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THE PHYSIOLOGY OF THE RESPIRATION OF FISHES IN RELATION TO THE HYDROGEN ION CONCEN- TRATION OF THE MEDIUM.*

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INTRODUCTION.

Within recent years much has been added to the knowledge concerning the mechanism of the respiratory function of the blood. Haldane and Priestley (1905) have shown that, at least in the higher animals, the respiratory movements are affected by the carbon dioxide tension of the arterial blood. It has been shown definitely (Hasselbalch, 1912 and citations) that the exciting agent is the hydrogen ion concentration of the blood bathing the respiratory center.

Krogh and Leitch (1919) undertook to study the respiratory function of the blood of fishes in view of the knowledge of the influence of temperature upon the dissociation curve of oxyhemoglobin as investigated by Barcroft and Hill (1909) and Barcroft (1914). These workers found that the blood of the fish was especially adapted to its needs.

Certain marine fishes are known to react to a gradient of acidity and alkalinity (Shelford and Powers, 1915). It has been found that certain species react positively to a definite range of hydrogen ion concentration of the sea water, others are less definite in their reaction, and still others seemingly do not respond to differences in alkalinity and acidity (Powers, 1921).

In view of these facts experiments were undertaken to determine the ability of marine fishes to extract oxygen from the sea water at different hydrogen ion concentrations. Interest in this question was

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further stimulated by the theory held by Roule (1915) that the salmon (*Salmo salar* L.) does not respond to salinity or temperature but that it always reacts in such a way as to bring it into water having a higher oxygen content.

Method.

A very simple technique was employed. A fish was placed in a 2 quart Mason jar filled with sea water and made air-tight with a rubber stopper. The jar was then immersed in a water bath of running sea water in which the temperature was almost constant. The oxygen content of the water at the beginning of an experiment was always sufficiently high so that the fish did not at first suffer from oxygen want. The hydrogen ion concentration was determined by the colorimetric method; and the oxygen, by the Winkler method immediately after all movements of the fish had ceased.

The hydrogen ion concentration of the sea water was varied by aerating with carbon dioxide-free air or by the addition of a small amount of sea water made alkaline by the addition of sodium hydroxide and by the introduction of carbon dioxide.

The fishes used in these experiments were kept in a small aquarium of running sea water. They were allowed to rest from 6 to 12 hours, so that they might recover from any shock suffered when collected. All were rejected after being in the laboratory 2 or 3 days so as to avoid as far as possible erratic results due to the ill effect of keeping them under unnatural conditions.

EXPERIMENTAL.

The mean oxygen content of the sea water of all experiments having approximately the same pH at the time of death of the fish was calculated. That is, if the highest oxygen content of the sea water at the time of death of the cunner at 7.22 to 7.25 pH was 0.30 cc. per liter, and the lowest 0.20 cc. per liter, the cunner was taken to be able to absorb the oxygen from the sea water down to 0.25 cc. per liter at a pH from 7.22 to 7.25. This was taken to be more nearly exact and to eliminate to a greater extent the factor of individual variation than if individuals were taken alone. Loeb (1912) has shown that the mortality curve of *Fundulus* embryos under the in-

fluence of acids, alkalis, and potassium salts, and Loeb and Northrop (1917) that the mortality curve of the fruit fly (*Drosophila*) under the influence of food and temperature are probability curves. The probable cause of the variations in the ability of different individual fish of the same species to absorb oxygen from the medium at low oxygen pressure at a given hydrogen ion concentration and temperature will be taken up later.

The figures are graphic representations of the experimental data.

The Ability of Fishes to Extract Oxygen from the Sea Water at Different Hydrogen Ion Concentrations.

(a) *The Cunner* (*Tautoglabrus adspersus* Walbaum).—The cunner was able to extract oxygen from the sea water down to approximately 0.25 cc. per liter before asphyxiation at all hydrogen ion concentrations up to about 6.5 pH. From this point on there seems to be a rapid loss in the ability of this fish to extract oxygen from the sea water at low oxygen pressure (Fig. 1).

