH distribution more than does diffusion in the so-called rhizosphere.

Flow Over Sessile Organisms

For sinking diatoms and swimming microorganisms we asked about why creatures did what they did. In some other situations we can test claims about the physical situations in which they live, in particular about local flows. How fast must air or water flow over an organism to affect exchange processes significantly? To put the matter in sharper terms, can calculating Péclet numbers help us evaluate a claim that extremely slow flow matters? After all, neither producing nor measuring very low speed flows is the most commonplace of experimental procedures so, at the least, cited speeds should be viewed with a skeptical eye.

For instance, consider the claim that a flow of 10 millimeters per second significantly increases photosynthesis in a green alga, *Spirogyra* (plate 1.2 left), consisting of threadlike filaments about 50 micrometers in diameter (Schumacher and Whitford 1965). Inserting the diffusion coefficient of CO_2 gives a Péclet number around 100 and suggests that far slower flows should also matter. Now one wonders about the opposite issue, whether so-called still water, the control in such comparisons, is still enough to achieve truly negligible flow. My own experience suggests that thermal convection and persistence of currents left from the initial filling of a tank can complicate attempts to prevent water from flowing. Still water doesn't just happen, and that may afflict laboratory investigations as well as classroom demonstrations.

Another paper reports that a flow of 0.2 to 0.3 millimeters per second, about a meter per hour, significantly increases photosynthesis in an aquatic dicot, *Ranunculus pseudofluitans* (Westlake 1977; plate 1.2 right). Its finely dissected, almost filamentous, leaves are about 0.5 millimeters across. A Péclet number of about 300 gives credibility to an otherwise eyebrow-raising report. One again guesses that even slower flows should be significant. The tables turn—one now becomes skeptical of any casual assumption of effectively still water in ponds and lakes.

A third paper (Booth and Feder 1991) considers the influence of water flow on the partial pressure of oxygen adjacent to the skin of a salamander, *Desmognathus*. The authors found that currents as low as 5 millimeters per second increased that partial pressure, facilitating cutaneous respiration. With a diameter of 20 millimeters, that flow produces a Péclet number of 50,000. Even assuming instead a 1-millimeter thick mixed regime at its skin gives a Péclet number of 5,000. A sessile *Desmognathus* may need flow, but it surely doesn't need much. Once again, the quality of any still-water control becomes important—something best checked, perhaps by watching a blob of colorant, before submitting a paper explicitly or tacitly assuming it.

Two Functions for Gills

Many aquatic animals both respire, exchanging dissolved gases, and suspension feed, extracting edible particles from the surrounding waters. Structures such as gills, with lots of surface relative to their volumes, can perform either function. While most suspension-feeding appendages may look nothing like gills, some not only look like gills but share both name and functions. No easy argument suggests that bifunctional gills balance their two functions. Quick calculations of Péclet number can tell us which function dominates a particular design and can thus point to the features that distinguish a respiratory gill from a dual-function gill.

Consider a keyhole limpet, *Diodora aspera*, a gastropod mollusk that uses its gills for respiration. With gill filaments about 10 micrometers apart, a flow rate of 0.3 millimeters per second (according to Janice Voltzow), and the diffusion coefficient for oxygen, the Péclet number comes to about 2. That's about as good as it gets for a respiratory gill. The dual-function gills of a bivalve mollusk, the mussel *Mytilus edulis*, contrast sharply. They have an effective distance of about 200 micrometers and a flow speed of about 2 millimeters per second (Nielsen et al. 1993). For oxygen access, that gives a Péclet number around 100. Clearly, mussel gills pump far more water than would be necessary were respiration the design-limiting function.

One can do analogous calculations for fishes, a few of which use gills for suspension feeding as well as respiration. A typical teleost fish has sieving units 20 micrometers apart (Stevens and Lightfoot 1986) with a flow between their lamellae of about 1 millimeter per second (calculated from the data of Hughes 1966). For oxygen transport, the resulting Péclet number is 5.5, not an unreasonable value for an oxygenating organ. One gets quite a different result for a fish that uses its gills for suspension feeding. While a somewhat higher 80 micrometers separates adjacent filtering

elements, the main difference is in flow speeds. Flows run around 150 millimeters per second for passive ("ram") ventilators (Cheer et al. 2001) and 550 millimeters per second for pumped ventilators (Sanderson et al. 1991). The resulting Péclet numbers, 6,500 and 20,000 (again using oxygen diffusion), exceed anything reasonable for respiratory organs.

