

Living in a physical world VIII. Gravity and life in water

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1. Introduction

Life was born in water, and aqueous habitats still hold most of life's diversity. The near-aqueous density of most organisms ensures something close to suspension by the surrounding water. A creature might be twice as dense as the medium but never, as on land or in the air, a thousand times as dense. Gravity? We might expect it to exert only a minimal impact on design and deportment. But that contrast in relative density between aquatic and non-aquatic life may mislead us.

As touched on in connection with the ascent of sap in trees in the last essay (Vogel 2006), gravity induces a change in hydrostatic pressure with height or depth of roughly $10,000 \text{ Pa m}^{-1}$, an atmosphere for every 10 m. How potent must that gradient be in oceanic water columns of hundreds or thousands of vertical meters! The hydrostatic squeeze will mercilessly compress a bubble of air or any other gas. Gases – pure or mixed – follow Boyle's law of 1662, the law that volume varies inversely with pressure. A bubble of air at a depth of, say, 10,000 m, that of deep ocean trenches, will have only about 0.1% of its volume at the surface – the 1000-fold pressure increase will result in a 1000-fold volume decrease. Unless the local water is air-saturated or the bubble is impermeably encapsulated, it will in short order redissolve, now a victim of Henry's law and Laplace's law, both of early 19th century origin. Henry's law declares that increased pressure leads to increased solubility of gases in liquids; Laplace's law (as we now know it) says that the smaller a bubble, the greater the internal pressure due to the squeeze of surface tension. Maintaining a gas under water thus bumps into the twin difficulties of depth-dependent volume (Boyle, augmented by Laplace) and dissolution rates (Henry).

That implies major effects of gravity on aquatic life. Again, we can easily be misled. What about a bubble of

some liquid, perhaps a vacuole of lipid? Or a cell, separated from the ocean by a lipid membrane? Or some solid material such as bone or chitin? For liquids and solids, no analogous rule links pressure and volume, and their responses diverge dramatically from that of a gas. Pressure increase produces almost no volumetric change. The descriptive variable here (lacking a general rule) is the bulk modulus, K (or its reciprocal, the compressibility). K is the ratio of change in pressure, Δp , to change in volume, ΔV , relative to original volume, V_o :

$$K = \frac{\Delta p}{\Delta V/V_o}. \quad (1)$$

Most liquids and solids have very high bulk moduli. It is often said that water is incompressible, but the implied infinite modulus is an exaggeration. Fresh water has a bulk modulus of about 2.1 GPa, seawater about 5% more (sources vary on the next significant figure). So seawater is about 4% denser at the bottom of a deep ocean trench than at the surface. These are ordinary values for liquids – the bulk moduli of pure hydrocarbons (octane, for instance) run about half water's value, but such oils as cells might put in vacuoles (vegetable oil, in one tabulation) differ little from water. Solids run one to two orders of magnitude higher, which is to say that they compress even less easily – glass has a bulk modulus of about 40 GPa and steel about 160 GPa. Even allowing for some pressure-dependent variation of values, in its hydrostatic manifestation gravity should matter little to either liquids or solids.

Pressure exerts slightly more influence on chemistry. At a depth of 10,000 m, altered hydrogen bonding of water increases its dissociation constant, 2.5-fold at 20°C, for instance (Hills 1972). Thus at extreme depths life faces significant – but not overwhelming – changes in buffering, protein configurations, membrane permeabilities, and so

forth. DNA is stable at up to ten times the 1000-atm pressure of that depth; while less barostable, proteins still denature only slightly at that pressure (Suzuki and Taniguchi 1972). By comparison, the fall in temperature with depth (and the lowered metabolic rates) causes substantially greater changes.

What about the surface of a pond or ocean, with air above and water below? Again, gravitational effects can range from profound to trivial. We know that a liquid's surface prefers to be horizontal and smooth. Gravity provides the main impetus for both, but smoothing involves another agency as well. Surface tension demands that work be done to create additional interfacial area, so it contributes another smoothing force. Disturbances of the smooth surface propagate as waves, and surface tension as well as gravity determines their behaviour. For water beneath air, surface tension sets the predominant rules for what we call "capillary waves," those with wavelengths below 17 mm. For instance, among these waves, shorter wavelength means faster rather than slower propagation. Before dismissing capillary waves as of relevance only to whirligigs and water striders, bear in mind that every big wave started small, with a wavelength at which surface tension ruled.

Nonetheless, most phenomena at the interface between sky and sea can be attributed to gravity. I mention their existence and note their importance before putting that interface aside for another occasion – here I mean to look only at what happens well beneath the water's surface. Even so, what follows must be recognized as an idiosyncratic selection of phenomena. No space will be given to density gradients caused by depth-dependent changes in temperature or salinity and thus to thermoclines and salt-wedges. Nor to the depth limitations of a chest-powered breathing snorkel, nor to the increasing effectiveness with depth of suckers such as those of an octopus. Attention will be limited to a few interrelated situations – problems of handling undissolved gases and of ballast and buoyancy control.

Of particular interest, as we will see, are the diverse instances in which submerged organisms maintain stores of air or other gases. They do so for either (on occasion, both) of two main reasons. For some, air breathers, what matters is the gaseous oxygen in the mix. Others use a gas to counteract body densities greater than that of the surrounding water – for flotation. Organisms may store gases internally, in cuttlebone and diverse bladders, or externally, as bubbles or body sheathing. Gas stores may be long-lasting or require periodic replenishment, the latter from secretion or transport downward from the surface. Only the shallowest and most turbulently moving water will be gas-saturated at pressures corresponding to their depths rather than contain gas equilibrated with the atmosphere above. Aquatic organisms containing gas can face Henry's law from either direction. Sometimes gas must be kept from disappearing into solution

lest an air breather sink or asphyxiate; sometimes gas must be kept in just such solution lest it tear up tissue or impede circulation. However, one categorizes the schemes, the possibilities are many.

A final prefatory note – in moving from the aerial and surface worlds of the previous essays, we need to shift from forces and accelerations to changes in pressures, volumes and solubilities.

2. Using surface tension to extract gases from water

Surface tension can provide the functional equivalent of waterproofing, doing the job well enough to prevent bulk gas loss from a bubble and leaving dissolution as the remaining concern. In my youth, I was taught that one could knot each leg of a pair of pants, wet the fabric, and use it, held upside down, as a float – not that I ever knew anyone driven to do it. (A pillow case needs no knots and provides an easy test of the device.) Either air or water passes through the pores in the fabric with little resistance, but the interface between them cannot do so, at least if the fabric contains no trace of a laundry-day surfactant. At least one spider, *Argyroneta aquatica*, uses an analogous air store. It makes its web within the submerged vegetation of ponds. An obligate air-breather like other spiders, it fills a silken bell, analogous to an old-fashioned diving bell, with air that it carries down from the surface. Periodically it adds air to the bell to offset both oxygen use and dissolution.

How fine a mesh must the web have to prevent escape of air, assuming (as seems to be the case) high hydrophobicity? Surface tension (0.073 N m^{-1} in fresh water at 20°C) keeps the air contained; hydrostatic pressure forces the air upward through the mesh. For a spherical shell whose radius of curvature is r and corresponding diameter is d , the pressure developed by surface tension (γ) is

$$\Delta p = \frac{2\gamma}{r} = \frac{4\gamma}{d}. \quad (2)$$

Hydrostatic pressure, of course, is simply

$$\Delta p = \rho gh, \quad (3)$$

where ρ is the density of water and h is the depth beneath the surface. Thus

$$d = \frac{4\gamma}{\rho gh}, \quad (4)$$

so the tighter the mesh (lower d), the deeper the spider can dwell. For depths up to 10 cm, the strands should be no more than 0.3 mm apart – not a particularly daunting requirement. [Alternatively one can set up a dimensionless ratio for the practicality of using surface tension to maintain air under water by dividing eq. (2) by eq. (3).] Neither its overall curvature nor the volume of air in the bell make a difference.

