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Changes of Scaling Pattern in Oxygen Uptake in Relation to Body Weight of an Estuarine Goby, *Pseudapocryptes lanceolatus* (Gobiidae, Perciformes)

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The regression analyses data on aquatic oxygen uptake rate (ml O_2 hr^{-1}, ml O_2 Kg^{-1} hr^{-1}) on different weight groups of amphibious goby, *Pseudapocryptes lanceolatus* revealed variations in the scaling pattern for VO_2 in relation to body weight: for smaller (2 - 5 g) and larger (8-18 g) fishes under surfacing allowed and surfacing prevented conditions these were 1.045 & 0.731 and 0.688 & 0.358 respectively. However, in surfacing allowed static water conditions the scaling pattern for smaller fishes were greater (0.321) than the larger ones (0.158). Larger fishes showed comparatively steeper falls in regression line than for smaller ones for VO_2 per unit body weight under surfacing allowed (b = -0.269, 0.045) and surfacing prevented (b=-0.643, -0.312) conditions with flowing water, and under surfacing allowed conditions with static water (b = -0.843, -0.679). Point of inflexion for the regression line relating oxygen uptake per unit time and per unitbody weight is variable under various experimental conditions and ranges from 4-10 g body weight. Variation in the scaling pattern for VO_2 in relation to body weight has been discussed in the light of efficacy of aquatic gas exchange at different growth stages under various experimental conditions.

Key Words: Scaling pattern, Oxygen uptake, *Pseudapocryptes lanceolatus*, Amphibious goby

Introduction

The majority of gobies spend about 16 hr on flat muddy surfaces and self-made burrows and extract O_2 directly from air by ventilating their opercular and suprabranchial chambers (Singh & Munshi 1969, Tamura et al. 1976, Biswas et al. 1979, Haque 1984, Hughes & Al-Kadhomiy 1986 and Yadav & Singh 1989). They also ventilate their gills with estuarine water and obtain O_2 from it when they are submerged (Biswas et al. 1979, Haque 1984). Some of these fishes are also entrapped in wetlands of these estuaries during low tide and use their gills and skin for aquatic O_2 uptake and opercular and suprabranchial chambers for aerial respiration (Yadav & Singh 1989). Some information is available on the scaling pattern of the dimensions of the respiratory organs in relation to body weight for such gobies (Hughes and Al-kadhomiy 1986; Yadav et al. 1990). However, there is paucity of information on the scaling pattern of VO_2 in relation to body weight (Biswas et al. 1979) and the growth of gobies. This forms the basis of the present investigation on the estuarine goby, *Pseudapocryptes lanceolatus*.

Materials and Methods

Live specimens of *P.lanceolatus* collected from the wetlands of the fisheries complex at Digha (West Bengal, India) were transported to a field laboratory stationed near the collection spot and were maintained in glass aquaria containing estuarine water. Self-designed respirometers were used to measure the aquatic O_2 uptake of the fishes under surfacing allowed or surfacing prevented conditions in flowing or static water system. In the first series of experiments a rectangular plexiglass respirometer (500 ml) with a small air chamber (9 cm^3) at its top (figure 1A) was used to allow free access to air to the fishes. In the second series of experiments a cylindrical respirometer (500 ml) without the air chamber was used to prevent access to air to the fishes. For surface-allowed and surface-prevented experiments with flowing water conditions, the respirometers were connected to a constant level water tank to maintain the flow of water under constant pressure of about 834 mm Hg (atmospheric pressure, 760 mm Hg) + (pressure exerted on fish by a water column of about 1000 mm, 1000/13.6 = 74 mm Hg). The flow of water through the respirometers was adjusted according to the size of the fish through valves to avoid any stress of asphyxiation. The fishes were acclimatized to their respective respirometers for at least two hours before the readings were taken. Water samples were collected unaerobically in conical flasks (100 ml) connected at the inlet and outlet points of the respirometers. For experiments with static water condition the water flow in the respirometer was stopped by valves. A submersible stirrer was used to mix water of the respirometer.

