RESPIRATION OF AN AIR-BREATHING CATFISH
CLARIAS BATRACHUS (LINN.)

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INTRODUCTION

The Asian species of air-breathing catfish, *Clarias batrachus*, lives in freshwater pools which usually have low O_2 and high CO_2 content and may also dry up during summer. Like several other fishes, this species has an air-breathing organ which functions in direct gas exchange with the atmospheric air. Munshi (1961) made a detailed study of the structure of the respiratory organs and also described the mechanism of ventilation. The accessory organs chiefly comprise (*a*) the supra-branchial chambers situated dorsally to the gill cavities and lined by the respiratory membrane, (*b*) the fan or gill plates borne on each arch and (*c*) the respiratory tree or dendritic plates borne by the second and fourth gill arches.

The African species (*C. lazera*) seems unable to obtain enough O_2 via the gills alone for long periods even when submerged in air-saturated water, as it died after 14–17 h (Moussa, 1957). Recently it has been observed that *Anabas testudineus* and *Saccobranchus fossilis* can survive in air-saturated water, exchanging gases with water alone for 6–8 h or for longer in *Saccobranchus*, without showing much sign of stress or struggling (Hughes & Singh, 1970, 1971). Moreover, *Saccobranchus* can survive even in hypoxic water (P_{O_2} 50–110 mmHg), depending on aquatic respiration alone. Since *Clarias batrachus* and *Saccobranchus fossilis* occur in similar habitats, often sharing the same ponds, it is of interest to compare their respiratory behaviour and gas exchange. The experiments were also designed to find out the suitability of this animal for life in water and on land under various environmental conditions.

MATERIALS AND METHODS

Live specimens of magur (*Clarias batrachus*) were collected in India and transported by air to England in Polythene bags containing water and charged with O_2. The fishes were kept in large aquaria at 25 ± 1 °C and acclimated to laboratory conditions. They were fed at regular intervals with tropical fish food and meat. Oxygen uptake ($\dot{V}_{O_2}$) and CO_2 release from water and/or air were measured by methods similar to those previously described (Hughes & Singh, 1970, 1971). The P_{O_2} measurements in water were made using a Beckman O_2 macroelectrode with a 160 physiological gas analyser. O_2 and CO_2 contents in air were determined using a 0·5 ml Scholander gas analyser. A total of 12 fish were used and some experiments were repeated using the same individuals under similar conditions. All experiments were carried out at 25 ± 1 °C.

RESULTS

Clarias batrachus is an obligate air-breather, coming to the water surface at irregular intervals to gulp air. Intervals between air breaths usually vary between 2 and 20 min, in relation to the O_2 content of the water and of the air. When exchanging gases with normal tap water and air, the opercular frequencies are 24–32/min but their amplitude is very low. In air of low O_2 content (5–10 vols %), air-breathing frequencies increase and the intervals vary from 15 sec to 5 min. When the fish is given free access to N_2 but maintained in air-saturated water, the air-breathing intervals are reduced to between 20 sec and 2 min, especially 7–8 h after the beginning of an experiment. Moreover, the fish often repeats a nitrogen breath as if 'not satisfied'.

When prevented from surfacing, *Clarias* can survive in air-saturated water for at least 6–8 h without showing many signs of stress or struggling. The opercular frequency and amplitude increase during such submersion. When exposed to air, *Clarias* breathes quietly for 5–6 h; the air-breathing intervals are irregular during this period.

$\dot{V}_{O_2}$ in water when access to air prevented

(a) *Air-saturated water*. The fish were a little restless at the start of an experiment but quickly settled down following attempts to gain access to the air. The opercular frequencies increased (38–50/min) as did their amplitude. Individual variations in frequency and amplitude were also observed. The fish can live under resting conditions, breathing water alone, for 6–8 h. During the later part of some experiments the fish started struggling and rising to the air tube apparently in search of air. The mean $\dot{V}_{O_2}$ of six fishes was 64·9 cc/kg/h (Table 1); there was no good correlation between the weight of the fish (80–157 g) and the O_2 consumption/gm.

(b) $\dot{V}_{O_2}$ *via skin in air-saturated water*. The mean rate of O_2 consumption through the skin was 10·71 cc/kg/h. As deduced from the total $\dot{V}_{O_2}$ in air-saturated water, $\dot{V}_{O_2}$ via the skin constitutes about 16·6 % of the total, and the remainder occurs via the gills when the fish is not allowed free access to air.

(c) $\dot{V}_{O_2}$ *in a continuous flow of hypoxic water*. When *Clarias* is kept in hypoxic water with access to air prevented, the frequency and amplitude of gill ventilation increase considerably (Fig. 1). $\dot{V}_{O_2}$ in nearly 50 % saturated water is reduced to almost half that in fully saturated water. At a WP_{O_2} of 40 mmHg, $\dot{V}_{O_2}$ is reduced to 16·9 cc/kg/h. The amplitude of the ventilatory movements becomes very marked and the fish begins to struggle and rises repeatedly to the air tube.

If after breathing hypoxic water (WP_{O_2}, about 40 mmHg) for about 1 h the fish chamber is flushed with air-saturated water, the opercular amplitude and frequency return to normal (32–40/min) in 5–7 min as the fish comes to rest.

