Proc. Indian natn. Sci. Acad. **B 46** No. 5 pp 621–635 (1980)

Morphometrics of the Respiratory Organs of an Air-breathing Catfish, *Clarias batrachus* (Linn.) in relation to Body Weight*

J S DATTA MUNSHI, FNA, J OJHA and ASHA L SINHA
Post-Graduate Department of Zoology, Bhagalpur University,
Bhagalpur 812007

(*Received* 10 *March* 1980; *after revision* 15 *September* 1980)

Measurements of the dimensions of the bimodal gas exchange machinery of *Clarias batrachus* have been made and the data analysed with respect to body weight using logarithmic transformations ($\text{Log } Y = \log a + b. \log. W$). Total respiratory area of gills, skin, gill fans, lining of the suprabranchial chambers and the dendritic organs increased by powers of 0.781, 0.743, 0.707, 0.736 and 0.840 respectively. The slope values for the surface areas of the 1st, 2nd, 3rd and the 4th gill arches were 0.692, 0.662, 0.929 and 0.826 respectively. The exponent value of total air-breathing organs was greater ($b=0.790$) than the total water-breathing organs ($b=0.755$).

These results throw light on the variations in growth pattern for the dimensions of the different gills. The exponent values and the diffusing capacity of water and air-breathing organs reveal that the air-breathing pre-dominates over water-breathing as the fish grows in size.

Key Words: *Clarias batrachus*, **Respiratory organs Air-breathing catfish, Diffusing capacity**

Introduction

Many tropical fresh-water fishes have developed accessory respiratory organs for air-breathing. The relative importance of the two modes of respiration (aquatic and aerial) varies in different species depending upon the efficiency of their bimodal gas exchange machinery. The gill dimensions of purely aquatic fishes have been studied in detail by many workers (Hughes 1966, Muir 1969, Hughes & Morgan 1973, Jager et al. 1977). Information on the effect of growth on the relative importance of bimodal respiratory surfaces in teleosts is somewhat limited (Hughes et al. 1973, 1974a, a Hakim et al. 1978). The present study was undertaken to investigate the functional relationships between body weight and various dimensions of the gills and air-breathing organs of "magur fish", *Clarias batrachus*, the

---

*This work was supported by a research grant from the University Grants Commission, Delhi

morphology of which is well known (Munshi 1961, 1976). It belongs to the order Cypriniformes, and the family Clariidae. The fish lives in swamps, pools and chaurs of the eastern part of India. They have developed special dendritic organs inside suprabranchial chambers for air-breathing. The fish can extract O_2 from water through skin and gills and from air by periodic ventilation of its air-breathing organs.

Materials and Methods

Large numbers of live specimens of magur were collected from the swamps of North Bihar and maintained in glass aquaria and acclimatized to laboratory conditions.

Morphometrics of water-breathing organs

Gills: Fresh body weights were determined and the fishes divided into six weight groups, the range of the sample being 15-77 g. The fishes were killed, opercula removed, and fixed in 5% formalin. After about 2 days fixation, the four gills of one side were dissected out carefully and were washed thoroughly in running tap water, and slowly processed through the ascending series of ethanols and preserved in 70% alcohol and stained with borax carmine. Measurements of the dimensions of the four gills were made according to the methods described by Muir and Hughes, 1969 and Hughes and Morgan, 1973.

Skin: The surface area of 12 weight groups of fishes was measured by removing the entire skin and tracing its outline on graph paper.

Morhpometrics of air-breathing organs

Surface areas of gill fans and the respiratory membrane lining the supra-branchial chambers of different weight groups of fishes were measured by removing them in pieces and tracing their outline on graph papers under camera lucida. With the help of a random table the branches of the dendritic organs were selected and their surface areas were determined using two formulae, one for open cylinder ($S=2\pi rh$) and the other for cylinder closed on one side ($S=2\pi rh+\pi r^2$).

Volume of the suprabranchial chambers and dendritic organs

The suprabranchial chambers of different weight group of fishes were exposed. The dendritic argans were carefully dissected out and the volume of the chamber was measured by filling it with fine sand. The volumes of the dendritic organs were determined by water displacement methods. The functional volume of the suprabranchial chamber was determined by deducting the volume of the dendritic organs from that of suprabranchial chamber.

Characteristics of the regression line relating the logarithms of each parameter of bimodal gas exchange machinery in relation to body weight were calculated by least-squares method using Moscal 1204 (DCM) electronic calculator.

Diffusing capacity of various respiratory surfaces was estimated using modified Fick equation :

$$\textit{Diffusing capacity}=\frac{K.A.}{t}$$

where K = Krogh permeation co-efficient (0.0000015ml O_2/min/μm/mm^2/mmHg at 20°C), A the respiratory area and t the diffusion distance. The necessary data for such calculations were available from the results of measurements described in this paper and those of Munshi (1976).

Results

Clarias batrachus exchanges gases in water by means of well-developed gills and naked skin and has air-breathing organs which function in direct gas exchange with atmospheric air. The accessory respiratory organs are in the form of a pair of suprabranchial chambers lined by respiratory membrane, the gill fans borne by each arch and two pairs of dendritic organs (figure 1).

Dimensions of the water-breathing organs

Gills: The different dimensions of the gills appear to increase with an increase in body weight. The dimensions in any particular specimen vary from first to fourth branchial arches. The filament length of the oral and aboral hemibranchs vary along the length of each of branchial arch (figure 2).

