

## Influence of ambient oxygen and random swimming activity on metabolic rates and quotients in the freshwater mullet *Rhinomugil corsula* (Hamilton)\*

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**Abstract.** Oxygen consumption and carbon dioxide production increased with increase in random (spontaneous) swimming activity in mullet, *Rhinomugil corsula* in high oxygen (normoxia), but the oxygen consumption in low oxygen (hypoxia) was negatively correlated with swimming activity in tests at both 30 and 35°C. The RQ of mullet under hypoxia always remained over unity and increased with increase in activity, clearly indicating intense utilization of anaerobic energy. The RQ under normoxia remained near unity irrespective of random swimming activity change. The AQ of normoxic and hypoxic mullet showed opposing trends, the quotient increasing with decreasing activity in the former and increasing with activity increase in the latter. The AQ change suggests increased protein utilization in quieter fish when adequate ambient oxygen is available, but the hypoxic mullet utilizes more protein the more active it is. The latter change in AQ is consonant with the change in hypoxic RQ and it is likely that increased anaerobic energy utilization demanded by the increased activity is accompanied by increased protein breakdown and ammonia release, thereby helping in acid-base balance and ionic (Na<sup>+</sup>) regulation. Results obtained at 30 and 35°C are almost identical. Within the small range temperature does not seem to cause a marked metabolic difference in mullet.

**Keywords.** Ambient oxygen; normoxia; hypoxia; respiratory quotient; ammonia quotient; swimming activity; *Rhinomugil corsula*.

### 1. Introduction

The metabolic quotients, RQ and AQ<sup>‡</sup> in fish have been used as indices of anaerobic metabolism (Kutty 1968, 1972; Kutty *et al* 1971a; Peer Mohamed and Kutty 1981; Peer Mohamed 1982; Peer Mohamed and Kutty 1983a, b) and protein utilization (Stroganov 1956; Kutty 1972; Kutty and Peer Mohamed 1975; Sukumaran and Kutty 1977; Peer Mohamed and Kutty 1981, 1983a, b), respectively. While there are several studies on the influence of random (spontaneous) activity on oxygen consumption in fish (Spoor 1946; Beamish and Mookherjee 1964; Beamish 1964; Smit 1965; Peer Mohamed *et al* 1978; Peer Mohamed 1982; Peer Mohamed and Gupta 1984) the influence of random activity on RQ has been studied only in a few cases (Kutty 1968; Kutty and Peer Mohamed 1975; Peer Mohamed and Kutty 1981, 1983a, b; Peer Mohamed 1982).

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‡RQ and AQ denote Respiratory Quotient and Ammonia Quotient which are mole to mole relations of carbon dioxide produced to oxygen consumed, and ammonia excreted to oxygen consumed, respectively.

Under aerobic conditions random activity did not appear to have any effect on the RQ of goldfish and rainbow trout (Kutty 1968), but the AQ might change with random activity (Kutty and Peer Mohamed 1975; Peer Mohamed 1982). Intense forced activity has been shown to influence both RQ and AQ in fishes (Kutty 1968, 1972; Sukumaran and Kutty 1977). Also it is not known how random activity and ambient oxygen would together influence anaerobic energy utilization and protein degradation. A study of RQ and AQ in mullet under random activity under various oxygen conditions would throw light in this regard. In the present study simultaneous measurements of oxygen consumption, carbon dioxide output, ammonia excretion and random swimming activity have been made in the mullet, *Rhinomugil corsula* at various ambient oxygen concentrations below air saturation at two temperatures, 30 and 35°C. Since most of the nitrogen excreted by the freshwater fish is in the form of ammonia (Black 1957) as shown in the present material (*Rhinomugil corsula*) as well (Sukumaran and Kutty 1977) it is felt that a reasonable pattern of protein degradation can be obtained from measurements of ammonia excreted.

In freshwater fish under anaerobiosis, ammonia produced may be of use in combating acidosis and also in conservation of Na<sup>+</sup> (Prosser and Brown 1961; Garcia Romeu and Motais 1966; Forster and Goldstein 1969; Kutty 1972; Peer Mohamed and Kutty 1981). In this context as well, the present study on changes in RQ and AQ in mullet especially under hypoxia will be of interest.