(d) $\dot{V}_{O_2}$ *from still water in a closed chamber*. The effect of gradual hypoxia is clearly seen under such conditions with the fish breathing water alone. About ½ h after having made unsuccessful attempts to gain access to the air, the fish rests at the bottom of the respirometer breathing water as WP_{O_2} is gradually reduced to 70–80 mmHg. Below this level the fish becomes restless and struggling increases with further decline in WP_{O_2}. $\dot{V}_{O_2}$ is reduced from 95·6 cc/kg/h at 151 mmHg to 44·0 cc/kg/h at 70 mmHg.

When the fish was given free access to air after WP_{O_2} had been gradually reduced to about 32 mmHg it took several air breaths within a few minutes. After such re-

peated air breaths, it stopped water-breathing for some time but later continued with a normal pattern of aquatic and aerial respiration.

It is of interest that, when the fish is subjected to gradual hypoxia in a closed respirometer, $\dot{V}_{O_2}$ is slightly raised (Fig. 2) compared to its level at the same WP_{O_2} in a continuous flow system (Fig. 1). The opercular frequency and amplitude of breathing increase under gradual hypoxia in a closed respirometer (Fig. 2).
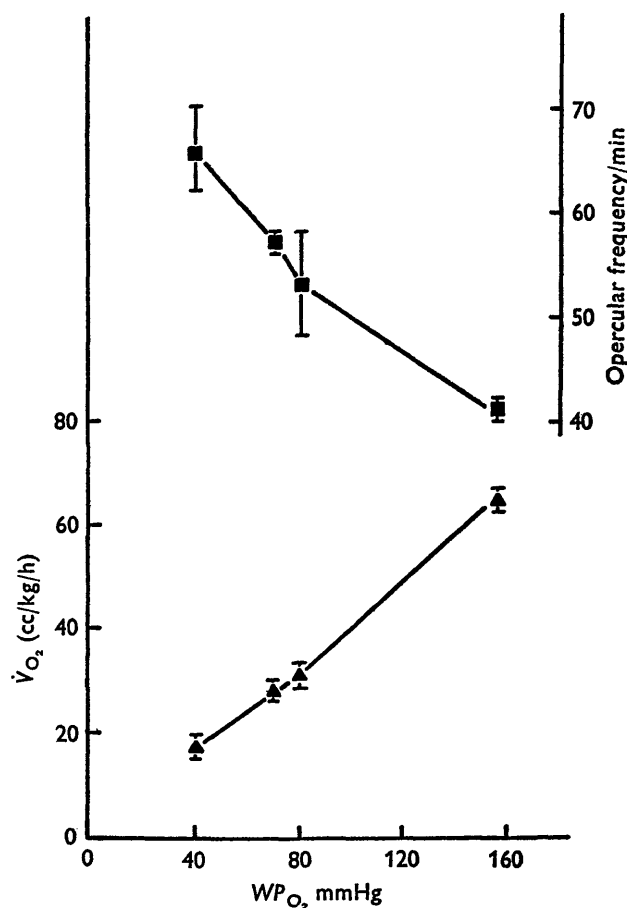

Fig. 1. Reductions in the rate of O_2 consumption (▲) with lowering of O_2 tension in water. The opercular movements (■) and the depth of gill ventilation increase in low O_2 tension but the effect of hypoxia is quite apparent throughout the range (156–40 mmHg WP_{O_2}) studied. The range of the determinations at each WP_{O_2} level are given in each case.

$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ in air-saturated water with free access to air

The mean $\dot{V}_{O_2}$ from air and water is 93·3 cc/kg/h; the fish consuming more O_2 via the air-breathing organs (58·4 %) than from water (41·6 %) (Table 1). However, in one fish, which became very active during the experiment, $\dot{V}_{O_2}$ increased to about 170 cc/kg/h during a period of observation (Table 1) as compared with its mean resting $\dot{V}_{O_2}$ of 97·14 cc/kg/h. The amount of O_2 obtained from air (63·14 %) was still greater than from water (36·86 %) during this active period. Opercular frequency rose to 56–60/min and the amplitude of the gill ventilatory movements was very great. Air-breathing intervals were much reduced.

The rate of CO_2 release ($\dot{V}_{CO_2}$) to the air from the air-breathing organs was $5 \cdot 88$ cc/ kg/h. The gas-exchange ratio for aerial respiration was only $0 \cdot 11$. The amount of CO_2 released into the water was not determined as it was not possible to measure the small changes in CO_2 content of the water circulated through the respirometer.
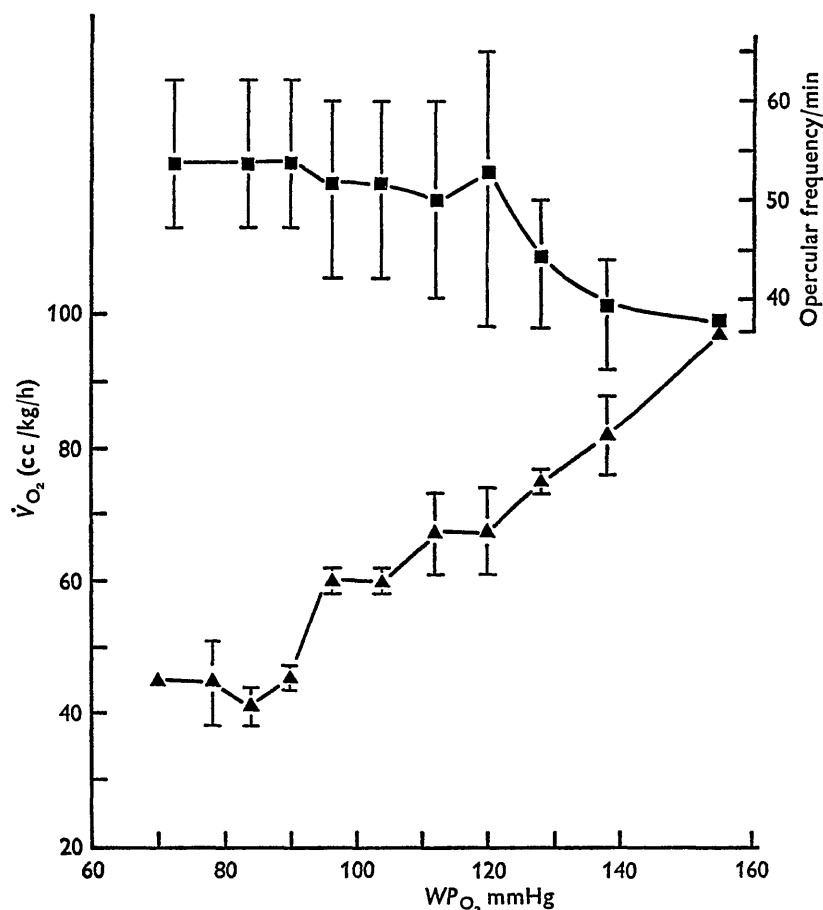