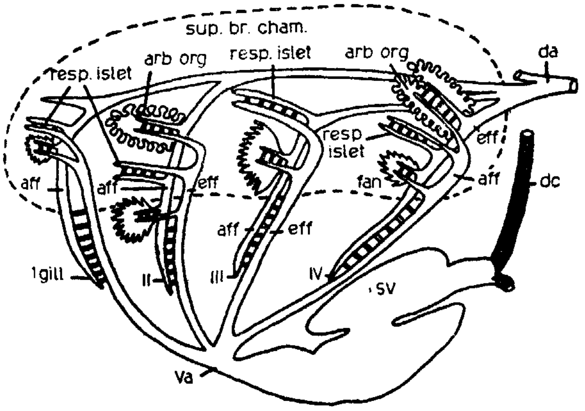

Figure 1 Diagrammatic representation to show the various respiratory surfaces and their blood supply in *Clarias batrachus*, **aff**, afferent branchial artery, **arb org**, arborescent organs, dc-ductus cuvierii; **eff**, efferent branchial artery; **resp. islet**, respiratory islet; ***Sup. br. cham.***, Suprabranchial chamber; **Sv**, Sinus venosus; **a, a.**, ventral aorta

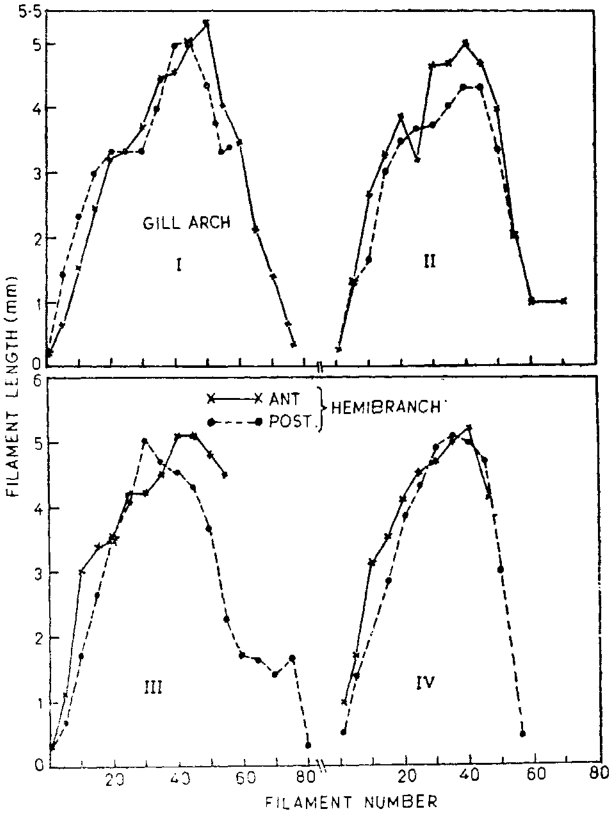

Figure 2 Graphic representation to show the variations in the filament length in the anterior and posterior hemibranchs of the four gill arches of 100 g *C. batrachus*

Relationships between body weight and various parameters of the gills

The relationships between body weight and various parameters of the gills are summarized in table 1 and shown in figures 3-7. In all the branchial arches the total filament number and average filament length increased with increasing body weight. In the former case the slope values ranged from 0.058 to 0.101 and in the latter they ranged from 0.321 to 0.377 respectively (table 1). Products of these two sets of measurements gave values for the total filament length. Results of the total filament lengths in relation to body

Table 1 *Relationship between body weight* (w) *and other component parameters* (Y) *of the different is the slope value of the regression line. The correlation coefficients* (r) *have also been shown*

Body weight(W) vs. Gill dimension parameter(Y)	1st Gill Arch (a)	Slope (b)	Correl. coeffi. (r)	2nd Gill Arch (a)	Slope (b)	Correl. coeffi. (r)
Total Gill filament number	143.310	0.101	0.826	160.47	0.072	0.974
	$Y=143.31W^{0\cdot101}$			$Y=160.47W^{0\cdot072}$		
Average filament length (mm)	0.951	0.321	0.980	0.884	0.336	0.974
	$Y=0.951W^{0\cdot321}$			$Y=0.884W^{0\cdot336}$		
Total filament length (mm)	135.31	0.423	0.972	141.77	0.408	0.976
	$Y=135.31W^{0\cdot423}$			$Y=141.77W^{0\cdot408}$		
No. of second lamellae/mm (both sides)	49.965	-0.074	-0.856	54.402	-0.102	-0.911
	$Y=49.965W^{-0\cdot074}$			$Y=54.402W^{-0\cdot102}$		
Total No. of secondary lamellae	6762.0	0.348	0.954	7722.0	0.306	0.963
	$Y=6762.0W^{0\cdot348}$			$Y=7722.0W^{0\cdot306}$		
Bilateral surf. area of an average lam. (mm^2)	0.011	0.349	09.18	0.011	0.362	0.845
	$Y=0.011W^{0\cdot349}$			$Y=0.011W^{0\cdot362}$		
Gill area (mm^2)	78.925	0.692	0.952	90.113	0.662	0.993
	$Y=78.925W^{0\cdot692}$			$Y=90.113W^{0\cdot662}$		
Gill area/g (mm^{2}g)	78·611	-0·307	-0·812	89·886	-0·338	-0·800
	$Y=78\cdot611W^{-0\cdot307}$			$Y=89.886W^{-0\cdot338}$		