Calculation for Aquatic O_2 Uptake

VO_2 (ml O_2 hr^{-1}) was calculated using the equation :

$$VO_2 = V_w (CIO_2 - CEO_2)$$

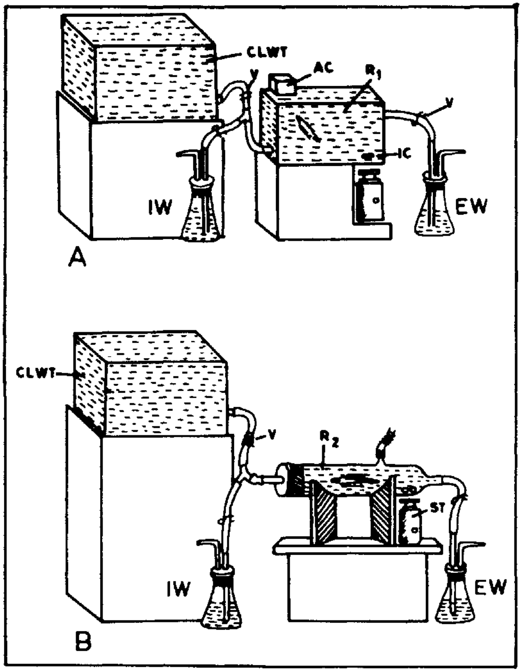

Figure 1 Experimental set up for measuring aquatic O_2 uptake with (A) and without (B) air-breathing. Valves (V) were closed to obtain static condition. (*AC*,.air chamber; *CLWT*, constant level water tank; *EW*,.expired water; R_1., respirometer with access to air; R_2, respirometer without access to air, *ST*, stirrer; *V*, valve)

where VO_2 is the O_2 uptake, V_w the water flow (ml min^{-1}) and CIO_2 & CEO_2 the concentration of oxygen in inlet and outlet waters of the respirometer respectively. The dissolved O_2 in water was estimated by Winklers volumetric method (Welch 1948). The experiments were conducted from 7-10 AM to minimize temperature fluctuation (28 ± 1°C).

Statistical Model

Data on aquatic O_2 uptake rate for eleven average weight groups (n = 3 in each weight group) were analyzed by linear logarithmic transformations using least square regression method. The general equation $Y = aw^b$ or $\log Y = \log a + b \log W$ was used to show the various scaling patterns for VO_2 against body weight, where Y is the parameter (O_2 uptake) analyzed, W is the body weight, log a and b were respectively the intercept and slope of the regression line (Rao 1965). Separate regression analyses were made for small (2-5 g) and large (8-18 g) fishes to test the validity of two component curves for the gills of *P. lanceolatus* (Yadav & Singh 1989). F-test was applied to test the difference between two exponent values (b) for the fishes of small and large weight groups at 5% and 1% level of significance.

The test statistic is:

$$\frac{R_2^2 - R_1^2}{R_1^2} \times \frac{n_1 + n_2 - 4}{1} \sim F_{1_o} n_1 + n_2 - 4$$

Drowning Experiment

Drowning experiments were performed in different weight groups of fishes under normoxic estuarine water (Do = 6.9mg $O_2 l^{-1}$; *p*H 7.4) to ascertain the intraspecific variation in the asphyxiation time. Fishes of different weight groups were also exposed to air to determine their survival time out of water.However, these fishes were occasionally sprayed with estuarine water to avoid desiccation.

Results

Data on aquatic VO_2 for eleven weight groups (n=3, in each weight group) of fishes under various experimental conditions are presented in table 1 and figures 2 & 3.

O_2 Uptake Rate from Flowing Water with Access to Air

Under this experimental condition the fishes extract oxygen from ambient water and also visited the water-air interface at irregular intervals to ventilate their supra-branchial and opercular chambers for air-breathing. The O_2 uptake rate (ml O_2 hr^{-1}) showed positive correlation (r = 0.988; P < 0.001) with a . slope of 0.758 (figure 2A). The scaling pattern of VO_2 in relation to body weight for smaller fishes (1.045) was significantly (P < 0.01) different from that of larger ones (0.731; figure 2B). However, VO_2 (ml O_2 Kg^{-1} hr^{-1}) showed negative correlation with body weight (r= -0.899; P < 0.01) with a slope of -0.241 (figure 3A). The scaling pattern of VO_2 (ml O_2 Kg^{-1} hr^{-1}) for smaller fishes (0.045) was not significantly (P > 0.05) different from that (-0.269) of larger ones (figure 3B).

