

THE TRANSITION BETWEEN BRANCHIAL PUMPING AND
RAM VENTILATION IN FISHES:
ENERGETIC CONSEQUENCES AND DEPENDENCE ON
WATER OXYGEN TENSION

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SUMMARY

1. Ram ventilation has been demonstrated in rainbow trout, *Salmo gairdneri*. The swimming speed eliciting the transition in mode of ventilation increased with declining ambient water oxygen tension (P_{wO_2}).

2. The mode of ventilation of fish swimming at a constant speed could be altered by controlled variations in P_{wO_2} .

3. Oxygen consumption (\dot{V}_{O_2}) decreased by 10.2% when rainbow trout, swimming at a constant speed, shifted from active to ram ventilation. This difference can be ascribed to a lowering of the energetic cost of active ventilation as well as improved drag characteristics.

4. Water velocity required for the transition from active to ram ventilation in the resting sharksucker, *Echeneis naucrates*, increased with decreasing P_{wO_2} .

5. The results show that water oxygen tension is an important stimulus for setting the ventilatory mode in rainbow trout and sharksucker.

INTRODUCTION

Many species of fish are known to ventilate by keeping an open mouth when swimming, or by remaining stationary in a fast water current. Muir & Kendall (1968) termed this phenomenon 'ram ventilation'. Ram ventilation has been reported for mackerel (*Scomber scomber*, Hall, 1930), *Remora remora* (Strasbourg, 1957), sockeye salmon (*Oncorhynchus nerka*, Stevens & Randall, 1967; Smith, Brett & Davis, 1967) and a sharksucker (*Echeneis naucrates*, Steffensen & Lomholt, 1983).

The factors that regulate the transition from active to ram ventilation are not well understood (Ballintijn & Roberts, 1976; Roberts, 1978). Roberts (1974) reported ram ventilation in several species and presented evidence suggesting that the shift in mode of ventilation was independent of water oxygen tension and temperature. In a

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later study he concluded that the reflex transfer from active to ram ventilation is initiated by mechanoreceptors, and not by chemoreceptors (Roberts, 1975*b*).

The advantage of shifting the mode of ventilation is that this is likely to reduce the energetic cost of gill ventilation by transferring the work of breathing from the buccal and opercular pumps to the swimming muscles. Several approaches have been employed to estimate the cost of ventilation in resting fish and values from 0.5 to 45% of standard oxygen consumption have been reported (Van Dam, 1938; Schumann & Piiper, 1966; Alexander, 1967; Cameron & Cech, 1970; Davis & Randall, 1973; Jones & Schwartzfeld, 1974). Steffensen & Lomholt (1983) reported an increase in standard oxygen consumption from 3.7 to 5.4% when the sharksucker shifted from ram to active ventilation. By contrast, there have been few studies of the cost of ventilation in swimming fish. Brown & Muir (1970) studied ram ventilation in skipjack tuna (*Katsuwonus pelamis*) and estimated the energetic cost of ventilation to lie between 1 and 3% of total metabolism. In swimming bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*) the cost was estimated to be 8.1 and 8.4%, respectively (Freadman, 1981).

The objectives of the present study have been to examine if the change in mode of ventilation in rainbow trout (*Salmo gairdneri*) and the sharksucker (*Echeneis naucrates*) depends exclusively on swimming speed or water velocity, or if it is also influenced by ambient water oxygen tension. If the latter is the case, both mechanoreceptors and chemoreceptors would be involved in eliciting the reflex transition in mode of ventilation. Furthermore, the energetic consequence of shifting to ram ventilation has been estimated for rainbow trout swimming at a constant speed.

MATERIAL AND METHODS

Eight specimens of rainbow trout, *Salmo gairdneri*, were obtained from a local fish farm, and three specimens of the sharksucker, *Echeneis naucrates*, were collected in Florida and air freighted to Denmark. Total length and weight were A: 60 cm, 820 g, B: 63 cm, 1275 g and C: 65 cm, 1500 g. The sharksuckers were maintained at 23°C and fed trout fillets *ad libitum* (Steffensen & Lomholt, 1983). The rainbow trout, weighing between 620 and 890 g, were kept in well-aerated large aquaria (1000 l) supplied with recirculating filtered water. The fish were fed trout pellets and the temperature was kept at 14–16°C.

Two types of experiments were done. First the water velocity at which the transition from active to ram ventilation takes place was determined by increasing the velocity in steps of 1 cm s⁻¹ at different levels of water oxygen tension.