## 2. Material and methods

*Rhinomugil corsula* (Hamilton), chosen for this study, is a fresh-water mullet abundant naturally in Gangetic and Mahanadhi river systems in North India; the fish was transplanted to Vaigai Dam by The Tamil Nadu Department of Fisheries (Kutty *et al* 1971b), and now the fish are breeding and thriving in freshwater in the Vaigai reservoir (Narayanan 1974). *R. corsula* collected from Vaigai Dam, were acclimated to freshwater at 30 ± 1°C and 35 ± 1°C for atleast 15 days before experiment, and tested under acclimation temperature. The fish were deprived of food for 36 hr (Fromm 1963; Beamish 1964; Kutty 1972; Peer Mohamed and Kutty 1981) before experiments.

Thirty-two mullet were used in these tests; they ranged in weight from 33.9–53.1 g (mean 41.2 g) and total length from 16.7–19.3 cm (mean 17.4 cm).

### 2.1 Apparatus

A modification of Fry's respirometer (Kutty *et al* 1971b) was used for the present experiments. Mainly it consisted of two units, an electronic counter and a transparent 'Perspex' annular respirometer having a capacity of 3 litres. When the fish moved it cut the light beams focussed on photocells in the centre of the annulus and the event was recorded by the electronic counter (more details of the apparatus are given in Kutty *et al* 1971b).

### 2.2 Fish medium and recirculation

The natural well-water available was very hard and it was unsuitable as fish medium for accurate determination of carbon dioxide production of fish. Therefore, as explained in

Kutty *et al* (1971a) decarbonated water of controlled pH (Bosworth *et al* 1936; Kutty 1968) was prepared and used as fish medium. The medium was pumped from a ground level reservoir (70 L) to an overhead reservoir of the same size. The latter was provided with a thermostat and a constant level device (Electric Control Equipment Co., Madurai) which activated the pump. Water from the overhead reservoir flowed through the respirometer to the ground level reservoir from which it was recirculated.

### 2.3 *Experimental procedure*

The experimental fish was transferred to the respirometer and the fish medium at the acclimation temperature, was circulated through the respirometer overnight. At the start of the experiment, initial water samples of run I were collected and circulation of water through the respirometer was cut off. After an interval of 60 min final samples were collected. At each sampling (initial and final of each run), 3 separate water samples were collected for analyses of dissolved oxygen, total carbon dioxide and ammonia. The size of each sample was 30 ml for dissolved oxygen, 60 ml for total carbon dioxide and 60 ml for ammonia (25 ml collected first as rinse was discarded). The figure in the activity counter was recorded immediately after each sampling. After taking the final samples of run I the respirometer was not opened to the circulating water for complete flushing but approximately 175 ml of fish-medium was circulated once or twice through the respirometer for mixing it with the water remaining unflushed in the respirometer. Then the initial samples of next run (run II) (as described above) were collected. The overall time for sampling and adding water was about 3 min. During the last run, the final samples were collected only after the fish reached the asphyxial oxygen level, as indicated by the beginning of equilibrium loss of the fish. Then the respirometer was flushed with air-saturated decarbonated water to revive the animal.

Data from the test runs were categorised into 2 groups, depending on the mean ambient oxygen concentration: (i) those with ambient oxygen values below air saturation but above 50% air saturation (referred here as 'normoxia') and (ii) those with oxygen values below 50% air saturation down to asphyxial oxygen (referred here as 'hypoxia'). Subsequent analyses of data are done accordingly.

### 2.4 *Methods of water analyses*

2.4.1 *Dissolved oxygen:* The unmodified Winkler method was followed (American Public Health Association 1965). The size of the sample used for titration was 25 ml.

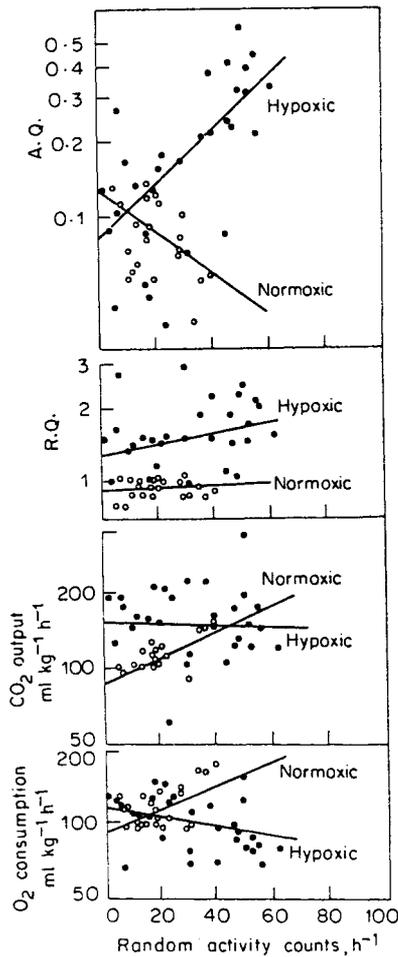
2.4.2 *Total carbon dioxide:* Direct measurement of total carbon dioxide by distillation and subsequent titration was made by the method described by Kutty *et al* (1971a), which is a modification of Maros-Schulek technique (Maros *et al* 1961).