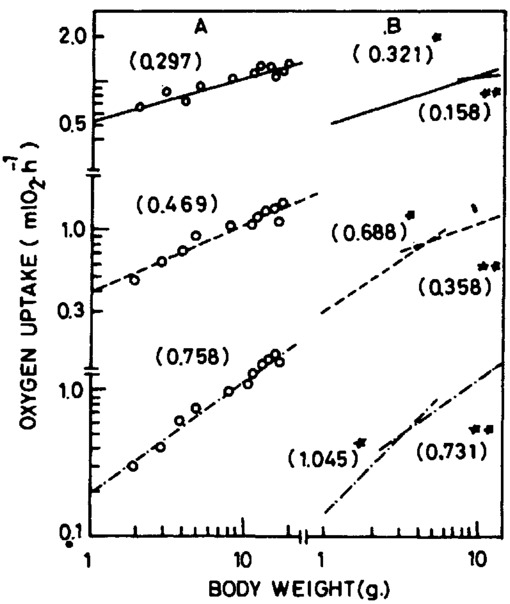

Figure 2 Bilogarithmic plots to show the relationship between VO_2 (ml O_2 hr^{-1}) and body weight under surfacing allowed (- . -) and surfacing prevented (---) conditions of flowing water system and surfacing allowed condition of static water (—). Values in parentheses indicate the regression coefficients for pooled data (A) and those obtained for bicomponent curves (B) for small (*) and large (**) weight groups of fishes

O_2 Uptake Rate from Flowing Water without Access to Air

Under this experimental set up, the ventilation of the suprabranchial and opercular chambers to air was not allowed and the fishes could ventilate

Table 1 *Aquatic oxygen uptake rate (mean values ±SD) under surfacing allowed and surfacing prevented conditions of flowing and static water systems of different weight groups of an estuarine goby,* ***Pseudapocryptes lanceolatus***

Weight (g)	Oxygen uptake rate: Flowing system, Surfacing allowed, $ml O_2 hr^{-1}$	Flowing system, Surfacing allowed, $ml O_2 kg^{-1} hr^{-1}$	Flowing system, Surfacing prevented, $ml O_2 hr^{-1}$	Flowing system, Surfacing prevented, $ml O_2 kg^{-1}$	Static system, Surfacing allowed, $ml O_2 hr^{-1}$	Static system, Surfacing allowed, $ml O_2 kg^{-1} hr^{-1}$
2.0	0.307±0.01	153.5±4.90	0.475±0.02	237.5±12.25	0.637±0.01	318.5±6.94
3.0	0.407±0.03	135.7±11.76	0.637±0.01	212.3±2.45	0.817±0.06	272.3±19.84
4.0	0.643±0.03	160.7±7.14	0.735±0.03	183.7±6.33	0.735±0.07	183.7±16.74
5.0	0.768±0.02	153.6±3.27	0.912±0.01	182.4±3.10	0.912±0.03	182.4±5.55
8.0	0.968±0.01	121.0±1.54	1.056±0.05	132.0±6.25	1.056±0.03	132.0±3.27
11.25	1.101±0.10	97.9±9.07	1.130±0.06	100.4±4.90	1.130±0.02	100.4±1.31
12.0	1.316±0.02	109.7±2.11	1.232±0.01	102.7±0.49	1.272±0.09	106.0±7.63
14.0	1.513±0.06	108.1±2.20	1.370±0.06	97.9±4.37	1.232±0.04	88.0±2.49
15.0	1.620±0.09	108.0±4.37	1.472±0.12	98.1±7.92	1.112±0.07	74.1±4.90
17.0	1.657±0.01	97.5±0.82	1.162±0.19	68.3±11.19	1.162±0.05	68.3±3.18
18.0	1.620±0.09	90.0±4.90	1.500±0.07	83.3±3.76	1.287±0.04	711.5±2.25