Thus for a given surface tension, density, and gravitational acceleration, depth and mesh size vary inversely with each other. Dissolution rate, of course, cares nothing about mesh size and will increase with depth; dissolution rate and the distance air must be transported downward probably limit the arrangement more than does web mesh. Schuetz and Taborsky (2003) note that these spiders seem bothered by excessive buoyancy when they bring air down to their bells, so they appear to pay for transport.

Many insects do much the same thing, if on a less impressive scale. Virtually all adult insects and many of their aquatic larvae, nymphs and pupae require access to gaseous as opposed to dissolved oxygen. Many hold air bubbles, periodically renewed by trips to the surface, in their various external irregularities – between body segments, beneath wings and elytra, and so forth.

A serendipitous physical phenomenon increases the persistence of such bubbles. Even in water that flows almost unnoticeably (Vogel 2004), solubility rather than diffusion coefficient determines how fast gases diffuse in or out of a bubble. And much less nitrogen than oxygen dissolves in a given volume of water (1.7% versus 3.5% by volume at 15°C and 1 atm; Krogh 1941). A bubble thus loses nitrogen more slowly than oxygen. Since air is mostly nitrogen (about 80%), the presence of nitrogen thus increases the persistence of a bubble compared to one of pure oxygen. In a classic experiment of Ege, in 1918 (cited by Thorpe and Crisp 1947), water bugs with air-filled bubbles could manage 7 h submergences. By contrast, bugs with bubbles of pure oxygen lasted only 35 min – oxygen consumption paled beside its outward dissolution, which rapidly decreased bubble size and hence effective surface area.

Could the respiratory depletion of an external air store be offset by net inward diffusion or some other device instead of periodic renewal at the surface? Harpster (1941) and Brown (1987) suggest that photosynthetically-produced oxygen might be acquired from aquatic plants, but no quantitative investigation seems to have been done. Still, we do know of at least two ways to compensate for outward diffusion and respiration. One depends entirely on surface tension and was established in a series of papers by Thorpe and Crisp (1947), the first of them being of greatest present interest; see also Thorpe (1950). The other, more unusual, depends primarily on a hydrodynamic effect and is a consequence of Bernoulli's principle. Stride (1955) showed how it works.

3. Surface tension and plastrons

First, let us consider the role of surface tension. It has long been known that a thin film of air covers some submerged adult insects, a layer conspicuous as a silvery sheen, much as one sees on a suddenly submerged leaf of nasturtium or lotus. Evidence for its respiratory role goes back at least to Comstock (1887), and Harpster (1944) proved that some insects could maintain the film without periodic replacement, at least in water with dissolved gases at atmospheric partial pressures.

The mechanism depends on the relationship expressed by eq. (2). Usually we apply the equation to bubbles convex on the outside – as they normally are. The smaller the bubble, the greater the component of pressure inside caused by surface tension. So tiny ones can spontaneously disappear as that pressure drives their gaseous contents into solution. For this thin film of air, or 'plastron' (Thorpe and Crisp

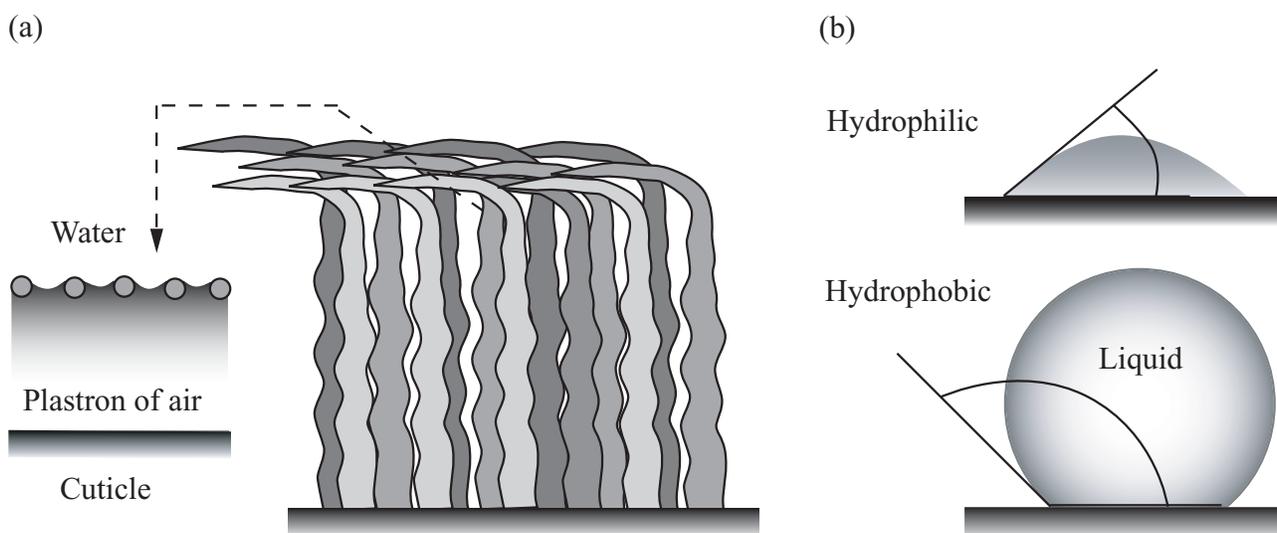


Figure 1. (a) Diagrammatic representation of a plastron; (b) contact angles for an aqueous liquid on hydrophilic and hydrophobic surfaces.

1947), one has to look at the implication of eq. (2) for a bubble of a seemingly unlikely geometry, one concave rather than convex on the outside. Smaller will now imply lower, not higher, internal pressure. With sufficiently small and numerous bubbles of this sort, enough oxygen could diffuse inward to supply an air-breathing animal's respiratory needs.

So submerged adult insects need a lot of tiny, concavely curved bubbles or else some kind of air layers characterized by interfaces with such curvature. They create such layers by coating themselves with air, forming air-water interfaces at the periphery of a dense layer of short, hydrophobic, cuticular hairs, as in figure 1a. In their initial report, Thorpe and Crisp (1947) estimated that *Aphelocheirus*, a naucorid bug, had about 2,000,000 hairs mm^{-2} – thus individual hairs less than 1 μm apart.

Using newer and better imaging equipment and the same species, Hinton (1976) revised that to 4,000,000 hairs mm^{-2} , with hairs tapering from 0.4 to 0.2 μm in diameter and extending 3 μm outward from the body. As in figure 1a, their distal portions are bent parallel to the surface, with little space between them. Treating the erect parts of the hairs as columns with the typical stiffness of arthropod cuticle (10 GPa) and assuming that a hair is vulnerable to Euler buckling, Hinton (1976) calculated that buckling such an array of hairs would require a pressure of about 40 atm. So the buckling strength of the hairs would impose a depth limit for use of a plastron of 400 m, which poses no problem for an entirely freshwater fauna. That hydrophobicity is less than perfect, so failure of surface tension restricts plastron use to lower hydrostatic pressures and thus shallower depths. Both Thorpe and Crisp (1947) and Hinton (1976) found that, in practice, plastrons break down through wetting at about 3 atm (above ambient pressure). Still, 3 atm corresponds to a depth of about 30 m, fairly deep by the freshwater standards of insects.