Fig. 2. Dependent form of respiration in water in a closed chamber when *Clarias* is prevented from surfacing. $\dot{V}_{O_2}$ (▲) is lowered throughout a WP_{O_2} range between 70–155 mmHg, although the frequency of opercular movements (■) and the amplitude of breathing are increased at low O_2 tensions. However, significantly different rates of O_2 consumption at the same WP_{O_2} are found in a continuous flow of water (Fig. 1) and the closed system (Fig. 2). Range of determinations in each case is also given at different O_2 tensions.

$\dot{V}_{O_2}$ *and* $\dot{V}_{CO_2}$ *of air-exposed fish*

When *Clarias* is exposed to air, $\dot{V}_{O_2}$ is $71 \cdot 17$ cc/kg/h (Table 1). Measurements were made after about $\frac{1}{2}$ h when the fish had settled in a closed air respirometer. The fish consumed a little more O_2 during the first $1\frac{1}{2}$ h when aerial P_{O_2} was 134–152 mmHg (Fig. 3). In the later part of the experiment it consumed a nearly constant level of oxygen at P_{O_2} between 134 and 79 mmHg (Fig. 3). During the $5\frac{1}{2}$–6 h of observation the P_{CO_2} in the closed respirometer gradually increased from 7 mmHg to $52 \cdot 4$ mmHg as a result of breathing and rebreathing the same air, but the increased CO_2 levels did not appear to have any marked effect on the $\dot{V}_{O_2}$ of this fish (Fig. 3).

The mean rate of CO_2 release appears to be related to the rate of O_2 consumption

Table 1. *Summary of results obtained for the rate of oxygen consumption and carbon dioxide release in* Clarias batrachus *when exposed to different experimental conditions*

(The values in parentheses indicate range of determinations and percentage values represent mean percentage O_2 uptake from water and air.)

Body weight (g)	Experimental conditions	$\dot{V}_{O_2}$ from water (cc/kg/h)	$\dot{V}_{O_2}$ from air (cc/kg/h)	Total mean $\dot{V}_{O_2}$ (cc/kg/h)	$\dot{V}_{CO_2}$ in air (cc/kg/h)	RQ Water	RQ Air	RQ Total	References
99.0 (87.0–105.0)	Air-saturated water (cont. flow) with access to air	38.85 (22.2–58.8) 41.60%	54.54 (38.95–76.76) 58.40%	93.39	5.88 (3.12–12.60)	?	0.11	?	Hughes & Singh (1970)
105	*Air-saturated water (cont. flow) with access to air	62.40* (58.80–66.01) 36.86%	106.88* (99.42–121.23) 63.14%	169.28*	—	—	—	—	Hughes & Singh (1971)
116.3 (80.7–157.0)	Air-saturated water (cont. flow) surfacing prevented	64.94 (58.45–75.60)	—	64.94	—	—	—	—	Present authors
88.5 (87–90)	Still water, surfacing prevented	60.85 (57.52–64.15)	—	60.85	—	—	—	—	
83.76 (76.0–88.0)	Air (kept moist)	—	71.17 (63.76–78.70)—	71.17	37.47 (16.00–66.78)	—	0.52	0.52	
114.0 (100.0–128.0)	Deoxygenated water; access to still air	—	40.84 (22.04–76.00)	40.84	17.24 (5.00–33.00)	—	0.51	0.51	

* When fish becomes active for few hours.   ? Not determined.

Table 2. $\dot{V}_{O_2}$ *in different experimental respiratory media of three air-breathing teleosts studied at* $25 \pm 1\ °C$

Species	$\dot{V}_{O_2}$ (cc/kg/h)				Quotient between $\dot{V}_{O_2}$					References
	Air and water	Water (cont. flow)	Air (air-exposed)	Air (de-O_2 water)	$\dfrac{\text{Water}}{\text{Air+water}}$	$\dfrac{\text{Air}}{\text{Air+water}}$	$\dfrac{\text{Air (de-}O_2\text{ water)}}{\text{Air+water}}$	$\dfrac{\text{Water}}{\text{Air}}$	$\dfrac{\text{Air (de-}O_2\text{ water)}}{\text{Air-exposed}}$	
Anabas testudineus	113.42	75.50	104.78*	132.83*	0.67	0.92	1.17	0.72	1.27	Hughes & Singh (1970)
Saccobranchus fossilis	84.50	66.35	54.50	35.09	0.79	0.64	0.42	1.22	0.64	Hughes & Singh (1971)
Clarias batrachus	93.39	64.94	71.17	40.84	0.69	0.76	0.44	0.91	0.57	Present authors

* Active state.

at a particular time of observation during 5–6 h of exposure (Fig. 3). Mean $\dot{V}_{CO_2}$ was 34·77 cc/kg/h at an RQ of 0·52 (Table 1).