2.4.3 *Ammonia:* The method followed was described by Kutty (1972) in which some modifications were incorporated as suggested by Stroganov (1962), which was in general agreement with that given in Standard Methods (American Public Health Association 1965). Fifty ml of water samples were distilled, the distillate nesslerised, and the optical density read in a Bausch and Lomb spectrophotometer (Spectronic-20) at a

wavelength of  $420 \mu$ . Ammonia free water (American Public Health Association 1965) was always used for blank and to prepare the reagents.

### 3. Results

Data on oxygen consumption, carbon dioxide production, RQ and AQ in relation to random swimming activity in mullet *R. corsula* exposed to oxygen concentration near air saturation (normoxia) and below 50% air saturation down to asphyxial oxygen concentration ( $0.8 \text{ mg l}^{-1}$ ) (hypoxia), are plotted in semilogarithmic graphs and are displayed in figure 1 ( $30^\circ\text{C}$ ) and 2 ( $35^\circ\text{C}$ ). The regression equations concerned are presented in table 1. The data on ammonia excretion are not indicated in figures 1 and 2



**Figure 1.** Oxygen consumption, carbon dioxide production, RQ and AQ in relation to random swimming activity in mullet, *Rhinomugil corsula* (acclimation and test at  $30^\circ\text{C}$ ) exposed to oxygen concentration near air saturation (normoxia) and to oxygen concentration below 50% air saturation down to asphyxial oxygen concentration ( $0.8 \text{ mg l}^{-1}$ ) (hypoxia). Data for normoxia and hypoxia are indicated by open and closed symbols respectively. Regression lines are fitted to plots in the figure by the method of least squares.

**Table 1.** Regression equations of logarithms of O<sub>2</sub> consumption, CO<sub>2</sub> production, NH<sub>3</sub> excretion (ml kg<sup>-1</sup> hr<sup>-1</sup> in each case), RQ and AQ (Y) on random swimming activity (counts hr<sup>-1</sup>) (X) in the mullet, *Rhinomugil corsula*, under 'hypoxia' (ambient O<sub>2</sub> below 50% air saturation down to asphyxial oxygen concentration) and 'normoxia' (ambient O<sub>2</sub> near air saturation) at 30°C and 35°C.

	30°C	35°C
<i>Hypoxia</i>		
O <sub>2</sub>	: log Y = 2.07044 - 0.00245 X	log Y = 2.00307 - 0.00036 X
CO <sub>2</sub>	: log Y = 2.17358 - 0.00031 X	log Y = 2.14488 + 0.00057 X
NH <sub>3</sub>	: log Y = 0.92250 + 0.01000 X	log Y = 0.83530 + 0.00820 X
RQ	: log Y = 0.10799 + 0.00197 X	log Y = 0.12856 + 0.00361 X
AQ	: log Y = -1.06161 + 0.01056 X	log Y = -1.01085 + 0.00361 X
<i>Normoxia</i>		
O <sub>2</sub>	: log Y = 1.96761 + 0.00503 X	log Y = 2.04390 + 0.00125 X
CO <sub>2</sub>	: log Y = 1.93430 + 0.00446 X	log Y = 1.99140 + 0.00292 X
NH <sub>3</sub>	: log Y = 0.95080 + 0.00250 X	log Y = 1.03220 + 0.00110 X
RQ	: log Y = -0.03010 - 0.00068 X	log Y = -0.03720 - 0.00056 X
AQ	: log Y = -0.89420 - 0.00898 X	log Y = -1.01080 - 0.00020 X

