Buoyancy in Deep-Sea Fish

The mass of an organism can be expressed in terms of its density (or mean tissue density) ρ and its volume V as:

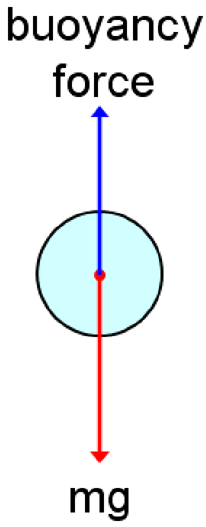
$m = \rho V$

and its weight can be expressed as:

$w = mg = \rho V g$

Where: g is the acceleration due to gravity.

If the animal is immersed in water then the force of its weight is countered by the buoyancy force. According to **Archimedes' principle**: fluid exerts an upward force on an object immersed in it equal to the weight of the displaced fluid:



Where the buoyancy force is given by:

$$F_{buoyant} = \rho_w V g$$

Where: ρ_w is the density of the displaced water.

The effective weight of an organism in water is thus given by:

$$w = Vg\rho - Vg\rho_w = Vg(\rho - \rho_w)$$

If the density of the organism, ρ, is equal to the density of the water, ρ_w, then the organism has no weight in water and is **neutrally buoyant**. Such an organism will float effortlessly in the water column. If, however, $\rho > \rho_w$, then the organism will tend to sink.

To counter this sinking, the organism needs to generate a minimum amount of lift, L, given by:

$$L = Vg(\rho - \rho_w)$$

One way to achieve this lift is to generate **hydrodynamic lift**. A swimming fish generates hydrodynamic lift by means of its pectoral fins acting as hydrofoils. The lift, L, generated by a hydrofoil is given by:

$$L = C \cdot S \cdot \frac{\rho_w}{2} \cdot U^2$$

Where:
S = surface area of hydrofoil,
U = speed of locomotion
C = lifting force coefficient

The lifting force coefficient depends on such parameters as the aspect ratio of the hydrofoil (the foil's span divided by its chord length, chord length is a measure of hydrofoil width, or equivalently span^2 / foil area) and also on angle of attack.

A long and narrow foil, i.e. one with a high aspect ratio, generates more lift for a given speed. For example, t he aspect ratio of the pelvic fins of tuna may be as high as 6. However, this high aspect ratio comes at the expense of maneuverability. For this reason many fish have much lower aspect ratios.

The other cost is the need to be moving to generate hydrodynamic lift and the energy cost of utilising pectoral fins as hydrofoils to generate hydrodynamic lift depends on the drag acting on the hydrofoils which increases with swimming speed. This metabolic energy cost, E_m, is given by:

$$E_m = 4L^2 / \eta \pi \rho_w U \lambda^2$$

Where:
η is the efficiency coefficient for the conversion of metabolic energy into mechanical energy and λ is the span of the hydrofoil.

One problem deep sea fish have this mode of generating lift is that food is scarce in the abyssal and hadal depths and temperatures are also typically very low, making it difficult to obtain the necessary energy.

Another way fish can generate lift is by increasing buoyancy by reducing mean tissue density. Many fish achieve this using a buoyancy organ such as a **gas bladder**. If V_b and ρ_b are the volume and density of the buoyancy organ, respectively, and V_s, ρ_s the volume and density of the rest of the fish's body, then in order to obtain neutral buoyancy (assuming $\rho_b < \rho_w$ and $\rho_s > \rho_w$) the following conditions need to be met (see: Randall and Farrell, 1997. Deep-Sea Fishes. Academic Press):

$$(V_S \rho_S + V_b \rho_b)/(V_S + V_b) = \rho_w$$

That is: the total density of the organism must equal the density of the surrounding water (note: $V\rho = m$);

$$V_b / V_S = (\rho_S - \rho_w)/(\rho_w - \rho_b)$$

That is: the volume of the buoyancy organ relative to the rest of the animal's volume increases as the density of the rest of the tissue increases (relative to water) and decreases as the density of the buoyancy organ decreases (relative to water) as expected. (This equation can be derived from the first by dividing by V_s and rearranging);

$$V_b /(V_S + V_b) = (\rho_S - \rho_w)/(\rho_S - \rho_b)$$

That is: the volume of the buoyancy organ as a fraction of the total volume of the animal increases as the density of the rest of the tissue increases (relative to water) and decreases as the density of the buoyancy organ decreases (relative to the rest of the animal). This last equation is less intuitive, but inserting some values (e.g. using $\rho_s = 2.0$, $\rho_w = 1.0$ and $\rho_b = 0.5$) to calculate $V_b / (V_b + V_s)$ (which is 2/3 in this case) demonstrates the correctness of this equation.

However, there is another problem to consider with gas bladders, which particularly affects deep-sea fish: the cost of excreting the gas to fill them. As depth increases, so does pressure and this pressure compresses the gases in the gas bladder, increasing ρ_b. This means that to maintain buoyancy the gas bladder must be larger. Increasing both the density of the gas within and the required volume makes gas bladders expensive to maintain at great depths. Increasing the volume also increases the drag on the fish, making it more expensive to swim.

Fish from the deepest waters have generally done away with gas-filled swim bladders and instead use other low-density materials to increase their buoyancy, such as lipids (fats and oils). Lipids may be stored in the swim bladder, in the bones, in cells of such organs as the liver, or in a variety of lipid sacs which appear to be modified lymph ducts. The skeleton is generally the densest parts and bones can be surprisingly dense in some fish (for although they don't need to support their weight on land they do need to support powerful swimming muscles). Many deep-sea fish have reduced their skeletal density and their muscle density to match. Muscle makes up the bulk of the tail of fish and the contractile proteins in muscle makes it quite a dense tissue. Many deep sea fish have watery muscles with low protein content. (This can also significantly facilitate oxygen diffusion across the muscle as in the haemoglobinless ice fish *Chaenocephalus aceratus* since proteins hinder oxygen movement).

Reducing muscle and bone is fine if you don't need to use these tissues as much. Consequently, many deep-sea fish are largely inactive ambush predators. This makes sense when prey is scarce: why waste energy searching for prey that is so hard to find? For example, deep-sea angler fishes may lay motionless in wait of potential prey lured to them by means of their bioluminescent lures. Powerful movements may only be required in a final lunge for prey or when escaping from danger. Low density bodies can indeed maintain their position in the water column with little energy expenditure. This energy economy helps compensate for the scarcity of meals at these depths and deep-sea fish may wait a long time between meals. The tendency towards low density bodies seems to solve a number of problems for deep-sea fish.