The Ability of Fishes to Extract Oxygen at Different Hydrogen Ion Concentrations of the Medium.

By

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POWERS,* working on some marine fishes, arrived at the important conclusion that the ability of fishes to absorb oxygen at low pressures is more or less dependent upon the hydrogen ion concentration of the water. His method of research was briefly as follows: a fish was placed in a two-quart jar filled with water, which was closed airtight with a rubber stopper. The pH and the oxygen determinations were made immediately after all the movements of the fish had ceased. The amount of oxygen left at death represented, according to Powers, the pressure below which the fish at the particular pH could not extract any more oxygen from water. Powers did not control the amount of oxygen at the beginning of an experiment; he says, "it was always sufficiently high so that the fish did not at first suffer from oxygen want."

While working recently on the influence of some physical and chemical conditions of water on May-fly larvæ, I observed that the amount of oxygen which was left at death at a particular pH depended on the amount of oxygen which was originally present in the water; for instance, if at pH 4·0, starting with 6 c.c. per litre of oxygen, 3 c.c. per litre was left, only 1·0 c.c. was left if the original amount was 4·0 c.c. per litre. If in the first case the larvæ at the concentration of 3 c.c. per litre died for lack of ability to absorb any more oxygen, as Powers' conclusions will warrant us to assume, in the second case also the individuals should have died when that tension was reached. Moreover, it was noticed that the time for which the larvæ lived in two waters having the same pH but different amounts of oxygen was almost the same. This strongly suggested that the larvæ died, not on account of the fact that they could not at that pH extract any more oxygen at the particular pressure, but due to some other cause, presumably the direct influence of the hydrogen ions.

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* *Journ. Gen. Phys.*, IV, p. 305.

As this point is of great physiological importance, to verify the above hypothesis a fish, *Gasterosteus aculeatus*, the common "stickleback," was chosen for detailed experiments, which are reported below :—

The most crucial test by which Powers could have tested his results and their interpretation was to observe on a fresh fish the effect of the water in which one had died previously, presumably on account of the fact that it could not absorb oxygen at that pressure, i.e. for instance, if the herring, *Clupea*, was observed to die at pH 7·1, leaving 2·5 c.c. per litre of oxygen, before concluding that *Clupea* at pH 7·1 cannot extract oxygen below 2·5 c.c. per litre concentration, Powers should have put another herring in the same water to see whether the fish died in a short time, which it should have done if his view was correct. Powers did not test his conclusion in this manner.

In the case of sticklebacks I have performed a long series of experiments on these lines, which are detailed in Tables 1–5 (p. 744). The pH of water was varied by adding small amounts of dilute HCl. Under Column I of the tables is given the time for which the first lot of stickles lived at a particular pH. Under Column II is given the time for which the second lot lived when put in the same waters in which the first lot had died. The mouth of the jar was opened, fresh specimens introduced, and the mouth was closed again as quickly as possible. As many as six lots were introduced in some jars in this way. An inspection of the tables will show that, contrary to what one would expect from the conclusions of Powers, the fish of the successive lots lived for almost the same time. If the first lot had died because it could no longer extract oxygen at that pressure, the second when introduced in the same waters should have died within a short time, and the third in any case should have done so at once.

It may be added that in all the above experiments the pH and oxygen content were checked before starting a fresh lot ; the jars opened for this purpose were, of course, not used during the rest of the series. Moreover, on account of the fact that the fish as a product of respiration added some CO_2 to the water, the pH at the beginning of a fresh lot would be slightly lower than that at the start of a previous one, but the specimens being small (0·20–1·5 gm.) and the experimental jars quite big (200 c.c.), and because some CO_2 went out when the jars were opened and fresh fish introduced, no appreciable change in pH was noticed during the duration of the series detailed in the tables.

The problem was tackled by another method as well. As will be evident from Table 2, stickles when put in water at pH 3 and having 6·5 c.c. of O_2 per litre die within 40–45 minutes, leaving about 5·8 c.c. per litre of oxygen—a concentration below which, according to Powers' interpretations, stickles should not be able to absorb oxygen at this pH. But when these fish were actually introduced in water of this pH and having as low a concentration of O_2 as 1·36 c.c. per litre, they lived almost as long as in the above water (Table 3). These experiments were repeated with even lower concentrations of oxygen, the fish lived about the same time unless the pH was lower (Table 4).

The ordinary suction pump was employed for reducing the amount of oxygen.

Thirdly, several pH ranges were prepared by adding HCl to waters having different amounts of dissolved oxygen. An examination of Table 5 will show that in each range the fish die leaving absolutely different amounts of oxygen. If the ability to extract oxygen at any pH depends upon the amount of O_2 present, then at a particular pH the individuals in the different ranges should leave almost the same amount of oxygen at their death.

It is interesting to add that in all the above-mentioned experiments the fish of the different ages behaved similarly, except very tiny ones (below 0·15 gm.), or those which were ready to breed (above 1·8 gm.)—see the weight columns in the different tables.

It may be pointed out, however, that the amount of oxygen which the fish absorb per hour per unit weight is not the same at different hydrogen ion concentrations. For instance, at a pH like 3 it is much less than at pH 7. This suggests that the hydrogen ions kill the fish by interfering with the respiratory system. But what the above-described experiments establish is that this interference is independent of the amount of oxygen present in the surrounding medium, unless its concentration goes down to 0·30–0·50 c.c. per litre, when the fish die of asphyxiation at any pH.