Of the five fishes that were exposed to air on one or more occasions for periods of 5–6 h, none showed signs of restlessness when kept in moist conditions. Considerable changes in skin coloration were found in most individuals, particularly in the later part of an experiment. Two fish died 24 h after having been returned to water following
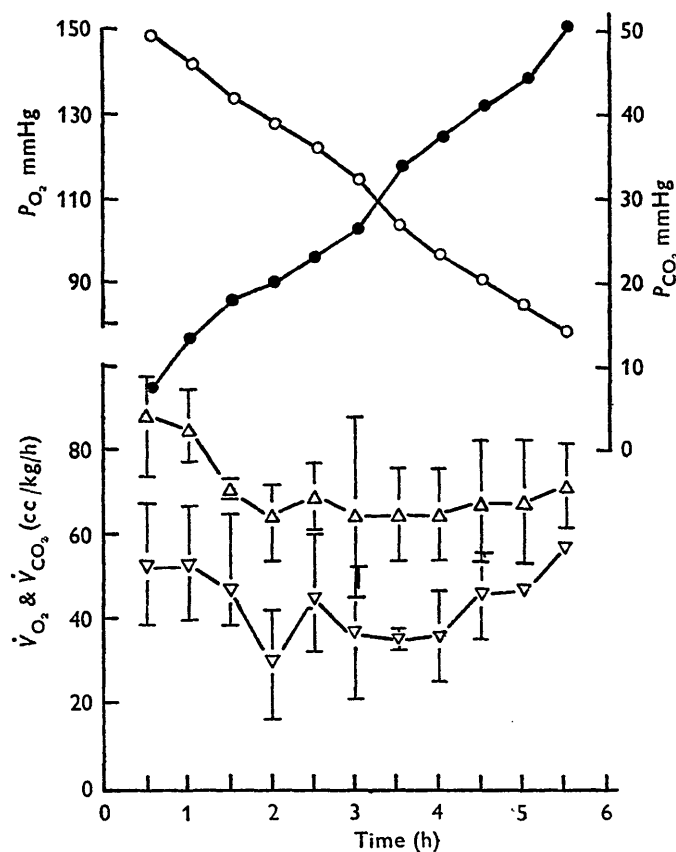

Fig. 3. The rate of O_2 consumption ($\triangle$) and CO_2 elimination ($\triangledown$) in the air-exposed fish over a period of about 6 h in a closed respirometer. The fish consumes little more O_2 in the first 1½ h but later $\dot{V}_{O_2}$ is levelled at about 65–70 cc/kg/h. $\dot{V}_{CO_2}$ shows a clear dependence on $\dot{V}_{O_2}$ throughout the observations. The P_{O_2} (O) in the closed air-space declined from about 150–80 mmHg and P_{CO_2} (●) rose to about 51·5 mmHg, but neither of these appear to have any marked effect on $\dot{V}_{O_2}$. The range of determinations at each ½ h is given for $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ and only mean values are plotted for P_{O_2} and P_{CO_2}.

a 5–6 h period of air exposure. There appeared to have been considerable damage to the skin of these fish which might have been due to the long periods of exposure to air. The remainder of the fish survived for at least several months when returned to water after air exposure.

$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ from still air of fish in deoxygenated water

When Clarias is kept in still deoxygenated water with free access to air, in a closed respirometer, its $\dot{V}_{O_2}$ is very much reduced (mean = 40·84 cc/kg/h) (Table 1). The air-breathing frequencies increased markedly when the P_{O_2} of the air was below

80 mmHg. But it was observed that *Clarias* can live for 4–5 days or more in nearly deoxygenated water so long as it is free to come to the water surface and breathe air.

$\dot{V}_{CO_2}$ from air is low (17·24 cc/kg/h) when a fish was kept in deoxygenated water. $\dot{V}_{CO_2}$ decreased from the beginning of an experiment as is clear in Fig. 4. The fish consumes less O_2 at the lower levels of P_{O_2} and the amount of CO_2 released decreases. It is interesting to find that the resulting gas-exchange ratio with air was 0·51, which is almost identical with the value obtained for fish exposed to air (Table 1).
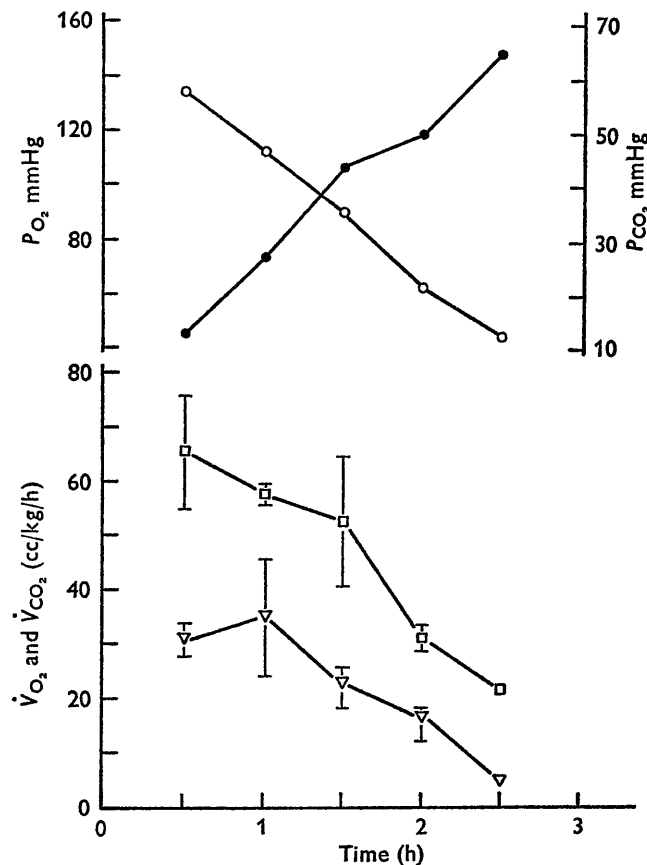