In the second series of experiments, the rate of oxygen consumption was compared for trout practising either active or ram ventilation while swimming at a constant speed. This was possible because, as shown below, trout swimming at a certain speed can be made to employ either active or ram ventilation by altering the water oxygen tension.

The experiments were conducted in a modified Brett-type swimming respirometer (Brett, 1964), with interchangeable swimming sections made from transparent PVC-tubing. For rainbow trout, a swimming section with an inner diameter of 15 cm was used and swimming speeds could be regulated up to 55 cm s⁻¹. When

working on sharksuckers, a swimming section of inner diameter 12 cm provided with a convex surface at the top part was used, because the fish does not attach to a concave surface. In this case, water velocities up to 90 cm s^{-1} could be obtained. Experimental temperatures were $15.0 \pm 0.2^\circ\text{C}$ for rainbow trout and $23.0 \pm 0.2^\circ\text{C}$ for sharksucker.

Water oxygen tension in the respirometer was measured continuously by recirculating a small fraction of the water through a thermostatted O_2 -electrode cuvette (Radiometer, D-616, E-5046) by a small roller pump fitted with gas-tight tygon tubing. The O_2 -electrode was connected to a Radiometer PHM 71 acid-base analyser and the signal fed to a Hewlett-Packard computer (A9825). The computer was also used to regulate water oxygen tension to the desired level prior to a measurement of oxygen consumption. This was done by opening or closing a magnetic valve controlling the amount of water shunted through an 'artificial lung' (Sci-Med Kolobow membrane gas exchanger with a 3.5 m^2 surface area). In addition, the computer controlled two valves directing either nitrogen or an air/oxygen mixture to the gas exchanger. After the preset P_{O_2} level had been reached and maintained for a preprogrammed period of time, the gas exchanger was shut off. The computer sampled P_{O_2} data every second and averaged values for periods of 30 s. This resulted in 30 values of P_{O_2} during a test period of 15 min. From the regression line based on these 30 values describing the decline in O_2 -tension with time, oxygen consumption (\dot{V}_{O_2}) was calculated and printed out. After a 15-min run, the oxygen tension was brought back to the original level by again letting a fraction of the water through the gas exchanger. The volume of the swimming respirometer (V) was 40.1 l , and oxygen consumption was calculated as follows:

$$\dot{V}_{\text{O}_2} = V \cdot (\Delta \text{Pw}_{\text{O}_2} / \Delta t) \cdot \alpha.$$

In addition, the computer was used to sample information about water velocities, correct these for the solid blocking effect of the cross-sectional area of the fish (Bell & Terhune, 1970), and display the actual swimming speed continuously. The swimming speed never varied more than $\pm 0.2 \text{ cm s}^{-1}$ during a test period.

Mode of ventilation was determined by visual inspection of mouth and opercular movements. This way of monitoring the mode of ventilation may be criticized on the basis that very shallow ventilatory movements may not be detected. However, since the energetic cost of such possible undetected ventilatory movements must be very small, this will be of no consequence.

The energy saved by switching from active to ram ventilation was calculated as follows:

$$\text{energy saving} = \frac{\dot{V}_{\text{O}_2} (\text{active}) - \dot{V}_{\text{O}_2} (\text{ram})}{\dot{V}_{\text{O}_2} (\text{active})} \times 100 \%$$

Feeding the fish was stopped 3 days before transfer to the respirometer in order to ensure that the fish were in the post-absorptive state, and to avoid excrements in the respirometer. The fish were allowed to adjust to the respirometer for a period of 10–15 h in normoxic water ($\text{P}_{\text{O}_2} = 150 \text{ mmHg}$) at a low swimming speed (5 cm s^{-1}).

RESULTS

Swimming speeds at which the transition from active to ram ventilation takes place at different ambient oxygen tensions for eight rainbow trout are summarized in Table 1. At the lowest O_2 tension (50 mmHg) some fish (II and IV) never showed steady ram ventilation even at the highest swimming speed of 55 cm s^{-1} . In these cases there was no upper limit of the transition zone [indicated by ir, (irregular ventilation)]. Similarly, in hyperoxic water some individuals never showed regular active ventilation at the lower swimming speeds. Hence there was no lower

