Life 22 - Respiration in Water - Raven & Johnson Ch. 53 (part)

Objectives

1: Understand the partial pressure of a gas in a mixture, and the properties of gases in solution

2: Describe Fick's law of diffusion and understand how the variables have altered as animals evolved more efficient respiratory systems

3: Understand how simple invertebrate, advanced invertebrate, and vertebrate respiratory systems maximize the rate of diffusion

4: Explain the principle of countercurrent exchange between water and blood across a respiratory surface

5: Understand how unidirectional flow of water is maintained across the fish gill by buccal and opercular pumps

Respiration in water
Seen the biochemistry of respiration - oxidation of organic molecules in the cells to release energy (saved as ATP). Oxygen as the final electron acceptor, carbon dioxide waste product

Now the physiology of respiration - process of uptake of oxygen and release of carbon dioxide by an organism - how oxygen reaches the cells from the environment, and carbon dioxide is excreted (also termed gas exchange)

Also use Schmidt-Nielsen, K. (1997). Animal Physiology. 5th edition. Cambridge University Press, if doing more animal physiology later

Need to distinguish clearly between:
Oxygenation - presence of molecular oxygen (in water, blood, haemoglobin etc). Oxygenated (with O_2) / deoxygenated (without O_2)

Oxidation - transfer of electrons (between atoms or molecules). Oxidised (lost e^-) / reduced (gained e^-), in cellular respiration

Properties of gases

Source of oxygen is the atmosphere, ultimately from photosynthesis. The prebiotic earth had an anaerobic atmosphere of methane, ammonia etc

Composition of air today is:

Oxygen	20.95%
CO_2	0.03%
Nitrogen	79.02%

Where "nitrogen" includes all the physiologically inert gases including argon (nearly 1%), helium & others. The open atmosphere has a very constant composition at all altitudes

Quantities of gases usually expressed as pressures, in millimetres of mercury (mmHg). At sea level atmospheric pressure is 760 mmHg, = 1 atmosphere (1 torr), or 101 kPa (kiloPascals, the SI unit)

Pressure of a gas in a mixture is the partial pressure. Equal to total pressure × the proportion of the gas in the mixture. Partial pressure of oxygen in air at sea level is thus $20.95/100 \times 760 = 159$ mmHg

Atmospheric pressure decreases with height above sea level in an exponential way. Every 6000 m of altitude halves atmospheric pressure, and partial pressures of each gas in the mixture, e.g. oxygen (Fig. 53.3)

Gases in solution
Gases are soluble in water. If water is exposed to a gas, molecules enter the water until equilibrium is reached between the numbers entering & leaving. This equilibrium depends on:

1: **<u>Solubility</u>**. The solubility coefficient α is the volume of gas in 1 L of water, in equilibrium with gas at a partial pressure of 1 atmosphere

Units of mL L^{-1} atm^{-1}. Solubility coefficients of the common gases in water at 15 C are:

Oxygen	34
CO_2	1020
Nitrogen	17

CO_2 is 30 times as soluble as oxygen in water. In fact there is more CO_2 in a litre of water than in a litre of CO_2 at any given pressure (i.e. $\alpha > 1000$)

2: **Pressure** of gas above the water. The amount of gas in solution is directly proportional to the pressure of the gas it is in equilibrium with (Henry's Law):

$$V_G = \alpha \times (P_G / 760) \times V_W$$

(P_G is the partial pressure of the gas in mmHg and V_w is the volume of water)

3: **Temperature**. Solubility decreases with increasing temperature. Oxygen content of water equilibrated with air at 1 atm:

0 C	10.3 mL L^{-1}
10	8.0
20	6.6
30	5.6

The oxygen content of fresh water in equilibrium with air at 1 atm thus decreases by nearly half from 0-30 C. Note different values to α above (34 mL L^{-1} atm^{-1}), which was for water in equilibrium with oxygen at 1 atm

The amount of gas in solution can be expressed as a concentration, in mL L^{-1}, or as a tension

The tension of a gas in solution is the partial pressure of gas which it would be in equilibrium with. A different term is used because gas does not exert a pressure in solution

Diffusion

It used to be thought that gas exchange involved the active absorption of oxygen and secretion of CO_2. This is now known to be untrue

The basic process in the movement of gases into and out of cells is diffusion. A physical process where gas molecules move down a concentration gradient

This may be helped by the bulk movement of the medium, e.g. breathing or blood circulation. But diffusion is the ultimate driving force for gas exchange

Fick's Law of Diffusion **$R = D \times A \times \Delta p / d$**

Where R is the rate of diffusion; D is the diffusion coefficient;
A is the area, Δp the concentration difference, and d the distance, over which diffusion takes place

D is a constant for a given gas and medium. The rate of diffusion of oxygen is 300 000 times slower in water compared to air for the same gradient of partial pressure/tension

And in water the rate of diffusion of CO_2 is 25 times faster than that of oxygen for the same gradient of tension

R can be increased by increasing the area **A** or the concentration difference Δ**p**, or decreasing the distance **d**

A small animal can rely on diffusion at the body surface for gas exchange. Unaided, this is adequate for a distance up to about 0.5 mm (Fig. 53.2a), so single-celled organisms need no special adaptations for respiration