Fig. 4. $\dot{V}_{O_2}$ (□) and $\dot{V}_{CO_2}$ (∇) plot in fish living in deoxygenated water but given free access to still air. $\dot{V}_{O_2}$ in this condition is sharply reduced after P_{O_2} (○) has fallen below 80 mmHg and P_{CO_2} (●) raised above 45 mmHg as a result of breathing and rebreathing of still air. The fish shows a dependent form of respiration in such a condition, which is markedly different when it is exposed to the air (Fig. 3).

DISCUSSION

The present study has shown how *Clarias batrachus* can survive some of the respiratory stresses which it might encounter in its normal environment. Survival is achieved in several ways; for example, by lowering the total metabolic rate when exposed to air or completely immersed in water (Table 2), or modifying the pattern and depth of its ventilatory movements. The relative rates of O_2 uptake, and CO_2 release through the gills and air-breathing organs may also change in air or water. Changes in O_2 uptake and CO_2 release by these routes can be related to their suitability

as respiratory media. Similar adjustments in metabolic rate have been found in other air-breathing fishes such as *Anabas* (Hughes & Singh, 1970) and *Saccobranchus* (Hughes & Singh, 1971).

In *A. testudineus*, *C. batrachus* and *S. fossilis*, the total $\dot{V}_{O_2}$ is reduced in fish prevented from surfacing in air-saturated water. The total $\dot{V}_{O_2}$ under water at 25 °C is 64·94 cc/ kg/h in *Clarias*, which is very close to the values obtained for *Anabas* (75 cc/kg/h), *Saccobranchus* (66·5 cc/kg/h) and in water-breathing fishes such as the bluegill sunfish, rainbow trout, and brown bullhead catfish (about 70 cc/kg/h) by Marvin & Heath (1968). However, the figures obtained for the rainbow trout by other authors have been lower than this (Hughes & Saunders, 1970). Lowering of the total $\dot{V}_{O_2}$ when these air-breathing fishes are submerged may be related to the thickness of the gill epithelium and their smaller surface area, but also the fish is less active because it does not come to the surface.

Munshi & Singh (1968) reported a very high haemoglobin content in the blood of *Clarias batrachus* and *Saccobranchus fossilis* and a few other air-breathing teleosts. Some preliminary determinations of the O_2 capacity of the blood of *Clarias* and *Saccobranchus* have shown that the O_2 capacity of the blood in these fishes is indeed high (*Clarias*, about 18·0 vols % and *Saccobranchus*, 17·5 vols %) (unpublished observations). This similarity in an important respiratory characteristic of the blood indicates that features of the water/blood pathway are important factors reducing the rate of O_2 transfer from water in the gills of *Clarias* relative to *Saccobranchus*.

From Table 3 of *Saccobranchus* (Hughes & Singh, 1971) it can be seen that among both air-breathing teleosts and lungfishes the amount of O_2 entering from the water (via the gills and/or skin), and from air (via the air-breathing organs and/or skin), vary a great deal in different species. This variation appears to be related to the nature and development of the gills and air-breathing organs and also to the ability of the skin to participate in gaseous exchange. As mentioned earlier, about 16 % of the total $\dot{V}_{O_2}$ occurs through the skin and 84 % by the gills in both *Clarias* and *Saccobranchus* when exchanging gases with air-saturated water alone (Table 3).

The effect of hypoxia in water is quite apparent in *Clarias* between tensions of 80–150 mmHg when the fish is breathing in a closed chamber (Fig. 2). The effect is also clear in a continuous flow of hypoxic water (Fig. 1). Dependent aquatic respiration is also found in *Anabas* (Hughes & Singh, 1970) but *Saccobranchus* shows an independent respiration in water (Hughes & Singh, 1971). This similarity in behaviour during hypoxia of *Clarias* and *Anabas* is shown in Fig. 5 by the graph for the three species measured under similar conditions. The more linear decline in WP_{O_2} with time in *Saccobranchus* is similar to that found in *Electrophorus* by Farber & Rahn (1970).

It is interesting to notice the slightly different effects of hypoxic water on *Clarias* by these two methods, i.e. still water in a closed respirometer and a continuous flow of hypoxic water (Figs. 1, 2). In rainbow trout, $\dot{V}_{O_2}$ changes with different O_2 tensions in water and has been shown to be related to the rate at which WP_{O_2} is changed (Hughes & Saunders, 1970). The same process appears to be involved in the two methods of producing water hypoxia in the present study. However, as the rate of O_2 consumption at the same O_2 tension appears to be higher in still water, perhaps it suggests that the fish may extract O_2 more readily under these conditions. This

could be advantageous for fish like *Clarias* and *Saccobranchus* and others which are found in still-water ponds of tropical countries.