***gill arches as based on equation** $Y=aW^b$, **where 'a' is the value for lg fish (log Y intercept) and** 'b'*

3rd Gill Arch			4th Gill Arch			Total Gill Arch		
(*a*)	Slope (*b*)	Correl. coeffi. (*r*)	(*a*)	Slope (*b*)	Correl. coeffi. (*r*)	(*a*)	Slope (*b*)	Correl. coeffi. (*r*)
161 99	0.058	0.522	146.20	0.062	0.533	609.54	0 074	0.808
$Y=161.99W^{0\cdot058}$			$Y=146.20W^{0\cdot062}$			$Y=609.54W^{0\cdot074}$		
0.757	0.377	0.929	0.957	0.328	0.863	0.881	0.340	0.955
$Y=0.757W^{0\cdot377}$			$Y=0.957W^{0\cdot328}$			$Y=0.881W^{0\cdot340}$		
120.38	0.439	0.886	139.15	0.391	0.852	537.03	0.415	0.938
$Y=120.38W^{0\cdot439}$			$Y=139.15W^{0\cdot391}$			$Y=537\cdot03W^{0\cdot415}$		
48.103	-0.073	-0.878	50.576	-0.083	-0.886	50.70	-0.083	-0.886
$Y=48.103W^{-0\cdot073}$			$Y=50.576W^{-0\cdot088}$			$Y=50.70W^{-0\cdot083}$		
5822.0	0.365	0.860	7080.0	0.306	0.804	27289.78	0.322	0 812
$Y=5822.0W^{0\cdot365}$			$Y=7080.0W^{0\cdot306}$			$Y=27289.78W^{0\cdot322}$		
0.005	0.568	0.958	0.007	0.524	0.986	0.00836	0.450	0.964
$Y=0.005W^{0\cdot568}$			$Y=0.007W^{0\cdot524}$			$Y=0.00836W^{0\cdot450}$		
32.915	0·929	0 960	48.784	0.826	0.968	227.51	0.781	0.970
$Y=32.915W^{0\cdot929}$			$Y=48.784W^{0\cdot826}$			$Y=227.51W^{0\cdot781}$		
53.172	-0·203	-0.687	48.53	-0.173	-0.629	227.51	-0.219	-0 746
$Y=53.172W^{-0\cdot203}$			$Y=48.53W^{-0\cdot173}$			$Y=227.51W^{0\cdot219}$		

weight for all 4 branchial arches showed correlation co-efficients exceeding 0.852; $P < 0.01$. Log-log plots of body weight and total filament length gave straight lines with slopes ranging from 0.391 to 0.439 (figure 3).

The secondary lamellae which are the actual sites of gaseous exchange form one of the vital components of the gill structure. Secondary lamellae per unit area is one of the gill parameters which determines the gaseous exchange efficiency. In all the four gill arches the number of secondary lamellae/mm decreased with increasing body weight, the slopes ranging from —0.073 to —0.102 (table 1, figure 4). Product of secondary lamellae per unit area and total filament length gave the value for total secondary lamellae. When the values for total secondary lamellae for all the gills and body weights were plotted on log-log coordinates they gave straight lines with slopes ranging from 0.306 to 0.365 (figure 5). The two variables showed positive correlation (table 1).

Average bilateral surface area of a secondary lamella is also an important parameter in the determination of total gill area. Bilogarithmic plots of body weight and average bilateral surface area of a secondary lamella for the four gill arches gave straight lines with slopes of 0.349, 0.362, 0.568 and 0.524 for the 1st,

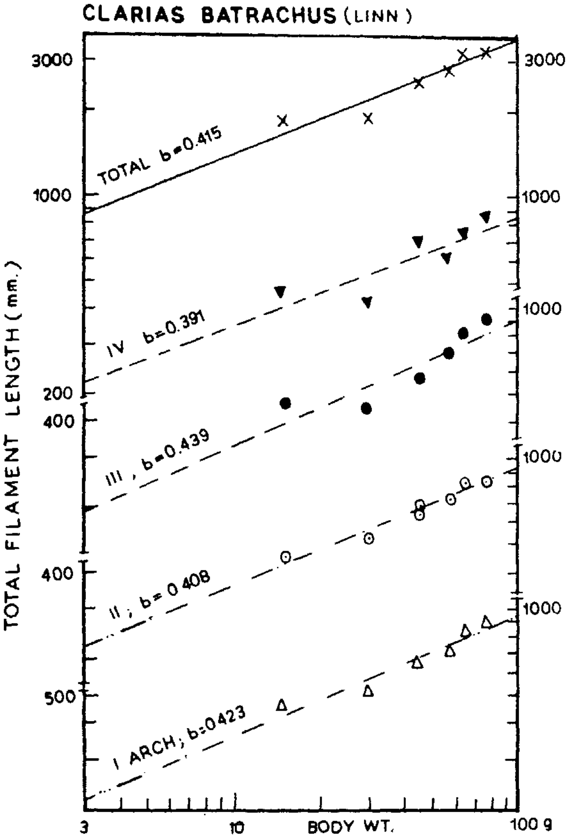

Figure 3 Log/log graphs showing the relationship between body weight and total filament length

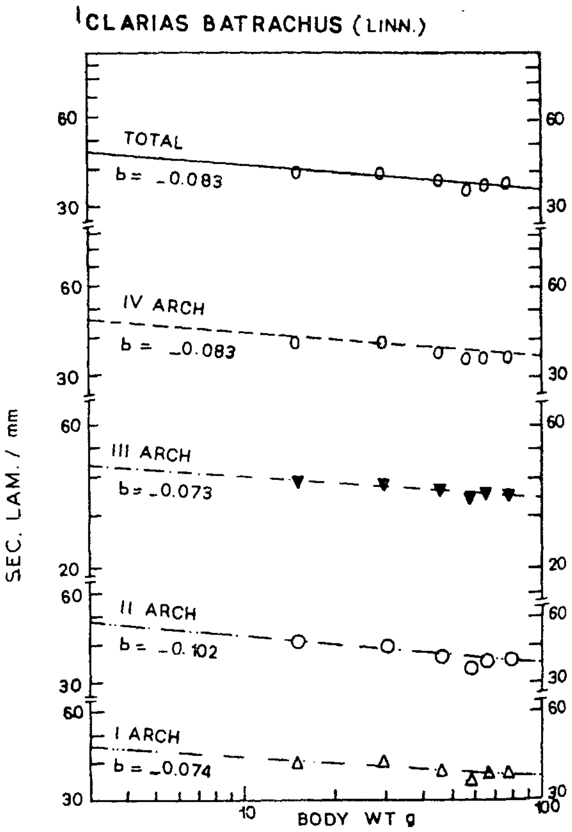

Figure 4 Bilogarithmic plots to show the relationship between body weight and secondary lamellae per mm

2nd, 3rd and 4th gill arches respectively (figure 6), and for all gill arches combined it gave a value of 0.450 (table 1). The correlation coefficients *(r)* exceeded 0.845 for all gill arches (table 1).