Air Movement and Stomatal Exchange

All the previous cases looked at diffusion and convection in liquids. Of course the same reasoning should apply to gaseous systems as well—fluids are fluids, and diffusion and convection happen in both phases of matter.

Leaves lose or "transpire" water as vapor diffuses out though their stomata and disperses into the external air. Transpiration rates depend on a host of variables, among them wind speed and stomatal aperture, with this last under physiological control. Right next to a leaf's surface, the process depends, as does any diffusive process, on concentration gradient—here from the saturated air at the stomata to whatever the environmental humidity might be. The stronger the wind, the steeper the concentration gradient as the so-called boundary layer gets thinner.

Consider a bit of leaf 20 millimeters downstream from the leaf's upwind edge. Assume a wind about as low as air appears to move for any appreciable length of time, as my slightly educated guess, 0.1 meter per second. The effective thickness of the velocity gradient outward from the leaf's surface, δ, can be calculated using the semi-empirical formula (Vogel 1994b)

$$= 3.5\sqrt{\frac{x\mu}{v\rho}}, \tag{1.4}$$

where x is the distance downstream, and μ and ρ are the air's viscosity and density, respectively, 18×10^{-6} pascal-seconds and 1.2 kilograms per cubic meter. The thickness comes to 6 millimeters. (The datum must be regarded as the crudest approximation; among other things, the formula assumes a thickness that is much less than the distance downstream.) For that thickness, that wind speed, and the diffusion coefficient of water vapor in air, 0.24×10^{-4} meters squared per second, the Péclet number is 25. So even at that low speed, wind suffices to produce a convection-dominated system.

What might that tell us? For one thing, it implies that changes in wind speed should have little or no direct effect on water loss by transpiration. If water loss does vary with wind speed, one should look for something other than a direct physical effect, something such as changes in stomatal aperture. For another thing, it implies that a leaf in nature won't have adjacent to its surface very much of a layer of higher-than-ambient humidity.

So-called vapor caps are not likely to mean much with even the most minimal of environmental winds. It also rationalizes observations that changes in stomatal aperture area have considerable effects on transpiration rates—vapor diffuses through them, and in an otherwise convection-dominated process, diffusion becomes rate-limiting.

Growth and Development

Hydrodynamics and Growth

In a multicellular organism, developmental patterns depend on both genetic control and an organism's environmental situation, with a diversity of feedback mechanisms integrating the two. Where the environment appears to rule, one may have trouble separating direct physical effects from those mediated by active sensing and responses, linked by such feedback. But sometimes the value of a Péclet number can argue the case for direct action.

A particularly nice illustration comes from work on the accretive growth of stony corals. Like such other sessile animals as sponges, corals are suspension feeders, gathering food over their external surfaces. The effectiveness of feeding depends on overall form, whether of individuals, as in sponges, or of colonies, as in corals. And intraspecific form depends strongly on the local situation—particularly on currents around individuals or colonies. In the stony corals, colonies of branching forms from quiescent locations tend to have more open branches with thinner and, eventually, longer branches. By contrast, colonies of a given species subjected to higher average flows are considerably more compact and spherical.

One might expect the degree of compactness to track the Reynolds number of flow in the immediate habitat. But a series of simulations (Kaandorp and Sloot 2001; Merks et al. 2003) found that variation in Péclet number much better describes what happens. So flow—advection—relative to diffusion, not just flow per se, must be important. One might then wonder about the meaning of diffusion where the key items are motile microorganisms such as unicellular algae. These investigators found that they could use effective diffusion coefficients for such ingestibles, with values, figured from several starting points, well above those of even the smallest of molecules. For instance, the green alga *Chlamydomonas*, 10 micrometers in diameter, has an effective D of 5×10^{-8} meters squared per second, and a 1-millimeter mover, a D of 3.5×10^{-5}. So it looks as if an analysis based on Péclet number has value even under circumstances in which the variable might seem inapplicable. And a particular abiotic mechanism provides a sufficient (if not necessarily complete) explanation of quite a lot of morphological variation.