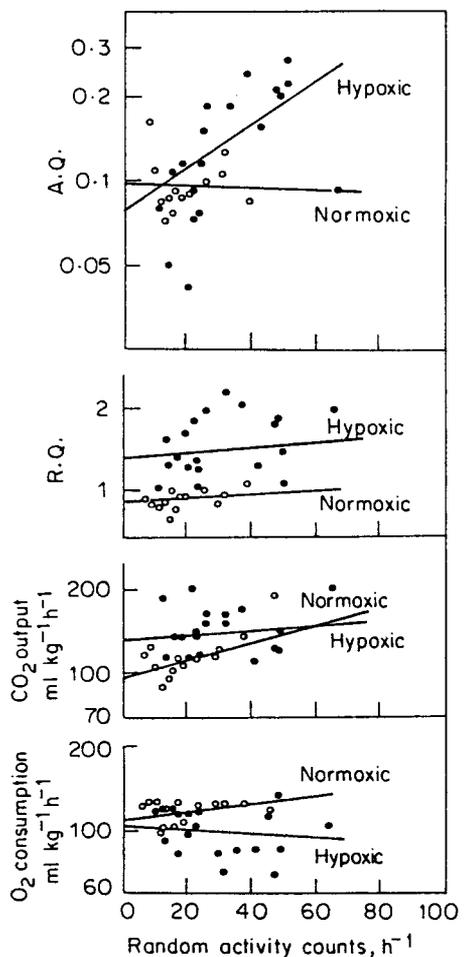
to avoid crowding in the figures, but their extent can be judged from a comparison of AQ and corresponding values of oxygen consumption.

It is interesting to check if the changes in the metabolic rates and quotients can be correlated with changes in random swimming activity at different ambient oxygen concentrations. Extrapolation of a line drawn through such plots of metabolic rates to 'zero' activity can be used for estimating the standard metabolism (Spoor 1946; Smit 1965; Kutty 1968; Kutty *et al* 1971b; Peer Mohamed *et al* 1978; Peer Mohamed and Gupta 1984). For such estimations, usually data obtained from simultaneous measurements of metabolism and activity of a single fish are used for plots. In the present study, the data available for individual fish are too small for such treatment. Therefore data for all individuals of mullet tested under similar oxygen concentrations are pooled. This we believe is permissible in view of the fact that the fish used were almost of similar size and some useful information can thus be made out with the present results. The trends of metabolic rates and quotients are essentially same in mullet at 30 and 35°C (figures 1 and 2). So there is some uniformity of results obtained, in spite of pooling of data from different fishes.

The standard (basal) values of metabolic rates and quotients of normoxic and hypoxic *R. corsula* at 30 and 35°C are given in table 2 as estimated from the regression equations in table 1. It is seen that the standard values at 30 and 35°C are remarkably close to each other, suggesting that temperature effect between the test temperatures is minor, probably because these temperatures are close to each other and are within the upper range to which the mullet is normally exposed during a good portion of the year. In general this is true of the other routine metabolic rates presented as well.

#### 4. Discussion

Slopes of regression lines of oxygen consumption and carbon dioxide production in mullet under adequate oxygen (normoxia) (figure 1) indicate that both rates increase



**Figure 2.** Oxygen consumption, carbon dioxide production, RQ and AQ in relation to random swimming activity in mullet, *Rhinomugil corsula* acclimated to and tested at 35°C. For further explanation see legend to figure 1.

**Table 2.** Estimated standard metabolic rates and quotients of mullet, *Rhinomugil corsula* acclimated to and tested at 30 and 35°C under high (normoxia) and low (hypoxia) oxygen.

Metabolic rate/quotient (ml kg <sup>-1</sup> hr <sup>-1</sup> )	Normoxia		Hypoxia	
	30°C	35°C	30°C	35°C
Standard O <sub>2</sub> consumption	93	111	118	101
Standard CO <sub>2</sub> production	86	98	149	140
Standard NH <sub>3</sub> excretion	9	11	8	7
Standard RQ	0.93	0.92	1.28	1.34
Standard AQ	0.13	0.10	0.09	0.10

