

ENERGETIC COST OF ACTIVE BRANCHIAL VENTILATION IN THE SHARKSUCKER, *ECHENEIS NAUCRATES*

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SUMMARY

1. Sharksuckers use active branchial ventilation when swimming or at rest in stationary water. When attached to a moving object or when placed in a water current, they shift to ram gill ventilation as water velocity exceeds a certain threshold.

2. Water velocities required for the transition from active to ram gill ventilation were from 10–50 cm s⁻¹, depending on the size of the fish.

3. Oxygen consumption increased between 3.7 and 5.7 % when the fish shifted from ram gill ventilation to active branchial pumping.

4. When water velocity was increased beyond the threshold for ram gill ventilation, no further increase in oxygen consumption was observed.

5. It is concluded that the energetic cost of active ventilation in sharksuckers is lower than has previously been reported for fish in general.

INTRODUCTION

Since the early paper by van Dam (1938) the energetic cost of ventilation in fish has generally been viewed as being high in comparison to that of air breathing vertebrates. The high density and viscosity of water as well as the large ventilatory requirement of fish resulting from the low oxygen solubility of water are factors contributing to a high cost of ventilation.

Estimation of the cost of ventilation in fish is difficult. At least three different approaches have been used to assess the cost, giving values ranging from 0.5 to 70 % of the standard oxygen consumption (Alexander, 1967; Davis & Randall, 1973; Cameron & Cech, 1970; Schumann & Piiper, 1966; Jones & Schwartzfeld, 1974), though the most generally accepted values are between 5 and 15 % (Holeton, 1980).

In contrast to most fish, which produce a ventilatory current by movements of the buccal cavity and opercula, some pelagic fish like tuna and mackerel ventilate by swimming with an open mouth and show no opercular movements. This mode of ventilation has been termed ram ventilation by Muir & Buckley (1970). Strasburg (1957) found that a jet of water aimed at the mouth of suckerfish, *Remora remora*, caused the ventilatory rate to decrease markedly, and at high water velocities to cease

Key words: Ram ventilation, cost of breathing, sharksucker.

completely. He proposed that the 'suckerfish would obtain other benefits from sharing than just transportation and the chance to dine with a shark.'

The aim of the present study has been to estimate the cost of ventilation in the sharksucker, *Echeneis naucrates* L., by measuring and comparing oxygen consumption during active branchial ventilation and during ram ventilation. The sharksucker is an ideal experimental animal for investigating the cost of ventilation. When introduced into a swimming respirometer they attach to the wall and, depending on the water velocity, either ventilate by active branchial pumping or use ram ventilation without any other muscular activity. Thus evaluation of the cost of ventilation in this species is based on measurements requiring a minimum of interference with the experimental animal.

MATERIALS AND METHODS

Sharksuckers, *Echeneis naucrates* L., were collected from their hosts, large sharks, which were caught on longline off the coast of Miami, Florida, and air freighted to Denmark. In the laboratory they were kept in a 1500 l tank containing well aerated, filtered sea water at 24–25 °C and 33–35 ‰ salinity. A PVC tube 100 cm long and 20 cm in diameter was suspended in the tank and a swift current of water was directed along the tube by a submersible pump. The sharksuckers spent most of the time attached to this tube, which acted as a substitute for a swimming shark. They were fed fillets of trout and herring, gained weight and appeared to be in good health.

Measurements of oxygen consumption at different ventilatory modes were made in two different types of respirometers, depending on the size of the fish. Experiments with four small specimens, weighing from 32–87 g, were performed in respirometers made from Plexiglass tubing and ranging in volume from 2–6 l. The respirometer had to be provided with a convex surface along its upper part, because the fish were unwilling to attach to the concave inner surface of the cylinder. Oxygen consumption was measured by open respirometry. Aerated water ($P_{\text{inO}_2} > 145$ mmHg) was passed through the respirometer by a pump of variable output and the flow (\dot{V}_R) adjusted to produce an oxygen tension in the outflow (P_{outO_2}) of about 120 mmHg. A second pump of high output (15 l min⁻¹) was used to recirculate the water at a velocity sufficient to elicit ram ventilation. At steady P_{inO_2} , P_{outO_2} and \dot{V}_R , oxygen consumption could be calculated as:

$$\dot{V}_{\text{O}_2} = (P_{\text{inO}_2} - P_{\text{outO}_2}) \alpha \dot{V}_R$$

where α is the solubility of oxygen in sea water of 35 ‰ salinity at 24 °C. Water oxygen tensions were measured continuously by siphoning a fraction of the water current via PE-160 polyethylene tubing through a thermostatted cuvette (Radiometer, D-616) holding an oxygen electrode (Radiometer, E-5046) and connected to a Radiometer acid-base analyser and recorder. The flow through the respirometer was determined by means of a measuring cylinder and a stop-watch. The experimental temperature was 24.0 ± 0.2 °C. Values of oxygen consumption are mean ± s.d. of from 8–9 determinations based on periods of steady state of at least 5 min duration.

