

GILL TISSUE O₂ UPTAKE IN CRUSTACEANS: APPLICATION TO THE FICK PRINCIPLE FOR ESTIMATING BLOOD FLOW

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Abstract—1. Since gill tissues receive their O₂ supply directly from the ambient medium, gill O₂ consumption in crustaceans should be excluded from total O₂ uptake for estimating blood flow by the Fick principle.

2. Gill O₂ consumption in two crustaceans accounts for 5–6% of total O₂ consumed.

3. Behavioral and environmental variables are likely to affect the quantitative relation between gill respiration and total O₂ uptake.

INTRODUCTION

Blood flow in aquatic organisms is now routinely estimated by a procedure which relies on accurate measurements of oxygen uptake in the whole animal and blood oxygen concentrations of both arterial and mixed venous blood. From these measurements blood flow is calculated according to the Fick principle where

$$\text{Blood flow} = \frac{\text{Oxygen uptake}}{\text{Arterial O}_2 \text{ conc.} - \text{Venous O}_2 \text{ conc.}}$$

Mangum (1977) has pointed out that the validity of this equation rests upon the two assumptions that oxygen uptake is confined to O₂ transported by the blood and that no oxygen enters directly from the external medium into the tissues.

In many aquatic organisms gas exchange occurs primarily at the gills. The oxygen consumption of the gill tissues themselves is generally included in O₂ uptake measurements made on whole animals and used for estimating blood flow by the Fick principle. However, the influx of oxygen from water to blood at the gill, down a concentration gradient, precludes an O₂ supply to the gill tissues from the blood. Rather, the gill tissues meet their own oxygen needs directly from the external medium. Thus, gill respiration should not be included in values of oxygen uptake entering the Fick equation. If the contribution of gill tissue respiration to oxygen uptake is neglected, the numerator in the Fick equation for blood flow will be greater than the assumptions justify (Mangum, 1977) resulting in erroneously high values for blood flow. The degree to which blood flow is overestimated depends upon the magnitude of the participation of gill tissues in total oxygen consumption.

Recent interest in the respiratory physiology of the decapod crustaceans has led to the application of the Fick principle for estimating blood flow (Johansen *et al.*, 1970; Mangum & Weiland, 1975; McMahon & Wilkens, 1975; Taylor, 1976; Burnett, 1979; McMahon & Burggren, 1979). In the present study,

the quantitative role of gill tissue respiration in overall oxygen uptake, the numerator in the Fick equation, is evaluated in the freshwater crayfish, *Procambarus clarki* (Girard), and the marine crab, *Pachygrapsus crassipes* (Randall).

MATERIALS AND METHODS

Procambarus clarki were obtained from a local bait store and maintained in well aerated tap water at room temperature (23°C ± 1). Specimens of *Pachygrapsus crassipes* were collected in Mission Bay, San Diego and maintained in well aerated sea water (35‰ salinity) at room temperature. Animals were fed fish at least twice each week.

Oxygen uptake was measured by placing individual specimens in a 300 ml respirometer submerged in 6 l. of the appropriate air saturated medium. Air saturated water was siphoned through the respirometer by gravity and returned to the 6 l. container. The P_{O₂} of water in the respirometer was continuously monitored (Radiometer PHM71) by passing a portion of the siphoned water across a P_{O₂} electrode (Radiometer E5046/0) enclosed in a thermostatted cell (23°C ± 0.1). Respirometer P_{O₂} was adjusted by altering the flow of water through the chamber and was never allowed to fall below 130 Torr. Care was taken to position the animal such that its ventilation stream was pointed away from the excurrent tap of the respirometer. Adequate mixing of water in the respirometer by the animal's ventilation was confirmed by injecting a suspension of carmine particles into the chamber. A shield was erected around the respiration apparatus to minimize animal disturbance and animals were acclimated to respirometers for at least 90 min prior to O₂ uptake determinations. Oxygen uptake was then determined over a period of 1.5–2 hr and calculated by multiplying the flow rate of water through the respirometer by the inflow–outflow O₂ concentration difference.