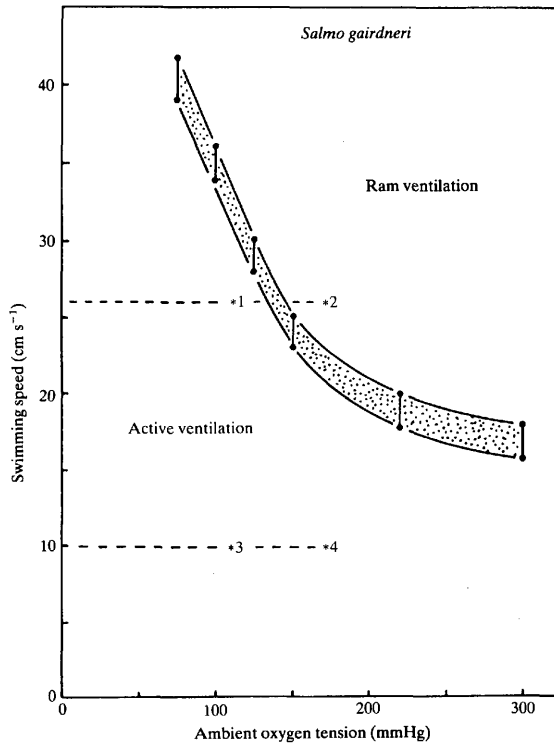


Fig. 1. The ventilatory mode of rainbow trout (no. VI) at different ambient oxygen tensions plotted against swimming speed. The vertical bars indicate the range of water velocities within which transition between ventilatory modes takes place. At water velocities above or below the dotted area (the transition zone), ram or active ventilation is used, respectively. The asterisks indicate the combination of Pw_{O_2} and speed at which V_{O_2} was measured.

Table 1. The dependence of the velocity threshold for ram ventilation on water oxygen tension

Fish number	Total length (cm)	Body weight (g)	Ambient oxygen tension (mmHg)											
			50	75	100	125	150	200	250	300				
I	33	430	34/41	27/33	22/27	—	15/20	11/16	9/13	ir/10				
II	34	520	38/ir	—	23/28	—	15/22	—	9/14	—				
III	36	640	27/32	23/27	19/23	—	13/17	ir/15	ir/15	—				
IV	30	430	39/ir	—	25/29	—	20/24	16/20	ir/17	ir/16				
V	38	705	—	34/41	32/37	28/32	23/27	—	19/23*	18/22				
VI	36	670	—	38/43	32/37	27/31	22/26	17/21†	—	15/19				
VII	40	805	—	41/47	30/36	—	22/27	17/22	—	12/17				
VIII	40	740	—	36/40	29/33	—	23/27	16/20	—	10/15				

The paired numbers show the upper and lower limits of a range of swimming speeds within which the transition between ram and active ventilation takes place. Each of these numbers is the mean of three determinations, the range of which never exceeded 3 cm s⁻¹. At velocities within the paired numbers ventilation was irregular.

ir, irregular ventilation.

* PwO₂ = 230 mmHg; † PwO₂ = 220 mmHg.

For further explanation see text.

limit to the transition zone, again indicated by *ir* in the table (fish I, III and IV).

The swimming speed required for transition from active to ram ventilation at different water oxygen tensions (P_{wO_2}) for trout VI is shown in Fig. 1. When swimming speed exceeds the lower limit of the transition zone, single breaths were dropped out. With increasing speed the drop-out sequences became longer, and when swimming speed rose beyond the upper limit of the transition zone, only ram ventilation was employed. In normoxic water ($P_{wO_2} = 150$ mmHg) this fish was ram ventilating at swimming speeds above 26 cm s^{-1} . In hypoxic water ($P_{wO_2} = 75$ mmHg) the threshold for ram ventilation was increased to a swimming speed of 43 cm s^{-1} , whereas in hyperoxia ($P_{wO_2} = 300$ mmHg) it was decreased to 19 cm s^{-1} .

The asterisks in Fig. 1 indicate the combinations of swimming speed and oxygen tension at which oxygen consumption (\dot{V}_{O_2}) was measured. When swimming at 26 cm s^{-1} at P_{wO_2} 113–114 mmHg (*1) this trout ventilated actively and \dot{V}_{O_2} was $139.77 \pm 4.70 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$. By increasing P_{wO_2} to 171–173 mmHg (*2) active ventilation was replaced by ram ventilation and \dot{V}_{O_2} decreased to $127.01 \pm 3.75 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$. The energy saving calculated as the percentage decrease in \dot{V}_{O_2} when shifting from active to ram ventilation was 9.1% ($P > 0.005$).