Preliminary experiments were carried out at the University of Miami, Florida, using a somewhat similar arrangement.

Experiments with one big sharksucker (487 g) were performed in a modified Brett type swimming respirometer (Christiansen, Lomholt & Johansen, 1982) containing 32 l of water (V). Water velocity could be regulated between zero and 80 cm s⁻¹. To insure adequate mixing the lowest velocity used was 3–4 cm s⁻¹. Water temperature was 24 ± 0.15 °C. Between periods of measurement, portions of water could be shunted through a membrane oxygenator in order to monitor O₂ tension and maintain it at a stable high level. To determine oxygen consumption, the oxygenator was shut off and oxygen tension was measured every minute for a minimum of 12 min. A straight line was fitted to these measurements by linear regression and the slope of this line ($\Delta P_{O_2}/\Delta t$) was used to calculate oxygen consumption according to the formula:

$$\dot{V}_{O_2} = V (\Delta P_{O_2}/\Delta t) \alpha$$

Water P_{O_2} never fell below 120 mmHg. Values of oxygen consumption are mean ± s.d. based on three determinations.

Breathing frequency was determined by direct counting. The cost of active branchial breathing was calculated as:

$$\text{cost of ventilation} = \frac{\dot{V}_{O_2} (\text{active}) - \dot{V}_{O_2} (\text{ram})}{\dot{V}_{O_2} (\text{active})} 100 \%$$

After transfer to the respirometer, a fish was allowed 2–3 h to settle down at a water velocity just above the level causing the fish to switch to ram ventilation. Usually the sharksucker would be firmly attached at all water velocities, but if it became restless and started moving about in the respirometer, the experiment was interrupted.

The water velocity necessary to elicit ram ventilation was determined for all fish in the swimming respirometer.

RESULTS

Table 1 summarizes the results of measurements of oxygen consumption during active pumping and ram ventilation as well as values of cost of active ventilation.

Fish no. I–III were tested in the flow-through respirometer at a water velocity below 0.5 cm s⁻¹ resulting in full active ventilation, and at a velocity above the threshold for ram ventilation. In all cases the oxygen consumption of the actively breathing fish was significantly elevated compared to that of the ram ventilating fish. The difference was, however, relatively small, resulting in values of cost of ventilation ranging from 1 to 5.6 % of the oxygen consumption during ram ventilation. The low value of 1 % obtained in fish no. I may be atypical. This specimen was unwilling to remain attached for periods sufficiently long to record oxygen consumption. Hence more data could not be collected from this specimen.

The larger specimen, fish no. IV, was tested in the swimming respirometer, where water velocity could be accurately controlled. Cost of breathing calculated from measurements of oxygen consumption at low water velocities of 4–10 cm s⁻¹ ranged from 3.7 to 5.1 % (expts no. 8, 10, 11 and 12) in agreement with the values obtained from fish no. II and III.

Preliminary experiments performed in Miami yielded values of 3.7 and 5.4 % in one specimen weighing 300 g and 4.7 % in another specimen of 230 g.

Table 1. *Ventilatory frequency and rate of oxygen consumption of sharksuckers during active branchial and ram ventilation (mean \pm S.D.)*

N indicates number of experiments. Body weight: I = 32 g, II = 37 g, III = 87 g, IV = 487 g. Threshold velocity = t.v. N.S. = not significant.

