

GAS EXCHANGE IN THE SWIMBLADDER OF THE
MUDMINNOW

Umbra limi (Kirtland)

VIRGINIA SAFFORD BLACK

Ontario Fisheries Research Laboratory,
University of Toronto

and

Department of Physiology, Dalhousie University

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ABSTRACT

Experiments were carried out to determine the extent and manner of gas exchange during asphyxiation in the swimbladder of the mudminnow, *Umbra limi* (Kirtland.) Under conditions of respiratory stress provided by lack of oxygen and presence of carbon dioxide in the environmental water the mudminnow drew extensively on the oxygen in the swimbladder. During asphyxiation in the presence of carbon dioxide, carbon dioxide entered and oxygen left the swimbladder; the rate of exchange of these gases increased at high environmental carbon dioxide tensions. Some data were obtained on oxygen consumption from the water and rate of respiratory movements during these experiments.

INTRODUCTION

Fish belonging to the genus *Umbra* are often found in stagnant waters and are able to live in water containing less oxygen and more carbon dioxide than most teleost fishes can tolerate. Investigations by Rauther (1914) and Geyer and Mann (1939) on European species have shown that the swimbladder acts as a supplementary organ for respiration thus enabling fish of the genus *Umbra* to use oxygen from the air when oxygen in the water is insufficient.

Rauther (1914) made the first extensive investigation of the swimbladder using the species *U. krameri* Fitz. His work on the histological nature of the swimbladder is especially significant since it gives a morphological basis for evidence he obtained that air intake into the swimbladder could maintain life when the oxygen content of the water is low.

The respiration of *U. lacustris* Grossinger is considered in two papers by Geyer and Mann (1939). They found that the oxygen consumption from the water increases when access to air is cut off and also when the swimbladder gas is removed by decompression. They concluded from their data that the swimbladder supplied $\frac{1}{4}$ to $\frac{1}{2}$ of the normal oxygen consumption. When the oxygen in the water is decreased, the use of the swimbladder for aerial respiration increases. On the other hand, in well oxygenated running water their fish did not come to the surface for air but employed only gill respiration.

It becomes apparent from the investigations of Rauther, and Geyer and Mann that the swimbladder of *Umbra* is an organ capable of accessory respiration which allows the fish to survive in a habitat in which it could not otherwise exist. The present investigations add to this knowledge by confirming the use of oxygen during asphyxiation from the swimbladder of the mudminnow, *Umbra limi* (Kirtland). In addition some experiments have been carried out to show the relation between the gases in the swimbladder and in the water during various conditions and stages of asphyxiation.

MATERIAL

Mudminnows are found in swamps and weedy brooks in Canada and north-eastern United States. The mudminnows used in these experiments were obtained from the Troyer Natural Science Service operating in the vicinity of Toronto, Ontario. The fish were of both sexes. The average weight was 4 grams, the range being from 0.5 grams to 13.6 grams. The fish were acclimatized to the temperature of the experiment, the overall time allowance for acclimatization being no more than 1° C. increase in temperature per day. Mudminnows kept at 10° C. were never observed gulping air at the surface of the water. The fish at 19° C. and 20° C. occasionally came to the surface.

METHODS

A. Fish completely asphyxiated at various carbon dioxide tensions.

Methods were identical to those used in similar experiments by Fry and Black (1938), Safford (1940) and Black (1942). Each fish was sealed in a bottle of water (275 ml. capacity) containing a known amount of dissolved carbon dioxide and having an oxygen tension of at least 100 mm. Thus there was no opportunity for renewing air in the swimbladder during the experiments. When all respiratory movements had ceased, the water was analyzed for carbon dioxide and oxygen. The swimbladder gas was withdrawn under water by syringe and needle at the conclusion of each experiment. The gas was analyzed immediately in the micro-gas-analyzer (after Krogh, 1908), using $\frac{1}{4}$ N potassium hydroxide to absorb the carbon dioxide and Oxsorbent to absorb the oxygen.

The carbon dioxide in the water was determined by equilibrating a small bubble of air (0.2-0.5 ml) with 35 ml of the water. The bubble was then analyzed for carbon dioxide by absorbing the carbon dioxide in the micro-gas-analyzer as above. Pressures were calculated by multiplying per cent gas by the barometric pressure less vapor tension at the temperature of the experiment.

The oxygen content of the water was determined by the Winkler method using a 50 ml sample of water. The pressure of oxygen was calculated by relating the quantity of oxygen found to the solubility at the temperature of the experiment and multiplying the fraction by the barometric pressure (760 mm. used in all these calculations though the actual barometric pressure varied from 750 mm. to 765 mm.).

B. Fish partially asphyxiated at various carbon dioxide tensions.

The mudminnows were placed in 275 ml bottles completely filled with water and sealed as above. The water in the bottles contained known tensions of carbon dioxide and oxygen. Each

bottle was opened after a definite time (column 2, Tables 3, 4). The fish was alive in every case. Water for carbon dioxide and oxygen samples was withdrawn as shown in Figure I, to prevent the fish from gulping air. This apparatus was devised with the assistance of Dr. R. R. Langford. As the water was drawn from the bottle through the rubber tube,

