Morphometrics of the Respiratory Organs of an Estuarine Goby, Boleophthalmus boddaerti

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Abstract Measurements of the dimensions of the different gills, skin and the opercular chambers of an estuarine goby, Boleophthalmus boddaerti, were made and the data were analysed with respect to body weight using allometric transformations $(Y=aW^b)$. The slope (b) for area of the total gill surface was 0.709, for skin 0.687, for the opercular chambers 0.544, and for their combined respiratory surface 0.686. The slope values for the surface area of the 1st, 2nd, 3rd and 4th gill arches were 0.757, 0.758, 0.615 and 0.570, respectively. The slope for secondary lamellae per mm was -0.083 and that for the bilateral surface areas of an average sized lamella 0.498.

These results indicate differences in growth patterns for the dimensions of the different gills. The growth-related decreases in the number of secondary lamellae per mm and size of an average secondary lamella, together with evidence from "drowning" experiments and diffusing capacity calculation, suggest that this estuarine goby is better adapted for aquatic respiration.

Boleophthalmus boddaerti (Pallas) is an estuarine amphibious gobiid species locally known in India as "dafur". It lives in the muddy shores of West Bengal and Orissa. Its skin is thin, highly vascular and covered with small cycloid scales. B. boddaerti has four pairs of gills. The 4th pair of gills is very much reduced. The opercular chambers are especially modified for aerial breathing and work as accessory respiratory organs.

The gills of fishes have shown a wide variation in the extent of gill surface area (Pütter, 1909; Price, 1931; Schöttle, 1931;

Gray, 1954; Oliva, 1960; Hughes, 1966). Recently, much attention has been paid to different components of the gill sieve in relation to body weight (Muir and Hughes, 1969; Hughes, 1970, 1972; Landolt and Hill, 1975). Though a few works are available on the gill dimensions of Indian air-breathing fishes (Hughes et al., 1973; Ojha and Munshi, 1974; Hakim et al., 1978), very little is known about amphibious estuarine fishes (Schöttle, 1931; Milton, 1971; Graham, 1973; Tamura et al., 1976).

The present study was undertaken to investigate the functional relationships between

Table 1. Summary of the relationships between bcdy weight and other component parameters of lg fish (log Y intercept); b, slope value of the regression line; W, body weight in g). The

Body weight	First gill arch			Second gill arch		
gill dimension parameters	Intercept	Slope	(<i>r</i>)	Intercept	Slope	(<i>r</i>)
Gill filament number	104.45	0.074	0.972	112.00	0.085	0.956
Average filament length (mm)	1.0314	0.321	0.934	1.355	0.317	0.952
Total filament length (mm)	107.40	0.396	0.948	154.47	0.398	0.987
Number of secondary lamellae/mm (both sides)	50.777	-0.131	-0.912	45.049	-0.071	-0.560
Total secondary lamellae	5465.99	0.265	0.931	6835.5	0.336	0.933
Bilateral surface area of a secondary lamella (mm²)	0.0116	0.492	0.930	0.0136	0.428	0.905
Gill area (mm²)	63.244	0.757	0.960	92.684	0.758	0.945
Gill area/g (mm²)	64.744	-0.263	-0.789	92.628	-0.241	-0.675

the body weight and various dimensions of the gills and accessory respiratory organs of Boleophthalmus boddaerti.

Materials and methods

Live specimens of Boleophthalmus boddaerti in the weight range of $1 \sim 12 \, \mathrm{g}$ (5.52 $\sim 11.0 \, \mathrm{cm}$ in total length) were collected from the estuary of the Subarnarekha River and banks of a navigational canal near Digha, West Bengal, India. They were kept for some time in a glass aquarium containing clear tap water in a continuous flow system in order to clear their gills of mud.

Measurements of the dimensions of the different gills were made according to the weighted method described by Muir and Hughes (1969). The surface area of the skin of different weight groups of fish was determined by directly tracing the entire skin on a graph paper. The opercular surface areas were measured by tracing the shape of the membrane pieces on graph paper by means of a camera lucida. The surface areas of all the membrane pieces were summed up and doubled and divided by the magnification to obtain the total surface area of the opercular chambers of the fish.