Fish no.	Expt no.	Water Velocity (cm s ⁻¹)	Breathing frequency (min ⁻¹)	Oxygen consumption (mgO ₂ /kg h)	<i>N</i>	Significance level (<i>t</i> -test)	'Cost of breathing' (%)
I	1	>t.v.	0	288.6 \pm 1.3	9	0.05	1.0
		<0.5	98 \pm 2	291.6 \pm 0.6	9		
II	2	>t.v.	0	254.7 \pm 2.9	9	0.001	3.9
		<0.5	109 \pm 2	265.1 \pm 6.0	9		
II	3	>t.v.	0	228.8 \pm 3.3	9	0.001	4.5
		<0.5	106 \pm 2	239.6 \pm 4.3	9		
II	4	>t.v.	0	251.3 \pm 1.2	9	0.001	5.6
		<0.5	105 \pm 1	266.2 \pm 2.4	9		
III	5	>t.v.	0	215.9 \pm 2.7	9	0.001	4.8
		<0.5	119 \pm 1	226.7 \pm 1.3	9		
III	6	>t.v.	0	220.0 \pm 1.5	8	0.001	3.8
		<0.5	122 \pm 3	228.6 \pm 2.9	8		
III	7	>t.v.	0	224.5 \pm 2.0	9	0.001	3.9
		<0.5	121 \pm 1	233.6 \pm 1.1	9		
IV	8	25	0	111.1 \pm 3.3	3	0.05	4.7
		10	68 \pm 4	116.6 \pm 2.3	3		
IV	9	30	0	126.7 \pm 0.3	3	0.05	2.1
		15	62 \pm 1	129.4 \pm 1.6	3		
IV	10	25	0	120.1 \pm 1.4	3	0.05	5.1
		10	67 \pm 5	126.5 \pm 2.5	3		
IV	11	45	0	110.3 \pm 1.3	3	N.S.	0
		30	0	110.3 \pm 0.9	3		
		15	74 \pm 4	113.4 \pm 0.3	3	0.01	2.7
		10	74 \pm 1	116.0 \pm 1.9	3	0.01	4.9
		4	73 \pm 2	115.7 \pm 2.0	3	0.025	4.7
IV	12	25	0	105.5 \pm 0.2	3	0.025	2.2
		15	71 \pm 3	107.8 \pm 1.0	3		
		7.5	73 \pm 1	109.6 \pm 1.4	3		
IV	13	25	0	104.0 \pm 1.7	3	0.05	3.2
		15	72 \pm 2	107.4 \pm 1.8	3		

When calculation of cost of breathing was based on the higher water velocity of 15 cm s⁻¹, smaller values ranging from 2.2 to 3.2% were obtained (expts no. 9, 11, 12 and 13). Thus, as water velocity approaches the threshold for the transition to ram ventilation, a gradual decline in the cost of ventilation was observed.

In Fig. 1 the results of experiment no. 11 are shown graphically. While the oxygen consumption declined as water velocity approached the threshold for ram ventilation, the frequency of branchial breathing remained constant. As water velocity was further increased beyond the threshold from 30 to 45 cm s⁻¹, no change in oxygen consumption occurred.

The threshold for the transition to ram ventilation had the character of a ran

7–21 cm s^{-1} in Fig. 1) of water velocities within which breathing frequency became irregular. The threshold increased with increasing size of the fish as shown in Fig. 2, where the transition range is plotted as a function of body length. The value for the largest specimen of 98 cm and 7.5 kg body weight was obtained from observations in the Miami Seaquarium. A similar, although not particularly clear, tendency was found by Muir & Buckley (1967) in the closely related suckerfish (*Remora remora* L.). However Freadman (1979) did not find any weight effect on the threshold velocity in