(b) *The Butter-Fish* (*Poronotus triacanthus* Peck).—Fig. 2 shows that the butter-fish was not able to extract the oxygen from the sea water at quite as low a level as the cunner. The general trend of the curve indicates that the butter-fish is able to absorb oxygen at the lowest concentrations at a pH of about 7.6 to 7.8. This was shown even more strikingly when individuals were considered, the lowest point at which oxygen was absorbed being 0.36 cc. per liter at 7.58 pH and 0.35 cc. per liter at 7.57 pH. There was a slight falling off in the power to extract the oxygen at low concentrations, as the hydrogen ion concentration of the sea water was lowered from a pH of about 7.6 or 7.8 to 9.0. The falling off was much more rapid when the hydrogen ion concentration was increased from a pH of about 7.6 to 6.3, being most rapid from 7.1 to 6.35. At the higher hydrogen ion concentrations but very little of the oxygen had been absorbed before asphyxiation took place.

(c) *The Mackerel* (*Scomber scombrus* L.).—There was only a slight variation in the ability of the mackerel to extract oxygen from the sea water at low tension from about 7.7 pH to about 8.2 pH within an optimum at about 8.0 pH. There was a more or less falling off in

this ability when the pH of the water was either raised above or lowered below this range (Fig. 1).

(d) *The Alewife (Pomolobus pseudoharengus Wilson)*.—The optimum pH for the absorption of oxygen at low oxygen tension for the

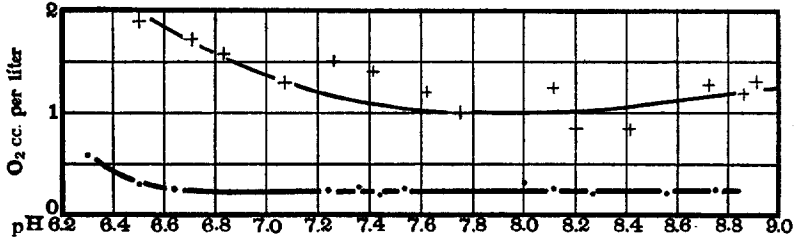


FIG. 1. The circles represent the experimental data of the cunner (*Tautoglabrus adspersus* Walbaum) and the plus signs those of the mackerel (*Scorpaenopsis diabolus* L.). The abscissæ give the hydrogen ion concentration; and the ordinates the oxygen in cc. per liter at the end of the experiment.

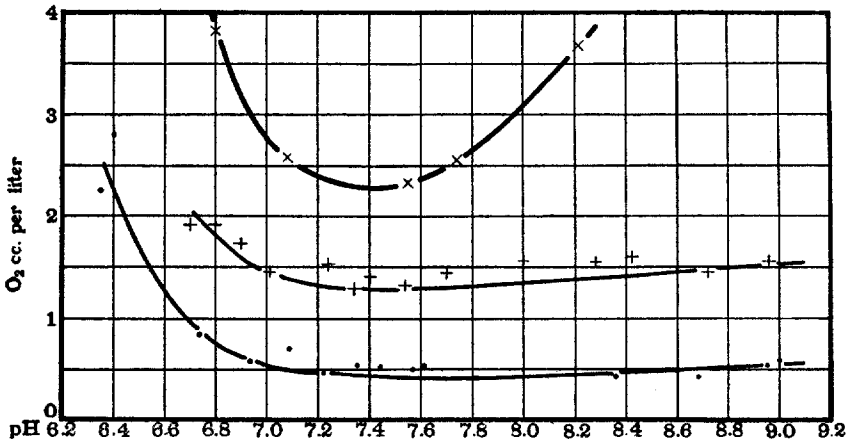


FIG. 2. The circles represent the experimental data of the butterfish (*Poronotus triacanthus* Peck), the plus signs those of the alewife (*Pomolobus pseudoharengus* Wilson) and the crosses those of the herring (*Clupea harengus* L.). The abscissæ give the hydrogen ion concentration; and the ordinates the oxygen in cc. per liter at the end of the experiment.

alewife was about 7.3 or perhaps 7.3 to 7.6 (Fig. 2). The falling off from this optimum was greatest when the hydrogen ion concentration was raised above this optimum. The falling off was less marked when the hydrogen ion concentration was lowered.

(e) *The Herring (Clupea harengus L.)*.—The herring (?) used in these experiments averaged from 3 to 4 gm. This fish appeared in great numbers for only a few days. Their sudden disappearance terminated the experiments and prevented the writer from having his identification of the species verified by a specialist. The young of the alewife were running at the same time and were taken by members of the U. S. Bureau of Fisheries.