In order to determine whether this change in \dot{V}_{O_2} could be attributed solely to the cost of active ventilation and improved drag characteristics, or partly to a general increase in \dot{V}_{O_2} caused by an increased ventilatory requirement at the lower P_{wO_2} , oxygen consumption was measured at the same P_{wO_2} values as above, but at a swimming speed of only 10 cm s^{-1} (asterisks 3 and 4). At this speed, the fish was only showing active ventilation, and \dot{V}_{O_2} was $90.66 \pm 5.38 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ at 114–126 mmHg and $90.86 \pm 9.92 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ at 167–173 mmHg. A similar experiment was carried out on trout V. Student's *t*-test showed no significant difference between these values. P. G. Bushnell (personal communication) likewise found identical oxygen uptake in trout swimming at 22 cm s^{-1} at P_{wO_2} of 60 mmHg and 120 mmHg, respectively. Consequently, the decrease in \dot{V}_{O_2} when swimming at 26 – 28 cm s^{-1} is an expression of the energy saved by the switch to ram ventilation.

Table 2 summarizes the experimental conditions and results of oxygen consumption measurements at different modes of ventilation. The calculated energy saving for fish V–VIII when swimming at 24 – 28 cm s^{-1} varies from 8.4 to 13.3% of total oxygen consumption (mean \pm s.d. = $10.2 \pm 2.2\%$).

The velocity threshold required to elicit the transition to ram ventilation for three sharksuckers (Fig. 2) is clearly dependent on ambient oxygen tension in a manner similar to that seen in the trout (Fig. 1).

Correcting the water velocities is complicated when the solid blocking effect of the fish is high (Bell & Terhune, 1970). Hence in Fig. 2 uncorrected water velocities have been used. These will be lower than the velocities to which the fish have actually been exposed.

Since the water velocities in Fig. 2 are not corrected for the solid blocking effect of the fish, the velocities for the transition to ram ventilation in normoxic water read from Fig. 2 cannot be directly compared to the values in our previous study of the sharksucker (Steffensen & Lomholt, 1983), where the fish were so small that a correction was unnecessary. In fact the fish of the present study are the same animals which have, in the meantime, to some extent 'outgrown' the apparatus.

Table 2. Experimental conditions, mode of ventilation, oxygen consumption ($\bar{X} \pm s.d.$) and energy saved by rainbow trout after transition to ram ventilation

Fish no.	Expt no.	Oxygen tension (mmHg)	Swimming speed (cm s ⁻¹)	Mode of ventilation	Oxygen consumption (mg O ₂ kg ⁻¹ h ⁻¹)	N	Significance <i>t</i> -test (<i>P</i> <)	Saved energy ΔV_{O_2}
V	1	114-121	27.6-28.0	active	223.20 ± 4.36	3	0.005	9.9
	2	175-181	27.5-28.0	ram	201.00 ± 2.22	3		
	3	118-120	10.5-11.0	active	108.78 ± 4.34	10	NS	—
	4	182-184	10.4-11.2	active	106.15 ± 3.20	3		
VI	5	113-114	25.7-26.2	active	139.77 ± 4.70	4	0.005	9.1
	6	171-173	25.8-26.2	ram	127.01 ± 3.75	6		
	7	114-126	9.7-10.0	active	90.66 ± 5.38	4	NS	—
	8	167-173	9.7-9.9	active	90.86 ± 9.92	4		
VII	9	120-123	25.0-25.2	active	146.85 ± 2.29	4	0.001	13.3
	10	164-171	25.0-25.3	ram	127.39 ± 4.38	3		
VIII	11	121-123	23.9-24.2	active	222.94 ± 3.72	4	0.001	8.4
	12	166-171	23.9-24.2	ram	204.14 ± 1.20	3		

Cost of ventilation (*N* = 4) \bar{X} = 10.2 ± 2.2% (s.d.) at velocities between 23.9-28.0 cm s⁻¹ for fish with total length of 36-40 cm. *N* indicates number of experiments.
NS = not significant.

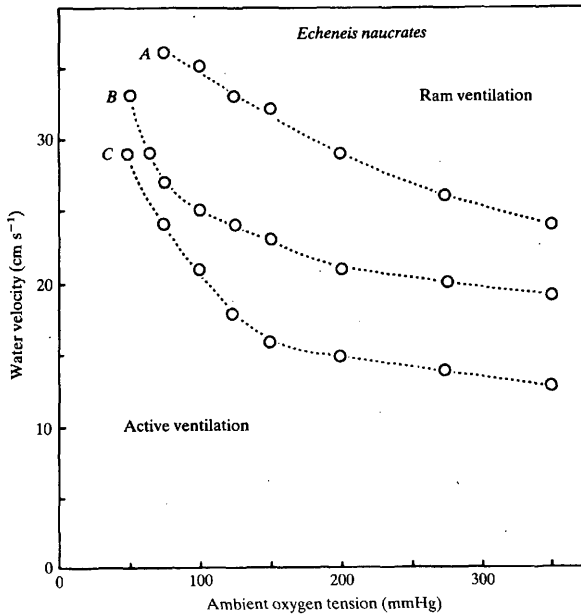


Fig. 2. Velocity threshold for ram ventilation at different ambient oxygen tensions, for three sharksuckers, A, B and C. Each point is the mean of three determinations, the range of which never exceeded 3 cm s^{-1} .