Measurements of average bilateral surface area of a secondary lamella and total secondary lamellae multiplied together gave values for total gill area. The slopes of the regression line relating total gill area for all gill arches and body weights ranged between 0.662 and 0.929 (figure 7). Correlation coefficients between the two variables ranged between 0.952 and 0.993 (table 1). The results of the regression analyses (table 1) indicated that the gill area per unit body weight decreased with increase in body weight both for individual gill arch as well as for the total gill arches. The two variables showed negative correlation (table 1).

Skin: Skin of *Clarias batrachus* is scaleless and therefore exchanges gases with water. The skin surface area increased by a power of 0.743 (table 2) with unit increase in body weight. Skin area and body weight showed positive correlation ($r=0.991$; $P<0.001$).

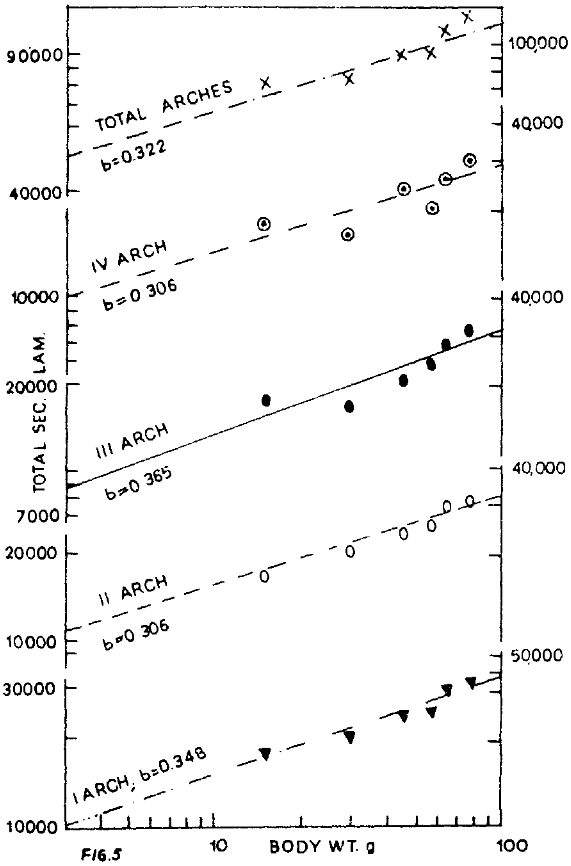

FIG.5

Figure 5 Log/log graphs to show the relationship between body weight and total secondary lamellae

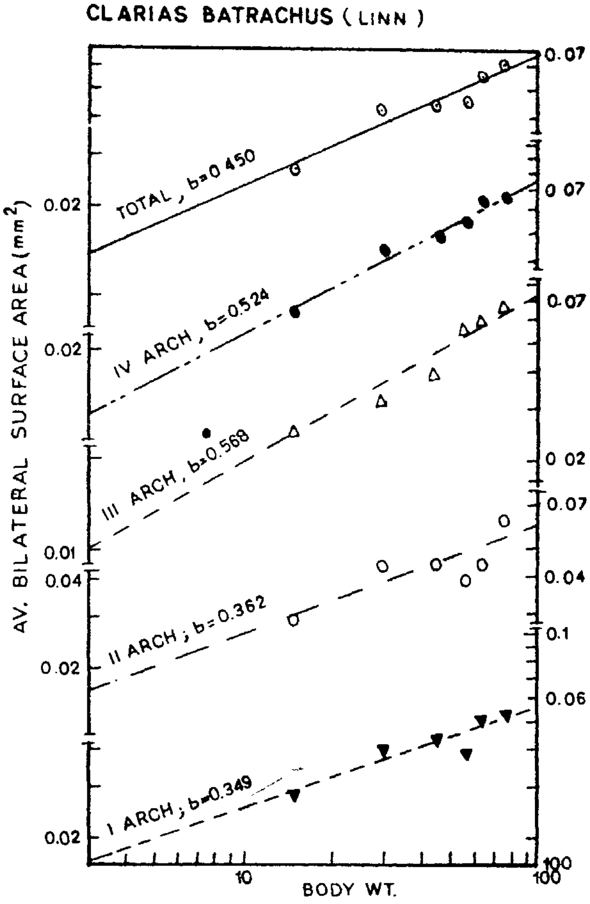

Figure 6 Log/log graphs to show the relationship between body weight and average bilateral surface area of a secondary lamellae

The sum of gill and skin area gave the value for total water-breathing surfaces. When these values were plotted against body weight on log-log coordinates, they gave a straight line with a slope of 0.755 (figure 10). The two variables showed high correlation ($r=0.999$; $P<0.001$).

Dimensions of the air-breathing organs in relation to body weight

Like water-breathing organs, the air-breathing surfaces also showed increasing trend with increase in body weight. The slope of the regression line relating area of total gill fans and body weight was 0.707 and for individual pair of gill fans the slope values ranged between 0.649 and 0.769 (table 2). Correlation between body weight and gill fan areas ranged between 0.934 and 0.975.