The relative role of the geometry of the outer part of the plastron and of its wettability remain uncertain. The usual measure of hydrophobicity is contact angle, that between the surface of a bubble and the surface it contacts, as in figure 1b; an angle of 180° would indicate perfect hydrophobicity. The hairs (and cuticle generally) cannot be perfectly hydrophobic – we know nothing that extreme. Contact angles for ordinary waxy coatings range between 105° to 110°, the range assumed in most calculations of plastron performance. Recent work, though, has shown that some biological systems achieve higher angles. The surfaces of the leaves of lotus and some other plants that have complexly sculptured waxy cuticles can reach 160° (Barthlott and Neinhuis 1997; Neinhuis and Barthlott 1997). A recently developed biomimetic super-hydrophobic coating, 'lotusan', (Sto Corp., Atlanta, GA, USA) is similarly and usefully self-cleaning. Of especial relevance here, Wagner *et al* (1996)

reported angles as high as 155° on insect wings, and Gao and Jiang (2004) reported an angle of 168° for the legs of a water strider – an insect for which high hydrophobicity should be particularly advantageous. These high values depend on surfaces with roughness of the same scale (Feng *et al* 2002) as the conspicuous bumps on the plastron hairs in Hinton's (1976) scanning electron micrographs.

Plastrons turn out to be widespread among arthropods and have undoubtedly evolved many times, perhaps because a hydrophobic exoskeleton with minute outgrowths represents nothing out of the ordinary and because no more diverse group of air-breathers occurs elsewhere in nature. They occur among eggs and larvae that suffer occasional floods (Hinton 1976), and they appear as well in some millipedes, mites, and whip scorpions (Hebets and Chapman 2000). I wonder about plant leaves, most of which have hydrophobic outsides and many of which have fuzz as well as stomata on their undersides (or on both surfaces), but I know of no data indicating any analogous functional arrangement. I also wonder whether diffusion alone can adequately transport oxygen to the spiracles through a gas layer only 3 μm thick or whether some additional physical device awaits recognition. (An earlier essay, Vogel 2005, raised the possibility of an analogous transport limitation within leaves.) Diffusion-augmenting bulk gas motion within the plastron might be induced by movement of an insect through the water or by such things as local water pumping by hindleg motion, the latter as reported by Harpster (1941).

4. Using flow to extract gases from water

Far less common than plastrons as a way to maintain air under water is flow-induced local pressure reduction. Only one case has been well documented, a few others remain conjectural; as we will see, all too few locations meet its physical requirements.

In addition to hydrostatic pressure, the surface of an object in a flowing fluid feels the pressures of that flow. The specific pressure on a location on the surface depends on its location. At some upstream point pressure is maximal, with a value that corresponds to the local hydrostatic pressure plus a component from conversion of the flow's kinetic energy to pressure. Bernoulli's principle gives the pressure increase (over the local hydrostatic pressure) at that point as

$$\Delta p = \frac{\rho v^2}{2}, \quad (5)$$

where v is the speed of flow before slowing by the object. Downstream, pressures are inevitably lower, with specific values determined by location and the object's shape.

These downstream pressures (Δp 's) are commonly expressed as their ratios to that maximum; the resulting dimensionless variable goes by the name "pressure

coefficient," C_p :

$$C_p = \frac{2 \Delta p}{\rho v^2}. \tag{6}$$

Thus a graph of pressure coefficient versus distance on the surface from upstream to downstream must always start at the y-axis with a value of $C_p = 1.0$, as in figure 2. In effect, pressure coefficients adjust pressures for the effects of speed and fluid density.

Not only does the pressure coefficient never reach 1.0 anywhere downstream, it drops below zero over much (usually most) of the rest of the body. The positive region turns out to be surprisingly limited, not even extending back to where the body is thickest. (For unstreamlined objects the pressure coefficient remains below zero back to the rear end, while for streamlined objects it gradually returns to positive territory, eventually approaching but not reaching 1.0.) Of present relevance, the overall pressure coefficient, integrated over the entire body, will almost always be negative; the particular value depends mainly on the body's shape. As a result, a bubble held stationary in a flow develops a net outward pressure coefficient. That coefficient ought to lie between about -0.1 and -0.3, with more negative

values for broader and less tapered bubbles. In short, the pressure inside will drop below the pressure outside (Vogel 1994).

(By integrating over the surface, taking local surface orientation into account, one can calculate drag, the downstream force on an object. Here we are concerned, instead, with transmural pressures.)

Here we see another way to extract gas from solution, a way whose operating range can be defined quite simply. Assume, as is common in rapidly moving, shallow water, saturation with air at atmospheric – or surface – pressure. If the flow-induced pressure drop in a bubble exceeds the local hydrostatic pressure increase due to depth, then the bubble should act as a gas extractor. The condition, then, for gas extraction, can be expressed quite simply by combining eq. (3) and eq. (6) as a ratio,

$$\frac{\Delta p_{flow}}{\Delta p_{hydrostatic}} = \frac{-C_p}{2} \frac{v^2}{gh} > 1.0. \tag{7}$$

(The minus sign on the right reflects the comparison of a pressure drop with a pressure increase.) Incidentally, the dimensional variables on the right form the Froude number, the ratio of inertial force to gravitational force, mentioned in