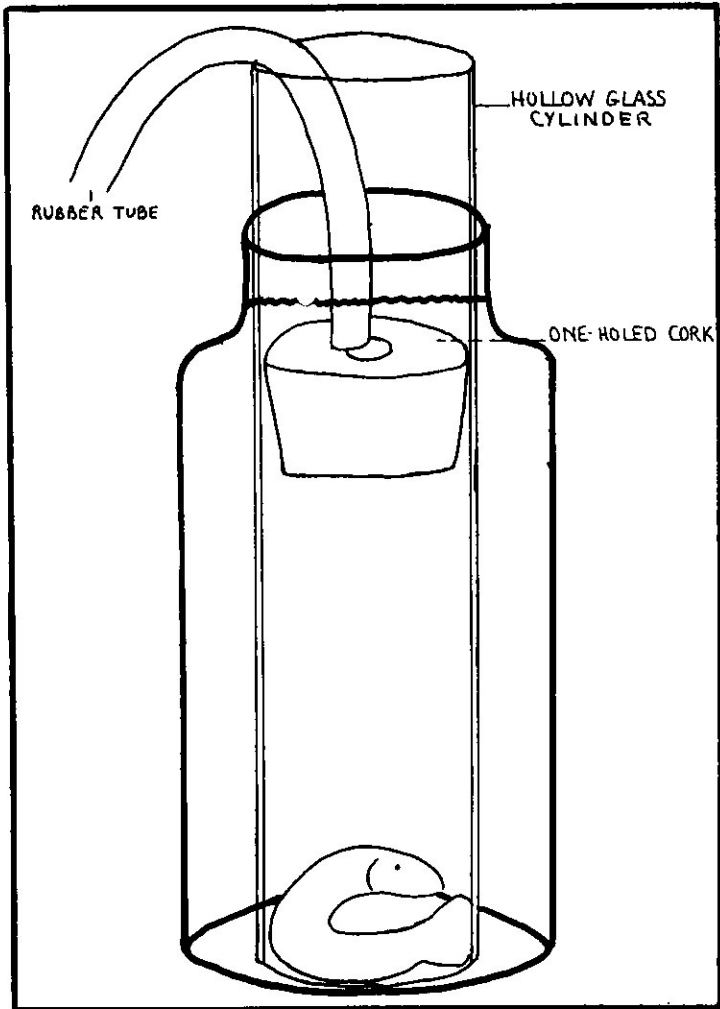


Figure I. Apparatus used for obtaining water sample without permitting mudminnow to gulp air.

the end of the rubber tube in the bottle was kept under the lowering water level by pressing down on the cork. When the samples had been taken, the entire apparatus (Fig. I) was carefully submerged in a water bath, the cork and glass tube were removed, and the fish killed by crushing its head against the side of the bottle. Swimbladder gas was obtained and analyzed as described above. The approximate volume of gas was noted.

The count of respiratory movements per minute was taken just before opening the bottle at the end of the experiment.

RESULTS AND DISCUSSION

A. Fish completely asphyxiated at various carbon dioxide tensions, 19°C.

This type of experiment was devised by Fry and Black (1938) to measure the carbon dioxide tolerance of a number of species of freshwater fish. Of these, the cold water fish (trout, suckers) tend to be most sensitive to carbon dioxide; the stream and lake minnows are moderately sensitive, while the bullhead (*Ameiurus nebulosus*), found in weedy lakes and sluggish rivers, is very hardy, being able to use practically all available oxygen in the presence of up to 200 mm. carbon dioxide (Fry, 1939).

Of some thirty-five species whose carbon dioxide tolerance has been determined only the mudminnow compares with the bullhead in ability to use oxygen in the presence of carbon dioxide. The mudminnow also occurs in sluggish waters, ponds and streams. Figure II shows that the mudminnow, by gill respiration, can use practically all the oxygen in water containing up to 200 mm. carbon dioxide at 19° C. Tensions of carbon dioxide greater than this affect the ability of fish to take the oxygen from the water, *i.e.* the asphyxial oxygen tension for the mudminnow increases when the environmental water contains more than 200 mm. carbon dioxide at 19° C.

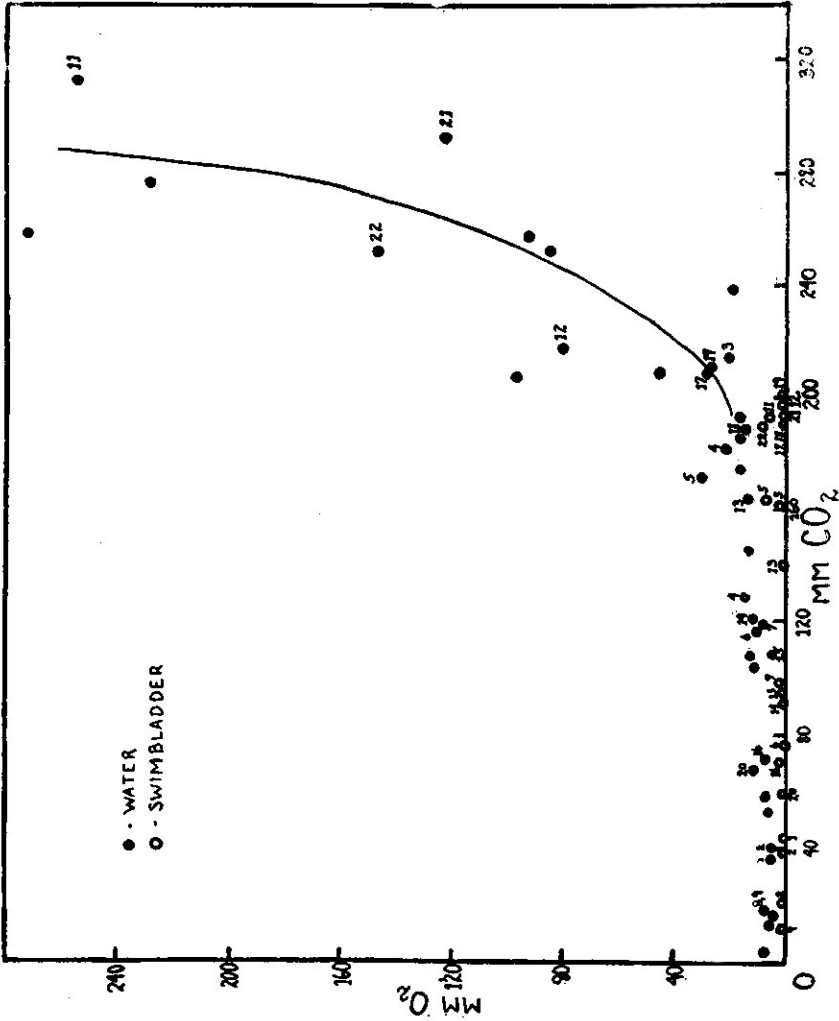


Figure II. The relation between carbon dioxide and oxygen in the water and in the swimbladder of the mudminnow after asphyxiation at 19° C.