Another somewhat counterintuitive way the mix of diffusion and convection affects growth has been uncovered in nonmotile phytoplankton. These, of course, move passively with the surrounding water, eliminating an obvious role for local flow. Moreover, the flows in which they're embedded will be laminar rather than turbulent, simply as a matter of scale. The minimum size of a turbulent eddy depends on the rate of energy dissipation in a fluid and is described by the so-called Kolmogorov scale. For natural waters it runs around 1 millimeter, roughly the upper end of the size range of phytoplankton. Thus, they should see little if any of the cross-flow mixing concomitant with turbulence. But the strong local velocity gradients that they will experience will make them rotate and even cause such detrimental things as cell aggregation and cell destruction (Hondzo and Lyn 1999). The same local, small-scale flows can still facilitate growth by enhancing nutrient uptake—mainly when Péclet numbers exceed unity (Warnaars and Hondzo 2006).

Chemosensory Systems and Yet Other Possible Relevancies

Where else might calculations of Péclet numbers provide useful insight? We haven't considered, for instance, olfactory systems, either aerial or aquatic—in short, chemosensation in moving fluids. For these, I've found few relevant data. Several things have come up recently that suggest anything but the kind of match between convection and diffusion that we've been treating as in some way or another optimal. But that mismatch may be instructive.

A look at Mead (2005) or Woodson et al. (2007) will provide a good sense of what goes on, at least in relevant aquatic systems. Fishes most often detect dissolved odorants in a pair of chambers atop their heads, just behind their—to use the term figuratively—noses. By some mix of active pumping and hydrodynamic induction, in each water flows in an anterior opening and out a posterior one. Cox (2008) calculated Péclet numbers between 20 and 3,000, indicating severe biases toward convection. Decapod crustaceans do chemoreception with quite different machinery, locating the receptors ("aesthetascs") on their antennules, flicking these to improve effective contact with odor-laden water. (See, for instance, Mead and Weatherby 2002.) For crayfish, Kristina Mead (personal communication) calculates *Pé*'s in the thousands.

Perhaps two factors, in combination, underlie that bias. First, as Cox (2008) points out, the cost of pumping water should be insignificant relative to overall metabolic rates. Furthermore, pumping ought to reduce the lag time between encountering signal-carrying water and detecting the chemical information. And whether looking for prey or looking out for predators, response speed should be accorded very high priority.

Beyond chemosensation, one wonders about yet other systems. Might we usefully consider the speeds and distances of movement of auxins and other plant hormones? Might we learn anything by comparing systems in which oxygen diffuses within a moving gas with ones in which it diffuses in a flowing liquid? Here one thinks of systems such as, on the one hand, our alveoli and bronchioles (see, for instance, Federspiel and Fredberg 1988), the tubular lungs of birds, and the pumped tracheal pipes of insects and, on the other, the gills of fish, crustaceans, and the like.

The Sizes of Morphogenetic Fields and Synaptic Clefts

A variation of the Péclet number may provide insight into such things as the development of animals and characteristic biological times. Much of pattern formation depends on the diffusion of substances, morphogens, whose concentration gradients establish embryonic fields. Establishing larger fields not only means lower gradients (or takes higher concentrations of morphogens) but (for a given concentration) would take more time, a non-negligible resource in a competitive world. Breaking up velocity into length over time we get:

$$\frac{l^2}{Dt}. \tag{1.5}$$

(The reciprocal of this expression is sometimes called the mass transfer Fourier number.)

To define the limits of excessively diffusion-dependent systems, we might assume a value of 1. A typical morphogen has a molecular weight of 1000; its diffusion coefficient when moving through cells (a little lower than through water) ought to be around 1×10^{-10} meters squared per second. A reasonable time for embryonic processes should be a few hours, say 10^4 seconds. The numbers and the equation imply that embryonic fields should be around 1 millimeter across, about what we find. I think this basis for the embryonic field size (although put somewhat differently) was first argued by Crick (1970).

In effect, the calculation produces what we might consider a characteristic time for a diffusive process. Consider ordinary synaptic transmission in a nervous system. The most common transmitter substance, acetylcholine, has a molecular weight of 146 and a diffusion coefficient around 7×10^{-10} meters squared per second. With a synaptic cleft of 20 nanometers, the corresponding time comes to 0.6 milliseconds. That value matches cited values for overall synaptic delay, between about 0.5 and 2.0 milliseconds, consistent with the textbook attribution of much of the delay to transmitter diffusion.