Drowning experiments: The term drowning is used in the same context as used by Hora (1935), i.e., when an air-breathing fish is prevented from coming to the surface for air and ultimately dies. Two sets of drowning experiments were performed in different groups of fish in the size range of $6 \sim 11$ cm

 $(2\,\mathrm{g}, 6\,\mathrm{g}, 9\,\mathrm{g})$ and $(2\,\mathrm{g})$ under normoxic $(0_2=6.9\,\mathrm{mg}\cdot\mathrm{l^{-1}}, \mathrm{pH})$ 8.0) water to analyse intraspecific variations if any on asphyxiation time. In the first series of experiments the fish were placed in four separate beakers of 300 ml capacity and the mouth of the beakers were tied up with pieces of mosquito net. The four beakers were then submerged under water in a large glass aquarium, where a continuous flow of normoxic sea water was maintained.

In the second series of experiments the fish were not allowed to breathe air and were kept under water in a system where there was no continuous flow of water.

Results

Anatomy.

Boleophthalmus boddaerti is a mud dweller of estuaries having broad wing-shaped secondary lamellae on both sides of primary gill filaments (Fig. 1). The gill rakers are wide leaf-like structures and are vascular. In many specimens the gills were found to be infected with parasitic nematodes. The infected specimens were not accounted for gill measurements.

The gills receive their blood (mixed) supply from the ventral aorta through four pairs of afferent branchial arteries and oxygenated blood returns to the dorsal aorta through four pairs of efferent branchial arteries. The opercular chambers and the buccal epithelium get a mixed blood supply directly from the first afferent branchial artery through bucco-opercular artery while the pharyngeal epithelium receives oxygenated blood from the first

the different gill arches in *Boleophthalmus boddaerti* as based on the equation $Y=aW^b$ (a, value for correlation coefficient (r) is also shown.

Third gill arch			Fo	Fourth gill arch			Total gill arches		
Intercept	Slope	(<i>r</i>)	Intercept	Slope	(r)	Intercept	Slope	(<i>r</i>)	
114.39	0.097	0.902	117.42	0.084	0.919	450.99	0.084	0.962	
1.384	0.200	0.586	0.813	0.210	0.849	1.148	0.278	0.918	
158.28	0.296	0.742	95.486	0.294	0.924	517.69	0.362	0.961	
45.884	-0.044	-0.384	59.141	-0.112	-0.768	49.155	-0.083	-0.872	
7206.8	0.257	0.735	5648.6	0.182	0.821	25150.0	0 285	0.951	
0.0115	0.357	0.771	0.0068	0.378	0.956	0.0111	0.430	0.952	
82.928	0.615	0.793	38.449	0.570	0.981	281.28	0.709	0.964	
82.928	-0.385	-0.631	38.466	-0.430	-0.968	281.52	-0.291	-0.829	

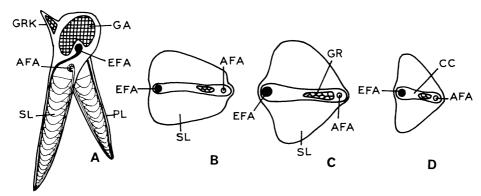


Fig. 1. Diagrammatic views of the gill of Boleophthalmus boddaerti. A: Longitudinal section (optically reconstructed) of a gill. B: Cross section of primary lamella through base. C: Cross section of primary lamellae through middle region. D: Cross section of primary lamella through tip region. AFA, afferent filamentar artery; CC, central canal; EFA, efferent filamentar artery; GA, gill arch; GR, gill ray; GRK, gill raker; PL, primary lamella; SL, secondary lamella.