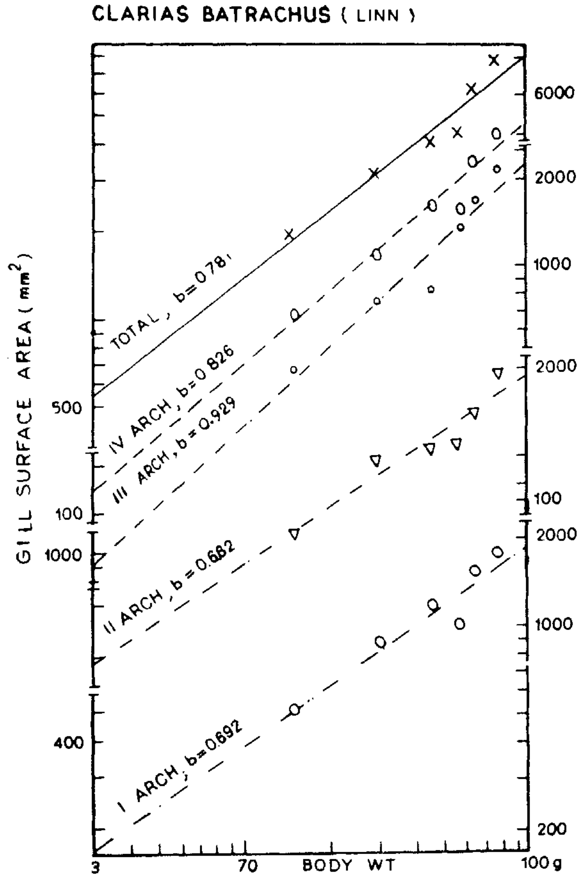

Figure 7 Bilogarithmic plots to show the relationship between body weight and gill surface area

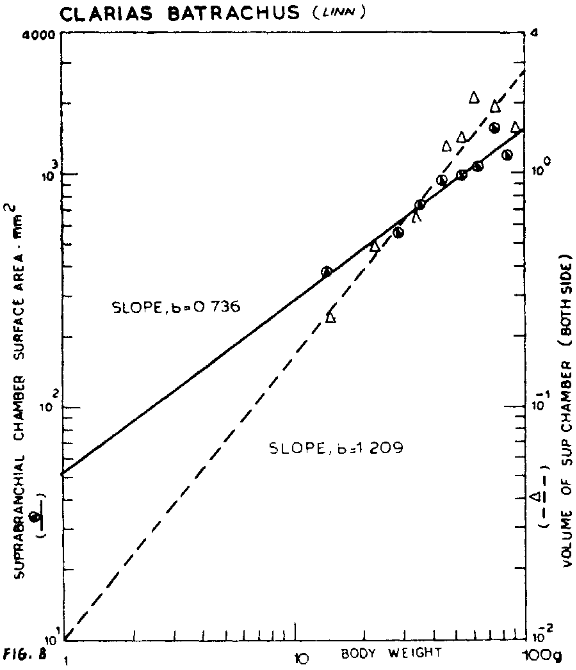

Figure 8 Log/log plots to show the relationship between body weight and the area and the volume of the suprabranchial chamber

The surface area and the volume of the suprabranchial chambers increased by powers of 0.736 and 1.209 respectively (figure 8). Surface area and the volume of suprabranchial chambers showed positive correlations (table 2).

Number of the branches of the dendritic organs, their total surface areas and volume also showed positive correlations (table 2). The slopes of the regression lines relating body weight and the number of branches for the first and second dendritic organs were respectively 0.586 and 0.638; for both dendritic organs combined, the slope value was 0.629

Table 2 *Intercept* (a) *slope* (b) *and relationship equations of the different dimensions of the respiratory organs based on equation* $Y=aW^b$. *Correlation coefficients* (r) *have also been shown*

Body wt.(*W*) vs. Dimensional parameters(*Y*)	(*a*)	Slope (*b*)	Equations	Correlation coefficient (*r*)
(a) Skin area (mm²)	564.94	0.743	$Y=564\ 94W^{0\cdot748}$	0.991
(b) Total water-breathing area (gill+skin) (mm²)	792.50	0.755	$Y=792.50W^{0\cdot755}$	0.999
(c) *Air-breathing area*				
(i) *Gill fan area* (mm²)				
1st gill fans	0.439	0.691	$Y=0\cdot439W^{0\cdot691}$	0.975
2nd gill fans	4.236	0.649	$Y=4.236W^{0\cdot649}$	0.934
3rd gill fans	5.346	0.724	$Y=5.346W^{0\cdot724}$	0.947
4th gill fans	1.452	0·769	$Y=1.452W^{0\cdot769}$	0.948
Total fans	13.120	0.707	$Y=13.120W^{0\cdot707}$	0.967
(ii) *Suprab. Chamber*				
Total surface area (mm²)	52.24	0.736	$Y=52.24W^{0\cdot736}$	0.970
Volume (ml)	0.011	1.209	$Y=0.011W^{1\cdot209}$	0.963
(iii) *Dendritic organs*				
No. of bulbs :				
1st tree	7.161	0.586	$Y=7.161W^{0\cdot586}$	0.942
2nd tree	29.717	0.638	$Y=29.717W^{0\cdot638}$	0.971
Total bulbs (1st + 2nd trees)	36.898	0.629	$Y=36.898W^{0\cdot629}$	0.970
Surface area (mm²)				
1st tree	8.551	0.909	$Y=8.551W^{0\cdot909}$	0.907
2nd tree	50.234	0.825	$Y=50.234W^{0\cdot825}$	0.914
Total area	59.979	0.840	$Y=59.979W^{0\cdot840}$	0.920
Volume :				
1st tree	0.010	0.751	$Y=0.010W^{0\cdot751}$	0.924
2nd tree	0.015	0.869	$Y=0.015W^{0\cdot869}$	0.970
Total	0.025	0.832	$Y=0.025W^{0\cdot882}$	0.964
(D) Total air-breathing area (mm²)	124.74	0.790	$Y=124.74W^{0\cdot790}$	0.999
(E) Total resp. area (mm²)	916.22	0.760	$Y=916.22W^{0\cdot760}$	0.999

Bilogarithmic plots of body weight and surface area of the dendritic organs gave straight lines with slopes of 0.909, 0.825 and 0.840 for 1st, 2nd and both the trees respectively (figure 9). The slope values for body weight and the volume of the dendritic organs were 0.751 and 0.869 for 1st and 2nd dendritic organs respectively.