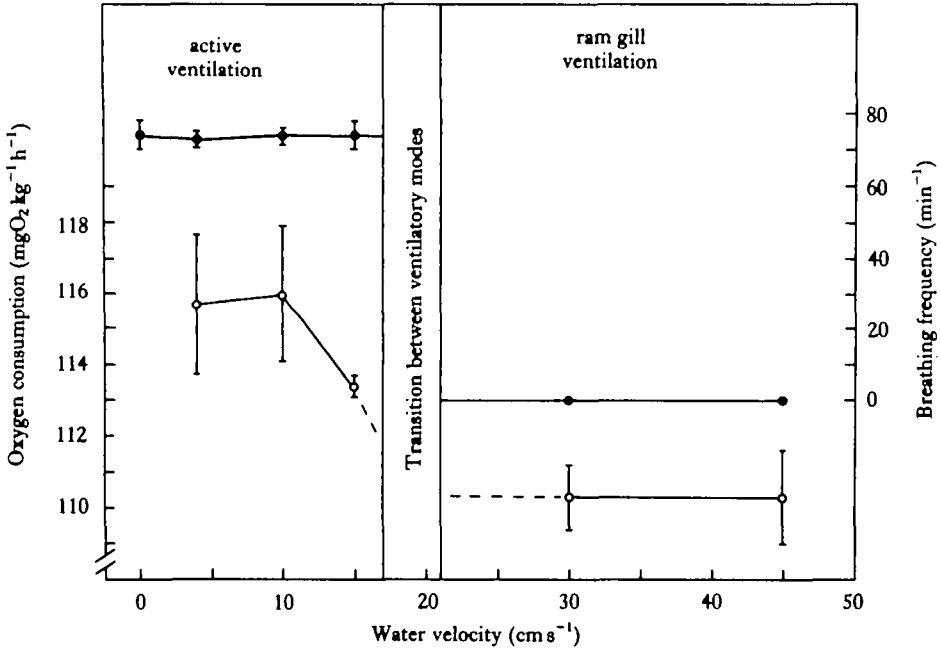


Fig. 1. Ventilatory frequency (●) and rate of oxygen consumption (○) of a sharksucker (#4, body weight, 487 g) as a function of water velocity. The vertical lines indicate the range of water velocities within which the transition from active to ram ventilation takes place (mean \pm s.d.).

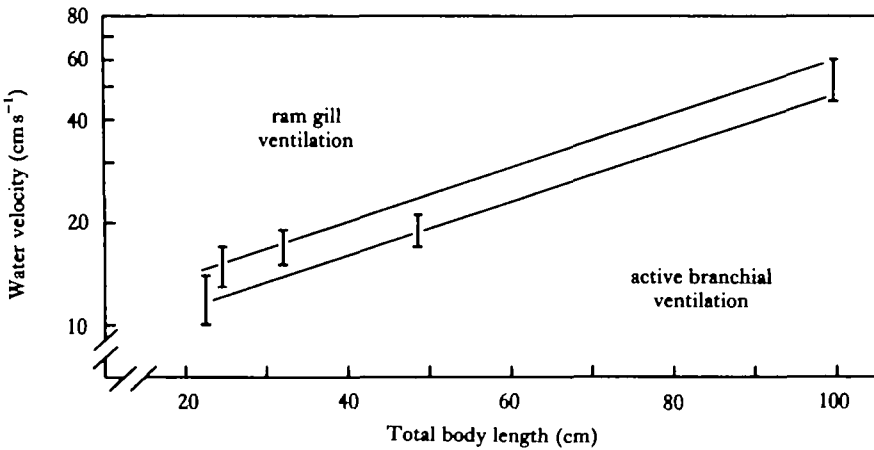


Fig. 2. Range of water velocities within which the change between active and ram ventilation takes place as a function of body length. Lines represent linear regression through endpoints of bars.

swimming bluefish (*Morone saxatilis* Walbaum) or striped bass (*Pomatomus saltatrix* L.). At present no functional significance can be attributed to this difference between the attached sucker fish and the free swimming fish with respect to the relationship of threshold velocity to body weight.

DISCUSSION

The large discrepancies between values for the cost of ventilation in fish reported in the literature may largely reflect differences in the approach used to obtain data for the calculations. According to Cameron & Cech (1970) the very high figures for the cost of ventilation of 30–50 % of total \dot{V}_{O_2} , given by van Dam (1938) and Schumann & Piiper (1966) may have been heavily influenced by excitement caused by the experimental situation as well as by side effects of anaesthesia. Likewise the very low estimate of 0.5 % by Alexander (1967) has been criticized for being based on assumptions of constant water flow, pressure gradient, and resistance to flow, conditions certainly not fulfilled in the naturally breathing fish (Cameron & Cech, 1970).

Based on the mass and probable metabolic rate of the respiratory muscles, Cameron & Cech (1970) proposed a cost of ventilation of 5–15 % of the standard oxygen uptake.

Edwards (1971) calculated a cost of breathing of 22 to 28 % in plaice based on a decline in oxygen consumption in artificially ventilated fish with paralysed ventilatory musculature. The artificially ventilated fish showed, however, a decrease in oxygen extraction which might well reflect a disruption of the functional integrity of the gills through interference with muscles responsible for keeping the gills in the correct position and hence with the pattern of water flow across the gills or through interference with the pattern of blood flow in the gills. If this is so, the decline in oxygen consumption does not reflect the cost of active ventilation, but rather a suppression of the ability of the fish to take up oxygen.

Jones & Schwartzfeld (1974) arrived at a cost of breathing of 10 % in trout, a value lower than most previously published, but still two to three times as high as the value presently found in the sharksucker. The difference may reflect a true difference between the two species, but it may also be the result of the more stressful experimental technique employed in the study by Jones & Schwartzfeld (1974), involving a rubber membrane sutured along the edge of the mouth, which might enhance the cost of breathing.