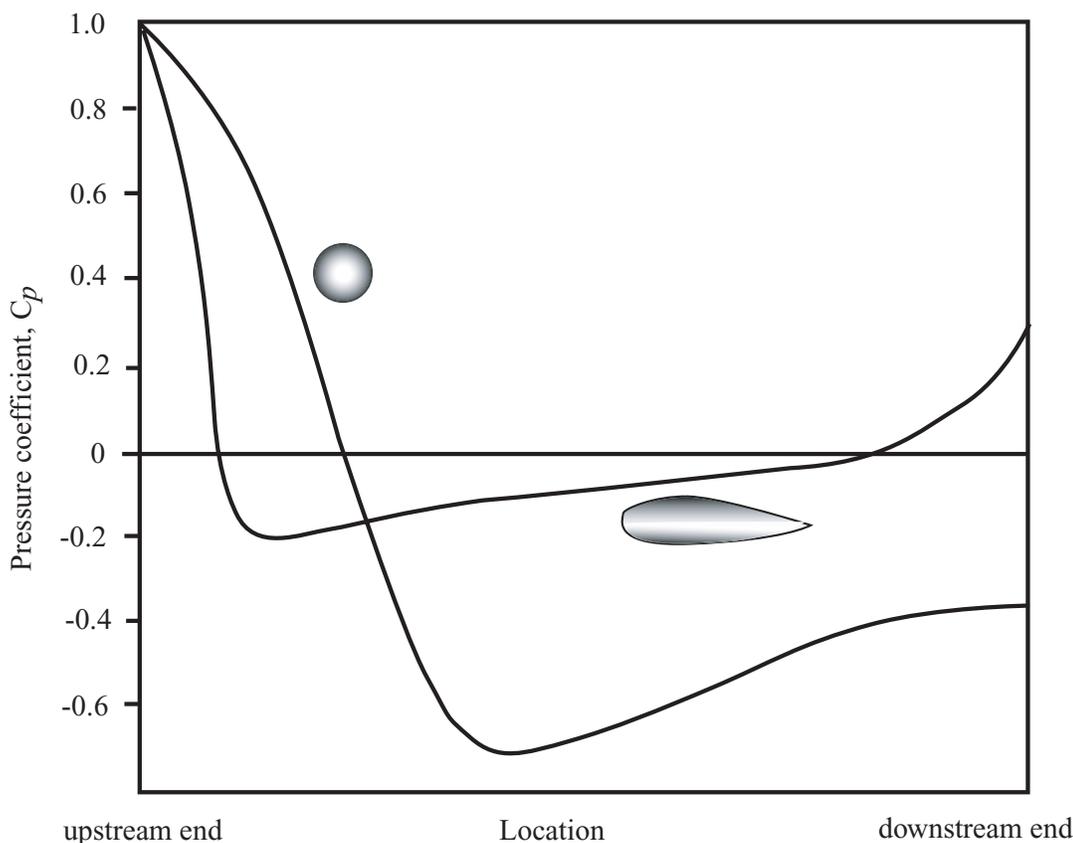


Figure 2. Pressure coefficient versus location on the surfaces of two objects – a sphere and a streamlined body of revolution. Both are about 40 mm in diameter. The data come from tests in air at 10 m s^{-1} and thus a Reynolds number (based on diameter) of 25,000.

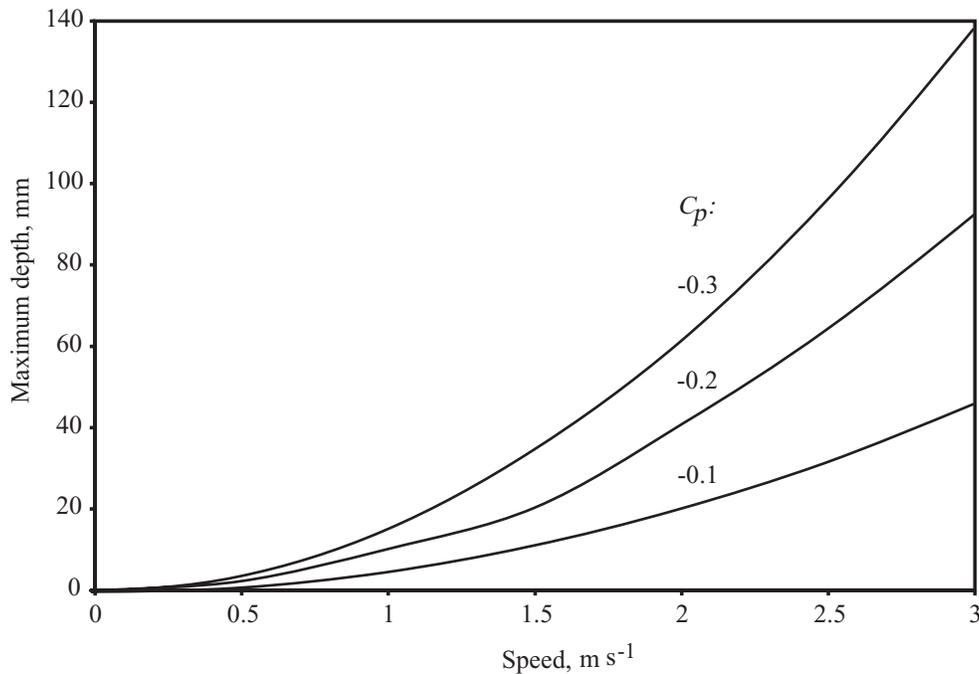


Figure 3. The maximum depth at which a bubble of air can be maintained by flow-induced gas dissolution for three different pressure coefficients. The water is assumed saturated with air at atmospheric pressure.

the previous two essays. Here it appears in the guise of flow force over hydrostatic force.

But eq. (7) defines a daunting condition. A bubble must be maintained despite the drag of the flow around it. And flow works far less effectively than surface tension as a pressure-reducer, at least when compared to surface tension acting across interfaces with minute radii of curvature. So the bubble must be held by an animal in the face of a substantial current, and it cannot be far from the surface. Figure 3 defines the limits for three possible pressure coefficients. It suggests that at a current speed of 1 m s⁻¹ a bubble could persist at depths between about 5 and 15 mm. Worse, given the inevitable velocity gradients near surfaces, an organism holding onto some solid surface may be exposed to a local flow substantially slower than that of the mainstream. Were it not for one well-documented case, we might dismiss the scheme as creative but impractical. That case, investigated by Stride (1955), merits some attention.

Working in Ghana, Stride (1955) noticed that adults of a particular kind of elm mid beetle, *Potamodytes tuberosus*, often “appeared to fly straight into the rushing water” of a rapid stream and then congregated on rocks just beneath the surface. Each faced upstream and carried “a large silvery air bubble”. In the laboratory, its bubble persisted indefinitely if – and only if – rapid, shallow flow enveloped the beetle. With some difficulty, Stride managed to measure the pressure within bubbles on restrained beetles subjected

to a range of flow speeds. At the test depth of about 10 mm, bubbles persisted at speeds above about 0.8 m s⁻¹.

I have reanalysed his data, extracting the flow-induced pressure reduction from the background hydrostatic pressure of 98 Pa (that 10 mm depth), and put his 34 points, in contemporary units, on figure 4. They do not correspond to a specific value of pressure coefficient: the faster the flow, the lower its apparent value. That must come in part from change in bubble shape with flow speed, as he notes; but changes in the air-water interface just above the beetles probably contribute as well. A linear regression nicely fits his data and as nicely misleads, implying, by extrapolation, an impossible flow-induced pressure drop of 69.3 Pa with no flow at all. Nonetheless, as the figure shows, the data do correspond to reasonable values of pressure coefficient, giving confidence in both his measurements and the present analysis.

Yes, the conditions may be daunting, but Stride noted that such beetles were common enough in his area, and Brown (1981) believes that beetles of the genera *Hispaniolara* and *Potamophilops* play the same game. Moreover, elm mids are not the only kind of riffle beetle. Adult riffle beetles use plastron respiration, so they already have spiracular connections to an outer store of air (Brown 1987). Furthermore, sub-surface photosynthesis (or dissolution of entrained bubbles from local waterfalls) can raise the partial pressure of oxygen beyond atmospheric level, which would allow a bubble to be maintained to greater depth – although Stride excluded