their gills alone for gaseous exchange through water. Under such condition O_2 uptake (ml O_2 hr^{-1}) and weight showed positive correlation ($r = 0.969$; $P < 0.001$) with a slope of 0.469 (figure 2A). Scaling pattern for smaller ($b = 0.688$) and larger fishes ($b = 0.358$) showed a significant difference ($P < 0.05$) (figure 2B). To the contrary the O_2 uptake rate (ml O_2 Kg^{-1} hr^{-1}) showed negative correlation with body weight ($r = -0.975$; $P < 0.001$) with a slope of -0.531 (figure 3A). Smaller ($b = -0.312$) and larger fishes ($b = -0.643$) showed variation in scaling pattern for VO_2 in relation to body weight (figure 3B).

O_2 Uptake Rate from Static Water with Access to Air

At the onset of such conditions the fishes used to break the water-air interface and gulped mouthfuls of air and retained itin the suprabranchial and opercular chambers. The presence of air in these chambers increased the buoyancy of head with respect to other parts of the body and fishes were suspended in water column with its snout touching the air column of the respirometer. Retention of air varied from 5 to 115 sec in fishes of different weight groups. Out of the total time (about 5 min) from the first air gulp to the end of experiment, the fishes spent about 84% time on air breathing and the rest (16%) was used for gill ventilation.

VO_2 and body weight showed positive correlation ($r = -0.952$; $P < 0.001$) with a slope of 0.297 (figure 2A). The two variables showed difference in the scaling for smaller ($b = 0.321$) and larger ($b = 0.158$) fishes (figure 2). However, such differences were not statistically significant ($P > 0.05$). VO_2 (ml O_2 Kg^{-1} hr^{-1}) showed negative correlation ($r = -0.991$; $P < 0.001$) with a slope of -0.703 (figure 3A). There was no significant variation ($P > 0.05$) in the scaling pattern for smaller ($b = -0.679$) and larger ($b = -0.843$) fishes (figure 3B).

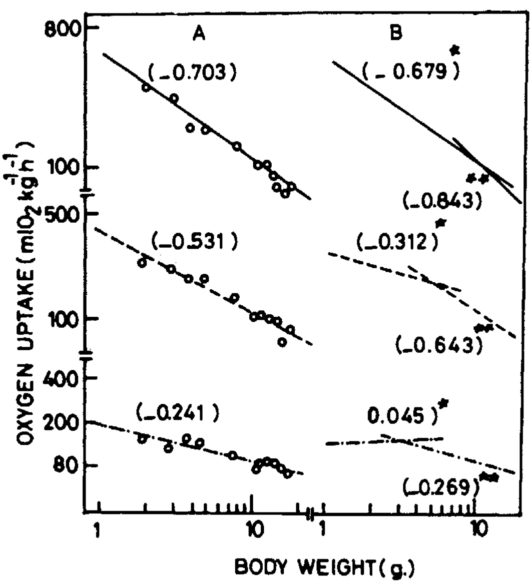

Figure 3 Bilogarithmic plots to show the relationship between VO_2 (ml O_2 Kg^{-1} hr^{-1}) and body weight under surfacing allowed(–.–)and surfacing prevented (– –) conditions for flowing water system and open condition of static water . Values in parentheses indicate the regression coefficients for pooled data (A) and those obtained for bicomponent curves (B) for small (*) and large (**) weight groups of fishes.

Respiratory Behaviour of Fishes in Static Water without Access to Air

At the start of the experiment the fishes were comfortable in the respirometer containing estuarine water with opercular frequency 100 min^{-1}. After about 30 min fishes started searching the water-air interface. Failing their attempt they settled down to the bottom of the aquarium to ventilate the ambient water vigorously (opercular frequency 123 min^{-1}). The fishes became uncomfortable and the experiments were discontinued and the data on VO_2 under such stressed condition were not processed for regression analysis.

Behavioural Response to Air-exposed and Drowning Conditions

Unlike obligate water breathers which react violently when exposed to air, *P. lanceolatus* remained motionless and gulped air at irregular intervals. At times the goby retained the air in the opercular chambers for 4 min 30 ± 20 sec. Sometimes opercula were closed and the bidirectional flow of air was maintained by periodically opening and closing the gape of mouth. Outside water the fishes in question survived for more than 12 hr if their skin was sprayed with estuarine water. The fishes also withstood the drowning condition and survived well even after 24 hr in surfacing prevented system with flowing estuarine water.