Incidentally, the above experiments suggest that in ponds and rivers where the oxygen content seldom goes down to such a low concentration as 0·30 c.c. per litre, fishes should not, as a rule, die of lack of oxygen, and that therefore other factors, e.g. pH, CO_2 pressure, poisons, etc., have more important ecological bearing than the amount of dissolved oxygen.

It is with great pleasure that I take this opportunity of thanking Dr. E. J. Allen, the Director of the Plymouth Laboratory, and Dr. W. R. G. Atkins, the head of the Physiological Department, who took a keen interest in this investigation, placed all facilities at my disposal and extended numerous courtesies during my stay at Plymouth.

TABLE 1.

pH 3·1, O_2 at start 6·5 c.c. per litre.

No. of Exp. jar.	I.		II.		III.		IV.		V.		VI.	
	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.
1	38	0·32	35	·27	42	0·21	35	0·23	40	0·20	34	0·25
2	32	0·35										
3	31	0·22	35	·21								
4	65	1·22	58	·25	60	0·23	60	0·20	65	0·20	67	1·00
5	47	0·28	48	·3								
6	60	0·20										
7	80	0·21	78	·2	70	0·2	75	0·2	65	0·18		
8	45	0·20	50	·29	51	0·23						
Average	50		51		56		57		57		51	

O_2 at the end of I lot 5·85 c.c. per litre (Nos. 2 and 6).
,, ,, II 5·2 ,, ,, (Nos. 3 and 5).
,, ,, III 4·8 ,, ,, (No. 8).
,, ,, V 4·0 ,, ,, (No. 7).
,, ,, VI 3·5 ,, ,, (Nos. 1 and 4).

Table 2.

pH 3·0, O_2 6·5 c.c. per litre.

	I.		II.		III.		IV.		V.	
	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.
1	40	0·27	41	·18	50	·18	30	·15		
2	35	0·20	42	·20	40	·21	45	·22		
3	45	·17								
4	59	·18	55	·75	56	·15	26	·11	50	·18
5	39	·25	40	·15						
6	54	·18								
7	48	·19	60	·20	58	·16	46	·13	55	·8
8	43	·17	50	·21	48	·17				
9	48	·17	47	·8						
10	38	·30	32	·2	52	·16				
11	67	·2								
12	56	·4	51	·2						
13	35	·2	35	1·2						
14	43	·8	38	·32	39	·22				
15	32	·3	54	·28						
16	32	·25	45	1·2						
17	45	·35	50	·3						
18	38	·30	35	·25						
19	47	·27	49	·22						
20	37	·45	39	·3						
21	40	·4								
22	47	·3	40	·2	45	·25				
Average	43		44½		48		36½*		51	

* Individuals No. 1 and 4 in IV below ·15 gms.

TABLE 3.

pH 3·0, oxygen at start 1·36 c.c. per litre.

	I.		II		III.	
Expt. jar No.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams
1	35	·35	30	1·0	34	1·3
2	35	·40				
3	39	·45				
4	52	·45	39	1·1	38	1·2
5	33	·45				
6	37	·30				
7	37	·40	36	1·8	39	1·5
8	36	·32				
9	40	·35				
10	50	·35				
Average	39·5		35		37	

TABLE 4.

pH 2·9, oxygen at start 1·4 c.c.

	I.		II.	
Expt. jar No.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.
1	27	·4	31	·30
2	39	·35	43	·25
3	25	·35	45	·25
4	37	·30	33	·30
5	36	·25		
6	35	1·20	34	·22
7	30	·27	31	·25
8	30	·25	30	·17
9	30	·25	31	·18
10	29	·25	30	·20
11	30	·30	30	·20
12	29	·27	17	·20
13	31	·25	29	·20
Average	30		29	

TABLE 5.

Expt. No. and amount of oxygen at start.	Low Oxygen Concentration.				Control—Oxygen 6·5—7 cc. per litre.		
	pH.	Oxygen left at death.	Dying time in minutes.	Size-weight in grams.	Oxygen left at death.	Dying time in minutes.	Size-weight in grams.
I Oxygen 3·0 c.c. per litre.	3·3	1·6	45	0·50	5·5	45	0·50
	3·0	2·7	30	0·50	6·0	29	0·50
	2·9	2·8	30	0·50	6·24	30	0·50
II Oxygen 2·50 c.c. per litre.	3·1	2·20	37	0·20	6·4	40	0·20
	2·9	2·25	33	0·20	6·4	35	0·20
	2·7	2·32	20	0·20	6·4	30	0·20
	2·5	2·40	30	0·20	6·5	30	0·20
	2·4	2·42	25	0·20	6·6	32	0·25
III Oxygen 2·0 c.c. per litre.	5·2	1·20	480	0·30	3·28	500	0·40
	3·9	1·40	270	0·30	4·4	245	0·30
	3·6	1·52	360	0·25	4·8	150	0·20
IV Oxygen 1·50 c.c. per litre.	3·1	0·96	46	0·20	5·00	48	·25
	3·0	1·00	40	0·20	5·36	35	·20
	2·9	1·04	32	0·20	6·08	40	·20
V Oxygen 1·75 c.c. per litre.	3·7	1·04	82	0·25	4·24	150	0·22
	3·4	1·20	75	0·30	4·70	80	0·23
	3·15	1·56	55	0·22	5·04	55	2·5