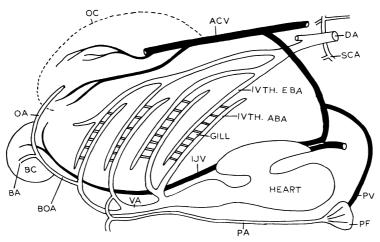


Fig. 2. A diagrammatic view of the vascular supply of the gills, buccal cavity, opercular chamber and the pelvic girdle of *Boleophthalmus boddaerti*. ABA, afferent branchial artery; ACV, anterior cardinal vein; BA, buccal artery; BC; buccal cavity; BOA, bucco-opercular artery; DA, dorsal aorta; EBA, efferent branchial artery; IJV, internal jugular vein; OA, opercular artery; OC, opercular chamber; PA, pelvic artery; PF, pelvic fin; PV, pelvic vein; SCA, subclavian artery; VA, ventral aorta.

suprapharyngeal artery. The oxygenated blood from opercular chambers is carried to the heart through the anterior cardinal vein and sinus venosus respectively (Fig. 2).

The two small baloon-like opercular chambers are situated to the lateral sides of the head, the ventral part of which is formed by the branchiostegal apparatus. The opercular chamber opens through a small slit. The

margin of the slit is thick and forms a valve-like structure for closing and opening the aperture. The pharynx communicates with the opercular chamber by the inhalant aperture lying in front of the first gill and is guarded by a plate formed by the inner extension of the same gill arch and is provided with gill rakers.

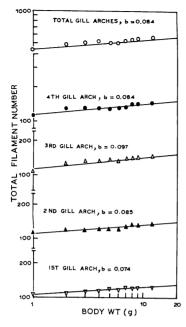


Fig. 3. Log/log graph showing the relationship between body weight and total filament number.

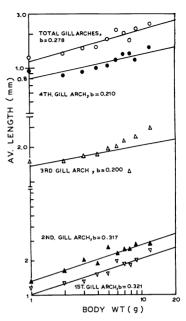


Fig. 4. Log/log graph showing the relationship between body weight and average length of the filament.

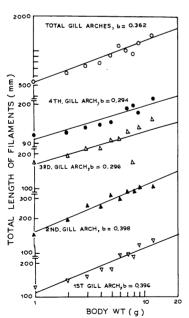


Fig. 5. Log/log graph showing the relationship between body weight and total length of filament.

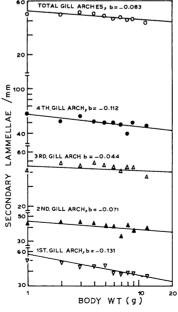


Fig. 6. Log/log graph showing the relationship between body weight and secondary lamellae/mm.

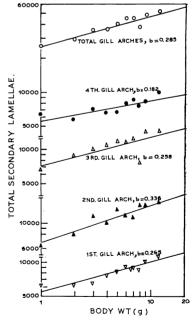


Fig. 7. Bilogarithmic graph to show the relationship between body weight and total secondary lamellae.

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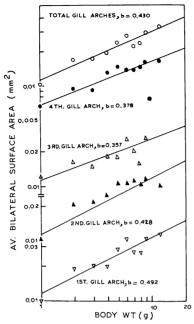


Fig. 8. Log/log graph showing the relationship between body weight and average bilateral surface area of a secondary lamella.

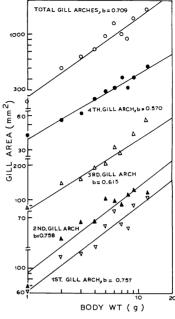


Fig. 9. Log/log graph showing the relationship between body weight and total gill area.

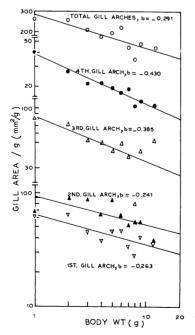


Fig. 10. Log/log graph showing the relationship between body weight and weight-specific gill area/g body weight.

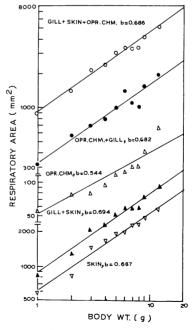


Fig. 11. Log/log graph showing the relationship between body weight and areas of various respiratory surfaces.

Morphometry.

The data obtained for 10 weight groups of fish for gill dimension, skin and opercular chamber area are summarised in Figs. $3\sim11$. The relationships based on the allometric equation are given in Table 1.

Gill morphometry. Relationships between body weight and total number and average length (mm) of the filaments: Regression analysis showed that, for all the gill arches taken together, the total number and average length of the filaments increased with increasing body weight by powers of 0.084 (Fig. 3) and 0.278 (Fig. 4), respectively, and showed significant correlations (Table 1).

