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**Investigations on the respiration of the Neotropical fish,
Colossoma macropomum (Serrasalminae)
The influence of weight and temperature on the routine
oxygen consumption**

by

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1. Introduction

The influence of weight and temperature on the oxygen consumption of fish has already been the subject of numerous scientific investigations. Reviews of these studies have been provided by such authors as WINBERG (1956), PALOHEIMO and DICKIE (1966), KAUSCH (1972), and FISCHER (1979). Plotted on a double logarithmic grid, oxygen consumption increases linearly with weight, with a mean slope of approximately 0.8 (WINBERG 1956; THONNEY et al. 1976). As the differences in this value among various species and under different experimental conditions are often great, FRY (1971) correctly warned that this value should not be taken as an absolute.

The majority of investigations concerning the relationship of oxygen consumption to weight were conducted exclusively with fish inhabiting temperate climate zones, which are characterized by high diurnal and seasonal temperature variations. Tropical regions, however, are noted for more stable temperature conditions. For example, the mean annual temperature in the Central Amazon area is 27 to 28° C with diurnal variations of 8 to 10° C, and the difference between the mean summer and winter temperatures is less than 2° C (REINKE 1962). GEISLER (1969) was one of the only researchers who measured oxygen consumption of obligatory gill breathing Neotropical fish.

Colossoma macropomum of the family Serrasalminae, commonly known as the tambaqui, is widely distributed in South America, ranging from the Rio de la Plata to the Orinoco River system. In the Central Amazon area, it has a high market value and seems to show great promise for future aquacultural development in Brazil (SAINT-PAUL and

BAYLEY 1979; SAINT-PAUL 1981, 1982). It inhabits primarily the floodplains in the whitewater regions of the Amazon River system, called várzea. Adult fish feed mainly on fruits and seeds, while juveniles (smaller than 4 kg) feed on zooplankton as well (HONDA 1974; GOULDING 1980; CARVALHO 1981; SAINT-PAUL 1982).

This typical and important representative of the Neotropical ichthyofauna was selected for determining the influence of weight and temperature on oxygen consumption.

2. Material and methods

Excluding anaerobic pathways, oxygen consumption is regulated directly by the metabolic rate of fish. Three levels of metabolism can be distinguished, depending on the fish's state of activity: these are termed "standard", "routine", and "active" (FRY 1971). In the present investigation, routine oxygen consumption was determined. This is the mean rate observed in fish with metabolic rates influenced by random activity under experimental conditions. This level is of interest because it reflects the normal oxygen consumption under natural conditions, or it can be the basis for its calculation.

2.1. Fish material

Fish were collected from the floodplains of the white-water River Solimões/Amazon close to Manaus. For several weeks before the start of the experiment, they were kept in tanks at an experimental culture station at temperatures between 26 and 29° C. They were fed a pelleted diet containing 34.9 % crude protein.

2.2. Apparatus

The effect of body weight and temperature on the routine oxygen consumption was determined in a flow-through respirometer patterned after KAUSCH's (1968) apparatus. The whole system used is divided into three parts: the water reservoir, the constant level tank, and the respiration chamber (Fig. 1).

Tap water in the water reservoir was vigorously aerated and filtered through activated charcoal and foam rubber. Water was adjusted approximately to the desired experimental temperature. The water then passed to the constant level tank, which maintained the flow rate. In this tank, water was well mixed by a rotary pump, and the water temperature was regulated exactly. Then the water passed through the respiration chamber at a constant flow rate. The smallest of these was an Erlenmeyer flask with a volume of 200 ml. The largest chambers used were rectangular with pyramidal shaped ends. Depending on the fish size, a 9,800, 15,600, or 37,100 ml chamber was used.

2.3. Experimental conditions

The water temperature inside the respiration chamber deviated from the desired value by no more than 0.5° C. The flow rate was adjusted so that the outflowing water had an oxygen content approximately 20 % less than the saturated inflowing water. The tap water was extremely poor in electrolytes and was weakly acid. The metabolic activity of the fish inside the chamber during the experiment caused a slight increase in the organic matter content of the outflowing water as determined by the titrimetric addition of KMnO_4 . The iron content decreased due to absorption either by humic substances or by the gills and skin of the fish. Some chemical parameters of the in and outflowing water are listed in Table 1.