During the course of these asphyxiation experiments the proportions of the various constituent gases in the swimbladder of the mudminnow change. The pressure of carbon dioxide normally found in the swimbladder gas of this group of mudminnows was about 9 mm., the average pressure of oxygen was 78 mm. (Table 1). The pressures of these gases in the swimbladder after complete asphyxiation is shown by hollow circles in Figure II. The numbers beside the hollow and solid circles show which gases in the swimbladder and water belong

TABLE 1
SWIMBLADDER GASES OF MUDMINNOWS UNDER "NORMAL" CONDITIONS

No. of Fish	% CO ₂		mm CO ₂ Average	% O ₂		mm O ₂ Average
	Range	Average		Range	Average	
A. Sept., 1942						
19°C. 20	0.8-1.9	1.28	9	3.2-15.9	10.6	78
B. Jan. May, 1944						
20°C. 5	0.3-1.4	0.95	7	11.0-18.8	15.6	116
10°C. 16	0.0-1.5	0.75	6	6.1-19.0	14.0	105

to the same fish. It is apparent from Figure II that practically all of the oxygen in the swimbladder disappears during asphyxiation.

The relation between the carbon dioxide tension in the water and the carbon dioxide pressure in the swimbladder is further analyzed in Figure III. This graph shows that the pressure of carbon dioxide in the swimbladder closely approximates the carbon dioxide tension of the water as long as the fish can remove all of the oxygen from the water. At tensions of carbon dioxide above 200 mm., however, complete equilibration does not take place before asphyxiation.

The disappearance of the oxygen in the swimbladder during asphyxiation is not typical of all species of fish. In Table 2 a comparison is given of the disappearance of swimbladder oxygen in several species of fish. The first group, the

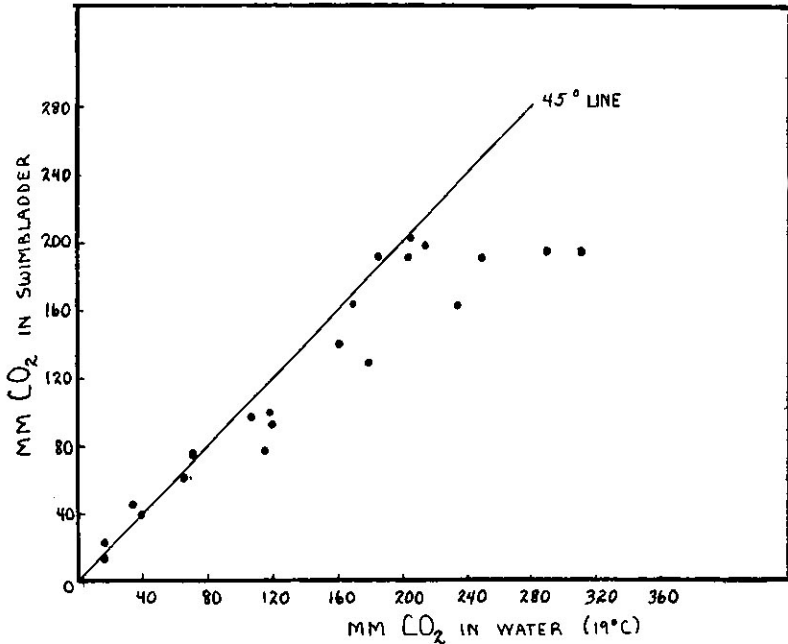


Figure III. Carbon dioxide in the water and in the swimbladder of the mudminnow after asphyxiation at 19° C.

physostomes, possess a swimbladder with a duct opening into the foregut where gas exchange may take place, but equipment for gas exchange between swimbladder lumen and blood appears to be limited in these species of physostomes. The second group, the physoclists, do not have any open duct but all gas exchange for the purpose of adjusting to changes in hydrostatic pressure must take place between the swimbladder and blood. These species possess vascular sections of the swimbladder wall which serve for the deposition and absorption of gases. The third group is represented in Table 2 by the mudminnow which has an open duct and a vascular swimbladder, both of which are essential to fulfill the function of respiration. The average percentages of oxygen found in the swimbladder of asphyxiated fish in this table are compiled from results of experiments at both high and low carbon dioxide tensions. Utilization of swimbladder oxygen was usually greater in the

TABLE 2

CHANGE IN OXYGEN CONTENT OF THE SWIMBLADDER GAS DURING ASPHYXIATION WITH AND WITHOUT CARBON DIOXIDE. AN AVERAGE OF ALL EXPERIMENTS COMPARED WITH THE AVERAGE OF THE CONTROLS