That Diffusion Coefficient

So far, values of the diffusion coefficient have materialized ex cathedra. In practice, one obtains them just that way—by appeal to higher authority or whoever bequeaths us the appropriate tables. That larger molecules have lower coefficients needs no further emphasis; it does tacitly anticipate some proper formula. No such luck, at least for ordinarily reliable predictions, but quantitative guidance isn't completely lacking. Uncertainty comes from the dependence of diffusion coefficients (and mean free paths of molecules, on which they directly depend) on molecular shape, no easy thing to specify. The following formula gives a rough sense of how the coefficient varies with molecular (here as molar) mass, assuming that the diffusing molecules are spherical, that the solution is quite dilute, and that some other conditions hold:

$$D = \frac{KT}{6\pi\mu r} = \frac{KT}{6\pi\mu} \sqrt[3]{\frac{4\pi\rho N}{3m}}. \tag{1.6}$$

Here K is the Boltzmann constant, T the Kelvin temperature, μ the viscosity of the solvent, r the molecular radius, ρ the density of the solute material, N Avogadro's number, and m the molecular weight of the solute.

Put as a rule of thumb, the diffusion coefficient varies inversely with the cube root of the molecular weight of the diffusing substance. In practice we get our diffusion coefficients from empirical measurement and thence, by inference, some idea of molecular shape. Incidentally, diffusion coefficients for transport through living material such as muscle and connective tissue are anomalously low (Schmidt-Nielsen 1997).

In fields such as fluid mechanics and chemical engineering, dimensionless numbers are pervasive and of proven utility. Biologists have been slow to exploit them as tools, perhaps because our initial or sole contacts with physical science have been with physicists, who use them only rarely. Or perhaps because we've for so long focused on scaling relationships, with their irregular and ambiguous dimensions. Dimensionless numbers will turn up again and again in the chapters that follow, in part as my argument-by-example (as briefly in Vogel 1998) that they can help us see the relevance of physical phenomena to biological systems. Some, such as the present Péclet number, have been bequeathed to us by engineers (here mainly chemical engineers), and we needn't even redefine the variables. Others (the Froude number, for instance, which will appear in chapters 6 and 7) have traditional applications in engineering that we can, by such redefinition, put to quite different uses. We can generate still other

dimensionless ratios without great formality, bearing in mind that the ultimate—indeed, the only relevant—test is whether the number gives some useful insight, perhaps permitting us to discern general relationships that would otherwise remain obscure.

Dimensionless numbers provide tools that, for the most part, tell us what matters. Is a flow going to be laminar or turbulent? At a given speed will an animal of a certain size find it easier to walk or run? Or, as here, will convective or diffusive processes prove predominant, so one or the other can be ignored, or does one's system appear designed to take best advantage of each? These chapters will argue (again by example) that these ratios prove especially useful where systems encompass wide size ranges. In particular, by not having any apparent or concealed length dimension, they can avoid contamination of comparative numbers with the confusing effects of size per se.

Finally, who was this person Péclet? One does not normally name a number after oneself. Someone may propose a dimensionless index, and then the next person who uses it names it after the first. Or else its originator may name it for some notable scientist who worked in the same general area. Péclet number is a case of the latter. Jean Claude Eugène Péclet (1793–1857) was part of the flowering of French science just after the revolution. He was a student of the physical chemists (as we would now call them) Gay-Lussac and Dulong—names yet remembered for their laws—and a teacher of physical science. He did noteworthy experimental work on thermal problems and wrote an influential book, *Treatise on Heat and its Applications to Crafts and Industries* (Paris 1829).

Putting his name on a dimensionless number happened a century later, by Heinrich Gröber, in 1921, in another important book, *Fundamental Laws of Heat Conduction and Heat Transfer*. That thermal version of the Péclet number antedates the mass-transfer version used here. The latter, as far as I can determine, first appears in a paper on flow and diffusion through packed solid particles, by Bernard and Wilhelm, in 1950. They note its similarity to the dimensionless number used in heat-transfer work and call their version a "modified Peclet group, symbolized Pe'". They shift, confusingly and deplorably, from an acute accent in "Péclet" to a prime ('), now usually omitted, at the end. Analogous indices for thermal and material processes are not unusual since the underlying transport processes are either the same (as convection) or analogous (as diffusion and conduction). But most often the two carry different names—such as Prandtl number and (as earlier) Schmidt number. Amusingly, most sources mention one of the versions of the Péclet number with no acknowledgment that there is any other.