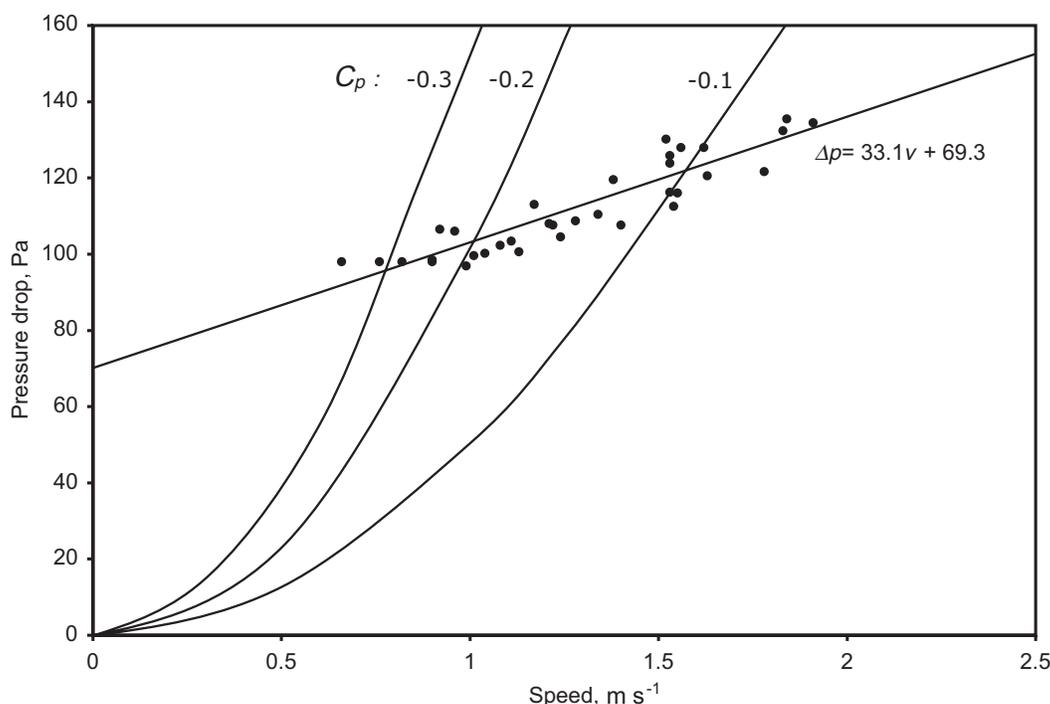


Figure 4. The pressure reduction caused by flow around a gas bubble – the predictions for three pressure coefficients and the measurements (points and fitted equation) by Stride (1955).

the possibility in his particular system. Finally, his beetles show no great anatomical adaptations, which implies both that such a trick can be done with behaviour alone and that lurking cases might easily be missed. Perhaps mere inattention explains why no others have surfaced in the intervening half-century. The composition of a diverse but globally consistent “torrential fauna” has been well-studied, although more with regard to who lives where than to any functional issues. The older accounts, especially Hora (1930) and Nielsen (1950), are still worth reading in any search for candidates.

Beyond the “plunge-and-grab-on” trick of *Potamodytes*, other ways of using current to maintain an underwater store of air must be possible. According to Pommen and Craig (1995), the plastrons of pupal net-winged midges (blepharicerid flies) produce bubbles that then persist in the low-pressure vortices behind their gills. Let me suggest yet another arrangement on the chance that it will either stimulate a specific investigation or consideration of still others.

The larval stages of many pyralid Lepidoptera (especially the Nymphulinae) are entirely aquatic, although pupae and adults typically live in air. In at least some genera – *Aulocodes* in northern India (Hora 1930) and *Elophila* and *Petrophila* (= *Parargyactis*, sometimes *Paragyactis*) in North and South America – the last larval instars spin tightly woven cocoons atop submerged rocks in rapids. The

pupa then rests on a shelf within the cocoon, as in figure 5. The space above the shelf is consistently and persistently air-filled, air of unknown origin as put by Nielsen (1950) and Resh and Jamieson (1988). All descriptions mention upstream and downstream holes that allow ingress and egress of water and flow beneath the shelf.

Since the openings are small and close to the substratum, I doubt if water flow through the cocoon would be rapid enough for oxygen extraction. But flow across the top could do the job. Pressure will be locally reduced by the velocity increase (shown in figure 5b as compression of streamlines) needed to bring water over the cocoon. Animals do use the locally reduced pressure as fluid flows over a protrusion for a variety of purposes – it has been shown in systems such as sponges (increasing flow for suspension feeding), keyhole limpets (increasing respiratory water movement), and giant termite mounds (increasing respiratory air movement) (Vogel 1994). Surface tension between air and water within the outer wall of the cocoon should add the equivalent of a plastron, one in which the lower pressures would permit a coarser mesh and weaker structure. Unlike the situation in an uncontained bubble, in a plastron a solid structure helps offset inward fluid pressure. That gives relevance to Lloyd’s (1914) comment that the outer walls of the cocoon “are spun of thick inflexible layers of silk.” Perhaps these lepidopteran pupae combine two mechanisms, the surface tension of plastrons with flow-induced persistent gas bubbles.

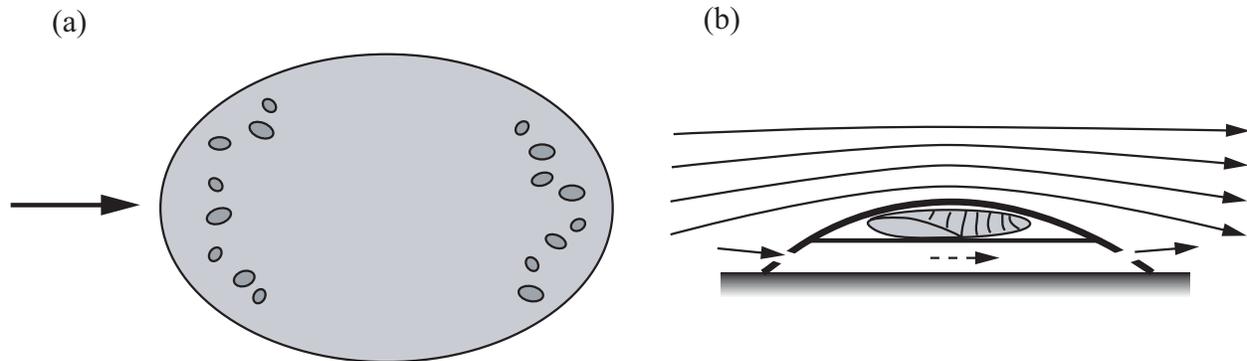


Figure 5. The cocoon (about 15 mm long) and pupa of a pyralid lepidopteran. (a) Top view of the cocoon, showing upstream and downstream openings. (b) A diagrammatic cross section of the cocoon, with the pupa resting on a shelf within an air-filled upper chamber (incorporating agreed-upon features from a variety of drawings and descriptions).

That raises the question of whether ordinary plastrons on insects that live in rapid flows take advantage of currents to reduce pressures still further than could surface tension alone – Pommen and Craig (1995) mention the possibility. My guess is that the effect, while inevitable, must be relatively minor except in very shallow water. After all, currents that an insect might encounter and withstand will generate at most a few hundred pascals of pressure, while unassisted plastrons can withstand pressures a thousand times greater.

5. Dealing with buoyancy

Gravity acts not so much on an organism's mass *per se*, as on the difference between that mass and the mass of the fluid that the organism displaces. While terrestrial organisms have densities much higher than that of the air around them, aquatic organisms differ little in density from water, and that displaced fluid cannot be ignored. Still, that difference varies from organism to organism and even, through both passive and active alteration, for a given organism over time.

Marine organisms without solid supporting materials have densities close to that of the surrounding fluid (around 1026 kg m^{-3}) and live in a weightless (although emphatically not massless) world. Minor adjustments in such variables as ionic composition can handle any residual weight (or buoyancy), often setting a slight downward bias. An equivalent freshwater organism can lower its density to that of the surroundings with a small body of one or another lipid, whose densities run around 900 kg m^{-3} . (Cholesterol, with a density of 1067 kg m^{-3} , cannot be used, while squalene, at 860 kg m^{-3} is especially effective.) Since lipids have about the same compressibility as water, buoyancy does not depend on depth.

Trouble can arise from either insufficient or excessive density. Thus the low densities of biological materials can hamper the ability of sedentary organisms to stay put as water flowing over them imposes both drag and lift or when

insufficient density limits locomotion by surface purchase at the bottom. The problem of insufficient density can be simply remedied by adding biosynthesized or environmental stony material to the system. For instance, various insect larvae (trichopterans, most notably) incorporate tiny pebbles into their cases. They reportedly use larger pebbles in swifter flows, although that may just be a result of differences in what they have at hand (Pennak 1978).