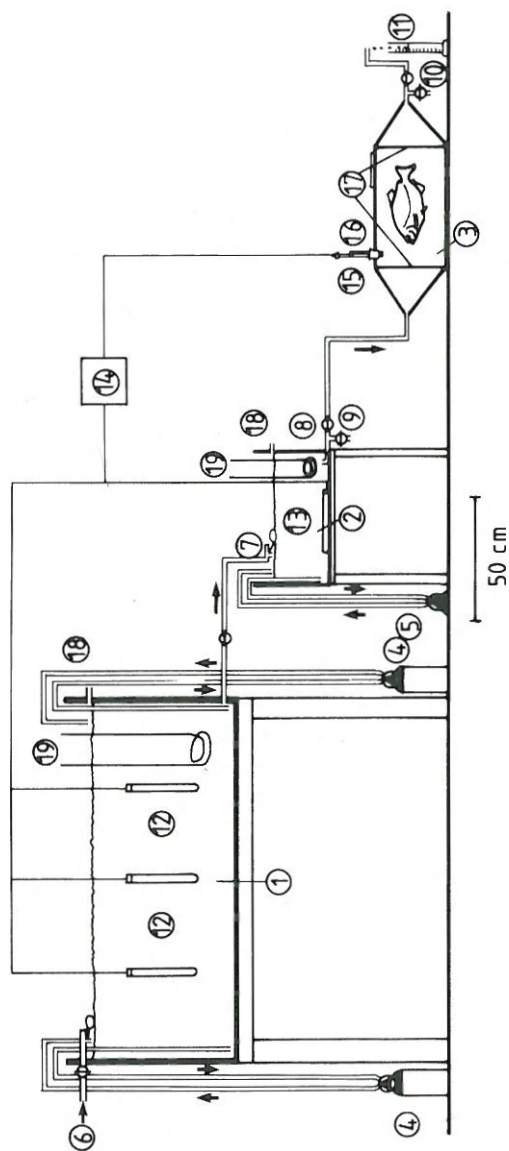


Fig. 1:
Constant flow respirometer for determining the influence of weight and temperature on the routine oxygen consumption of *Colossoma macropomum*.
1. 1,000 l water tank, 2. constant level tank, 3. respiration chamber, 4. water filter, 5. rotary pump, 6. tap water inflow, 7. float valve, 8. - 10. taps, 11. measuring cylinder, 12. - 13. heater, 14. relays, 15. contact thermometer, 16. control thermometer, 17. sieveplate, 18. overflow, 19. cooling unit.

Tab. 1: Some chemical parameters of the in and outflowing water of the respiration chamber. The water was filtered before being analysed.

chemical parameter	inflow	outflow
μS_{20}	38.0	43.7
pH	4.75	4.80
KMnO_4 consumption (mg/l)	17.1	21.5
NO_2^- ($\mu\text{g/l}$)	traces	20
NO_3^- ($\mu\text{g/l}$)	84	140
Total Fe ($\mu\text{g/l}$)	67	32
Soluble Fe ($\mu\text{g/l}$)	53	32
Total PO_4^{3-} ($\mu\text{g/l}$)	13	15
Soluble PO_4^{3-} ($\mu\text{g/l}$)	11	10
Si (mg/l)	1.94	1.94
Cl^- (mg/l)	4.5	4.9
SO_4^{2-} (mg/l)	1.3	0.8
Buffering capacity (mmol HCl/l)	0.10	0.05
Water hardness ($^\circ\text{dH}$)	0.75	0.85

2.4. Experimental procedure

The experimental fish were placed in the respiration chamber 24 hours after their last feeding for adaptation. The chamber was closed and covered to protect the fish from excessive light or other irritations during the experimental procedure.

After a 13 to 15 hour acclimatization period, samples of the inflowing and the outflowing water were taken at intervals of one hour, six to eight times a day. Oxygen content was determined by the Winkler method (GOLTERMAN 1971). Temperature and water flow were also measured.