Moussa (1957) found that the African species *Clarias lazera* could survive only 14–17 h when kept in aerated water and prevented from surfacing. During this period the fish struggled hard to gulp air and finally died. The present study shows that *C. batrachus* does not show any signs of stress for 6–8 h when maintained in air-saturated water and prevented from surfacing. During submersion *C. batrachus*, like
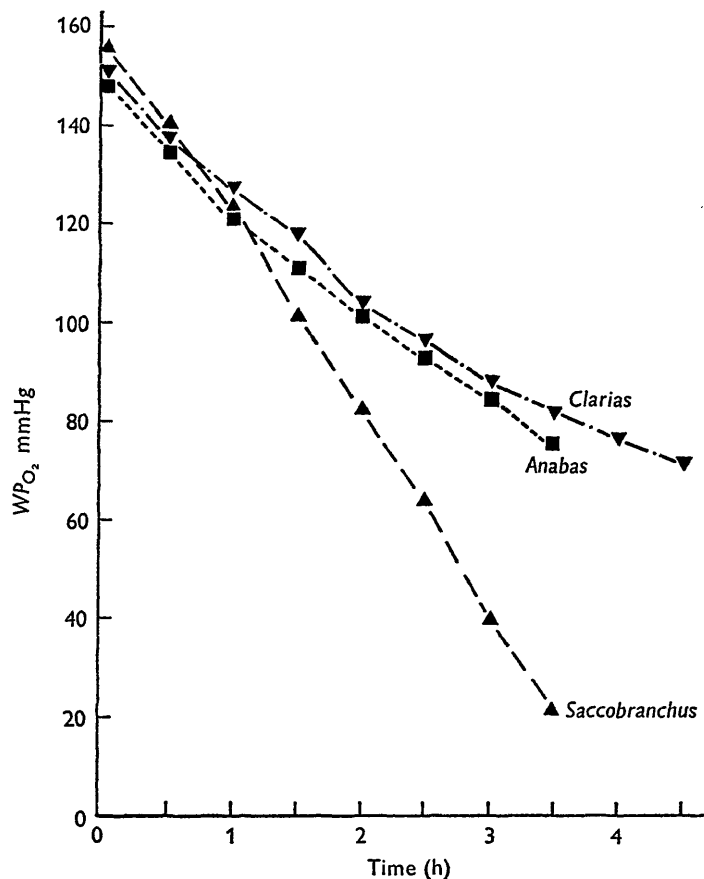

Fig. 5. A comparison between three air-breathing fishes, *Clarias batrachus* (▼), *Anabas testudineus* (■) and *Saccobranchus fossilis* (▲), in the process of O_2 uptake from water as indicated by lowering in WP_{O_2} after the onset of the experiment, when they are maintained in still water in a closed chamber and prevented from surfacing. *Clarias* and *Anabas* show dependent respiration and resemble each other, whereas *Saccobranchus* shows an independent water respiration and resembles more the O_2 independent water-breathing fishes. For details see text. Only mean values have been plotted and the values for *Anabas* and *Saccobranchus* are those determined by Hughes & Singh (1970, 1971).

C. lazera, initially showed an increase in opercular frequency but the depth of breathing increased only slightly in *C. batrachus* and once the frequency had risen to between 38–50/min it showed a fairly constant rate and depth of gill ventilation. This respiratory behaviour of *C. batrachus* differs from *C. lazera* (Moussa, 1957) as the latter showed a continuously increasing rate and depth of breathing and finally died of asphyxia. Magid (personal communication) also observed that *C. lazera* survived for several

days in air-saturated water without showing many signs of stress when prevented from surfacing.

The present observations show that *C. batrachus* does not usually attempt air-breathing until WP_{O_2} is reduced below 100 mmHg. Gill ventilation increases in hypoxic water and so maintains an optimal $\dot{V}_{O_2}$. The fish may depend on aquatic respiration alone at tensions as low as 60–100 mmHg, but below this level it must surface to gulp air. Thus *C. batrachus* can survive for longer periods, in both air-saturated and hypoxic waters exchanging gases with water alone than was observed for *C. lazera* by Moussa (1957). This adaptation is probably advantageous to *C. batrachus* as it inhabits stagnant waters with low O_2 content except in the rainy seasons when the waters may approach air-saturation.

Clarias in still deoxygenated water but given free access to still air has a very much reduced total $\dot{V}_{O_2}$ (40·84 cc/kg/h). The fish shows little activity and rests quietly and apparently waits for an air-breath with its head directed towards the air tube.
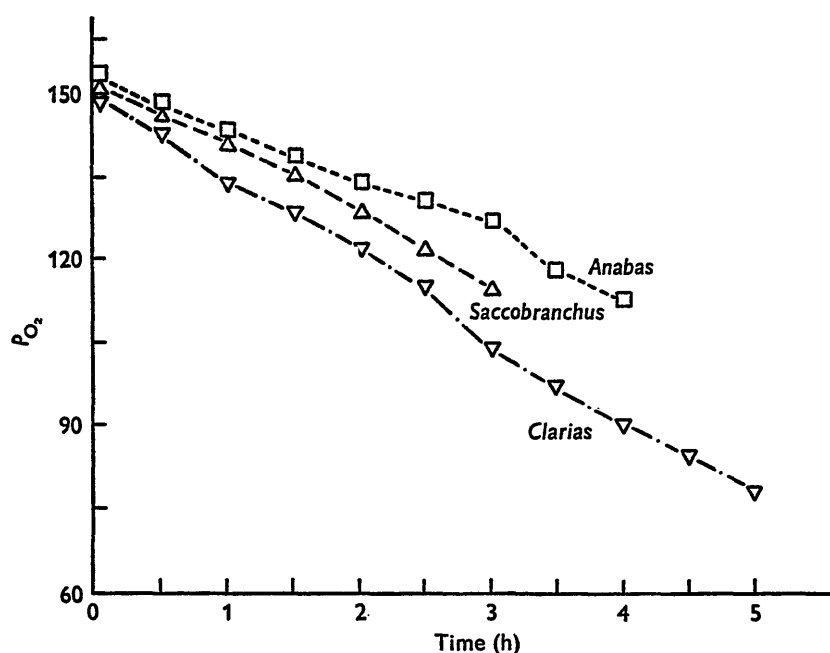