Still, one can recognize clear cases of deliberate density increase. A wide variety of air-breathing aquatic vertebrates, both fossil and living, swallow and retain stones ('gastroliths') to offset the buoyancy that comes with air-filled lungs – plesiosaurs, some crocodilians, some pinniped mammals, some penguins, and others (Taylor 1993). Marine gastropod and bivalve mollusks commonly have thick shells of calcium carbonate that at least on some occasions must help them hold position in currents. Sessile adult bivalves that lack specific attachment devices (such as the byssus threads that tie mussels to rocks) tend to be the ones with the thickest shells. One specific case may be instructive – a tiny surf clam (*Donax variabilis*) depends on staying near the substratum as wave swash or backwash moves it up or down a beach. According to Ellers (1995), its relatively thick and dense shell gives it an overall density of 1650 kg m^{-3} ; the densities of other bivalves, mostly larger, from the same beaches, range from 1170 to 1660 kg m^{-3} .

But density costs little in marine habitats, because sea water is usually either saturated or supersaturated with calcium, and because stones of greater density than calcium salts are common enough. The more aquatic mustelid mammals seem to have denser bones – but with ambiguous functional significance (Fish and Stein 1991). Good organisms for exploring functional increases in density might be the freshwater mussels – all shelled, diverse in size and flow speed preferences, and bottom-dwelling but not attached. Many, perhaps most, should be at some risk of dislodgement through sediment erosion during floods. One

encounters anecdotal statements about thicker shells beneath more rapid waters (as in Pennak 1978), but no systematic study that rules out some simple scaling rule for size versus density or shell thickness seems to have been done (M C Barnhart, personal communication).

Alternatively, the presence of solid supportive systems can raise densities enough to make pelagic organisms sink. Compensatory adaptations for increasing buoyancy seem to be more common than those for reducing it, perhaps because the macroscopic supportive systems of big animals usually reduce their buoyancy. (Hydroskeletons are the most widespread exception.) Bones and stony corals have densities around 2000 kg m^{-3} , mollusk shells of calcium carbonate (as calcite or aragonite) around 2800 kg m^{-3} , and crustacean exoskeletons of calcified chitin about 1900 kg m^{-3} (Wainwright *et al* 1976). In most groups, species with larger individuals devote a greater fraction of body mass to support – even, if less dramatically, in aquatic groups – so the problem gets worse with increasing size.

Some animals take a “brute force” approach, producing sufficient lift to offset their negative buoyancy while swimming uninterrupted. The paradigmatic examples are pelagic sharks. Lift comes from the combined action of asymmetrical caudal fins – larger lobes above than below – and a body pitched nose-upward. The fin asymmetry causes a downward tilt to the tail’s rearward force (29° below horizontal in a leopard shark), generating lift as well as the thrust needed for swimming. Trouble from the posterior line of action of that lift is offset by additional lift from a flattened head and upward body pitch (11° in a leopard shark), which has an anterior line of action (Wilga and Lauder 2002). Still, sharks minimize the need for lift with skeletons that are much less calcified than those of bony fish of similar size – ‘bony’ recognizes just that difference. And squalene (with an especially low density of 860 kg m^{-3} , as noted) makes up a large fraction of their lipid.

Squid, likewise, lack flotation devices to compensate for negative buoyancy, and they also make do with a minimum of stiff material. Their main skeletal element is a light, thin lengthwise ‘pen’ that keeps the upstream (posterior) end from bending when the jet gives a forceful squirt. Since it can direct its jet downward, a squid need not make headway to maintain enough lift, yet it must still work – hovering costs about twice as much as does resting, and almost as much as does normal locomotion (Webber *et al* 2000).

A few bony fish, members of an obscure group that lacks swimbladders, take the shark game a step further. These Antarctic notothenioids have bones with only a trace of ossification – the ashed skeletons weigh only around 0.4% of body weight rather than a typical 2%. And they are full of lipid, mainly triglycerides of about 930 kg m^{-3} , located subdermally and in intermuscular sacs (DeVries and Eastman

1978; Eastman and DeVries 1982). With near-perfect neutral buoyancy, they need produce no hydrodynamic lift.

6. Using gases at local pressure for buoyancy

Gases underlie the most space-efficient schemes for buoyancy augmentation since at ordinary pressures the densest gas weighs much less than the least dense liquid. At atmospheric pressure, air gives 700 times more buoyancy per unit volume than the best lipid, squalene; even at a depth of 1000 m, air (or, very nearly, oxygen or nitrogen) will be about 7 times better. And storing air will normally require a lower metabolic investment than storing lipids, whose synthesis is especially costly.

Several problems, though, come with that high volumetric efficiency and low cost. As already mentioned, the solubility of gases in liquids varies with pressure, so a quick reduction in pressure may bring dissolved gases out of solution – the origin of “the bends”, the name alluding to the stooped posture of human divers who surface suddenly: they suffer from painful gas bubbles trapped in their joints. We can equilibrate with local pressure at depths up to 100 m or so in a diving bell, caisson, or when using an aqualung. But we then need a slow ascent to allow time for dissolved gas to work its way out through the lungs rather than vaporize within our blood and other tissues. Of the gases in air, nitrogen makes the most trouble, partly because air contains so much of it – 80% by volume – and partly because of its substantial solubility in blood and tissues and its high solubility in body fat. Diving with helium works better since its lower solubility more than compensates for the rapidity of the diffusion of its smaller molecules into the body. Schmidt-Nielsen (1997) gives a particularly good account of the relevant physiology.

Nitrogen dissolution causes less trouble for diving animals than for us, mainly because they do not breath from tanks of air while deep underwater. So only gas already present in their respiratory passages can go into solution. And diving animals usually minimize that volume by exhaling before leaving the surface, tolerating the extra thoracic compression at depth that results. But not all do so. Penguins, conversely, inhale before diving; buoyancy demands that they work hard during the initial phase of descent. At least the buoyancy from air in their plumage and respiratory systems speeds upward gliding during the latter part of their ascents (Sato *et al* 2002).

That thoracic compression and the peculiar dynamics of descent and ascent in penguins brings us to the next problem. Gases compress all too readily, with volumes running almost exactly inverse with local pressure, in sharp contrast with the minor volume changes in other body constituents. Thus at only one depth can an organism containing air at local pressure be neutrally buoyant. Worse

yet is the metastability of that neutrality. Ascend, and the gas volume and thus buoyancy increases; descend, and buoyancy decreases. Putting the gas in a rigid container, as within our submarines, would solve the problem, but the necessary stiffness for the container's wall limits that route. Inextensible gas-filled bladders do serve many kinds of surface-living or rooted aquatic organisms, but these need only positive buoyancy above some minimal value. And being functionally inextensible takes only tension-resisting materials, which are relatively cheap to make and light in weight. Withstanding compression well below the surface (as elsewhere) is less easy than resisting tension – columns and beams cost more than ropes.

Consider the poor diving duck. It carries air in its plumage, so just beneath the water's surface it must struggle against excessive buoyancy. Deeper dives cost less to sustain – but reaching greater depth takes more time and energy, both precious resources for an actively swimming air-breather (Lovvorn and Jones 1991). A few birds such as anhingas have hydrophilic plumage and need deal only with internal gases. At the surface, the less buoyant anhinga swims with only neck and head exposed (hence 'snakebird', one common name) and with, one presumes, greater locomotory cost. In addition, it loses most of the insulating value of the plumage, restricting it to warm waters, and immediately after emersion it cannot readily fly (Hennemann 1982).