The herring (Fig. 2) showed greater differences in ability to absorb oxygen at low oxygen tension with variation in the hydrogen ion concentration of the sea water than any of the other fishes tested. There was a very rapid falling off of the power to absorb oxygen from the sea water when the hydrogen ion concentration was raised at least above a pH of 7.4. It was less rapid when the hydrogen ion concentration was lowered.

The experiments just described show that the lowest tension at which oxygen can be absorbed from the sea water by certain marine fishes is more or less dependent upon the hydrogen ion concentration of the sea water. Of the five species of fishes tested, the cunner, butter-fish, mackerel, alewife, and herring, the cunner and butter-fish were affected least by a change in the hydrogen ion concentration. The lowest point at which the butter-fish was able to absorb oxygen from the sea water was at 0.35 cc. per liter at a pH of 7.57.¹ The mackerel, alewife, and herring were most affected by the variation in the pH of the sea water; *i.e.*, have the narrowest optimum pH. These fishes are considered the most sensitive and most restricted in their migratory movements. On the other hand, the cunner which is least affected is more cosmopolitan as to habitat and is an all year resident (Sumner, Osburn, and Cole, 1911). The butter-fish which shows less resistance to the variation in the pH is somewhat less cosmopolitan than the cunner in its habitat and is a resident of the Woods Hole vicinity only from early summer to late fall.

¹ This could not be called the optimum pH of the sea water for carrying on the respiratory functions by this fish. At the same time oxygen is being absorbed from the sea water bathing the gills, carbon dioxide is being given off. The pH at the beginning of the experiment was 8.28. Thus it stands to reason that the optimum pH of the sea water for this fish would be some where between 8.28 and 7.57.

When the figures are examined more closely it is seen that the optimum pH for the absorption of oxygen at low tension varies with the different species. The herring has the lowest pH optimum which seems to be correlated with the habits of this fish.

Results of Experiments on the Pacific Herring (Clupea pallasii
Cuv. and Val.).

The foregoing experiments were performed at the Marine Biological Laboratory, Woods Hole, during the summer of 1920. It was thought desirable to test the Pacific herring, *Clupea pallasii*, in the same manner since its behavior was better known (Shelford and Powers, 1915 and Powers, 1921) than the Atlantic herring *Clupea harengus*. These experiments were performed at the Puget Sound Biological Station, Friday Harbor, during the summer of 1921. The methods employed in the experiments were similar to those at Woods Hole. In order to eliminate individual variation and make the time until death shorter, five 1.5 to 2.5 gm. fish were put in a 2 quart Mason jar of sea water instead of only one. The oxygen was determined immediately after the last fish had died. A total of three hundred and seventy-five fish were tested. Instead of taking the means of the extremes of the oxygen content at the end of an experiment, as was done in the preceding experiments, a curve, which is the mathematical mean of all experiments, was drawn (Fig. 3). The greatest deviation from the mean was 0.18 cc. per liter with the exception of three experiments. In two, one at 6.95 pH where the fish died when the oxygen content was 1.08 cc. per liter and another where the pH was 7.88 and the oxygen content was 0.98 cc. per liter at the end of the experiment, the variation from the mean was plus 0.25 cc. per liter. These two experiments seemed somewhat erratic but they have been included in all averages and calculations. In another, where the pH was 7.43, the variation from the mean was 0.20 cc. per liter. The average variations were plus 0.089 and minus 0.085 cc. per liter. This is less than 2 per cent of the total oxygen content of the sea water at the beginning of the experiments and less than 12 per cent of the difference of the extremes of the oxygen content of the sea water at the time of death of the fish. The

extreme variation from the mean is less than 33 per cent of the total variation in the experiments.

