THE RELATION OF RESPIRATION OF FISHES TO ENVIRONMENT—A REVIEW

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In this paper there will be an attempt to review certain work that has been done on the physiology of the respiration of fishes in relation to the environment. The original work will be found in *The Relation of Respiration of Fishes to Environment, Ecological Monographs,* Vol. 2, pages 385 to 473, 1932, by Edwin B. Powers, *et al.,* together with bibliography. The original data will not be given but will be discussed and summarized.

All animals are aquatic as far as their respiration is concerned. Gills and other structures functioning in gaseous exchanges in aquatic animals are bathed with water; and lungs, trachæ, book-lungs and other structures functioning in gaseous exchanges in terrestrial animals have membranes always kept moist, that is, covered by a fluid. Thus, gaseous exchanges in all animals, including protozoa—and in plants as well—are essentially the same in every detail. In all cases the gaseous exchange is by the process of osmosis; the rate and direction follow the laws of diffusion of gases through permeable membranes.

There is an essential difference in the morphology of the respiratory organs of lung and gill breathers. The alveolar space of lungs is more or less a closed system. The gills of gill breathers are more or less continuously exposed to the water and thus form a more or less open system. Apparently fishes have no means by which they can control the gaseous tensions to which their gills are exposed. This is determined by the gaseous tensions of the water in which the fishes are living, being, perhaps only slightly altered by the rate of bathing the gills with the water. Since there is no definite relation between the oxygen and carbon dioxide tensions of natural waters, fishes living in different waters experience entirely different oxygen and carbon dioxide complexes.

In lung breathing animals, the actual oxygen partial pressure of the alveolar air at any given time is determined by the barometric pressure and the rate and depth of respiration as modified by the rate of oxygen utilization. The carbon dioxide partial pressure of the alveolar air is determined by the rate of carbon dioxide production by the body and the velocity of ventilation of the lungs. The actual carbon dioxide partial pressure is in reality controlled by the alkali in use in the blood at any particular instant, which in turn is controlled by the oxygen pressure of the habitat. That is, the oxygen and carbon dioxide partial pressures of the alveolar air and the

blood as a physico-chemical system are interreciprocal and the three as opposing forces tend to reach equilibrium, *i. e.*, a dynamic-equilibrium. We may call this a physiological-dynamic-equilibrium. Since gill breathers are not able so well to control the oxygen and carbon dioxide tensions of the water bathing their gills, the greater burden of adjustment is placed upon the blood as a physico-chemical system. This physiological-dynamic-equilibrium merely means that an organism is able, within limits, to maintain an adjustment of its internal and external environment.

It has been determined that, at least in the blue cat (*Ictalurus punctatus*), the volume per cent of carbon dioxide of the (venous) blood increases with an increase in the oxygen content (tension) of the water and *vice versa*, and also with an increase in the carbon dioxide tension of the water and *vice versa*. The oxygen volume per cent of (venous) blood increases with an increase in the oxygen tension of the water and *vice versa*. No obvious relation between the oxygen volume per cent of the blood and the carbon dioxide tension of the water has yet been shown; however, a relation is suspected.

There is a definite relation of the number of red blood corpuscles to the oxygen tension and to the carbon dioxide tension of the water. The number increases with a decrease in the first and with an increase of the second and *vice versa*.

The oxygen and carbon dioxide dissociation curves of fish blood, as has been shown by various workers, are essentially the same as those of mammalian blood. There are certain obvious characteristics in the behavior of fish blood in its relations to carbon dioxide tensions. Fish blood reaches its isoelectric point at a very low carbon dioxide tension (from about .2% to .4% of an atmosphere) after which there is an increased affinity for oxygen with an increase in the carbon dioxide tension. However, very quickly a carbon dioxide tension (apparently about 1% to 1.6% of an atmosphere) is reached when the blood again loses its affinity for oxygen with increase in carbon dioxide tension. These characteristics are only apparent and not essentially different from mammalian blood. This is obvious when it is remembered that the carbon dioxide tension of natural waters in which fish live normally approximates .035% of an atmosphere and not 5±% as found in alveolar air. Two-tenths per cent to four-tenths per cent carbon dioxide is approximately ten times normal for fish blood. This, according to all formulæ used in calculating the p_H of blood, would mean approximately a decrease of 1 p_H in the blood. Human blood has been shown to reach its isoelectric point when passed over about the same range.

On the other hand, there are certain characteristics which are peculiar to fish blood. However, these on further investigation might again prove only apparent. First, blood when exposed to carbon dioxide partial pressures higher than normal, actually lowers its alkali reserve. This has been shown in two ways. The blood when

in equilibrium with atmospheric air has a lower pH and has a lower carbon dioxide content, provided it has first been exposed to a carbon dioxide partial pressure higher than normal. Second, the blood at carbon dioxide tensions higher than normal actually loses in its capacity to combine with oxygen. In certain sea-water fishes, this loss is as great as 75% of the original oxygen-loading capacity. From a few preliminary experiments, the indications are that the capacity of the blood to load oxygen is at least partially regained when its carbon dioxide tension is again reduced to normal. The physiological advantages of these characteristics of the blood will be more apparent when the mechanism of the deposition of gases into the swim-bladder is considered.