Most bony fishes maintain near-neutral buoyancy with a gas-filled swimbladder, either gulping air at the surface or (more commonly) secreting gas from circulating blood. Freshwater fishes have swimbladders that make up 5.5 to 8.3% of body volume, while the bladders of those living in the sea occupy 3.1 to 5.6% (Alexander 1966). For comparison, a pair of our lungs (our homolog of a swimbladder, incidentally) averages about 4% of our body volumes – even with their fine volumetric efficiency swimbladders are not tiny organs.

One can demonstrate the problem of maintaining buoyancy by putting a small goldfish in a large glass jar such a 40-liter carboy. Aspirate the air above the water even slightly and the fish rises abruptly and only slowly readjusts to the lower pressure. It may even belch a bubble (which will help readjustment) – goldfish have a connection, the so-called pneumatic duct, between swimbladder and esophagus. A fish that has readjusted to a lower pressure will sink when atmospheric pressure is restored, readjusting again after a short time. Readjustment offsets about a meter of depth (10,000 Pa) per hour (Fänge 1983). If you try the demonstration, do not use just any fish – only some, such as salmon, carp (including goldfish), pickerel, and eels, have pneumatic ducts. Others risk a ruptured swimbladder, which cannot be pleasant.

To put a few numbers on the problem, consider a neutrally-buoyant fish that lives near the surface and whose

swimbladder occupies 5% of its volume. If it descends to 10 m, pressure will double and the volume of the swimbladder will halve. As a result it will have a density about 2.5% greater than the surrounding water, enough for a bilaterally compressed body to sink further at an appreciable rate even when maintaining its long axis horizontal. If it descends to 90 m, pressure will go up 10-fold and swimbladder volume down by the same fraction, to about 0.5% of the body. Now 4.5% denser than the water, it will descend still faster. One need not consult a graph to recognize that the problem of depth metastability will be most severe near the surface. Abyssal fish should be able to ignore most depth-dependent volume change.

But how can a fish maintain a gas mixture in a bag at severely elevated pressures? The problem, the inverse of the outgassing of the bends, comes from the same high solubility of gases at high pressures. Blood with haemoglobin can transport a lot of oxygen for its volume, but it does so at a partial pressure no greater than that of the oxygen in the water that passes across the gills. Since the oxygen in deep waters has come either from the air above or from photosynthetic activities near the surface, it will be far below local saturation (partial) pressure. That strongly impels bladder oxygen to dissolve and diffuse into tissues and blood, thence to gills, and thence out to sea.

The solution (in both senses of the word) of fishes has two main components. First, fishes restrict the vascularization of the swimbladder to a tiny gas secreting gland, with thin layers of crystalline guanine that render the rest of the bladder almost completely impermeable to diffusing gas (Lapennas and Schmidt-Nielsen 1977). Second, they supply the gas gland with blood that has passed through a particularly efficient countercurrent exchanger – a device I described previously in connection with heat conservation (Vogel 2005). With such an exchanger, blood leaving the gland with dissolved gases at high partial pressures can lose gas, not to the gills and exterior, but to blood about to enter the gland. In effect, a bag containing oxygen (among other components) at very high partial pressure can be in diffusive contact with blood at nearly the same partial pressure rather than at the lower partial pressures of the ambient water, the gills, or elsewhere in the fish.

Nonetheless, some work does need to be done – a countercurrent exchanger can only minimize losses and secretory costs. The particular trick used by bony fishes consists of acidifying the blood in the gas gland with CO₂ and lactic acid. That reduces the haemoglobin's affinity for oxygen, driving oxygen into physical solution and increasing its partial pressure in the venous blood going from the gas gland into the exchanger. Even though the venous blood has less oxygen per unit volume than the arterial blood – some has passed into the swimbladder – its higher partial pressure means that net diffusion will move oxygen toward

the arterial blood. So oxygen will head back toward the swim bladder even as the blood that formerly held it goes gillward. (Bear in mind that solutions, unlike gases, have partial pressures, sometimes called ‘tensions’, that depend on solubility as well as fractional composition.) This version of an exchanger has been called a “countercurrent multiplier.” Schmidt-Nielsen (1997) again gives a succinct description, while Fänge (1983) supplies quantification and the details of the physiological chemistry. Again, the process still requires continuous work – clever machinery can only minimize the task.

7. Using gases at low pressure for buoyancy

In the ways they maintain buoyancy, as in so many respects, the cephalopod mollusks show us evolutionarily achievable alternatives to those of the animals of our own phylum. As noted earlier, squid, like sharks, make do with a minimum of stiff material and with continuous locomotory effort. More remarkable are the cuttlefish. They demonstrate that gas can be kept at pressures both much less than ambient and steady – circumventing both buoyancy loss due to gas compression and the metastability problem. And they do these things without sacrificing the ability to adjust gas volume.

While most bony fish put gas in a single chamber, cuttlefish put it in rigid foam – ‘cuttlebone’. With its small and rigid chambers, each about 0.1 mm wide and 0.6 mm high, cuttlebone represents much more material than does a swimbladder. But extracting its main material, calcium carbonate, from saturated seawater should cost little. The compartmentalization allows the cuttlefish to make a nearly incompressible float of lower density, about 620 kg m^{-3} , than that of any lipid, if somewhat denser than the gas plus swimbladder wall of a bony fish.

In a series of now-classic papers, Denton and Gilpin-Brown (1961 *et seq*) and Denton *et al* (1961) worked out how the system operates. Neither gas gland nor countercurrent multiplier plays any role. Cuttlefish balance the hydrostatic pressure difference between the surrounding water and the interior of the cuttlebone with a liquid (within part of it) that has an osmotic pressure below that of the blood. Since the liquid has a lower salt concentration than blood, water is drawn out of the cuttlebone osmotically with the same pressure as it is forced into it hydrostatically. As with a swimbladder, maintaining the system takes work – here the osmotic work of extracting Na^+ and Cl^- to keep the fluid hypoosmotic.

The organ as a whole must (and, of course, does) withstand the local hydrostatic pressure. The measured collapsing pressure, 24 atm, comfortably exceeds the hydrostatic pressure, about 15 atm, at the depths at which the animals live. Pet stores sell pieces of dry cuttlebone for caged birds, who sharpen their beaks on it, so one can

easily acquire a sample of this light, rigid, buoyancy tank. Its unusual mechanical properties have attracted attention from people interested in materials (Birchall and Thomas 1983; Gower and Vincent 1996).

We might compare different flotation media by calculating the fraction of body volume that each would require for a standard body density. If cuttlebone, with its density of 620 kg m^{-3} , makes up 9.3% of the volume of a cuttlefish swimming in seawater of 1026 kg m^{-3} (Denton and Gilpin-Brown 1961), then the rest of the body has a density of 1066 kg m^{-3} . Assuming that density for its body (excluding the gas in the swimbladder), a bony fish would need a swimbladder (containing essentially massless gas) of an internal volume of 3.9%, within the reported range. What if a creature used lipid for flotation – say fat or oil of 910 kg m^{-3} ? It would have to devote 27% of its volume to this anti-ballast. Even the best non-gaseous flotation material, squalene, would still occupy 20% of overall volume. While these amounts seem plausible (some fishes do contain large amounts of oil and small cetaceans have thick layers of fatty blubber), they amount to an energy investment comparable to that of all other body components combined. Moreover the investment cannot be cashed in during starvation without additional locomotory effort to prevent sinking.