Duplicate oxygen tests could not be made by the methods employed since only 2 quarts of sea water were used in each experiment. However, the accuracy of the method was determined in connection with other work done at the same time. In 88 duplicate oxygen tests, the average deviation from the mean was ± 0.024 cc. per liter. This is more than 27 per cent of the average variation of the oxygen content at end of experiment from the mean curve (Fig. 3). The extreme

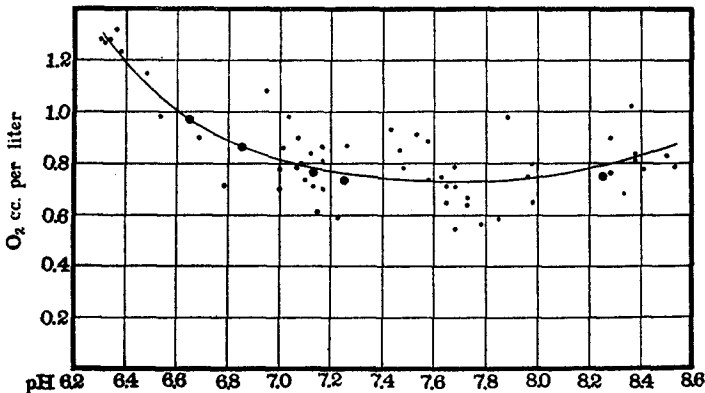


FIG. 3. The small circles represent the experimental data of the herring (*Clupea pallasii* Cuv. and Val.) when five fish were tested in a 2 quart mason jar, and the large circles when ten to twenty-five fish were tested in a 42 liter carboy. The abscissæ give the hydrogen ion concentration; and the ordinates the oxygen in cc. per liter at the end of the experiment.

deviations of the 88 duplicate tests were one 0.094 cc. per liter and four from 0.078 to 0.072 cc. per liter. This, again, is more than 33 per cent of the extreme deviations of the experiments from the mean curve. In other words, from 27 per cent to 33 per cent of the deviation of the experiments are probably due to the method employed and not the individual variation of the fish. Thus the average individual variation of the fish is less than 8 per cent and the extreme is less than 22 per cent of the difference of the total variations of the experiments. Further justifications for the form of the curve will be taken up in connection with the discussion of other experiments.

In order to determine whether or not the death of the fish was due to asphyxiation because of low oxygen tension of the sea water, the first set of experiments was checked by testing the fish where they would not suffer from oxygen want so quickly. Ten to twenty-five fish were placed in a carboy (capacity about 42 liters) of sea water at different hydrogen ion concentrations. The results of these experiments conform very markedly to the mean curve, although the time until death of the fish in the carboy was from 24 to 48 hours as compared with 1 hour and 23 minutes to 2 hours and 40 minutes when five fish were tested in the 2 quart Mason jars (Fig. 3). This shows that the fish died from asphyxiation due to low oxygen tension in the sea water and not to other causes.

The experiments performed at Friday Harbor corroborate in every way those done at Woods Hole. The results of these experiments conform strikingly with the behavior experiments and field observations made by the writer on the same fish during the summers of 1918 and 1919. The lowest tension at which the herring, *Clupea pallasii*, can extract oxygen from the sea water is when the hydrogen ion concentration is ± 7.68 pH. This fish reacts positive to sea water having a pH of from 7.68 to 7.73 and was found most abundantly in the sea water in the vicinity of the Puget Sound Biological Station that had a pH of about 7.73 to 7.76 (Powers, 1921).

DISCUSSION.

Workers on fish respiration have found that fishes are able to survive at rather low oxygen tension without any apparent ill effect (Powers, 1921, citations). Gaarder (1918) found that the actual oxygen consumption of an anesthetized carp was reduced only slightly, 0.62 cc. per kg. per minute, until the oxygen in solution in the water had been reduced from 15.4 cc. per liter to about 1.13 cc. per liter when the gills were artificially bathed with water at a constant rate. It is not known whether or not this slight falling off of oxygen consumption could have been corrected had the respiratory mechanism of the fish been free to respond normally. Packard (1905) showed that *Fundulus heteroclitus* injected with 5/16 M sodium carbonate were able to live longer in a liter flask of sea water

stopped tightly to exclude air than those not so injected. He also found that when the fish were injected with $m/250$ to $m/500$ solution of acetic acid, they did not live as long as the control fish. From these experiments Birge and Juday (1911) suggested that "if a fish possessed the power to alter the composition of its blood somewhat, it would be able to adapt itself to water which contains only a comparatively small amount of dissolved oxygen." Might it not be possible in these experiments, since the oxygen tension was lowered by the respiration of the fish, that the differences in survival time of the fish were due to the variations in their abilities to absorb oxygen from the sea water at low oxygen tension under the conditions of the experiment? That is, the fish whose blood was best adapted to absorb oxygen at low tension at the particular carbon dioxide tension of the experiment would survive longest. This ability would perhaps depend upon the alkaline reserve of the blood of the fish. That is, if the hemoglobin of the blood of all the fish of a given species had the same optimum pH to carry oxygen, the fish would be able to extract oxygen from the water at low oxygen tension in the direct order of the alkaline reserve of the blood at a carbon dioxide tension higher than the optimum and in the reverse order of the alkaline reserve in a carbon dioxide tension below the optimum. In these experiments the carbon dioxide tension would tend to increase above the optimum for the absorption of oxygen at low tension since ordinary sea water was used and, as the oxygen was absorbed by the confined fish, carbon dioxide would be given off.²