	Control % O ₂	Asphyxiated % O ₂	% Decrease in O ₂
Physostomes (swimbladder not adapted for respiration):			
Creek chub	6.4	8.9	..
Speckled trout	6.0	6.4	..
Common sucker	11.1	9.7	13
Finescale dace	12.1	9.7	20
Brown bullhead	7.5	6.0	20
Physoclists (swimbladder adapted for gas secretion):			
Scup	9.4	7.0	25
Smallmouth bass	26.0	17.6	32
Yellow perch	19.4	10.7	45
Cunner	25.8	13.2	49
Killifish	15.6	7.3	53
Pumpkinseed	21.2	9.7	54
Brook stickleback	19.6	5.6	72
Tautog	51.3	14.6	72
Toadfish	55.0	15.0	73
Sea robin	22.8	3.6	84
Physostome (swimbladder adapted for respiration):			
Mudminnow—19°C	10.6 (20)	0.2 (21)	98

low carbon dioxide range, except in the case of the mudminnow. During asphyxiation the first group of physostomes uses very little oxygen, the physoclists use from 25% to 84% depending on the species (Safford, 1940; Black, 1942), and in the mudminnow an average of 98% of the oxygen in the swimbladder disappears. Even when carbon dioxide in the water prevents complete utilization of oxygen from the water (Nos. 11, 12, 21, 22 in Fig. II) oxygen disappears from the swimbladder of the mudminnow. This lower oxygen pressure in the swimbladder than in the water indicates active respiration of oxygen. It is probable that the difference in the response of

these three groups (Table 2) is due chiefly to the extent of vascular surface exposed to the swimbladder lumen.

Rauther (1914) has shown that there are two reasons why the morphology of the swimbladder of *U. krameri* is better fitted for respiratory function than the swimbladder of most teleosts. Although the physoclists have highly vascular sections (*retia mirabilia*) in the anterior swimbladder wall, *Umbra*, a physostome, has in addition to these, inter-epithelial capillaries, *i. e.* a capillary between almost every epithelial cell over a large portion of the swimbladder wall. This arrangement provides lung-like efficiency for gas exchange between swimbladder and blood. The second morphological feature favoring respiration of swimbladder oxygen is the blood supply to and from the swimbladder. The coeliac artery and intercostal arteries supply respectively the anterior and posterior parts of the swimbladder as is the case for most teleosts. The oxygenated blood leaving the swimbladder, however, is collected in three large veins which unite and empty into the posterior cardinal vein just as it passes into the right Cuvierian duct, which in turn empties directly into the heart. Hence partially oxygenated blood enters and leaves the heart instead of only reduced blood as is the case in fish whose swimbladder is not adapted for respiration. In this latter group of fishes the blood usually leaves the swimbladder by way of the portal vein instead of going directly to the heart.

B. Fish partially asphyxiated at various carbon dioxide tensions, 10° C. and 20° C.

This series of experiments was performed in an attempt to discover how the respiration was divided between gills and swimbladder at various carbon dioxide tensions and at various stages in asphyxiation. As is evident from Tables 3 and 4 there are fairly large individual differences in the results which may be accounted for in part by the fact that activity of the fish in the bottle could not be controlled. There appeared to be no marked correlation in every individual

between oxygen consumption, respiratory rate and pressure of oxygen in the swimbladder. The data have therefore been analyzed on the basis of the *average* results for each group of carbon dioxide tensions.

TABLE 3
RESPIRATION OF MUDMINNOWS AT 20°C.

CO ₂ in Water mm.	Time in Bottle Hours	Weight gms.	O ₂ Consumption ml. O ₂ /kilo/hr.	Resp. Movements at End of Experiment Number per Min.	Swimbladder Gases		Final O ₂ in Water mm.
					CO ₂ mm.	O ₂ mm.	
9.	1.0	9.6	113.0	68	10	82	59
6.	1.5	13.6	77.4	130	8	22	16
1.5	2.5	2.9	24.3	30	11	78	136
2.5	3.3	6.4	68.9	105	7	64	28
0	5.8	2.5	102.5	111	7	38	24
Average:	3.8	7.0	77.2	89	9	57	52
91.	0.83	5.3	55.4	62	74	53	103
92.	1.75	3.4	103.0	60			70
99.	3.0	5.2	66.0	73	83	53	35
112.	3.	5.6	75.0	Irr.	107	10	14
Average:	98.	2.15	74.8	65	88	39	55
146	1.66	2.9	68.6	60	73	45	91
148.	6.0	3.2	52.5	63	116	10	30
Average:	147.	3.83	60.5	62	95	27	60
184.	1.3	3.0	20.4	Irr.	137	11	101
187.	2.5	3.4	19.8	Irr.	132	0	93
Average:	185.	1.9	20.1	...	135	6	97

1. Oxygen consumption from water and swimbladder.

In Figure IV the average oxygen consumptions from the water (A) and from the swimbladder (B) are plotted against the carbon dioxide tension of the water. The data for oxygen consumption from the swimbladder were derived as shown in Table 5. The average volume of the swimbladder for each average weight was taken from Figure V where the approximate volume of gas found in the swimbladder of several fishes is plotted against the weight of the fish. Figure IVB shows that the swimbladder provides only a minute portion of the total oxygen consumed when the oxygen in the swimbladder cannot be continually renewed by gulping air. However, there is a contrast in the effect of carbon dioxide on the utilization of oxygen from the water and from the swimbladder. At high carbon dioxide tensions the oxygen consumption from the water tends to decrease (cf. Hall, 1931) whereas oxygen consumption from the swimbladder, though

small, is greatest at the highest carbon dioxide tension, indicating utilization of swimbladder oxygen when carbon dioxide makes uptake of oxygen from the water difficult.

TABLE 4
RESPIRATION OF MUDMINNOWS AT 10°C.