with increase in random swimming activity. The fish is aerobic, maintaining an RQ close to unity (the change in RQ with random activity is negligible). In normoxic fish the AQ seems to increase with decrease in random activity, especially clear in the plot of values at 30°C (figure 1) suggesting a greater involvement of protein degradation, the quieter the fish, the proportionately higher its protein use as was also observed in *Tilapia mossambica* (Peer Mohamed 1982). This observation is in variance with the results of study on the influence of forced activity on AQ. In the latter case the AQ increased with increase in activity (Kutty 1972; Karuppannan 1972; Sukumaran and Kutty 1977). In *T. mossambica* it appeared that initial AQ (first hour of 5 hr exercise) at lower swimming velocity was less than the routine AQ (Kutty 1972; Karuppannan 1972). And it was suggested that in this case there might be a protective action of carbohydrates on protein. This might be the reason why the steady AQ (after 2–3 hr swimming) is correlated better with the initial RQ of fish under long-term exercise (Kutty 1972; Karuppannan 1972). It is not impossible that random activity (spontaneous random movement) and forced activity (intense exercise) have different relations to protein degradation and utilization, as indicated by NH<sub>3</sub> excretion. A quieter fish would utilize proteins more, but increase in random activity relatively more energy is required by the fish for several breaks and starts in swimming overcoming inertia each time (Brett 1964; Smit 1965; Kutty 1969). In this case carbohydrate utilization could be higher as long as adequate oxygen is available, thereby indicating lower AQ at higher random activity, more or less similar to the low initial AQ during the beginning of intense activity (continued exercise). In both these cases, fish under high random activity and initial phase of intense swimming (forced activity), the protective action of carbohydrates on proteins may be operative (Phillips 1970) and low AQs may result. In continued exercise a better correlation of AQ is always with the duration of exercise, protein utilization being high the longer the exercise, rather than with the increase in the intensity of exercise even though the latter does exist in apparent contrast with the AQ decrease with increase in random activity.

The trends of hypoxic metabolism with activity are quite different. The oxygen consumption of hypoxic mullet decreased with increase in random activity, and its RQ and AQ showed marked increase with increase in activity, in marked contrast with the trends of these parameters in normoxic mullet.

The level of carbon dioxide production in the hypoxic mullet is generally higher than the oxygen consumption, as indicated by the RQ plot. The anaerobic metabolism (RQ over unity) increased with increase in activity. The opposing trends of oxygen consumption and RQ in relation to random activity again suggest a compensatory increase in anaerobic energy utilization.

The negative slope of the oxygen consumption–activity relation of the hypoxic mullet can perhaps be explained as due to acid loading, or acidosis and subsequent reduction in oxygen capacity of the blood. Karuppannan (1972) also found that at high temperatures the relation of oxygen consumption and level of forced activity in *T. mossambica* may have a negative slope. There is evidence that the anaerobic metabolism was higher at higher activities in the hypoxic mullet, and therefore acid accumulation could also have been higher. The oxidative energy lack is compensated by increased protein degradation and anaerobic energy utilization. As has been suggested earlier herein, the coupling of increased protein degradation and anaerobic energy utilization may have significance in combating acidosis and also in conserving Na<sup>+</sup> during hypoxia, which may be specially required due to hypoxic stress on ion-osmotic mechanism.

From the scatters of hypoxic AQ values (figures 1 and 2) it is seen that the higher values were obtained in mullet at 30°C, some values going as high as 0.5. While it appears that much of the ammonia excreted by mullet under hypoxia was produced anaerobically, it is suggested that only values higher than a theoretically estimated maximum for anaerobic conditions can be confirmed as anaerobically involved (Sukumaran and Kutty 1977). In that context clearly anaerobic AQs (above 0.33) seem to occur in hypoxic mullet at 30°C only, but it is likely that under hypoxic conditions even the lower AQs are partially accounted for by anaerobically produced ammonia.

It is also interesting to compare the standard metabolism of the hypoxic and normoxic mullet. Because of the opposing trends in the slopes of the regression lines of oxygen consumption and random activity at both 30 and 35°C, the standard metabolism under normal and hypoxic conditions is not markedly different, but the standard carbon dioxide production and RQ are different, the latter being always higher in the hypoxic mullet, suggesting that anaerobic metabolism, can be intense in quieter fish as well under hypoxic conditions.

## 5. Conclusion

There does not appear to be any marked difference between the metabolic rates of mullet at 30 and 35°C, even though the RQ and AQ at the temperature range is perhaps close and is probably near a flattened optimum level. While further statistical treatment of the limited data available appears unwarranted, as explained, the general similarity of trends of metabolic rates and quotients in relation to random swimming activity in hypoxic and normoxic mullet, at 30 and 35°C, appears to confirm the validity of the present observations. There are no other similar observations on fish, as far as we are aware, and within the general framework of the present study the results are valid and clearly point out the need for further study in the area of organismal physiology. Taking this approach the ecophysiological or the autecologist would perhaps succeed in unravelling some of the unanswered questions in bioenergetics especially with reference to the coupling of anaerobic energy utilization and enhanced protein metabolism as it is related to the activity of the whole animal.

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