Relationship between body weight and total filament length: The total filament length is a multiplied product of the above two parameters. This section of gill dimension increased with the increase in body weight, and log/log plots in relation to these two variables for each gill arch gave straight lines with the slopes ranging between 0.294 and 0.398 (Table 1, Fig. 5). Results for all the four gill arches and the correlation coefficients are also summarised in Table 1.

Relationship between body weight and secondary lamellae/mm on both sides of a filament: When all the four gill arches and their combined results were plotted on log/log co-ordinates they gave straight lines and in all cases the number of secondary lamellae/mm decreased with the body weight, the slopes ranged from -0.083 to -0.131 (Table 1, Fig. 6). There were significant negative correlations obtained for the 1st, 4th and all arches taken together, but the 2nd and 3rd gill arches showed non-significant correlations (Table 1). The number of secondary lamellae/mm for total arches were 49.15, 40.56 and 33.47, respectively, for 1, 10 and 100 g fish.

Relationship between body weight and total number of secondary lamellae: The body weight and number of secondary lamellae were significantly correlated with one another. The correlation coefficients were 0.931, 0.933, 0.735, 0.821 and 0.951, respectively, for the 1st, 2nd, 3rd, 4th and the total gill arches. The slope for separate arches ranged from 0.182 to 0.336 (Fig. 7). The values of 1, 10 and 100 g fish were respectively 25150, 48451.8

and 93342.9.

Relationship between body weight and the average bilateral surface area of a secondary lamella: Average bilateral surface area increased with increasing body weight and slopes for the 1st, 2nd, 3rd and 4th gills were respectively 0.492, 0.428, 0.357 and 0.378 (Fig. 8). For combined gill arches the slope was 0.430 (Fig. 8). Correlation coefficients varied from 0.771 to 0.956 (Table 1). The average bilateral surface area of a secondary lamella of 1, 10 and 100 g fish were 0.011, 0.023 and 0.080 mm², respectively.

Relationship between body weight and gill surface areas (mm²): The correlation coefficients of two variables for all the four gill arches were significantly correlated (Table 1). The surface area for each arch increased at different rates in relation to body weight. The average value for the total gill area for all arches taken together ranged from 255.58 to 1703.46 mm² in the body weight range of 1 to 12 g, the average value of gill area being 1109.05 mm² for an average body weight fish of 5.7 g. The slope for the four gill arches ranged from 0.570 to 0.758 (Table 1; Fig. 9) and was 0.709 for combined gill arches. The surface area for the 2nd gill arch increased more rapidly with the increase in body size.

Relationship between weight specific gill area (mm^2/g) and body weight: The results of the regression analysis (Table 1, Fig. 10) showed that the gill area per unit body weight decreased with an increase in body weight, for the separate gill arch as well as for all the gill arches taken together. Correlation for these relationships ranged between -0.631 and -0.968.

Morphometrics of the accessory respiratory organs. The skin, total water-breathing area, opercular chamber area, total air-breathing area and total respiratory surface area increased in relation to body weight. The results of the regression analysis are summarised in Table 2, and depicted in Fig. 11. When the data of these variables were plotted against body weight on log/log co-ordinates, they gave straight lines with slopes of 0.687, 0.694, 0.544, 0.682 and 0.686 respectively for skin, gills+skin, opercular chambers, opercular chambers+gills and total respiratory surface area.

Correlation coefficients for all the parameters were high (Table 2).

Diffusing capacity.

The diffusing capacity (ml O2/min/mm Hg/

Table 2. Summary table showing intercept (a) and slope (b) of the surface (mm^2) of the accessory respiratory organs and body weight (g) as based on the equation $Y=aW^b$ in Boleophthalmus boddaerti. Correlation coefficients (r) are also shown.