Surface areas of gill fans, suprabranchial chambers and dendritic organs constitute total air-breathing organs. The total air-breathing organs of *Clarias* increased by a power of 0.790, whereas, the total respiratory surface increased by a power of 0.760 with unit increase in body weight (figure 10).

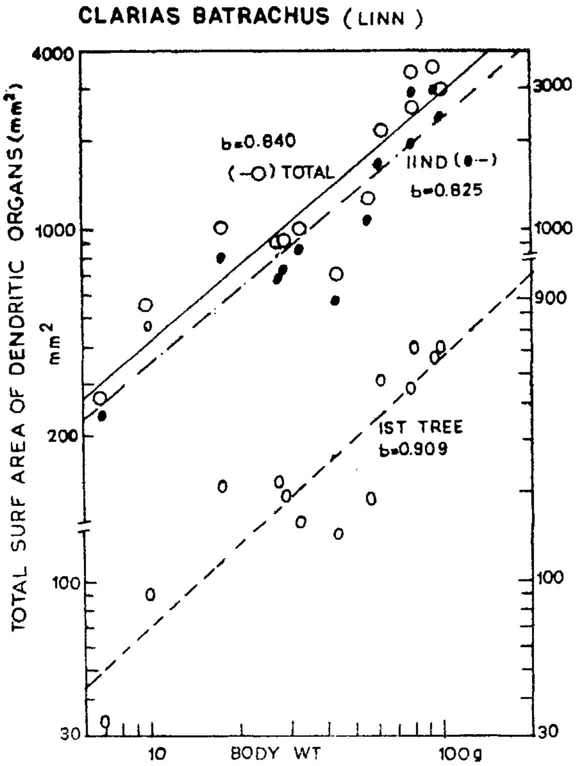

Figure 9 Log/log graphs to show the relationship between body weight and the surface area of the dendritic organs

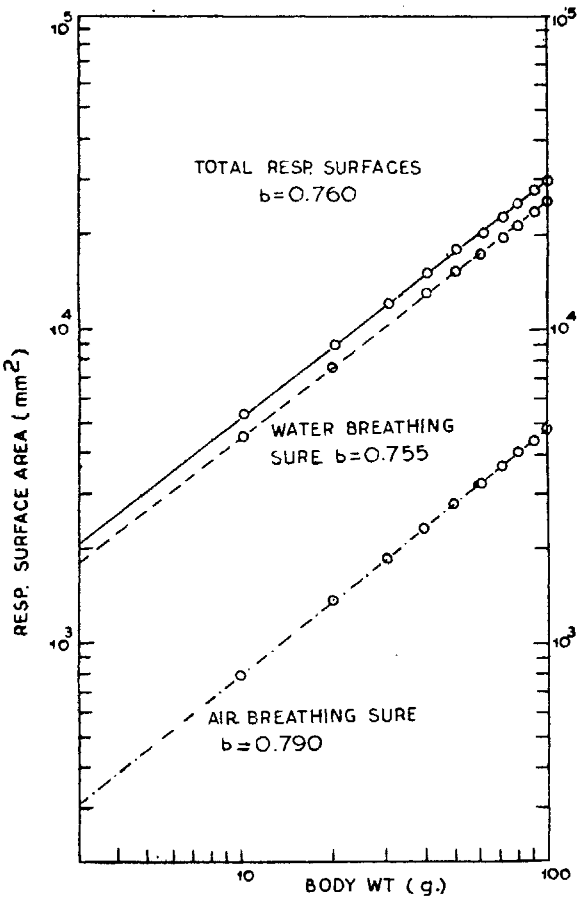

Figure 10 Bilogarithmic plots to show the relationship between body weight and water and air-breathing surfaces

Diffusing capacity of the respiratory organs

The diffusing capacity of the dendritic organs was greater than those of the respiratory membrane, gill fans, gills and skin (table 3).

Discussion

There is a persistent and widespread tendency for body size in animals to increase during their phylogeny (Cope 1885). The

Table 3 *Diffusing capacity (ml O_2.min^{-1}.mmHg^{-1}.kg^{-1}) for the tissue barrier of the respiratory organs as based upon morphometric findings of some air-breathing teleosts*

Fish species	Respiratory surf./g wt. for 100g fish (mm^2)	Thickness of tissue barr. t (μm)	diffusion capacity	Reference
Anabas testudineus				
(i) All gill arches	47.2	10.00	0.0071	Hughes et al. 1973
(ii) Suprabranch. Chamb.	7.6	0.21	0.0539	
(iii) Labyrinthine organ	32.0	0.21	0.2286	
Heteropneustes fossilis				
(i) Total gills	57.7	3.58	0.0242	Hughes et al. 1974a
(ii) Air-sac	30.7	1.6	0.0288	
(iii) Skin	200.0	98.00	0.0031	
Amphipnous cuchia				
(i) Air-sac	4.84	0.44	0.0165	Hughes et al. 1974b
Channa punctata				
(i) All gills	71.82	2.03	0.0530	Hakim et al. 1978
(ii) Suprab. Chambs.	39.17	0.78	0.0753	
Clarias batrachus				
(i) 1st gill arch	19.12	7.67	0.0038	Present paper
(ii) 2nd gill arch	18.95	7.67	0.0037	
(iii) 3rd gill arch	20.88	7.67	0.0041	
(iv) 4th gill arch	21.88	7.67	0.0043	
(v) Total gills	82.98	7.67	0.0162	
(vi) All gill fans	3.42	7.90	0.00065	
(vii) Skin	172.99	101.60	0.0026	
(viii) Suprabran. Chamb.	15.49	0.45	0.0516	
(ix) Dendritic organs	28.71	0.45	0.0957	