Fig. 6. A comparison between *Clarias batrachus* ($\triangledown$), *Saccobranchus fossilis* ($\triangle$) and *Anabas testudineus* ($\square$) of their O_2 uptake from still air as shown in terms of lowered P_{O_2} after the onset of observation in a closed chamber. Both *Clarias* and *Saccobranchus* show O_2 independence and follow the linear pattern while *Anabas* shows dependent respiration in which $\dot{V}_{O_2}$ is lowered as the P_{O_2} in air is reduced below 125 mmHg as a result of breathing and re-breathing of the still air. For details see text.

Low activity and low O_2 content in the air tube (reduced by breathing and re-breathing still air) might be the reason for such a low $\dot{V}_{O_2}$ from air under these conditions. The skin of *Clarias* is smooth, thin and well vascularized, so that some O_2 absorption probably occurs by this route in fish exposed to air and/or placed in oxygenated water. In fact, *Clarias* absorbs about 16% of its total O_2 cutaneously and the remainder through the gills when submerged in aerated water. In deoxygenated water O_2 exchange is not possible through the body surface. Consequently, not only is $\dot{V}_{O_2}$ very low in deoxygenated water but the effect of hypoxia is also more apparent (Fig. 4).

Table 3. *A comparison between certain air-breathing teleosts in respect of percentage $\dot{V}_{O_2}$ from water via the skin and via the gills when the fish is submerged under water and not allowed to surface*

Species	Temp. (°C)	Experimental conditions	$\dot{V}_{O_2}$ in water (%) Via skin	$\dot{V}_{O_2}$ in water (%) Via gill	Reference
Anguilla vulgaris	7–15	Submerged under water	10–15	85–90	Berg & Steen (1965)
Saccobranchus fossilis	25		16·82	83·18	Hughes & Singh (1971)
Clarias batrachus	25		16·61	83·39	Present authors

Table 4. *A comparison of the $\dot{V}_{CO_2}$ and RQ in water and air in some air-breathing fishes*

Species	$\dot{V}_{CO_2}$ (cc/kg/h) In water with access to air Water	Air	In water (access to N₂)	In air (air-exposed)	In de-O₂ water with access to air Water	Air	RQ In water with access to air Water	Air	Total	In water (access to N₂)	In air (air-exposed)	In de-O₂ water with access to air Water	Air	Reference
Protopterus aethiopicus (20 °C)	6·06	2·58	—	—	—	—	4·9	0·26	0·77	—	—	—	—	Lenfant & Johansen (1968)
Electrophorus electricus (25–27 °C)	24·57	5·65	—	—	—	—	3·65	0·25	1·01	—	—	—	—	Farber & Rahn (1970)
Anabas testudineus (25 °C)	120·44	12·26	137·56	74·62	113·66*	19·17	2·29	0·20	1·17	1·08	0·71	0·89*	0·15	Hughes & Singh (1970)
Saccobranchus fossilis (25 °C)	79·10*	5·40	—	31·78	21·92*	13·17	1·58*	0·17	1·00*	—	0·58	0·62*	0·38	Hughes & Singh (1971)
Clarias batrachus (25 °C)	87·51*	5·88	—	37·47	23·60*	17·24	2·25*	0·11	1·00*	—	0·52	0·58*	0·51	Present authors

* Assuming overall RQ = 1.

However, in *Anabas* $\dot{V}_{O_2}$ from air when it was maintained in deoxygenated water was very high (133 cc/kg/h) (Hughes & Singh, 1970). But the *Anabas* measurements were made using continuously flowing deoxygenated water and the fish was active during the experiments. Direct comparison of $\dot{V}_{O_2}$ levels and effects of P_{O_2} between *Clarias* and *Anabas* when in deoxygenated water is therefore not possible. However, under the same conditions $\dot{V}_{O_2}$ of *Clarias* is slightly greater than that of *Saccobranchus* (Table 2).

When *Clarias* was exposed to air $\dot{V}_{O_2}$ did not show much dependence on aerial P_{O_2} between 78 and 134 mmHg. It seems likely therefore that the skin of this fish helps O_2 absorption when exposed to air. A very similar response of metabolism under similar conditions was also observed in *Saccobranchus* (Hughes & Singh, 1971). Berg & Steen (1965) found an efficient absorption of oxygen via the skin in the air-exposed eel, *Anguilla vulgaris*. Moreover, it is interesting to note the linearity of P_{O_2} plots for air-exposed *Clarias* and *Saccobranchus*, both of which indicate O_2 independence whereas *Anabas* shows a dependence on P_{O_2} in air (Fig. 6). This similarity between *Clarias* and *Saccobranchus* is probably related to their ability for cutaneous respiration particularly at lower P_{O_2} levels (i.e. below about 125 mmHg).

