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Bimodal Oxygen Uptake in a Freshwater Air-breathing Fish, *Notopterus chitala*

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Abstract Measurements of bimodal oxygen uptake have been made in a freshwater air-breathing fish, *Notopterus chitala* at 29.0±1(S.D.)°C. The mean oxygen uptake from continuously flowing water without any access to air, was found to be 3.58±0.37 (S.E.) ml $O_2 \cdot h^{-1}$ and 56.84±4.29 (S.E.) ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ for a fish weighing 66.92±11.27 (S.E.) g body weight. In still water with access to air, the mean oxygen uptake through the gills were recorded to be 2.49±0.31 (S.E.) ml $O_2 \cdot h^{-1}$ and 38.78±1.92 (S.E.) ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ and through the accessory respiratory organs (swim-bladder) 6.04±0.87 (S.E.) ml $O_2 \cdot h^{-1}$ and 92.32±2.91 (S.E.) ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ for a fish averaging 66.92±11.27 (S.E.) g. Out of the total oxygen uptake (131.10 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$), about 70% was obtained through the aerial route and the remainder 30% through the gills.

Notopterus chitala, the featherback, is a freshwater dual breather belonging to the family Notopteridae of the order Osteoglossiformes. They are an important food fish of northern India and commonly inhabit the normoxic water of rivers. However, they can also thrive well in the hypoxic water of swamps. Preliminary studies have been made on the anatomy and physiology of the air bladder of these fishes (Dehadrai, 1960) but little is known on their relative role in aquatic and aerial oxygen uptake (Dehadrai, 1962). The present paper reports a detailed account of the quantitative measurement of bimodal oxygen uptake in *Notopterus chitala*.

Materials and methods

Experimental fishes and their maintenance. A large number of live *Notopterus chitala* were collected from river Ganga near Bhagalpur (India) during the post-monsoon period (September, 1982) and were transported to and maintained in plastic pools (1000 *l*) of the Ichthyology Laboratory. The fishes were acclimatized to the laboratory condition (water temperature: 28–30°C) for fifteen days and during that period they were fed on living aquatic insects, zooplankton and shrimps.

Methods. Oxygen uptake rate was measured at water temperature of 29±1°C (S.D.) under two experimental conditions, viz. (i) when access to air was prevented and (ii) when it was allowed. The first series of experiments give an estimate of only aquatic oxygen uptake through gills at the water flow of 150 ml·min^{-1} (9 *l*·h^{-1}). From the second experimentation bimodal oxygen uptake was measured. For the first series of experiments, a cylindrical glass respirometer (Fig. 1) was used (Munshi and Dube, 1973). In such experimentation the fishes were forced to aquatic breathing only by completely filling the respirometer with water.

For the second series of experiments a closed glass respirometer was used (Fig. 2). In the respirometer the water and air-phases were adjusted in the ratio of 5.5 *l* and 1.5 *l* respectively. The air-phase of the respirometer was connected to an aquous manometer which shows an imbalance when oxygen declines in the respirometer due to air-breathing of the fish. KOH pellets absorbed the expired CO_2. The oxygen was injected through a graduated syringe to restore the imbalance of manometer. The amount of oxygen required to restore the imbalance of manometer indicated the aerial oxygen uptake by the fish.

Oxygen uptake per unit time through aquatic route in the first experiment was estimated with the help of the equation:

$$V_{O_2} = Vw\,(CIO_2 - CEO_2)$$

where, V_{O_2}=oxygen uptake (ml $O_2 \cdot h^{-1}$), Vw= water flow (ml/m) and CIO_2 and CEO_2 respec-