increase in body size is coupled with higher oxygen requirement. This is associated with a large gas exchange surface and lower diffusion distance. The relationship between metabolism and body weight for many fishes have been summarised by Winberg (1956) as $\dot{V}o_2 = aW^{0.81}$. The exponent values (b) show a wide range of variations, depending on the size and activities of the fishes and the ambient temperature. The slope for the gill area is higher in *Clarias batrachus* (0.781) than the values reported for *Anabas testudineus* (0.615), *Channa punctata* (0.592) and *Heteropneustes fossilis* (0.746). The gills of *C. batrachus* have comparatively high rate of growth in comparison to other air-breathing fishes of India. However, this value is appreciably lower than those reported for active water-breathing teleosts (table 4). Comparatively lower slope value for *Clarias* is probably due to air-breathing habits of this catfish. Like other fish species the sum of the slope values for total filament length, bilateral surface area of a secondary lamella and the secondary lamellae/mm gave a value (0.782) which is almost similar to the slope value (0.781) obtained for gill area in relation to body weight (table 4).

Clarias shows a greater slope (0.415) for total filament length than *Anabas* (0.336) and indicates a greater dependence of this catfish on branchial respiration. As in most of the fishes, the frequency of secondary lamellae along the filaments

Tabel 4 *Regression coefficients slope* (b) *for total filament length, secondary lamellae/mm, bilateral surface area of an average secondary lamella and their sums in different fish species for comparison with slope* (b) *for the total gill area in relation to body weight*

Fish species	Slope(*b*) total filament length	Slope(*b*) secondary lam/mm	Slope(*b*) bi, surf. of an av. sec. lam.	Sum of Cols. 1,2 and 3	Slope(*b*) total gill area	References
Coryphaena hippurus	0.4310	−0.0360	0.3270	0.7220	0.7130	Hughes (1970a)
Scomber scombrus	0.4110	−0.0234	0.5560	0.9904	0.9970	Hughes (1970b)
Scyliorhinus canicula	0.3510	−0.0710	0.6840	0.9640	0.9610	
Tinca tinca	0.3190	−0.0160	0.1860	0.5210	0.5220	
Opsanus tau	0.4850	−0.0750	0.3720	0.7820	0.7900	Hughes & Gray (1972)
Anabas testudineus	0.3360	−0.1520	0.4260	0.6090	0.6150	Hughes et al. (1973)
Macrognathus aculatum	0.4670	−0.0690	0.3470	0.7450	0.7330	Ojha & Munshi (1974)
Heteropneustes fossilis	0.4350	−0.0950	0.4080	0.7480	0.7460	Hughes et al. (1974a)
Channa punctata	0.4253	−0.1376	0.3043	0.5920	0.5919	Hakim et al. (1978)
Clarias batrachus	0.4150	−0.0830	0.4500	0.7820	0.7810	Present authors

decreases with body weight. The estimated value for the number of secondary lamellae/mm from the regression lines for a 1g fish is 51 which is low in comparison to other air-breathing fishes and much less than that obtained for the fast swimming tunny (Muir & Hughes 1969). Lower values of secondary lamellae/mm in *Clarias* indicates greater physiological dead space between adjacent secondary lamellae. Thus in this catfish it is probable that quite a lot of water is shunted past the secondary lamellar system, thus decreasing the efficiency of oxygen uptake by the gills.

Comparison between different gill arches has shown some variations in surface area distribution during the growth of this species. The gill area of 3rd branchial arch increases more rapidly ($b=0.929$) than those obtained for other branchial arches. However, the number of gill filaments and secondary lamellae/mm showed little variation in different branchial arches. Perhaps the size and length of gill filaments matter much in determining the relative surface areas of different gill arches.

The slope for total secondary lamellae in *Clarias* is greater (0.322) than in *Channa* (0.289) and *Anabas* (0.177). The slope value for bilateral surface area of an average secondary lamella is also greater in *Clarias* (0.450) than *Channa* (0.304) and *Anabas* (0.426) indicating that the secondary lamellae in *Clarias* increases more rapidly than those of *Channa* and *Anabas* and thus providing more surface for gaseous exchange. *Clarias* has scaleless skin and therefore plays an important part in gaseous exchange. Skin area in this catfish increases by a power of 0.743, which is higher than that reported (0.698) for *H. fossilis* (Hughes et al. 1974a) and the average exponent value (0.67) suggested by Benedict (1938). It is interesting to note that out of total water-breathing surface about 68% is accounted by the skin area and gill comprises only 32%. However, in this fish only 16.6% of total aquatic oxygen uptake takes place through this route (Singh & Hughes 1971). Lower oxygen uptake by skin is obviously due to its lower diffusing capacity as a result of higher diffusion distance (101.6 μm).

Gill fans, respiratory membrane and the dendritic organs show different exponent values. The individual gill fans show more or less the same growth pattern as their respective gill arches. Because of their small surface area only a very small amount of oxygen could be extracted through these organs. These structures are useful in ventilation of air through the inhalent and exhalent apertures of the suprabranchial chambers (Munshi 1961). Higher exponent value ($b=0.736$) for the respiratory membrane lining the suprabranchial chambers of *Clarias* in comparison to those for *Anabas* (b 0.493) and *Channa* ($b=0.696$) indicates greater importance of the suprabranchial chambers in the former fish in comparison to latter fishes.

Out of all the respiratory organs, the dendritic organs are the most efficient organs for gaseous exchange. The second pair of dendritic organs are better developed. The total surface area of both the pairs of dendritic organs increases by a power of 0.840, which is greater than the values obtained for other respiratory structures. This finding indicates that as magur grows in size the dendritic organs become more and more dominant organ for oxygen uptake. The volume of the dendritic organs also increases at approximately the same rate to maintain the perfusion and diffusion balance. Higher exponent value (1.209) for the volume of the suprabranchial chambers signifies greater space to accommodate larger amount of air for efficient gaseous exchange.