Body weight vs surface parameters	Inter- cept	Slope	(<i>r</i>)
Skin (mm²)	601.04	0.687	0.988
Skin+gills (mm ²)	884.94	0.694	0.990
Operc. chambers (mm ²)	52.26	0.544	0.908
Operc. chambers+gills (mm²)	336.33	0.682	0.962
Total resp. surface area (mm²)	939.84	0.686	0.991

kg) of the tissue barrier (Dt) was measured for the gills, skin and the respiratory lining of the opercular chambers in 10 weight-groups of fish. Dt varied from 0.0055 to 0.0321 for all the four gill arches and for the combined gill arches it was found to be 0.0773 for a 100 g fish. The diffusing capacity of all the gill arches is compared with that for other species in Table 3. The diffusing capacity of the tissue barriers was comparatively lower in the skin and the respiratory linings of the opercular chambers (Table 3).

Drowning experiments.

Test fish survived for more than 24 hours in continuous flowing normoxic water (4.82 ml O_2 l⁻¹) when surfacing was prevented. However, in confined water without access to air, they died within 2 to 3 hours when the dissolved oxygen in the water went down to 1.79 to 2.34 ml O_3 l⁻¹.

Table 3. Diffusing capacity for the tissue barrier of the respiratory organs as based upon morphometric findings in *Boleophthalmus boddaerti*; corresponding data for *Anabas testudineus*, *Heteropneustes fossilis* and *Channa punctata* are also given for comparison.

Species	Respiratory surface for 1 g fish (mm ²)	Diffusion distance (µm)	Area/g weight 100 g fish (mm ²)	Diffusing capacity 100 g fish (ml/min/mmHg/kg)
Anabas testudineus ¹⁾				
All gill arches	278.00	10.0000	47.2000	0.0071
Suprabranchial chamber	55.40	0.2100	7.6500	0.0539
Labyrinthine organ	80.70	0.2100	32.0000	0.2286
Heteropneustes fossilis2)				
Total gills	186.10	3.5800	57.7000	0.0242
Air sac	145.90	1.6000	30.7000	0.0288
Skin	851.10	98.0000	200.0000	0.0031
Channa punctata31				
First gill arch	161.96	2.0333	25.1189	0.0185
Second gill arch	142.63	2.0333	20.4489	0.0151
Third gill arch	92.13	2.0333	15.5431	0.0115
Fourth gill arch	74.54	2.0333	10.3952	0.0077
Total gills	470.39	2.0333	71.8229	0.0530
Suprabranchial chamber	159.08	0.7800	39.1705	0.0753
Boleophthalmus boddaerti41				
First gill arch	63.24	1.43	19.30	0.020
Second gill arch	92.68	1.43	30.54	0.032
Third gill arch	82.93	1.43	14.08	0.015
Fourth gill arch	38.45	1.43	5.30	0.005
Total gill arch	281.28	1.43	73.72	0.077
Skin	601.04	22.50	14230.90	0.009
Opercular chamber	52.26	1.22	641.12	0.008

References: 1) Hughes et al. (1973); 2) Hughes et al. (1974); 3) Hakim et al. (1978); 4) Present study.

Discussion

Gills.

Analysis of measurements of gills of Boleophthalmus boddaerti shows a slope of 0.709 for the gill area, which is low when compared to other dual breathers (Tables 4, 5), except Channa punctata (0.591) and Anabas testudineus (0.615). The statistically estimated value for the gill area for a specimen of B. boddaerti weighing 1 g was found to be 281.2 mm²,

which is lower than Anabas testudineus (556 mm²), Channa punctata (470.4 mm²) and Lepisosteus (393.6 mm²) but higher than Heteropneustes fossilis (186 mm²), Clarias batrachus (227.6 mm²) and Macrognathus aculeatus (217.3 mm²). From these findings, it is evident that B. boddaerti is more active than many of these air-breathing fishes.

Boleophthalmus boddaerti shows a slope (-0.083) for secondary lamellae/mm, which is very similar to Clarias (-0.083), but is

Table 4. Comparison of the sum of the values of the slope of the regression line obtained for various parameters of gill sieve with that obtained for total gill area separately in different fish species.