CO ₂ in Water mm.	Time in Bottle Hours	Weight gms.	O ₂ Consumption ml. O ₂ /kilo/hr.	Resp. Movements at End of Experiment Number per Min.	Swimbladder Gases		Final O ₂ in Water mm.
					CO ₂ mm.	O ₂ mm.	
0.	1.2	10.0	89.0	47	10	92	75
2.5	1.25	11.3	94.0	68
1.5	1.5	2.9	85.0	..	10	78	138
4.6	1.5	2.5	94.0	Irr.	8	140	123
6.5	3.42	9.3	54.4	40
0.	3.5	5.1	49.4	..	3	112	87
0.	4.0	1.2	36.8	135
5.	6.0	6.3	48.0	34
4.	6.3	4.9	54.0	62	8	35	31
4.5	6.7	2.0	34.2	..	3	28	116
5.	8.0	6.1	39.2	..	10	57	27
Average:	3.	3.9	61.6	55	7	77	79
98.	0.75	6.8	18.1	36	76	75	125
83.	1.5	1.9	56.8	72	37	23	128
90.	2.3	2.5	42.1	43	51	68	115
87.	3.5	2.7	50.5	65	50	4	106
87.	5.5	2.0	54.5	60	75	11	97
95.	7.0	2.5	30.4	58	79	27	95
Average:	90.	3.4	42.1	56	61	35	111
111.	0.83	5.6	39.8	45	61	59	110
105.	1.3	1.7	40.8	60	29	81	116
110.	3.75	4.3	51.5	55	68	26	64
109.	4.17	2.5	41.5	57	77	37	92
110.	5.25	3.9	49.2	50	93	44	51
108.	5.75	1.6	38.5	70	72	30	98
115.	7.5	3.7	39.6	50	88	44	44
104.	8.0	9.0	51.0	44	73	19	65
Average:	109.	4.6	43.9	54	70	42	80
135.	1.0	2.5	37.0	36	55	42	119
136.	1.7	4.2	38.4	50	81	87	109
136.	2.25	1.8	46.0	48	63	43	112
147.	3.0	2.3	47.0	48	49	27	102
132.	4.3	3.1	48.8	51	76
145.	6.0	2.7	47.0	46	117	19	70
139.	7.2	3.4	48.4	51	100	65	38
Average:	139.	3.6	44.6	47	77	47	89
164.	0.85	1.9	67.0	50	48	16	120
159.	1.5	1.7	67.0	42	77	24	115
168.	1.5	5.0	10.2	..	53	33	102
157.	2.0	1.2	51.3	0	98	46	119
166.	4.0	5.9	9.5	0	142	21	92
159.	5.5	1.3	49.5	54	105	65	102
Average:	162.	2.5	42.4	29	87	34	106
183.	0.66	4.2	0.0	23	46	39	100
170.	1.25	2.5	0.0	32	46	22	109
Average:	181.	0.9	0.0	27	46	30	109

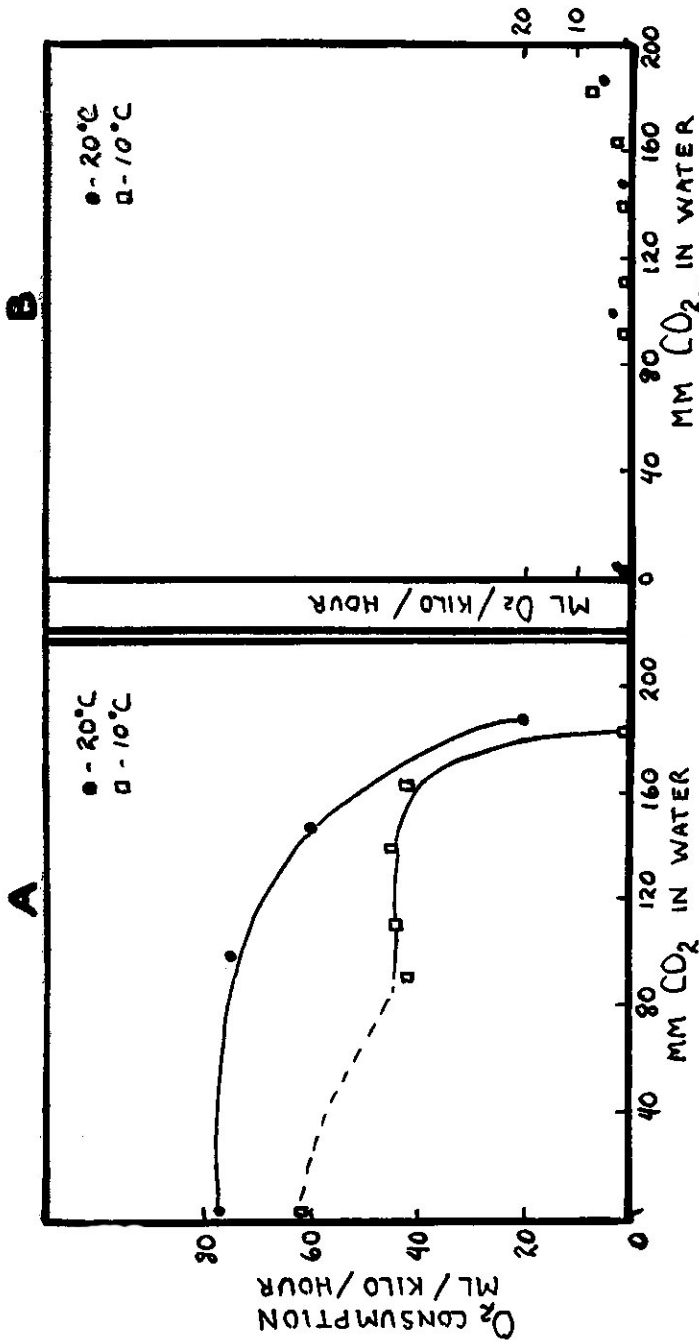


Figure IVA. The average oxygen consumption at the gills of the mudminnow at various carbon dioxide tensions in the water.

Figure IVB. The average oxygen consumption from the swimbladder of the mudminnow at various carbon dioxide tensions in the water.