In *Clarias* higher exponent value (0.790) for air-breathing organs in comparison to water-breathing organs (0.755) indicates that in this catfish the air-breathing predominates over aquatic respiration in higher weight groups of fishes.

The value for air-breathing organs of about 99g magur is quite low (4704. 98mm^2) in comparison to water-breathing organs (25451.26mm^2). However, this fish of the same body weight meets nearly 58.4 % of its total oxygen uptake through air breathing organs and rest (41.6%) through water-breathing organs. The higher oxygen uptake through air-breathing organs is obviously due to their greater diffusing capacity which is directly proportional to the respiratory area and inversely proportional to the diffusion distance. From the morphometric measurement of diffusing capacity we may have estimates of the relative oxygen uptake through various respiratory surfaces by multiplying the data with Δ PO_2 across the respiratory membrane. These theoretical values are directly proportional to the diffusing capacity and therefore the values are greatest (574.2 ml $O_2.kg^{-1}.h^{-1}$) for the dendritic organs and lowest (3.9 ml $O_2.kg^{-1}.h^{-1}$) for the gill fans. The theoretical metabolic rate (1000.2 ml $O_2.kg^{-1}.h^{-1}$) is about 12 times greater than the empirical data (80.0 ml $O_2.kg^{-1}.h^{-1}$) (table 5). This higher value is due to the fact that the theoretical data are based on the morphometry of tissue barrier alone and ignores the significant resistance to O_2 transfer in water-air and blood (Hill & Hughes 1970).

Table 5 *Morphometrically estimated oxygen uptake calculated from the diffusing capacity (ml $O_2.min^{-1}.mmHg^{-1}$ Kg^{-1}) of various respiratory surfaces of* Clarias batrachus

Respiratory surfaces	Diffusing capacity (*Dt*)	Oxygen uptake (ml$O_2.kg^{-1}.h^{-1}$) Estimated $VO_2 = Dt.\ \Delta\ PO_2$	Empirical
Gills	0.0162	97.2	
Skin	0.0026	15.6	
Gills + skin	0.0188	112.8	39.3
Gill fans	0.00065	3.9	
Lining of the suprabranchial chamber	0.0516	309.6	
Dendritic organs	0.0957	574.2	
Total air-breathing organs	0.1479	887.4	40.7
Total respiratory organs (Aquatic + Aerial)	0.1667	1000.2	80.0

References

Benedict F G, 1938 Vital energetics a study in comparative basal metabolism; *Publs. Cornegie Instn.* No. 503

Cope E D, 1885 On the evolution of the vertebrate; *Amer. Nat.* **19** 140-148. 234-247, 341-353

Hakim A, Munshi J S D and Hughes G M 1978 Morphometrics of the respiratory organs of the Indian green snake-headed fish *Channa punctata, J. Zool.* (Lond.), **184** 519-543

Hills B A and Hughes G M 1970 A dimensional analysis of oxygen transfer in the fish gill; *Resp. Physiol.* **9** 126-140

Hughes G M 1966 The dimensions of fish gills in relation to their function; *J. Exp. Biol.* **45** 177-195

——1970a Morphological measurements on the gills of fishes in relation to their respiratory function; *Folia morphologica* (Praha) **18** 78-95

——1970b Gill dimensions in relation to other respiratory parameters; *Int. Congr. Anat.* 9

——, Dube S C and Munshi J S D 1973 Surface areas of the respiratory organs of the climbing perch, *Anabas testudineus; J. Zool. Lond.* **170** 227-243

——, and Gray I E 1972 Dimensions and ultrastructure of toadfish gills; *Biol. Bull. mar. Biol. Lab.* (Wood Hole, Mass.) **143** 150-161

——, Morgan M 1973 The structure of fish gills in relation to their respiratory function; *Biol. Rev.* **48** 419-475

——, Singh B R, Guha G, Dube S C and Munshi J S D 1974a Respiratory surface area of an air-breathing siluroid fish, *Saccobranchus* (=*Heteropneustes*) *fossilis* in relation to body size; *J. Zool Lond.* **172** 215-232

——, Singh B R, Thakur R N and Munshi J S D 1974b Areas of the air-breathing surfaces of *Amphipnous cuchia* (Ham.) *Proc. Indian natn. Sci. Acad.* B **40** 379-392

Jager S D E, Smit Onel M E, Videler J J, Vangils B J M and Uffink E M 1977 The respiratory area of the gills of some teleost fishes in relation to their mode of life; *Bijdragen Tot De Dierkunde* **46** 199-205

Muir B S, 1969 Gill dimensions as a function of fishsize; *Jl. Fish Res. Bd. Can.* **26** 165-170

——, and Hughes G M 1969 Gill dimensions for three species of tunny; *J. exp. Biol.* **51** 271-285

Munshi J S D 1961 The accessory respiratory organs of *Clarias batrachus*; *Jl. Morph.* **109** 115-240

——1976 Gross and Fine structure of the respiratory organs of air-breathing fishes; in Respiration of *Amphibious Vertebrates* pp. 73-104 ed. G M Hughes (London) Acad. Press.

Ojha J and Munshi J S D 1974 Morphometric studies on the gill and skin dimensions in relation to body weight in a fresh-water mud-eel, *Macrognathus aculeatum* (Bloch); *Zoologischen Anzeiger* (Jena) **193** 364-381

Singh B N and Hughes G M 1971 Respiration of an air-breathing catfish *Clarias batrachus* (Linn.); *Jl.* Expt, *Biol.* **55** 421-434

Winberg G 1956, Rate of metabolism and food requirements of fishes, Belorussian University, Minsk (Fish Research Board of Canada Translation Series number 194)