	Slope						
Species	Total filament length	Secondary lamella	Bilateral surface area of secondary lamella	Sum	Total gill area (mm²)		
Water breathers:							
Scomber scombrus ¹⁾	0.4110	-0.0234	0.5560	0.9904	0.9970		
Scyliorhinus canicula1)	0.3590	-0.0710	0.6840	0.9640	0.9610		
Tinca tinca ¹⁾	0.3190	-0.0160	0.1860	0.5210	0.5220		
Opsanus tau ²⁾	0.4850	-0.0750	0.3720	0.8720	0.7900		
Dual breathers:							
Anabas testudineus ³¹	0.3350	-0.1520	0.4260	0.6090	0.6150		
Heteropneustes fossilis4)	0.4350	-0.0950	0.4080	0.7480	0.7460		
Macrognathus aculeatus5)	0.4670	-0.0690	0.3470	0.7450	0.7330		
Clarias batrachus6)	0.4150	-0.0830	0.4500	0.7820	0.7810		
Channa punctata7)	0.4253	-0.1376	0.3043	0.5920	0.5919		
Boleophthalmus boddaerti8)	0.3620	-0.0830	0.4300	0.7090	0.7090		

References: 1) Hughes (1972); 2) Hughes and Gray (1972); 3) Hughes et al. (1973); 4) Hughes et al. (1974); 5) Ojha and Munshi (1974); 6) Sinha (1977); 7) Hakim et al. (1978); 8) Present study.

Table 5. Slope for the total secondary lamellae and bilateral surface area of an average size secondary lamella and their sum in different fish species for comparison with the slope for the total gill area in relation to body weight.

	Slope						
Species	Total secondary lamellae	Bilateral surface of a secondary lamella	Sum	Total gill area			
Coryphaena hippurus ¹⁾	0.390	0.327	0.717	0.710			
Opsanus tau ²⁾	0.420	0.360	0.780	0.770			
Anabas testudineus³)	0.177	0.426	0.603	0.615			
Heteropneustes fossilis4)	0.336	0.407	0.743	0.745			
Macrognathus aculeatus ⁵⁾	0.404	0.347	0.751	0.733			
Boleophthalmus boddaerti ⁶⁾	0.285	0.430	0.715	0.709			

References: 1) Hughes (1970); 2) Hughes and Gray (1972); 3) Hughes et al. (1973); 4) Hughes et al. (1974); 5) Ojha and Munshi (1974); 6) Present study.

lower than Macrognathus aculeatus (-0.069). The secondary lamellae/mm decreases with age and as a result, in higher weight groups of fish, the spacing between lamellae increases, leading to the fall of gill resistance. But this may be an adaptation for the amphibious habits of the fish. The gills will not collapse as they are small and widely separated from each other.

The sum of the regression coefficients for total secondary lamellae (0.285) and bilateral surface area of a secondary lamellae (0.430) give a slope value (0.715) which approximates the value of total gill area (0.709). Similarly, the sum of the regression coefficients for total filament length (0.362), number of secondary lamellae/mm (-0.083) and bilateral surface area of an average secondary lamella (0.430) give an identical value (0.709) obtained for the gill area. This finding clearly indicates the validity of the application of the least square method for analysing data for different parameters of the gill dimensions against body weight.

The total gill filament length of *Boleophthal-mus boddaerti* has a low slope value (0.362) in comparison to other air-breathing fishes except those reported for *Anabas testudineus* (Table 4). The low slope value (0.084) for the total number of gill filaments indicates that only a few new filaments are added as the fish grows in size. In *A. testudineus* a similar trend is also seen (Hughes et al., 1973). However, the gill filaments grow in length at an appreciable rate (0.278) and are responsible for the increase of the gill area.

When the average values of four gill arches for different parameters are compared with each other, all the four gill arches show some changes in each parameter. The total filament length, total number of secondary lamellae and gill area are larger in the second gill arch than others (Figs. 5, 7, 9). The highest slope value for total gill filament numbers (0.097) is found on the 3rd gill arch (Table 1).