A longer lasting acclimatization period to the various experimental temperatures was not provided. In the prevailing tropical climate, short-term diurnal temperature changes are much greater than seasonal ones. It was therefore assumed, that *Colossoma macropomum* is able to adapt its metabolic rate to experimental temperature variations relatively rapidly.

At the end of the experiment, the anesthetized (MS 222, Sandoz) fish were weighed. Oxygen consumption was calculated using the equation recommended by NIIMI (1978) for constant flow systems. Oxygen consumption rates were determined at four different temperatures. The following groups of fish were used in the determination: for 20° C, 15 fish from 89.6 to 240.0 g; for 25° C, 40 fish from 0.5865 to 2086.0 g; for 30° C, 42 fish from 0.3470 to 1975.0 g; and for 35° C, 34 fish from 5.5 to 2170.0 g. Each fish was used for only one determination.

3. Results

The influence of weight on oxygen consumption was determined at three different temperatures: 25, 30, and 35° C. Plotted on a double logarithmic grid, routine oxygen consumption increased linearly with weight, according to the following equation,

$$Q = a \cdot W^k \quad (\text{mg/h})$$

where Q is the rate of oxygen consumption or some other quantitative index of metabolism for the whole organism, a is a coefficient equal to the total metabolism of an animal of unit weight, W is the weight of the animal, and k is a constant that indicates at what speed and in what direction the metabolic rate changes as weight increases (WINBERG 1956).

The results of this experiment are presented in Figure 2. They show that at temperatures of 25 and 30 °C, only the axis intercept of the two curves are different, while at the higher temperatures, from 30 to 35 °C, there is a 0.14 increase in the slope value (from 0.64 to 0.78). As these differences between the axis intercept and the slopes are significant at the 5 % level, a significant difference between all three equations can be demonstrated.

The influence of temperature on the routine metabolism was determined at 20, 25, 30, and 35 °C. The relation between metabolic rate and temperature is subject to a general quantitative law, which can be expressed by what has been called "Krogh's normal curve" (KROGH 1916). This empirically obtained curve can be described approximately by Q_{10} values, which are calculated by using following equation:

$$Q_{10} = \frac{K_2}{K_1} \frac{10}{t_2 - t_1}$$

where K_1 and K_2 are the metabolic rates (mg O_2 /100 g/h) measured at the two different temperatures t_1 and t_2 (°C). The differences in the Q_{10} values indicate an adjustment in the metabolic rate to temperature changes of 10 °C (WINBERG 1956).

Because oxygen consumption could only be measured over a limited weight range in the 20 °C trial, the data obtained had to be corrected to a standard weight. The mean oxygen consumption obtained for this experimental group was 13.10 mg/h (SD = 2.73), corresponding to an average-sized fish of 144.0 g (SD = 46.4). Assuming a proportionality of the routine oxygen consumption rate to weight $W^{0.64}$, as shown at 25 and 30 °C, a 100 g fish had a calculated oxygen consumption of 10.37 ± 2.16 mg/h.

Oxygen consumption at the three other temperatures was calculated using the equations shown in Figure 2. At 25 °C, a 100 g fish has an oxygen consumption of 19.15 ± 1.94 mg/h. This value increases to 28.97 ± 3.57 mg/h at 30 °C. Only at the highest temperature used (35 °C), did oxygen consumption (21.24 ± 2.18 mg/h) decrease to a level below that observed at 30 °C (Fig. 3). As the standard deviations of each individual mean do not overlap, a significant difference between all four values is apparent.

The normal curve for *Colossoma macropomum* can be described by the following Q_{10} values:

T °C	20 - 25	25 - 30	30 - 35
Q_{10}	3.41	2.29	0.54

The decrease in the Q_{10} value correspond to the decreasing metabolic rate with rising temperature.