Lenfant & Johansen (1968) observed that $\dot{V}_{O_2}$ in *Protopterus aethiopicus* is independent of CO_2 in air until the P_{CO_2} reaches 35 mmHg, but above this level $\dot{V}_{O_2}$ is reduced. In *Clarias* it can be seen that $\dot{V}_{O_2}$ of air-exposed fish is independent of P_{CO_2} in air as high as 51·0 mmHg (Fig. 3). Although there is some lowering in total $\dot{V}_{O_2}$ during the first few hours of air-exposure, this could not be accounted for by the increased aerial P_{CO_2}. In *Saccobranchus* also, $\dot{V}_{O_2}$ of air-exposed fish is independent of P_{CO_2} as high as 15–20 mmHg. This indicates that *Clarias* has even higher tolerance of P_{CO_2} in air than *Protopterus*.

Table 4 indicates that in almost all of the air-breathing fishes studied much more CO_2 is released into the water than into the air. If we assume a total RQ of about 1 from water and air in *Clarias* and *Saccobranchus*, as indeed is the case in *Anabas* and *Electrophorus*, then measurements made on CO_2 released into the air clearly indicate that in *Clarias* and *Saccobranchus* also much CO_2 is released into the water (Table 4). However, it must be borne in mind that as the skin takes part in gas exchange in *Clarias* and *Saccobranchus*, it is not improbable that some CO_2 is released into the water through the skin of these fishes.

When *Clarias* is exposed to air the gas-exchange ratio is low (0·52). Similar reduction in the RQ of air-exposed *Anabas* and *Saccobranchus* (Hughes & Singh, 1970, 1971) has also been determined. However, it is interesting to find that RQ with air in *Clarias* kept in deoxygenated water is also about 0·5, whereas in *Anabas* and *Saccobranchus* it is much lower (Table 4). Our control experiments have shown that there was no significant diffusion across water and air in the respirometers designed for *Anabas* and *Saccobranchus* (Hughes & Singh, 1970, 1971). The present study indicates that diffusion of gases across the two media in such experiments under these conditions is negligible, since the RQ in fish exposed to air and to deoxygenated water is nearly the same. The use of paraffin oil as a barrier in all these three fishes was avoided, as Spurway & Haldane (1963) reported that oil interferes with breathing in *Anabas*.

It has been observed that in nearly deoxygenated water and given free access to atmospheric air, *C. batrachus* can survive for 4–5 days or more. Moussa (1957) found

that when *C. lazera* was maintained in deoxygenated water and given free access to atmospheric air, it died after 11–16 h due to exhaustion because of its activity in taking frequent air-breaths. However, neither *Clarias* nor *Saccobranchus* died of exhaustion although showing increased air-breathing in our experiment when they had to swim upwards about 4 in. in order to obtain air.

It appears that when *Clarias* is in deoxygenated water it exchanges both CO_2 and O_2 through air-breathing organs and cuts down any exchange of gases through the skin or gill. This would of course be advantageous for the fish, since in eliminating CO_2 through the skin or gill in deoxygenated water these fishes would run a danger of losing O_2 from blood into the deoxygenated water. This could be achieved in *Clarias* probably by shunting the blood flow into the peripheral capillaries of the skin. A shunting of blood flow through a part of the respiratory organ which is not needed for gas exchange in an unsuitable environment has also been suggested by Johansen, Hanson & Lenfant (1970) and Hughes & Singh (1970). It may be concluded therefore that *Clarias* is probably more adapted for its life in water of very low O_2 tensions than is *Saccobranchus* or *Anabas*.

SUMMARY

1. The respiratory behaviour and the rate of O_2 consumption and CO_2 elimination has been studied in *Clarias batrachus* under different environmental conditions which were also designed to test its suitability for life in water and on land.

2. The mean V_{O_2} from water and air is about 93 cc/kg/h. It consumes more O_2 from air (58·4 %) than from water (41·6 %). The rate of CO_2 release through the air-breathing organs is very low (RQ = 0·11), much more CO_2 is released through the gills and skin in water.

3. When the fish is submerged under air-saturated water and prevented from surfacing V_{O_2} is low (about 65 cc/kg/h). However, the fish does not struggle to breath air over a period of 6–8 h in aerated water. It exchanges about 17 % of O_2 through the skin and the rest through the gills in aerated water.

4. If the fish is maintained in still water in a closed chamber V_{O_2} is about 61 cc/kg/h. It starts to search for air once the O_2 tension in water is reduced below 100 mmHg and this searching becomes vigorous below 60 mmHg (WP_{O_2}).

5. When exposed to air its V_{O_2} is about 71 cc/kg/h; V_{CO_2} in air-exposed fish is about 37 cc/kg/h; hence RQ in air is only 0·52. It shows independent respiration in air although P_{O_2} in ambient air was reduced to about 80 mmHg and P_{CO_2} rose to about 51 mmHg.

6. When the fish is kept in deoxygenated water but allowed free access to air, V_{O_2} is low, but RQ air is not reduced (0·51) from that of air-exposed fish. It shows dependent respiration under these conditions when aerial P_{O_2} is reduced below 80 mmHg and P_{CO_2} raised above 50 mmHg.

7. *Clarias batrachus* can live in deoxygenated water for several days if allowed free access to air, and appears to be more suited for life in poorly oxygenated water than *Saccobranchus fossilis* or *Anabas testudineus*.

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