When the total surface gill area of Boleo-phthalmus boddaerti in the weight range of $3\sim6$ g is compared with approximately similar weight groups of two estuarine fishes, i.e., Blennius $(2.6\sim6.2 \text{ g}; \text{ Milton}, 1971)$ and Mnierpes $(3.5\sim5.6 \text{ g}; \text{ Graham}, 1973)$, B. boddaerti

shows a lower gill area $(623.2 \sim 1290.6 \text{ mm}^2)$ than *Blennius* $(1622 \sim 3286 \text{ mm}^2)$ and *Mnierpes* $(1547 \sim 1684 \text{ mm}^2)$. This reflects that *B. boddaerti* is more amphibious than the other two estuarine fishes and it has to depend more on air-breathing for its total oxygen requirement.

The ratio of gill surface area to body surface area in *Boleophthalmus boddaerti* of 11.0 cm in total length obtained in this study (0.52) is quite lower than the ratios given by Schöttle (1931) on the same species of 12.1 and 12.6 cm in total length (0.83 and 0.68). This may be due to the different methods applied in the two studies.

Accessory respiratory organs.

Skin provides about 67% of total aquatic respiratory surface area in this fish, but its rate of growth (0.687) is much lower than gill area (0.709). This slope value is more or less close to that reported for *Heteropneustes fossilis* (0.698; Hughes et al., 1974).

The slope value for the opercular chamber area (0.544) is much lower than the gill area (0.709). The gills also take part in aerial respiration. As such, the gill and opercular chamber area together will form the total air-breathing surface area. The total air-breathing area increases by a power of 0.682 which is lower than the gill area (0.709) as well as the total respiratory surface area (0.686). Thus the gill area in relation to body weight increases more rapidly than accessory respiratory organs and, therefore, the gills play an important role in aquatic as well as aerial respiration.

Comparison of the exponent values relating the respiratory areas of total air-breathing and total water-breathing organs in relation to body weight shows that the exponent value for total air-breathing organ (0.682) remains smaller than that for total water-breathing organs (0.694). Similar results have been reported for *Heteropneustes fossilis* (Hughes et al., 1974) where water-breathing area develops at a greater rate than airbreathing organ.

The diffusing capacity of gills of Boleophthalmus boddaerti (0.077) is high in comparison to the capacities of other air-breathing fishes, such as Anabas testudineus (0.007; Hughes et al., 1973), Heteropneustes fossilis (0.024; Hughes et al., 1974) and Channa punctata (0.053; Hakim et al., 1978). The diffusing capacity of the opercular chambers of this estuarine goby is distinctly lower than that of the labyrinthine organs of A. testudineus, air sacs of H. fossilis, suprabranchial chambers of C. punctata and dendritic organs of Clarias batrachus. From this finding it can be suggested that the air-breathing organs of B. boddaerti are less efficient in oxygen uptake than those of other air-breathing fishes.

It has been found that the relationships between body weight and the total respiratory surface area (0.686) and those for oxygen uptake (0.791) is different when the fish is prevented for surfacing, but the relationship for the gill surface area (0.709) gives a value which is close to the value obtained for the metabolic rate (0.791) (Niva et al., 1979).

The banks of canals and shores of estuaries remain exposed for a long time from tidal waters almost twice a day. This long exposure may be the reason for the air-breathing habit of this fish. During tidal periods it remains submerged under water for a long time without taking any air gulp. Under experimental conditions the fish was found to survive for a long time when prevented from surfacing in a continuous flow system. In spite of being an inhabitant of normoxic waters, this fish has developed the habit of breathing air. This is because of the fact that the fish remains exposed to air for considerable periods of the day. Activities of Boleophthalmus boddaerti on land show that its heart rate does not decrease in air (Graham, 1976), indicating that the fish has adapted well physiologically for amphibious life.

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インド産ムツゴロウの呼吸器の形態計測学的研究 Biswas Niva・Jagdish Ojha・J. S. Datta Munshi

インド産のムツゴロウの1種について体表面積, 鰓腔表面積および鰓面積を計測し, 成長に伴う変化を調べた. またこの魚が水面へ浮上するのを抑制することによって、空気呼吸がこの魚にとって不可欠なものかどうかもあわせて研究した. その結果, 成長に伴う鰓面積の変化の様子が各鰓弓で異なることを明らかにするとともに, 鰓の酸素拡散量の推定値と浮上抑制実験とに基づいて, この魚は水中の呼吸に適応していると推察した.