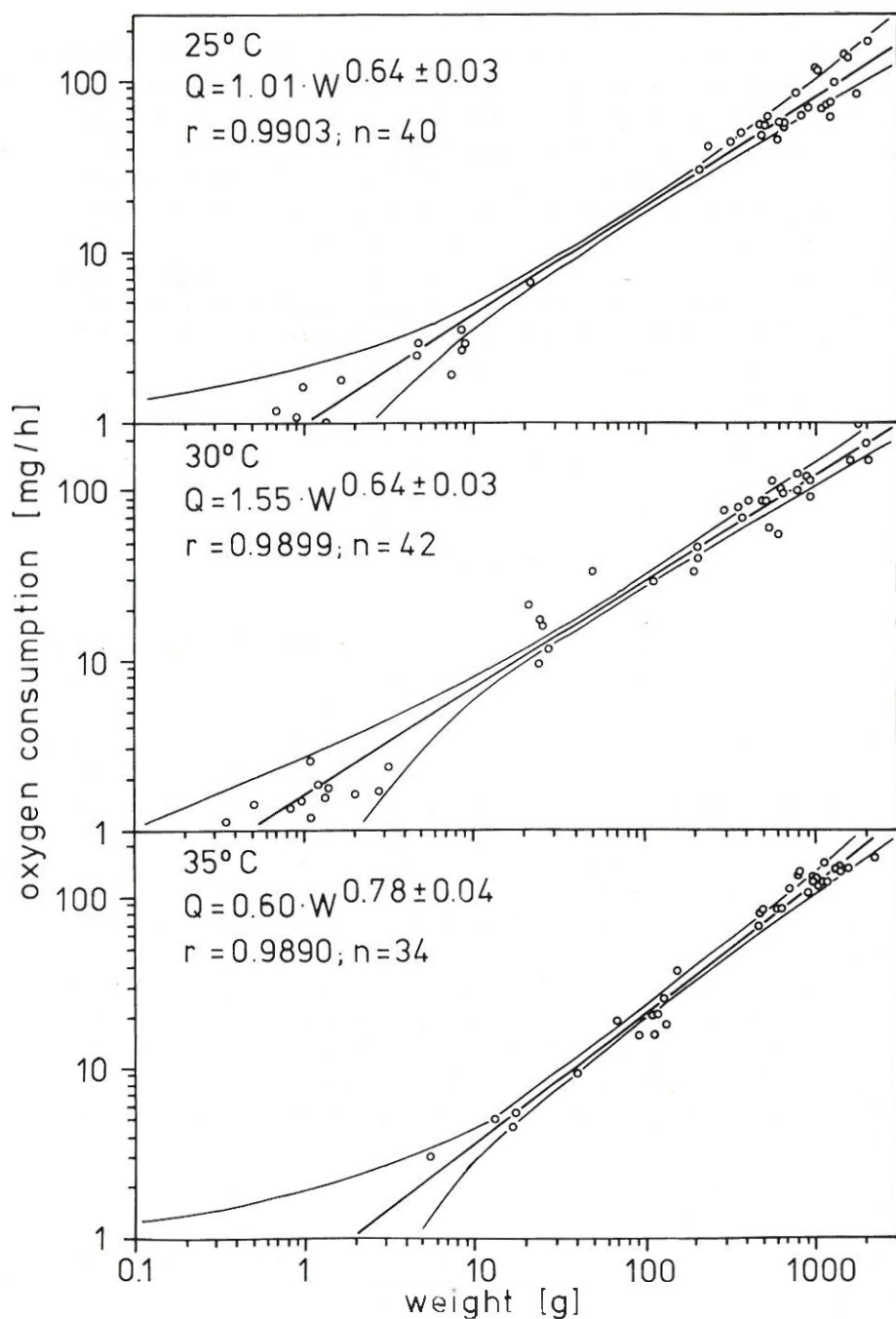


Fig. 2:

Influence of weight on the routine oxygen consumption of *Colossoma macropomum* at 25, 30, and 35 °C; 95 % confidence intervals are given. At 25 °C, two values (less than 1 mg/h), considered in the calculation, could not be included.