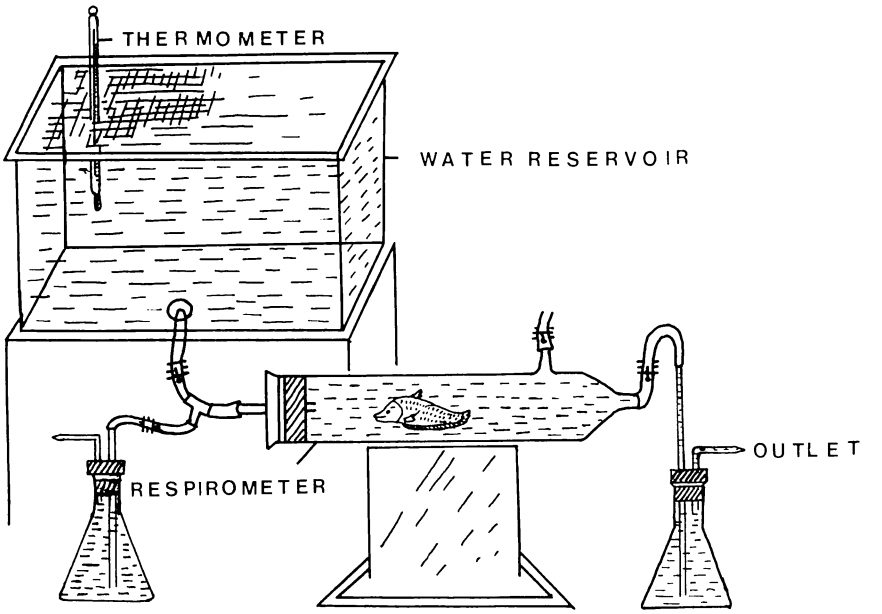

Fig. 1. Experimental set up for measuring aquatic oxygen uptake through the gills when access to air was prevented.

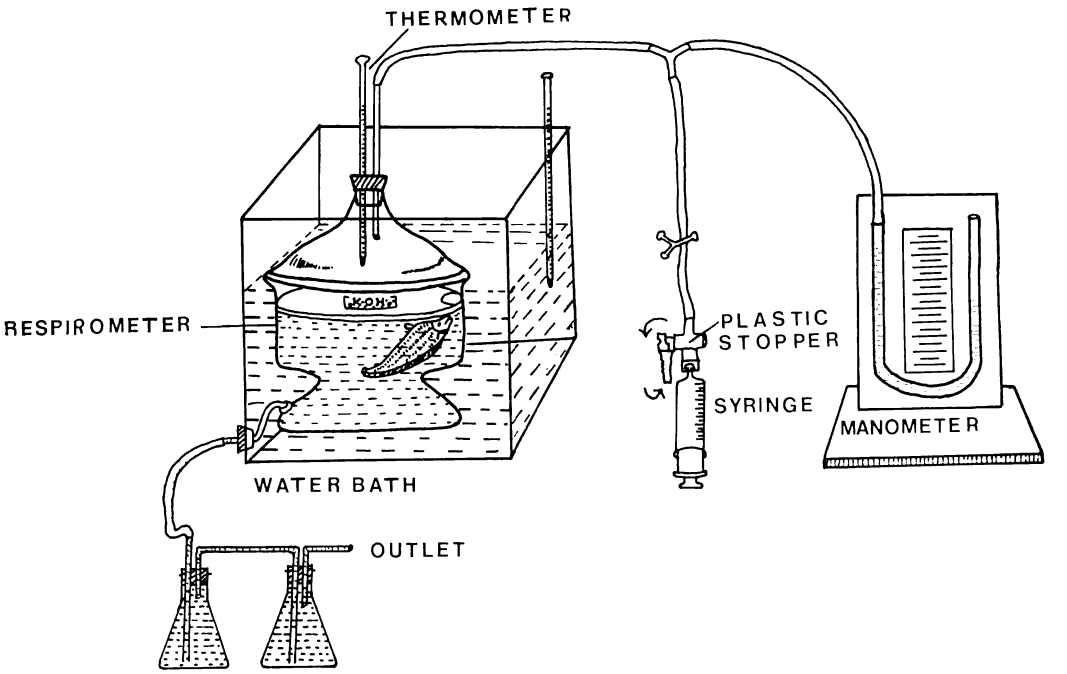

Fig. 2. Experimental set up for measuring bimodal oxygen uptake.

tively the oxygen concentration of inlet and outlet waters.

The aquatic oxygen uptake rate in the second experimental set up was estimated from the difference between dissolved oxygen of the ambient water before and after the experiment and the volume of water in the respirometer. Concentrations of the dissolved oxygen in various samples were estimated by Winkler's volumetric method (Welch, 1948).

Results

In the normoxic waters of the aquarium, the fishes used their gills for aquatic respiration and also visited air-surface at regular intervals to ventilate their swim-bladders for air-breathing. In a fish of 65 g body weight the opercular frequency ranged from 32 to 36 times per minute and the interval of two successive air-gulps was about six to eight minutes as was recorded in a glass aquarium which had access to air. However, the fishes showed increased opercular frequency when they were subjected to the respirometer without any access to air. It was recorded at 63 per minute for a fish of 67 g which is almost double from the normal.

Aquatic and bimodal oxygen uptake rate from continuously flowing (without access to air) and still (with access to air) water systems respectively are presented in Tables 1 and 2.

Oxygen uptake from continuously flowing water without any access to air. In such experimental conditions the fishes became restless with the inception of the experiment but soon settled with increased opercular frequency. The mean oxygen uptake rate (ml $O_2 \cdot h^{-1}$) ranged from 2.44 to 4.89 for *N. chitala* ranging between 35–105 g. For a fish of 66.92 g the mean oxygen uptake rates per unit time and per unit body weight were 3.58 ml $O_2 \cdot h^{-1}$ and 56.84 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ respectively. The average opercular frequency rate was about 63 per minute (Table 1).