TABLE 5
OXYGEN CONSUMPTION FROM THE SWIMBLADDER PER KILO
PER HOUR, AT 20°C. AND 10°C.

mm CO ₂ (average) at 20°C.	3.8	98	147	185		
Average weight, gms.....	7.0	4.9	3.1	3.2		
Average volume of swim- bladder (Figure V).....	0.5	0.35	0.18	0.2		
Average normal % O ₂ in swimbladder less average % O ₂ in swimbladder at end of experiment = Δ% O ₂	7.9	10.3	11.9	14.8		
ml. O ₂ used.....	0.04	0.036	0.021	0.03		
ml. O ₂ per kilo.....	5.7	7.3	6.8	9.3		
Average time in bottle, hours.	2.8	2.15	3.83	1.9		
ml. O ₂ /kilo/hour.....	2.0	3.4	1.8	4.9		
mm CO ₂ (average) at 10°C.	3.0	90	109	139	162	181
Average weight, gms.....	5.6	3.1	3.2	2.9	2.8	3.3
Average volume of swim- bladder (Figure V).....	0.4	0.18	0.2	0.17	0.16	0.2
Δ % O ₂ in swimbladder....	3.7	9.3	8.4	7.7	9.5	10.0
ml. O ₂ used.....	0.015	0.017	0.017	0.013	0.015	0.02
ml. O ₂ per kilo.....	2.6	5.4	5.2	4.6	5.4	6.1
ml. O ₂ /kilo/hour.....	0.7	1.6	1.1	1.3	2.2	7.1

2. *Exchange of carbon dioxide and oxygen to and from the swimbladder at known tensions of carbon dioxide in the water.*

To obtain comparable values for the pressure of carbon dioxide in the swimbladder at various tensions of carbon dioxide in the water, the average carbon dioxide pressure for each group of carbon dioxide tensions (Tables 3 and 4) was divided by the average weight of fish and average time of exposure to give the carbon dioxide pressure per gram per hour. These values are plotted in Figure VIA. There is a definite increase in the rate of entrance of carbon dioxide into the swimbladder at increased carbon dioxide tensions.

The rate of disappearance of oxygen from the swimbladder was obtained by calculating the average difference in oxygen pressure in the swimbladder per gram per hour

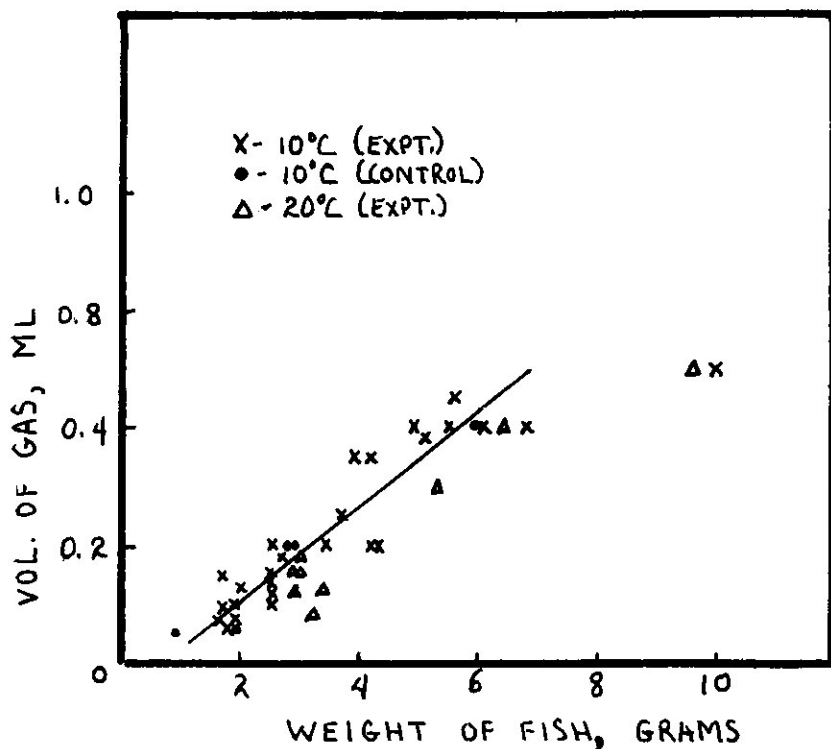


Figure V. The relation between body weight of the mudminnow and volume of gas in the swimbladder.

(Table 6). Differences in oxygen tension of the water are also plotted in Figure VIB. At both 20° C. and 10° C. the amount of oxygen taken from the water per gram per hour decreases as the carbon dioxide in the water is increased. Rate of oxygen utilization from the swimbladder, however, increases with increase in the carbon dioxide tension of the water. It is noteworthy that points which are out of line in Figure VIB are also out of line in the same direction in Figure VIA. This indicates that the rate of exchange of carbon dioxide is related to the rate of exchange of oxygen, a fact which is apparent also when the values for rate of entrance of carbon dioxide are compared with values of rate of disappearance of oxygen (Fig. VI). All experiments (Fig. II, Tables 3 and 4)

indicate that the oxygen in the swimbladder is determined to a greater extent by the requirements of the fish than by the tension of oxygen in the water. When the carbon dioxide in the water is high, the necessity for using oxygen in the swim-

TABLE 6
AVERAGE DIFFERENCE IN MM O₂ IN WATER AND IN SWIMBLADDER
PER UNIT TIME (HOUR) AT 20°C. AND 10°C.