It has been shown as far back as 1807 that oxygen was generally present in closed swim-bladders at percentages higher than present in atmospheric air, and that the percentages of oxygen increased with increase in depth at which the fish is found. It was also known that the deposition of all gases could take place against the enormous pressures at which deep sea fishes live. As long ago as 1896, it was known that the inert gases were present in the swim-bladder of these fishes in the same proportion as in atmospheric air, although at much higher partial pressures.

There is a rete mirabile and gas gland present in the walls of the swim-bladder of fishes that are able to deposit gases at all rapidly into their swim-bladders. The fundamental mechanics of the rete mirabile gas gland relations can be described as parallel arteries and veins which are split up into a large number of capillaries, the rete mirabile, in which the capillaries of the arteries run parallel to the capillaries of the veins. The capillaries of the veins and those of the arteries always approximate each other and are intercalated with the most astonishing regularity. At the end of the rete mirabile proximal to the gas gland the arterial and venous capillaries again form into arterioles and venules and arteries and veins. These are united by arterioles to epithelial capillaries in the gas gland. These in turn lead to venules and back to capillaries of the rete mirabile. A conception of this mechanism can be gained by referring to the diagram (Fig. 1).

The arterial blood which has been brought into equilibrium with the carbon dioxide and oxygen tensions of the water enters the rete mirabile. It is then distributed among the very large number of capillaries of the rete mirabile. The blood is then gathered up by arterioles to arteries and again distributed into arterioles and then into the capillaries of the gas gland. Here the carbon dioxide tension of the blood is brought to approximate that of the carbon dioxide partial pressure in the swim-bladder, which is generally if not always higher than the carbon dioxide tension of the arterial blood. The oxyhemoglobin will then give up a large part of its oxygen. The blood being in a closed system with surroundings having a metabolism almost nil, the excess oxygen must go into solution in a plasma

already in equilibrium with the external oxygen tension of the water. This automatically raises the oxygen tension of the blood. The oxyhemoglobin ratio is higher than it would have been had the oxygen tension remained constant. This excess oxyhemoglobin constitutes a potential back pressure against the carbon dioxide. This and the characteristic of the blood to lose a part of its alkali reserve at higher carbon tensions[1] in turn raise the tension of the carbon dioxide, which in turn lowers the oxygen-loading capacity of the blood. This further increases the oxygen tension of the blood plasma. The blood with its augmented oxygen and carbon dioxide tensions is carried to the venous capillaries of the rete mirabile. The excess oxygen and carbon dioxide will diffuse from blood in the venous capillaries to the blood in the arterial capillaries. By continuous circuits (see Fig. 1) of the oxygen and carbon dioxide from the
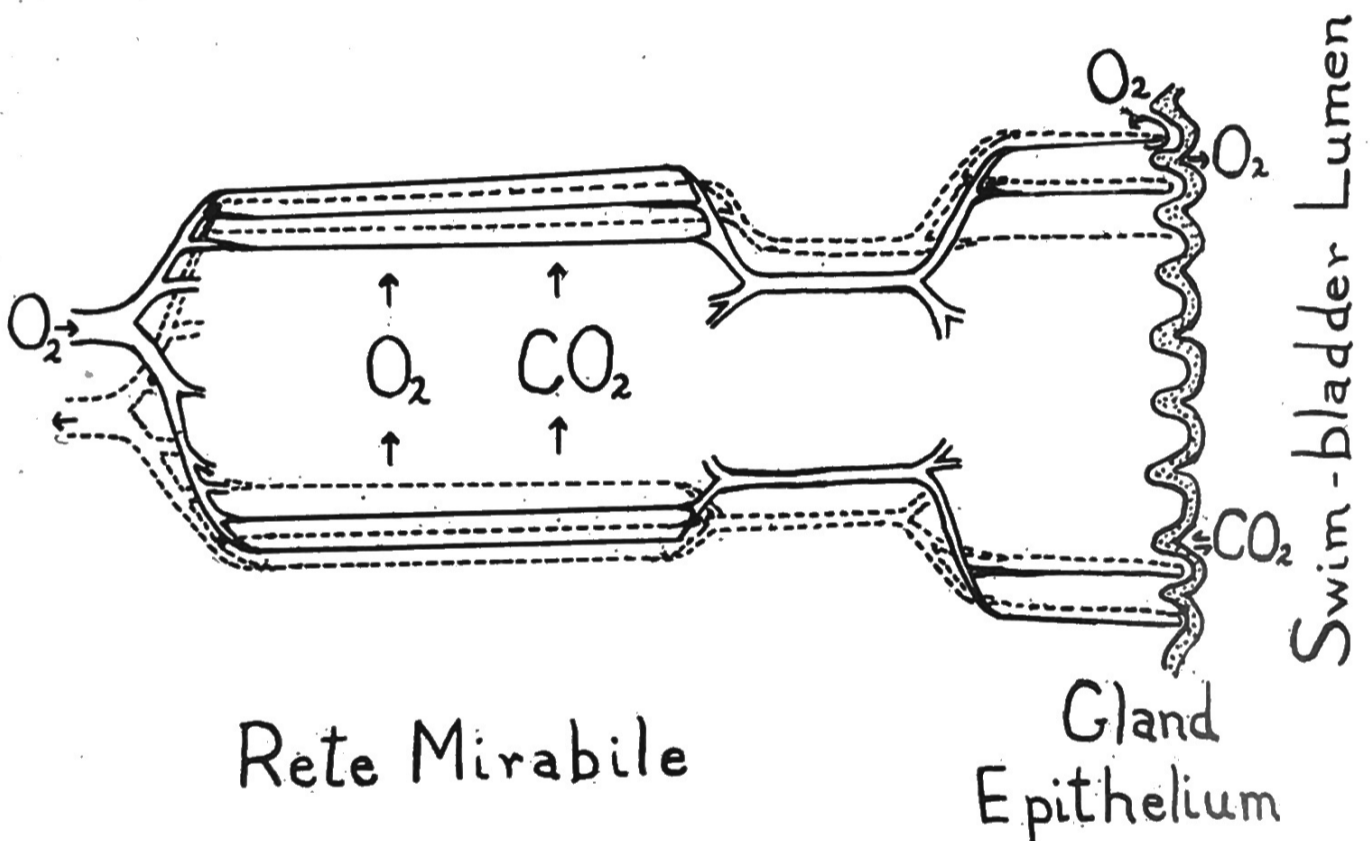