To measure gill O₂ uptake, gills were dissected from an animal, briefly rinsed in filtered (0.45 μ) tap water (dechlorinated) or sea water and placed in two or three 20 ml Gilson respirometer flasks. Care was taken to remove all gill filaments from each animal. Respirometer flasks were shaken in a water bath and oxygen uptake was measured at 23°C at 10 min intervals for 1 hr and the data averaged. Gill O₂ uptake was calculated on a per animal basis and expressed as a percentage of total animal respiration.

RESULTS AND DISCUSSION

Gill tissues take up a significant amount of oxygen when compared to the total organismal O_2 uptake in resting conditions (Table 1). In this case, a failure to take gill respiration into account would result in Fick estimates of blood flow 5–6% too high. These results are not surprising since gill tissues have an extremely large surface area due to their respiratory function and they experience P_{O_2} conditions at least as high as fully oxygenated blood. Gill tissues receive their O_2 supply directly from the ambient medium since extremely large P_{O_2} gradients (70–90 Torr) exist between water and blood across the gill (Cameron & Mecklenburg, 1973; Mangum & Weiland, 1975; Taylor, 1976; Burnett, 1979). Therefore, measurement of total organismal O_2 uptake for application to the Fick principle does not fulfil the assumption that no oxygen enter directly from the medium to the tissues. However, the quantity of O_2 which directly enters the gills from the medium can be measured and subtracted from total animal O_2 uptake. The resulting value for O_2 uptake expresses more correctly the quantity of O_2 taken up and transported to the tissues by the blood.

The relative contribution of gill respiration to the Fick equation may change, depending upon the O_2

demand of both the gill tissues and the animal. Previous studies are available on the O_2 uptake of both the organism and the excised gill tissues (Vernberg, 1956; Dehnel & McCaughran, 1964; King, 1965; Dehnel, 1974). However, their lack of information relating the total gill weight to crab weight in these instances prevents an evaluation of the role of gill respiration in total animal O_2 uptake. These studies do, however, point out the importance of habitat (Vernberg, 1956), salinity (Dehnel & McCaughran 1964; King, 1965; Dehnel, 1974) and season (Dehnel & McCaughran, 1964) in influencing the metabolic activity of gill tissues. Dehnel (1974), for example, demonstrated a two-fold increase in gill O_2 demand when the euryhaline crab *Eriocheir sinensis* was transferred from seawater to freshwater. These results emphasize the care that must be taken to evaluate the participation of gill respiration in total animal O_2 uptake in situations where gill O_2 demand may change. On the other hand, when the metabolic demand of the crab is high due to activity, gills may take up a smaller portion of the total O_2 taken up by the animal.

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Table 1. Gill tissue and total animal oxygen uptake in individual specimens of *Procambarus clarki* and *Pachygrapsus crassipes*

Weight (g)	<i>Procambarus clarki</i> 23°C freshwater		
	Gill O_2 uptake (ml/hr)	Animal O_2 uptake (ml/hr)	% Gill O_2 uptake
29.23	0.087	1.402	5.79
20.42	0.194	2.029	9.56
36.85	0.190	3.203	5.93
20.77	0.096	1.463	6.56
16.15	0.037	1.287	2.87
20.20	0.081	1.220	6.64
19.53	0.109	1.764	6.18
25.66	0.090	1.872	4.81
20.98	0.088	1.519	5.79
\bar{x} 23.31			6.01
SD 5.96			1.66
Weight (g)	<i>Pachygrapsus crassipes</i> 23°C 35‰ salinity		
	Gill O_2 uptake (ml/hr)	Animal O_2 uptake (ml/hr)	% Gill O_2 uptake
24.31	0.153	2.539	6.03
22.20	0.060	1.786	3.36
15.95	0.054	1.249	4.32
32.88	0.149	2.427	6.14
19.76	0.078	1.097	7.11
12.74	0.054	1.268	4.26
25.64	0.140	3.296	4.25
12.01	0.066	0.876	7.53
41.08	0.163	3.205	5.09
37.40	0.152	3.077	4.94
30.56	0.129	2.357	5.47
33.05	0.129	2.570	5.02
28.16	0.136	2.133	6.38
\bar{x} 24.58			5.15
SD 9.60			1.40

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