mm CO ₂ (average) at 20°C.	3.8	98	147	185		
Average initial O ₂ in water (mm.)	153.0	124.0	120.0	109.0		
Average final O ₂ in water (mm.)	52.0	55.0	60.0	97.0		
Δ mm. O ₂ in water	101.0	69.0	60.0	12.0		
Average weight in gms.	7.0	4.9	3.1	3.2		
Average time in bottle (hours)	2.8	2.15	3.83	1.9		
Δ mm. O ₂ in water per gram per hour	5.1	6.5	5.0	2.0		
Average initial mm. O ₂ in swimbladder	116.0	116.0	116.0	116.0		
Average final mm. O ₂ in swimbladder	57.0	39.0	27.0	6.0		
Δ mm. O ₂ in swimbladder	59.0	77.0	89.0	110.0		
Δ mm. O ₂ in swimbladder per gram per hour	3.0	7.4	7.1	18.1		
mm CO ₂ (average) at 10°C.	3	90	109	139	162	181
Average initial O ₂ in water (mm.)	154.0	135.0	123.0	124.0	122.0	109.0
Average final O ₂ in water (mm.)	79.0	111.0	80.0	89.0	108.0	109.0
Δ mm. O ₂ in water	75.0	24.0	43.0	35.0	14.0	0.0
Average weight in gms.	5.6	3.1	3.2	2.9	2.8	3.3
Average time in bottle (hours)	3.9	3.4	4.6	3.6	2.5	0.85
Δ mm. O ₂ in water per gram per hour	3.4	2.3	2.9	3.4	2.0	0.0
Average initial mm. O ₂ in swimbladder	105.0	105.0	105.0	105.0	105.0	105.0
Average final mm. O ₂ in swimbladder	77.0	35.0	42.0	47.0	34.0	30.0
Δ mm. O ₂ in swimbladder	28.0	70.0	63.0	58.0	71.0	75.0
Δ mm. O ₂ in swimbladder per gram per hour	1.3	6.6	4.3	5.5	10.1	26.8

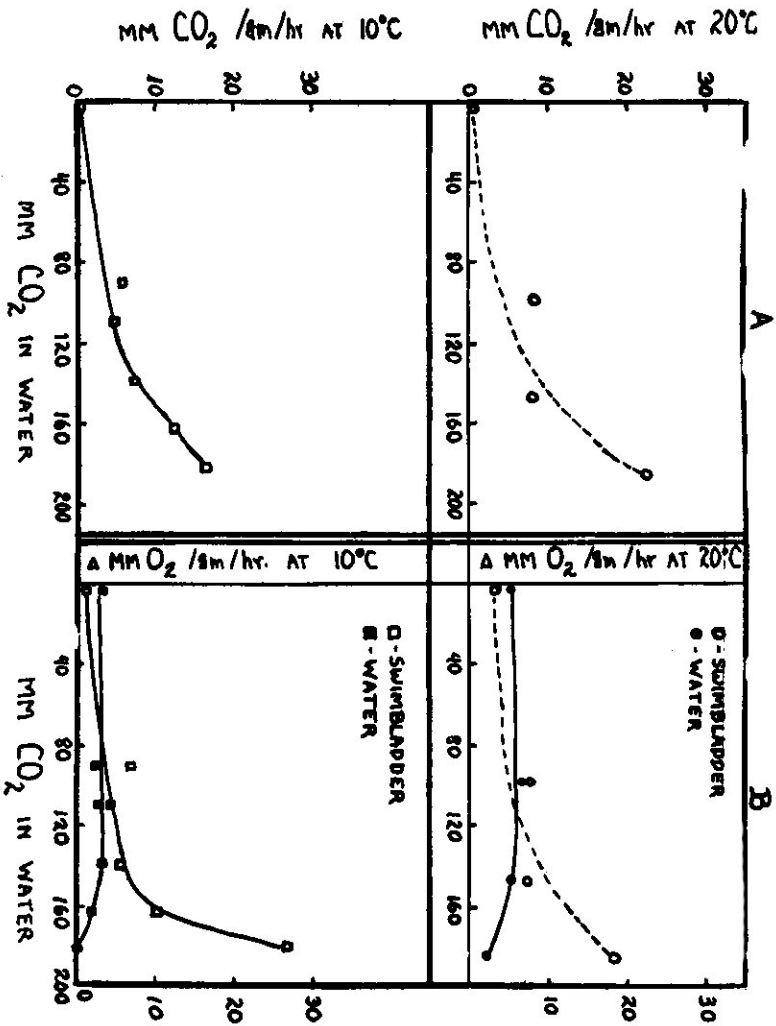


Figure VI. The average rate of gas exchange at the swimbladder of the mudminnow at various carbon dioxide tensions of the water.

A. Entrance of carbon dioxide into the swimbladder.

B. Utilization of oxygen from the swimbladder and from the water.

bladder early in the experiment becomes great and the lost oxygen is replaced by carbon dioxide.

The ability of the mudminnow to use oxygen from the swimbladder even when oxygen uptake at the gills is inhibited by the carbon dioxide tension of the water may be accounted for by the fact that the carbon dioxide in the swimbladder had not increased enough to inhibit oxygen uptake there. Even in the first set of experiments where asphyxiation was complete, the carbon dioxide in the swimbladder never exceeded 200 mm., the tension at which carbon dioxide begins to impair the ability of the mudminnow to extract oxygen from the water. At the highest carbon dioxide tensions the respiratory movements were irregular and sometimes stopped completely when the fish was first put into the bottle. It is conceivable that the fish was drawing on the swimbladder oxygen at such times.

3. Use of swimbladder oxygen at various stages of asphyxiation.

By examining Tables 3 and 4 it is difficult to ascertain exactly when, in the process of asphyxiation, the mudminnow draws most heavily on the oxygen in the swimbladder. In general, however, about half (or more) of the swimbladder oxygen has been used within the first hour of the experiment at both 10° and 20° when the fish is asphyxiated in the presence of carbon dioxide (90 mm. to 185 mm.). Even though the mudminnow is able, by gill respiration, to use all available oxygen up to 150 mm. carbon dioxide in the water (10° fish are more sensitive to carbon dioxide than 20° fish), respiration of swimbladder oxygen at carbon dioxide tensions in the water of 90 mm., or perhaps even less, indicates that the fish is conscious of its abnormal environment. However, when the fish is asphyxiated by lack of oxygen only, the oxygen in the swimbladder remains fairly high until the fish has lowered the oxygen in the water to about 50 mm.