Discussion

The surfacing allowed experimental set up simulates the natural conditions of the estuaries which gobies experience during high tide. In this period the air in the branchial and opercular chambers ensures higher buoyancy to the head with respect to other parts of the body and the fishes are carried passively in vertical posture alongwith denser water current (Biswas et al. 1979, Haque 1984). Such buoyancy of gobies reduces the energy expenditure to reach the water-air interface. Significant differences in the scaling pattern for the two variables (aquatic VO_2 and body weight) under surfacing allowed condition supports the validity of two component curves for gills of fishes below and above 6 g body weight (Yadav & Singh 1989). Higher exponent value for the two variables of smaller fishes suggest their preference for water breathing and supports the earlier findings of Hughes et al. (1986) that the dual breathers depend more on aquatic O_2 uptake in the early part of their life history. Comparatively smaller exponent value for larger fishes suggests gradual decline in aquatic respiration and their preference for air breathing. The urge for air breathing may be associated with the decline in lamellar number as some of them participate in the development of neomorphic air breathing organs (Yadav & Singh 1989). Higher exponent value for pooled data suggests overall greater efficacy of aquatic respiratory organs in this experimental condition.

The surfacing prevented condition of the flowing water in the laboratory approximates that in the estuaries during high tide where some of the gobies are entrapped in self-made burrows. On such occasions the fishes prefer to stay in their respective burrows and obtain oxygen entirely from the estuarine water. Such findings suggest facultative air breathing habit of the fishes. In this experimental condition smaller fishes extract comparatively more oxygen than in surfacing allowed condition. This may be related to complete dependence of fishes on water breathing in the former condition and option of air breathing in the latter. Lower oxygen uptake for larger fishes in surfacing prevented condition may be related to the decreased efficacy of gills and skin due to comparatively greater diffusion distance (Haque 1984). Significant difference in the scaling pattern for aquatic O_2 uptake for smaller and larger fishes under closed conditions of flowing water may be related to difference in the O_2 uptake efficacy of gills and skin and the contribution of lamellar units to the development of neomorphic air-breathing organs (Yadav & Singh 1989).

Significantly higher exponent value for pooled data for O_2 uptake in relation to body weight in surfacing allowed condition than that in surfacing prevented condition suggests the former conditions more congenial for aquatic VO_2 than the latter one. Variation in the scaling pattern for VO_2 per unit time in relation to body weight indicates more pronounced decrease in the efficacy of aquatic respiratory organs of larger fishes than the smaller ones.

The surfacing allowed system with static water approximates the condition prevalent in the wetlands of the estuaries during low tide. The fishes trapped in the stagnant water are free to ventilate their gills and opercular chambers for aquatic and air breathing respectively. Because of breathing and rebreathing the same static water there is gradual decline in the ambient O_2 level which in turn increases the surfacing frequency of the fishes to avoid the critical O_2 level (1.9 mg O_2 l^{-1}). Greater exponent values for smaller fishes in comparison to the larger ones again suggest dependence of the lower weight groups on aquatic breathing and the older ones on air breathing. Variation in the scaling pattern for O_2 uptake in relation to body weight in smaller and larger weight groups of fishes under various experimental conditions suggests differences in the O_2 uptake capacity of gills and skin of gobies in different stages of fish growth under varied ecological niches.

The steeper decline in the O_2 uptake per unit body weight in larger fishes than in smaller ones suggests judicious use of the dissolved oxygen in the ambient water to avoid critical O_2 level (1.9 mg O_2 l^{-1}). This critical O_2 level in the estuaries seems to be one of the decisive factors in the evolution of air breathing in such gobies.

The closed system with static water in the respirometer is not a natural phenomenon in the estuaries. However, this experimental condition indicates the critical oxygen level of the respirometer which monitors the air breathing in the gobies under question.

The respiratory behaviour during drowning experiments indicates that the fishes are comfortable in air as well as in normoxic estuarine water. Such findings suggest the facultative air and water breathing habit of *P. lanceolatus*.

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