DISCUSSION

Rainbow trout reared on fish farms have been reported to have lost the ability to ram ventilate and will do so only after intensive training at high swimming speeds (Roberts, 1975a). Freadman (1979) reported that active ventilation was the only mode of ventilation used by rainbow trout up to a swimming speed of 70 cm s^{-1} , and he never observed the trout to ram ventilate. By contrast, the rainbow trout presently studied showed ram ventilation at swimming speeds as low as $20\text{--}30 \text{ cm s}^{-1}$ in normoxic water ($P_{\text{wO}_2} = 150 \text{ mmHg}$) without previous training.

The control of the transition between active and ram ventilation has been thought to be initiated largely through the action of mechanoreceptors detecting water pressure or velocity, whereas the transition is notably insensitive to water oxygen tension except at extreme, near lethal hypoxic conditions (Roberts, 1974, 1975a).

The present results are not in agreement with these earlier contentions. On the contrary, the swimming speed or water velocity necessary to elicit the transition from active to ram ventilation increases with declining ambient oxygen tension (Figs 1, 2, Table 1). This indicates that a P_{O_2} stimulus is involved in controlling the

ventilatory mode in rainbow trout and sharksucker, not only at extreme levels of oxygen tensions, but over the entire range of water oxygen tensions tested (approx. 75–300 mmHg).

Mackerel increase the gape in response both to an increased oxygen demand after feeding and to a lowered oxygen content of the water (Brown & Muir, 1970). A similar adjustment of mouth gape in response to water P_{O_2} was observed during the present study in the swimming rainbow trout as well as in the resting sharksucker. This adjustment of mouth gape is clearly an indication that these fishes can also regulate gill irrigation in response to inspired P_{O_2} during ram ventilation.

The energetic advantage of shifting the mode of ventilation is likely to be a result of a transfer of the work of breathing from the cranial respiratory muscles to the swimming musculature. Also ram ventilation may improve the drag characteristics of the swimming fish (Roberts, 1975a, 1978; Jones & Randall, 1978). During ram ventilation, the respiratory pump muscles are not relaxed, but tonically active and the mouth gape continuously adjusted, though the energetic cost of these movements is probably negligible (Freadman, 1979; Steffensen & Lomholt, 1983).

The observed decline in oxygen consumption is a measure of the total energy saving when shifting from active to ram ventilation. This saving was found to be from 8.4–13.3% of total oxygen consumption (mean \pm s.d. = 10.2 ± 2.2 , Table 2). Since drag is most probably reduced because of improved boundary layer conditions resulting from a shift to ram ventilation (Roberts, 1975a, 1978; Freadman, 1979), a fraction of the 10.2% reduction can be ascribed to drag reduction. The exact magnitude of this fraction cannot be estimated at present. The remaining fraction of the average 10.2% reduction in \dot{V}_{O_2} can be ascribed to the cessation of activity of the branchial muscles. Consequently the oxygen consumption of the respiratory muscles must be somewhat less than 10% of total \dot{V}_{O_2} at a swimming speed just below the ram threshold. This low value is in good accord with the low cost of active ventilation seen in the sharksucker at rest which was 4–6% of standard oxygen consumption (Steffensen & Lomholt, 1983).

Ram ventilation is thus a mode of ventilation enabling the fish to save energy. This aspect of ram ventilation is particularly significant in the light of calculations by Jones (1971), which suggest that the oxygen consumption of the cardiac and branchial pumps may become so high as to limit maximal oxygen uptake.

The influence of ambient oxygen tension on the transition to ram ventilation as well as on the mouth gape during ram ventilation suggests that the control of this mode of ventilation forms an integral part of the control system of active branchial ventilation, which is primarily based on an oxygen-sensing mechanism (Dejours, 1975). The present study does not rule out the importance of mechanoreceptors for the initiation of ram ventilation, but indicates that these are strongly modulated by an oxygen-sensing mechanism.

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