Further analysis of the course of asphyxiation by oxygen lack is afforded by comparing the CO_2/O_2 ratio of the swimbladder gas of normal fish, derived from Table 1, with the same ratio for fish in various stages of asphyxiation. This comparison is made in Table 7A. The quotient tends to be greater when the oxygen tension in the water is very low, a result caused mainly by a decrease in oxygen in the swimbladder.

TABLE 7A

THE CO_2/O_2 RATIO OF THE SWIMBLADDER GAS OF THE MUDMINNOW UNDER NORMAL CONDITIONS AND DURING ASPHYXIATION BY LACK OF OXYGEN

Average Normal CO_2/O_2 Ratio

10°C.....	0.053
19°C.....	0.120
20°C.....	0.061

Individual Ratios for Fish at Decreasing Oxygen Tensions

	Oxygen Tension of the Water mm.	Swimbladder Gas CO_2/O_2 Ratio
20°C.....	136.	0.141
	59.	0.122
	28.	0.109
	24.	0.184
10°C.....	16.	0.364
	138.	0.128
	123.	0.057
	116.	0.107
	87.	0.027
	75.	0.109
	31.	0.230
	27.	0.175

There is, however, no gradual decrease in the ratio with decrease in oxygen tension of the water. This situation indicates that the use of oxygen from the swimbladder of the mudminnow is governed largely by the requirements of the fish, rather than the oxygen tension of the water.

CO_2/O_2 quotients for fish asphyxiated in the presence of carbon dioxide also increase at the lowest oxygen tensions in the few experiments at 20° C. At 10° C., however, there is little correlation between the ratio and the oxygen tension

of the water although the highest quotients are at medium or low oxygen tensions. In Table 7B the ratios for the average carbon dioxide and oxygen tensions in the swimbladder are recorded for each group of carbon dioxide tensions. The higher quotients at 20° C. are a result of both greater carbon dioxide and lower oxygen in the swimbladder, indicating a faster rate of exchange at the higher temperature.

TABLE 7B

THE CO₂/O₂ RATIO OF THE SWIMBLADDER GAS CALCULATED FROM THE AVERAGE PRESSURES FOR EACH GROUP OF CARBON DIOXIDE TENSIONS (TABLES 3 AND 4).

Average mm. CO ₂ in H ₂ O	3.4	90	98	109	139	147	162	181	185
20°C.....	0.16	2.25	3.5	22.5
10°C.....	0.09	1.74	1.67	1.64	2.56	1.53

SUMMARY

Mudminnows were completely asphyxiated in sealed bottles of water, each containing a known tension of carbon dioxide and at least 100 mm. of oxygen. After all respiratory movements of the fish had ceased the water in the bottle and gas in the swimbladder were analyzed for carbon dioxide and oxygen. The ability of the fish to use the oxygen in the water was not impaired by carbon dioxide at 19° C. until over 200 mm. were present in the water. In these experiments practically all the oxygen disappears from the swimbladder even when the carbon dioxide prevents complete utilization of the oxygen in the water. The carbon dioxide in the swimbladder increases during the experiment and after asphyxiation is approximately equal to the carbon dioxide tension in the water at tensions below 200 mm.; above 200 mm. carbon dioxide equilibration was not reached before asphyxiation occurred.

Another series of experiments was made in which the bottles containing the fish were opened after different lengths

of time but in all cases the fish was still alive. When the swimbladder gas cannot be renewed by gulping air, as was the case in all experiments, oxygen consumption per unit weight and time from the swimbladder constitutes an extremely small portion of the total oxygen consumption but is greatest at the highest carbon dioxide tensions, whereas oxygen consumption from the water is least at the highest carbon dioxide tensions. The rate of exchange of carbon dioxide and oxygen increased as the carbon dioxide in the water was increased, i.e. more carbon dioxide entered and more oxygen left the swimbladder per unit time when the carbon dioxide tension in the water was high. The CO_2/O_2 ratio in the swimbladder during asphyxiation with and without carbon dioxide tends to be greater than the normal ratio as a result of increase in carbon dioxide and loss of oxygen.

These experiments give evidence of the facility of gas exchange which makes the swimbladder of the mudminnow a valuable supplementary organ for respiration.

REFERENCES

- Black, V. S. The effect of asphyxiation under various tensions of carbon dioxide on the swimbladder gases of some fresh water fish. *Can. Jour. Res.*, **20**: (D): 209-219. 1942.
- Fry, F. E. J. The position of fish and other higher animals in the economy of lakes. *Am. Assoc. for the Adv. of Sci.*, Publ. No. 10: 132-142. 1939.
- Fry, F. E. J. and E. C. Black. The influence of carbon dioxide on the utilization of oxygen by certain species of fish in Algonquin Park, Ontario. *Anat. Rec.*, **72**: Supplement: 47. 1938.
- Geyer, F. and H. Mann. Die Atmung des ungarischen Hundsfisches (*Umbra lacustris* Grossinger). *Zool. Anz.*, **127**: 234-245. 1939.
- Geyer, F. and H. Mann. Beitrage zur Atmung der Fische. II. Weiteres zur Atmung des ungarischen Hundsfisches (*Umbra lacustris* Grossinger). *Zool. Anz.*, **127**: 305-312. 1939.
- Hall, F. G. The respiration of puffer fish. *Biol. Bull.*, **61**: 457-467. 1931.
- Krogh, A. On micro-analysis of gases. *Skan. Arch. f. Physiol.*, **20**: 279-288: 1908.

Rauther, M. Über die respiratorische Schwimmblase von *Umbra*
Zool. Jahrb., 34: 339-364. 1914.

Safford, Virginia. Asphyxiation of marine fish with and without
CO₂ and its effect on the gas content of the swimbladder.
Jour. Cell. Comp. Physiol., 16: 165-173. 1940.