The reason why these various approaches have been used is, in the words of Cameron & Cech (1970), that 'The exact cost, however, has not been directly determined due to the inability of the investigators to persuade an organism voluntarily to increase its ventilation rate without also increasing other factors adding to the oxygen demand'. This is, however, exactly what can be asked from the sharksucker. Without any experimental manipulations, other than a change in water velocity, it can be made to breathe by active pumping or by passive ram ventilation.

In order to calculate the cost of breathing from the rise in oxygen consumption observed when the sharksucker shifts from ram ventilation to active branchial pumping, two requirements should be fulfilled. Firstly, the measured rates of oxygen consumption should be resting rates. Secondly, ram ventilation should be associated with no significant energetic cost. Only results from experiments in which the f

showed no signs of moving about in the respirometer, have been included in the calculations. The very small standard deviations of the oxygen consumption values in Table 1 indicate that spontaneous variation in activity was small or absent. A possible energetic cost involved in ram ventilation might stem from attachment to the wall of the respirometer and from adjusting the mouth aperture in relation to water velocity (Fig. 3). In both cases this cost should be expected to increase with increasing water velocity. The observation that oxygen consumption remains constant when water velocity is increased well beyond the threshold for ram ventilation is evidence that ram ventilation is not associated with significant energetic cost (Fig. 1).

On the basis of the above considerations we feel that the estimate of the cost of ventilation in the sharksucker is a very direct one, derived from experiments involving only minor interference with the fish. A value between 3–5% of standard oxygen consumption leaves the sharksucker, and possibly other fish as well, with a cost of ventilation close to the 1–2% found in man (Agostoni, Campbell & Freedman, 1970).

The explanation for the relatively high cost of ventilation in fish has usually been sought in the characteristics of water as a respiratory medium. The oxygen solubility of water is low and the density and viscosity are high. Hence fish must ventilate a large volume of a heavy and viscous medium. The results obtained in the sharksucker indicate that, in spite of this difference between air and water as respiratory media, the work of breathing is not vastly different in fish and man.

This seemingly paradoxical finding calls for an explanation, which may rest with differences in flow resistance resulting from the structure of the respiratory organs, fish lacking the long narrow conducting airways characteristic of the mammalian lung. Additionally, work of breathing must not only overcome resistance to ventilatory flow; it must also balance the mechanical forces of the ventilatory apparatus. It may

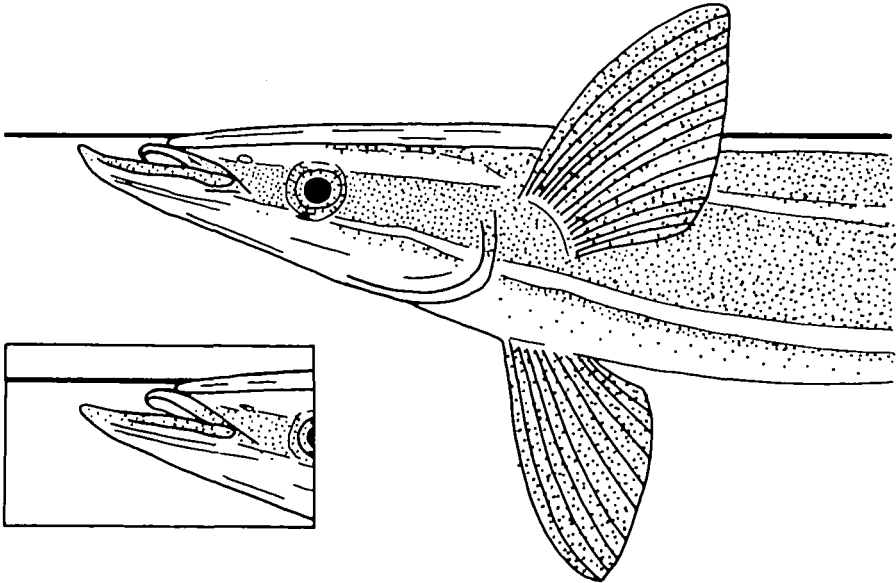


Fig. 3. Head of sharksucker to show position of the lower jaw during ram ventilation at high water velocity. As water velocity is decreased, the mouth is opened by lowering the lower jaw as shown in insert.

be that these mechanical forces are smaller in fish than in mammals, although no detailed analysis of the mechanical properties of the gill apparatus of fish appears to be available. Such differences could be a reflection of the very different mechanical conditions encountered by a terrestrial animal, which must carry its own weight in distinction to fish having a specific gravity very close to that of water.

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