Bimodal oxygen uptake from still water with access to air. In this experimental condition the fishes extracted oxygen from still water through the gills and from air through its specialized swim-bladder. The mean of aquatic oxygen uptake rate (ml $O_2 \cdot h^{-1}$) ranged from 1.58 to 3.43 whereas the mean of aerial oxygen uptake (ml $O_2 \cdot h^{-1}$) ranged from 3.48 to 9.02 for fishes ranging from 35 g to 105 g body weight. The oxygen uptake rates (ml $O_2 \cdot h^{-1}$) through gills and swim-bladder of an average 66.92 g fish were 2.49 and 6.04 respectively. Similarly the aquatic and aerial oxygen uptake rate per unit body weight for a 66.92 g fish were found to be 38.78 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ and 92.32 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ respectively. Out of the total oxygen uptake of 131.10 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$, the gills extract about only 30% whereas the major demand (70%) was satisfied by the swim-bladder. The quotient between aquatic and aerial respiration, i.e. 0.420 also suggested the dominance of aerial respiration over the aquatic respiration (Table 2).

Discussion

Most of the air-breathing fishes live and flourish in the adverse ecological conditions of the swamps. Unlike other dual breathers, *Notopterus chitala* prefers to inhabit normoxic flowing water of rivers. Its respiratory rhythm is adjusted according to the riverine ecosystem. In laboratory

Table 1. Mean values of aquatic oxygen uptake ($\dot{V}_{O_2}$) through the gills of *Notopterus chitala* at 29±1°C.

Serial number	Body weight (g)	Oxygen uptake ($\dot{V}_{O_2}$) without access to air		O.F. min^{-1}
		ml $O_2 \cdot h^{-1}$	ml $O_2 \cdot kg^{-1} \cdot h^{-1}$	
1	35.00	2.44	69.71	76
2	43.50	2.93	67.36	70
3	55.50	3.39	61.08	62
4	70.00	3.42	48.86	58
5	92.50	4.39	47.46	55
6	105.00	4.89	46.57	58
$\bar{X}$	66.92	3.58	56.84	63
S.E.±	11.27	0.37	4.29	3

O.F.=Opercular frequency; S.E.=Standard error

Table 2. Mean values of oxygen uptake ($\dot{V}o_2$) from still water through gills and swim-bladder (bimodal) of *Notopterus chitala*. S.E.=Standard error.

Serial number	Body weight (g)	Bimodal oxygen uptake ($\dot{V}o_2$)						Aquatic (%)	Aerial (%)	Aquatic / Aerial
		Aquatic		Aerial		Total				
		ml $O_2 \cdot h^{-1}$	ml $O_2 \cdot kg^{-1} \cdot h^{-1}$	ml $O_2 \cdot h^{-1}$	ml $O_2 \cdot kg^{-1} \cdot h^{-1}$	ml $O_2 \cdot h^{-1}$	ml $O_2 \cdot kg^{-1} \cdot h^{-1}$			
1	35.00	1.58	45.06	3.48	99.43	5.06	144.48	31.18	68.82	0.453
2	43.50	1.86	42.66	4.20	96.55	6.06	139.22	30.65	69.35	0.442
3	55.50	2.24	40.43	5.08	91.53	7.32	131.96	30.64	69.36	0.442
4	70.00	2.54	36.32	6.89	98.43	9.43	134.76	26.96	73.04	0.369
5	92.50	3.29	35.52	7.59	82.05	10.88	117.58	30.21	69.79	0.433
6	105.00	3.43	32.69	9.02	85.90	12.45	118.59	27.56	72.44	0.380
$\bar{X}$	66.92	2.49	38.78	6.04	92.32	8.53	131.10	29.58	70.42	0.420
S.E. (±)	11.27	0.31	1.92	0.78	2.91	1.17	4.47	0.74	0.74	0.02

Table 3. Mean values of total oxygen uptake, $\dot{V}o_2$ (ml $O_2 \cdot kg^{-1} \cdot h^{-1}$) during bimodal respiration and aquatic respiration (without access to air) of some common air-breathing fishes of India. 1, Munshi and Dube, 1973 (27.5±1°C); 2, Hakim *et al.*, 1983 (20.0±1°C); 3, Hakim *et al.*, 1983 (31.0±1°C); 4, Munshi *et al.*, 1976 (26.5±1°C); 5, Munshi *et al.*, 1978 (26.0±1°C).