Multicellular animals need other mechanisms. Simplest is to improve water movement across the body surface, e.g. by cilia. This maintains the concentration difference Δ**p**, e.g. in planarians (Platyhelminthes)

Larger animals have proportionately smaller surface area in relation to their mass, and must use respiratory organs to increase the area **A**, and internal circulation to reduce the diffusion distance inside the animal **d** (Fig. 53.2b)

These are of 3 main types:
1: Gills - projections from the body (Fig. 53.2 c,e)
2: Lungs - cavities within the body (Fig. 53.2f)
3: Air capillaries - in insects (Fig. 53.2d)

Respiration in water
Compare systems in different animals to see the general principles, firstly fish, have the most efficient respiratory system in nature

Mouth or buccal cavity has perforated walls, between the gill arches. The operculum covers the gills and forms a second chamber, the opercular cavity (Fig. 53.4)

Water enters the mouth, flows between the gills, and out behind the operculum. Valves at the mouth and operculum prevent back-flow, i.e. out of the mouth or in behind the operculum

Gill filaments are a stack of thin plates projecting from the sides of the gill arches. Smaller plates or lamellae project above and below the filaments. Lamellae contain capillaries, and are the site of gas exchange (Fig. 53.5)

Distance between the lamellae is about 20 μm, so the maximum diffusion distance **d** in the water is 10 μm (1/100 mm). This close spacing is a consequence of the slow diffusion of oxygen in water

If the lamellae were more widely spaced, water flowing midway between them would not give up oxygen to the gill, and the energy cost of moving this water would be wasted

Slow diffusion also means that the water over the gill must be changed frequently. Otherwise, a boundary layer of deoxygenated water would develop next to the gill

Water is pumped over the gills by muscular action of the buccal & opercular cavities. Look at the pressure changes in both cavities over two pumping cycles (Schmidt-Nielsen Fig. 1.10)

A complex pattern. The important point is the net pressure gradient across the gills (buccal ⇒ opercular). This is positive through most of the cycle, so water passes in one direction, not reversed

There is a brief period when the pressure gradient is reversed, but the high inertia of water keeps it flowing in the same direction

Two pumps - buccal & opercular cavities - act together to form a single pumping system, with the mouth & opercular valves. Simplified diagram of the system (Schmidt-Nielsen Fig. 1.9)

A: Buccal cavity has negative pressure, water enters mouth. Opercular cavity has even more negative pressure, pulls water through gills from the buccal cavity

Opercular valves close to stop direct entry of water from the outside. The system is acting as a suction pump. Position A on pressure graph

B: Opercular cavity has positive pressure, water is expelled through the operculum. Buccal cavity has higher positive pressure, pushes water through the gills into opercular cavity

Mouth valves closed to stop water being expelled through mouth. The system is acting as a pressure pump. Position B on pressure graph

Combination of the two phases gives continuous flow across the gills, although water only enters the mouth or leaves the operculum intermittently

As water flows in one direction only, there is the possibility for blood to flow in the opposite direction, with the advantage of countercurrent flow

As blood is about to leave the lamella, it encounters water which has had no oxygen removed, and the oxygenation of the blood can reach the highest possible level (Fig. 53.6)

As water passes across the lamella, it meets blood with lower and lower oxygen content, and can still give up oxygen to the blood

The whole length of the lamella takes up oxygen from the water, and 80-90% of the oxygen may be extracted. Blood leaving the gill has much more oxygen than water leaving the gill

Compare with parallel flow of water and blood. The maximum possible extraction is 50%, when the blood and water leaving the gill have the same oxygen tension

High extraction efficiency is a great advantage because of the high energy cost of pumping water, because of water is dense and has a low oxygen content. Ventilation accounts for 5-10% of the energy used by a fish at rest

Molluscs

The primitive pattern is a number of pairs of gills in the mantle cavity. Each gill has many lamellae, triangular plates on a supporting axis, one on each side of the gill. Skeletal rod prevents deformation of the lamella (OHP Figure)

Water currents over the gill are produced by cilia, and flow is continuous in one direction; more advanced molluscs have separate inhalent & exhalent siphons

Gill has afferent ("to") and efferent ("from") vessels, and blood passes between these through indistinct channels in the lamella. Blood flow is countercurrent to that of the water

Echinoderms

Sea urchins use tube feet, connected to a hydraulic system - the water vascular system. Most specialised are the heart urchins, which have sheet-like tube feet on the dorsal surface, form the 5-pointed star (OHP Figure)

Tube feet act as a double countercurrent exchanger; between the seawater and the water vascular system, and then with the coelomic fluid. The currents are produced by cilia

Mollusc & echinoderm systems similar in principle to fish, but use cilia instead of muscles to produce the water current. Three general principles of gas exchange across gills in water:

1: It is necessary to maintain a flow of water over the gill because of the slow diffusion of oxygen in water

2: It is efficient to keep this flow in one direction, because of the high density of water and high cost of reversing flow

3: One-way flow of water can be coupled to a countercurrent flow of blood through the gill for maximum extraction of oxygen