The experiments recorded in the figures show that the species of fish tested have an optimum pH of more or less narrow or wide range for absorbing oxygen from the sea water at low oxygen tension. The limiting factor is perhaps the carbon dioxide tension of the sea water. The pH of the sea water with a given alkaline reserve is dependent upon the carbon dioxide tension (Henderson and Cohn, 1916, and McClendon, 1917). The optimum carbon dioxide tension of the sea water for a species of fish as suggested above would perhaps depend upon the alkaline reserve and the optimum pH of its blood.

² The author has performed experiments which give strong evidence for this probability, which are reserved for further publication.

The individual variation of fish of a given species might depend upon the individual variation in the alkaline reserve of the blood.

These conclusions are further emphasized by FitzGerald's observations (1913, 1915), and recent experiments by Henderson (1919), Haggard and Henderson (1920), and Henderson (1920) on the part played by the alkaline reserve of the blood in the acclimatization to altitude. It might be further suggested that the species of fish having the greatest ability to vary the alkaline reserve of their blood would also have the greatest power to withstand a variation in carbon dioxide tension of the water. The rapidity of the change in the carbon dioxide tension which a fish would be able to withstand would depend upon the rapidity with which it is able to vary the alkaline reserve of its blood. In man (Henderson, 1920) this seems to be a rather slow process. This is a more logical explanation since the carbon dioxide and oxygen tension in the environment of the fish are not so intimately connected as with the air-breathing animals. But as a general rule when the oxygen content of the sea water is low the carbon dioxide is increased (Powers, 1920). However, further experiments are necessary to settle these points.

In the light of these experiments it is easily seen why Wells (1913) found that high carbon dioxide was more rapidly fatal to fishes than low oxygen and why fishes are able to sense out and detect variations in carbon dioxide tension more easily than the variations in the oxygen tension (Shelford and Allee, 1913). Bayliss (1918) states: ". . . if increase in carbon dioxide be prevented, as by respiration of pure nitrogen, a man may become unconscious before experiencing any unpleasant symptoms."

It is conceivable that the carbon dioxide tension of the water could be raised above the carbon dioxide tension of the tissue capillary blood of the fish. Under this condition the oxyhemoglobin would be reduced to hemoglobin in the capillaries of the gills of the fish rather than the hemoglobin being oxidised to oxyhemoglobin. The fish would then suffer oxygen want more quickly in water with a high carbon dioxide tension and ordinary oxygen tension than in water with a low carbon dioxide tension and a low oxygen tension. Thus the probabilities are that in Wells' experiments the high oxygen tension was not antagonistic to the high carbon dioxide tension, in

the true sense of the word, but that the oxygen tension was below on the one hand, and on the other it was above the tension at which hemoglobin could be oxidised to oxyhemoglobin in the presence of a high carbon dioxide tension.

SUMMARY.

1. The ability of marine fishes to absorb oxygen at low tension from the sea water is more or less dependent upon the hydrogen ion concentration of the water.

2. The ability of fishes to withstand wide variations in the range of hydrogen ion concentration of the sea water can be correlated with their habitats. The fishes that are most resistant to a wide variation in the hydrogen ion concentration are most cosmopolitan in their habitat. Those that are least resistant to a variation in the hydrogen ion concentration are the most restricted in their range of habitat.

3. There is a close correlation between the optimum condition of the sea water for the absorption of oxygen at low tension by the herring (*Clupea pallasii*), the condition of the sea water to which they react positive and that in which they are found most abundantly.

4. It is suggested that the variation in the ability to absorb oxygen at low tension at a given pH of individuals of a species is dependent upon the alkaline reserve of the blood of the individual fish.

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