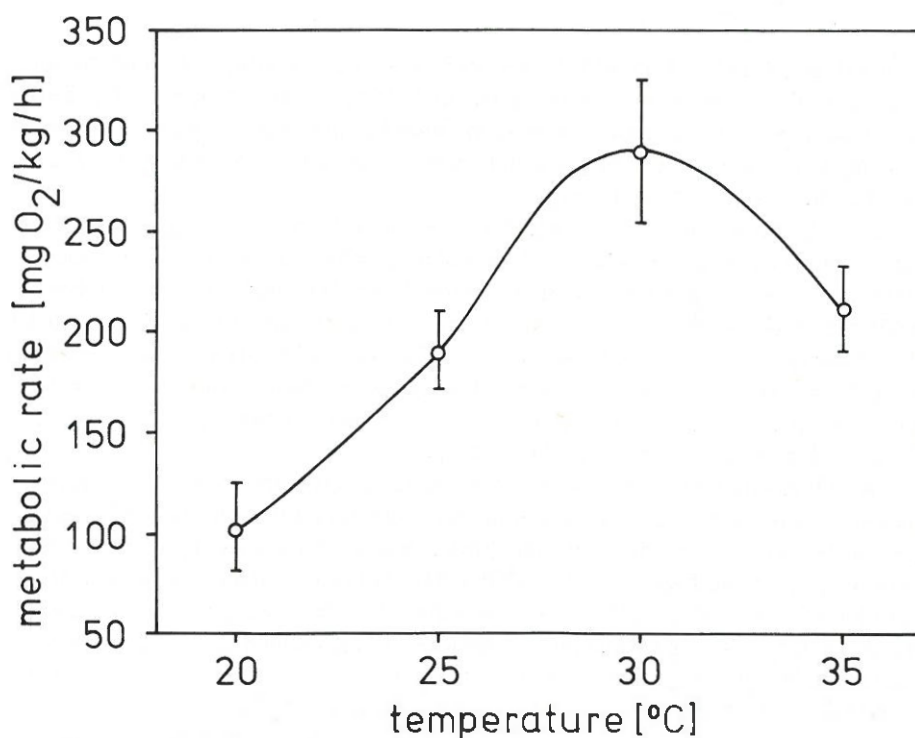


Fig. 3:
Influence of temperature on the routine oxygen consumption rate of a 100 g *Colossoma macropomum*. (Mean \pm 95 % confidence interval).

4. Discussion

The data show that oxygen consumption increases with weight. The slopes of 0.64 and 0.78 indicate that the oxygen consumption rate of smaller fish is greater than that of larger ones. The slopes at the three different experimental temperatures are not constant, but there is a significant increase at 35 °C. At 25 and 30 °C, the metabolic rate is proportional to the conventional surface index of the fish, 0.67. At 35 °C, however, the slope of 0.78 is close to 0.81, which was calculated by WINBERG (1956) from empirical data on freshwater fish. A comparison with GEISLER's (1969) data on Amazonian fish species is not possible, because he used pooled oxygen consumption rates of numerous species for his calculation. He obtained a slope of 0.76 at temperatures between 28 and 30 °C.

Different k-values at various temperatures were also found for other fish species (BEAMISH 1964; BEAMISH and MOOKHERJII 1964; RAJAGOPAL and KRAMER 1974). However, the changes are irregular, so the biological importance of this phenomenon is difficult to interpret. A generalized k-value for *Colossoma macropomum*, however, as shown for fish in general by WINBERG (1956), cannot be used because of the significant differences between the slopes. This is in agreement with BRETT's (1956) observation on active metabolism of sockeye salmon (*Oncorhynchus nerka*). PAILOHEIMO and DICKIE (1966) demonstrated a certain biological significance for a generalized k-value of 0.81,

interpreting a slope's change with temperature and feeding regime to be a reflection of the capacity of the fish for adaptation or acclimatization to new conditions. This means, that the metabolic rate of *Colossoma macropomum* becomes more dependent on weight with rising temperature, indicating a higher energy demand for larger fish. However, the reason for this has not yet been found.

The relationship between the metabolic rate of poikilothermal organism and temperature can be expressed by what has been called Krogh's normal curve. Experiments on fish species living in temperate climatic zones yield data that conform nicely to this curve (BEAMISH 1964). As the metabolic rate of *Colossoma macropomum* was determined at higher temperatures than those which the normal curve was calculated, a direct comparison is not possible. The Q_{10} values decrease with rising temperature in the same manner for both the normal curve and that plotted for *Colossoma macropomum*, but the two curves are displaced from each other along the abscissa.