Species	Temp. (°C)	Total aquatic oxygen uptake	Bimodal oxygen uptake			Aerial (%)	Aquatic / Aerial	References
			Total	Aquatic	Aerial			
Amphipnous cuchia	20.0	—	19.30	6.70	12.60	65.00	0.532	Lomholt and
Amphipnous cuchia	30.0	16.4	33.30	11.20	22.10	66.36	0.507	Johansen, 1976
Anabas testudineus	25.0	91.38[1]	113.42	52.62	60.80	54.00	0.865	Hughes and Singh, 1970
Boleophthalmus boddaerti	26.0±1	76.40	199.40	116.10	83.30	41.80	1.393	Biswas *et al.*, 1979
Channa gachua	29.0±1.5	11.00	60.70	26.31	34.39	56.66	0.765	Ojha *et al.*, 1978
Channa marulius	30.0±1	—	56.99	12.78	44.21	77.58	0.325	Ojha *et al.*, 1979
Channa punctata	21.0±1	65.81[2]	117.67	53.32	64.35	54.72	0.838	Ghosh, 1984
Channa punctata	31.5±1	103.40[3]	156.23	75.87	80.36	52.18	0.937	Ghosh, 1984
Clarias batrachus	25.0	75.17[4]	93.39	38.85	54.54	58.40	0.712	Singh and Hughes, 1971
Heteropneustes fossilis	25.0	66.88[5]	84.55	50.10	34.45	40.80	1.454	Hughes and Singh, 1971
Notopterus chitala	29.0±1	56.84	131.10	38.78	92.32	70.42	0.420	Present authors

conditions the fishes are expected repeat the same respiratory behaviour as that in their natural habitat. In the normoxic waters of the aquarium the fishes break the water-air interface to gulp air to compensate gill-breathing for their total metabolic oxygen requirement. Under surfacing prevented conditions the fishes survived but they increase their opercular frequency from 32 to 63 per minute. The increased opercular frequency in abnormal conditions of life is associated with pumping large volumes of water through gills to extract adequate oxygen for their total metabolic activities. Increased ventilatory rates have also been reported in *Anabas testudineus* (Munshi and Dube, 1973) and in *Channa punctata* (Hakim *et al.*, 1983). The value obtained for oxygen uptake through gills only (56.84 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$) is quite low from the value obtained for total oxygen uptake (131.10 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$) through bimodal gas exchange machinery in *Notopterus chitala*. Similar reports are also available for other air-breathing fishes of India (Table 3). From these findings it can be concluded that *N. chitala* under adverse conditions can drop down its metabolic activity and adjust itself even to lower oxygen availability. Obligate air-breathers fail to minimize the level of their metabolic activities in accordance with lower oxygen uptake through the gills and hence asphyxiate.

In *N. chitala*, the quotient between aquatic and aerial oxygen uptake is less than one (0.42) which indicates dominance of air-breathing over water-breathing. The value further indicates that *N. chitala* depends more on aerial breathing for total metabolic oxygen uptake. Higher percentage of aerial breathing is recorded in the present fish in comparison to other air-breathing fishes except *Channa marulius* (Table 3). Its lower quotient value is a unique feature for the fish inhabiting normoxic water of rivers.

Notopterus chitala never abandons aerial respiration but its extent and magnitude appear to vary according to the dissolved oxygen and free carbon dioxide contents of the water (Dehadrai, 1962). The continuous use of the accessory respiratory organs for aerial breathing may be attributed to its higher diffusing capacity of swim-bladder epithelia. With their continued use of air-breathing organs even in normoxic waters, it has become a natural instinct of the fishes to come to the surface.

The data on oxygen uptake for *N. chitala* will be helpful for its transportation and culture in ponds and lakes.

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淡水性空気呼吸魚 *Notopterus chitala* の 2 方式酸素摂取量

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淡水性空気呼吸魚 *Notopterus chitala* の 2 方式酸素摂取量を 29±1℃ で測定した．連続流水中で空気呼吸させない時の水相酸素摂取量は体重 66.92±11.27 g (SE) の個体で 3.58±0.37 mlO_2/h，即ち 56.84±4.29 mlO_2/kg/h であった．静水中で空気呼吸も行なわせるようにすると，鰓による水相酸素摂取量は，同じ体重で，2.49±0.31 mlO_2/h，即ち 38.78±1.92 mlO_2/kg/h であり，副呼吸器官（鰾）を介しての気相酸素摂取量は，同じ体重で，6.04±0.87 mlO_2/h，即ち 92.32±2.91 mlO_2/kg/h であった．全酸素消費量 (131.09 mlO_2/kg/h) の約 70% が気相呼吸，残りの 30% が鰓による水相呼吸であった．