8. Cartesian divers

The depth metastability that bedevils a bony fish and that a cuttlefish evades underlies a wonderfully clever device once well-known to physiologists. This manometric apparatus could measure such things as the rate of oxygen consumption of invisibly small organisms or their parts. Physicists have long recognized a “Cartesian diver” – even if Descartes should not be given credit for it. A ‘diver’, a floating body of minimally positive buoyancy, can be made to sink by applying a small pressure to a container of water. A version can be assembled from the simplest of everyday items, as in figure 6a, and something like it graces science classes at diverse educational levels.

Because of its fish-like metastability, one cannot easily make a diver that, unattended, neither sinks to the bottom nor floats to the top. While not the usual point of the demonstration, its incarnation as a measuring device depends on that metastability. As originally described by Linderstrøm-Lang (1937) and shown in figure 6b, a glass ‘diver’ exposed to the local pressure contains a small volume of air (and a respiring bit of life in water) and a droplet of oil as a pressure-transmitting seal. A larger, closed container of liquid (usually ammonium sulphate or lithium chloride to reduce gas exchange) envelops the diver.

Initially the operator holds the diver at some arbitrary depth in the container by manipulating the pressure within the container. If the specimen withdraws gas from the air in

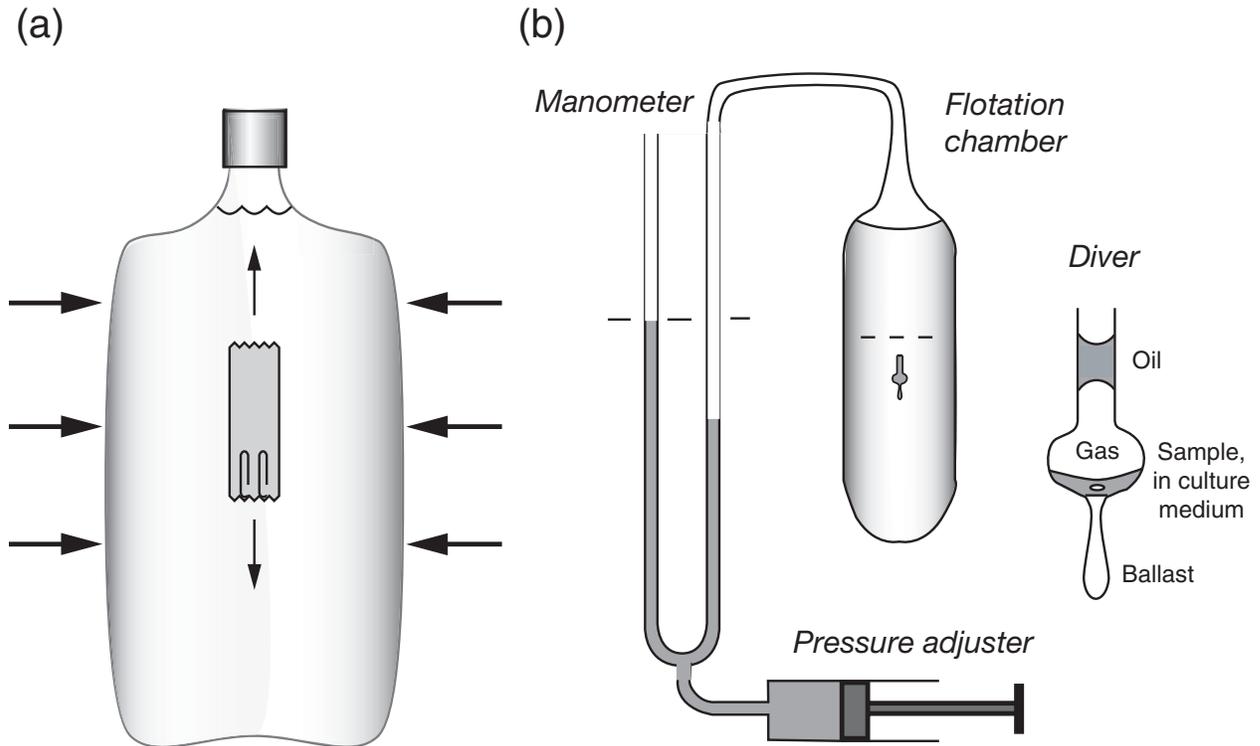


Figure 6. Cartesian divers. (a) One made from contemporary artifacts – a foil single-serving package of condiments ballasted just short of sinking with a few paper clips in a water-filled squeezable 2-liter plastic soft-drink bottle. (b) A diver used as a micro-respirometer, a simplified version of that described by Linderstrøm-Lang (1937). Today one would probably substitute an electronic manometer for the U-tube.

the diver, the diver becomes denser and plunges. Reducing the overall pressure will persuade the diver to return to the initial depth. Knowing that pressure and the initial volume of the gas within the diver then allows calculation of the volume of gas consumed. With a sensitive manometer, one indicating pressure differences of about 20 Pa, and with a good way to adjust pressure differences, a volume change of $2,000,000 \mu\text{m}^3$ ($2 \times 10^{-6} \text{ cm}^3$) can be measured. Zeuthen (1943) managed to increase its sensitivity to $2,000 \mu\text{m}^3$ and with it measured the oxygen consumption of single amoebae.

Some years later, Scholander *et al* (1952) improved the technique further, adding a reference diver for nulling the pressure and isolating the sample in a bubble whose volume could be measured with an ocular. This more complex version had yet greater sensitivity, about $200 \mu\text{m}^3$ – the volume of a sphere about $7 \mu\text{m}$ across or of a typical animal cell – good enough to measure the metabolic rate of still smaller cells. Per Scholander, of course, was the great master of manometry, both macro and micro – recall his device for measuring the extreme negative pressures in the vessels of

plants, described in the previous essay (Vogel 2006). These divers have not so much been superseded as shelved due to waning interest in what they could measure.

9. Gravity versus evolution

This extended consideration of the biology of gravity – three essays in all, with numerous facets left untouched – prompts one final note. Once established, we put theories or laws or definitive equations to two fairly distinct uses. Sometimes we ask that they explain phenomena in the world around us; sometimes we ask that they predict some future state of that world or the outcome of some deliberate manipulation. To explain is not necessarily to predict, and prediction need not depend on an intuitively satisfying explanation. Some theories do better at one task, some at the other.

Gravity, expressed as Newton's universal equation, does a splendid job of prediction. Our contemporary technology, especially in its larger manifestations, would be unthinkable without its reliable precision. But as an explanation, I think

it serves us poorly. Taken at face value, it requires that every bit of matter in the universe have some sense of the existence of every other bit of matter. Modern physics (so I am reliably informed) does not rely on such a metaphysical assertion, but its alternative explanation lacks intuitively satisfying persuasiveness.

Evolution, as defined by the concept of natural selection, has quite the opposite virtue. It does a fine job of explaining both the large- and the small-scale phenomena of life, including many subtle and even counterintuitive observations. It does make predictions, but their precision never approaches that of Newton's simple and succinct equation. The real phenomena whose futures we want to predict involve too many players, too much contingency, too much amplification of insignificant perturbations. This contrast plays a role both in determining the relative status of biology among the sciences and in fueling the criticism of evolution from some quarters outside the sciences.

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