Fig. 1. Diagrammatic representation of a rete mirabile gas gland mechanism of an eel. The arrows indicate the direction of transportation and diffusion of oxygen and carbon dioxide.

arterial capillaries of the rete mirabile through the gas gland and back to the venous capillaries of the rete mirabile and by diffusion back to the arterial capillaries of the rete mirabile, the total gaseous partial tensions of the plasma will finally reach and exceed the mechanical pressure on the blood. Gas bubbles will then be formed.

[1]From all observations made, one would conclude, although there is a potential back pressure due to oxyhemoglobin and the blood does lose alkali reserve with rise in carbon dioxide tension, that the blood will always hold more total carbon dioxide at higher carbon dioxide tensions than at lower tensions. This is not the case with oxygen. The total oxygen held by blood at higher oxygen tensions can be lowered below what it can hold at lower oxygen tensions by increasing the carbon dioxide tension of the blood. This explains how it is possible to have in the swim-bladder a very high partial pressure of oxygen and carbon dioxide partial pressure very low or even nil. This can be the case even though the partial pressures of the inert gases are much higher than their respective partial pressures in the atmosphere.

Perhaps before the total gaseous partial tensions has reached this value, the mechanical pressure on the blood, the oxygen diffusion pressure would be toward the lumen of the swim-bladder. Oxygen would thus be deposited into the swim-bladder by simple diffusion. If gas bubbles are formed, the bubbles would contain primarily oxygen. The inert gases would diffuse into the bubbles in proportion to their respective partial tensions in the plasma. When the gas bubbles are formed, the total partial gaseous pressures would be equal to or greater than the external pressure upon the blood. Water vapor pressure would augment the total gaseous pressures of the bubble, since the water vapor tension of a fluid is independent of the gaseous pressure on the fluid. The total internal pressure of the gas bubble would thus be greater than the internal pressure of the swim-bladder, which is balanced by external pressure. The gas bubble would then move and break into the lumen of the swim-bladder, since of necessity the gas bubble would always move from a higher to a lower pressure.[2]

The inert gases would thus be deposited into the swim-bladder regardless of their respective partial pressures in the swim-bladder. The oxygen being reabsorbed more rapidly than inert gases due to its chemical activity, the inert gases would be left behind in the swim-bladder. Their partial pressures would be determined solely by the mechanical pressure upon the swim-bladder. This is a clear-cut explanation as to why the inert gases are present in the swim-bladders of fishes in the same proportion as found in the atmosphere. This explains clearly how it is possible for inert gases to have higher partial pressures in the swim-bladder of fishes than their respective partial pressures in the atmosphere. This is also an explanation of the mechanism of the deposition of gases into the swim-bladder of fishes, without the aid of any vitalistic force, generally called "secretion."

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[2]It might be argued that gas plus vapor tension would expand the bubble until internal pressure of the bubble would equal the swim-bladder internal pressure. This being the case, the gas defussion pressure would be from plasma to bubble. Thus there is always a resultant pressure from bubble to swim-bladder.

ANNOUNCEMENT OF THE ANNUAL MEETING

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be voted on at the coming annual meeting. The proposed amendments are primarily for authorization of a Board of Trustees of the Tennessee Academy of Science and of a separate Board of Trustees, a Director, and a Curator for the Reelfoot Lake Biological Station. Copies of the proposed amendments may be obtained upon request from the Secretary of the Academy. With minor corrections the amendments are the same as those circulated among members in attendance at the last annual meeting.