SCHOLANDER et al. (1953) were the first to compare effects of temperature on the metabolic rate of tropical and arctic marine fish. They found that the metabolic rates of arctic species at 0 °C were 20 to 30 times higher than those obtained by simple extrapolation of data for tropical fish to 0 °C. WOHLSCHLAG (1960, 1964) assumed that the adaptation of arctic fish to cold is less complicated than the corresponding adaptation of tropical fish species to high temperatures. BRETT (1970) defined this kind of adaptation by fish living in different climatic zones as "compensation". According to his interpretation, poikilothermal arctic species have a relatively high metabolic rate compared to those living in temperate zones, while the rates of tropical species are relatively low. Comparing the different metabolic rates observed during the present investigations to the data of BRETT (1970) shows that there is a great similarity between the oxygen consumption rate of *Colossoma macropomum* and those of tropical marine fish species.

The routine oxygen consumption rate of *Colossoma macropomum* shows a distinct response to temperature changes, and the highest rate occurs at about 30 °C. Above this temperature, the rate decreases. BEAMISH and MOOKHERJEE (1964) found a comparable behavior for *Carassius auratus*, but the temperature of maximum routine oxygen consumption rate was 20 °C, and temperature increases above this led to a reduction in the spontaneous activity of the fish. The standard rate remained constant in spite of the temperature increase. The biochemical mechanism of temperature adaptation are still not very clear, but it can be assumed that significant temperature changes inhibit the activity of certain enzymes, resulting in a stagnation or even decrease in the animal's oxydative metabolic rate (HOCHACHKA and SOMERO 1973).

It can be assumed that the decrease in metabolic rate at a temperature above the approximately annual mean in this Neotropical region reflects an adaptation of *Colossoma macropomum* to constant climatic conditions. Furthermore, it is possible that this is also a form of adaptation to the lower oxygen concentrations in water at elevated temperatures. Changes of spontaneous activity with temperature could not be determined by the experimental method used.

Because the experiments conducted reflect only the effect of the relatively short-term temperature changes that occur in nature, it could be expected that after a longer lasting period of adaptation, different iso-enzymes optimally adapted to a new temperature might be mobilized.

5. Summary

The influence of weight and temperature on the routine oxygen consumption of *Colossoma macropomum*, a Neotropical fish species of the family Serrasalminidae, was investigated using a constant flow respirometer. Plotted on a double logarithmic grid, oxygen consumption increases linearly with weight. Slopes of 0.64 at 25 and 30 °C, and 0.78 at 35 °C were obtained. Because of the significant difference in the slopes, a general value could not be provided. The metabolic rate of a 100 g fish increases from 103.7 to 191.5 and 289.7 mg O₂/kg/h at 20, 25, and 30 °C, respectively. At 35 °C, the oxygen consumption rate decreased to 212.4 mg O₂/kg/h. The metabolic rate is comparable to those of other tropical fish species. Obviously, *Colossoma macropomum* is well adapted to the constant temperature conditions of its Neotropical habitats.

6. Resumo

A influência do peso e da temperatura sobre o consumo de rotina de oxigênio de *Colossoma macropomum*, uma espécie neotropical de peixe da família Serrasalminidae, foi investigada usando um respirômetro com fluxo permanente de água. Transcrito na escala logarítmica, o consumo de oxigênio aumenta linearmente com o peso. Foram obtidas inclinações de 0,64 com 25 e 30 °C e 0,78 com 35 °C. Não foi possível obter um valor geral por causa das diferenças significantes nas inclinações. O metabolismo de um peixe de 100 g aumenta de 103,7 a 191,5 e 289,7 mg O₂/kg/h com temperaturas de 20, 25 e 30 °C respectivamente. Com 35 °C, o consumo de oxigênio diminuiu até 212,4 mg O₂/kg/h. O nível metabólico é comparável aquele de outras espécies ictiológicas tropicais. Evidentemente, *Colossoma macropomum* está bem adaptado às condições constantes de temperatura do seu habitat neotropical.

7. Acknowledgments

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