HEAT TRANSFER BETWEEN FISH AND AMBIENT WATER*

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SUMMARY

1. The ability of fish gills to transfer heat was measured by applying a heat pulse to blood in the ventral aorta and measuring it before and after passing through the gills of a teleost, *Hemitripterus americanus*.

2. 80–90 % of heat contained in the blood is lost during passage through the gills.

3. The fraction of heat not lost during passage through the gills is due to direct transfer of heat between the afferent and efferent artery within the gill bar.

4. The major fraction of metabolic heat (70–90 %) is lost through the body wall and fins of the sea raven in sea water at 5 °C; the remainder is lost through the gills.

INTRODUCTION

Many authors have assumed that most of the metabolic heat produced by fishes is lost to ambient water as blood flows through the gills. The assumption is reasonable because body temperature is close to ambient temperature, blood and water have a high heat capacity (relative to air), the surface area of the gill epithelium is large and diffusion distance across the epithelium small, and because a large volume of water is pumped over the gills due to its relatively low oxygen content. In spite of the vast literature on gas-exchange at fish gills (see Hughes, 1970, 1973) the amount of heat lost as blood passes through fish gills does not appear to have been determined. We have measured this heat loss and, in addition, related it to the total heat production estimated by measuring oxygen uptake so that the fraction of heat lost at the gills, relative to that lost by other avenues, could be calculated. In the present experiments we show that most of the heat present in blood is lost as it passes through the gills, but that the major fraction of total heat loss occurs through the body wall and fins, not through the gills.

MATERIALS AND METHODS

Atlantic sea ravens, *Hemitripterus americanus*, were captured by trawl and held in large tanks at 3–7 °C for at least one week prior to use. This species was selected for
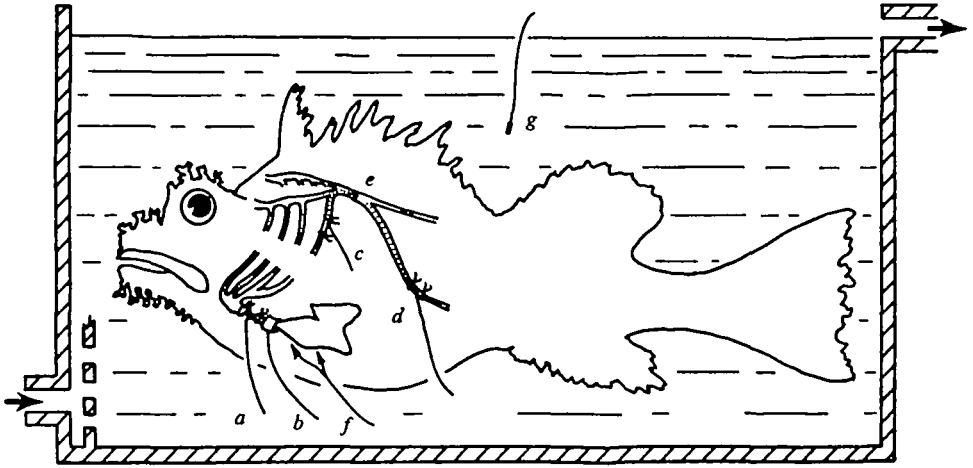
Fig. 1. The apparatus used to measure heat loss at the gills in sea raven. (a) thermistor in ventral aorta; (b) heater cuff around ventral aorta; (c) thermistor in fourth branchial efferent artery; (d) thermistor in coelico-mesenteric artery; (e) position of thermistor c or d in the dorsal aorta; (f) ventricle; (g) thermistor in ambient water.

these studies for several reasons. They can be obtained in large quantities in a size range of 10–3000 g. Their vascular anatomy permits cannulation and insertion of thermistors in blood vessels. They survive well in captivity, are docile and rarely struggle when confined.

Heat exchange across gills in situ

Heat exchange across the gills was determined by measuring the temperature in the blood of the ventral and dorsal aorta after applying a heat pulse to the ventral aorta (Fig. 1).

Thermistors (2 kΩ, ultra small bead, time-constant less than 1 s) were mounted in polyethylene tubing (O.D., 0·8 mm). Dorsal aortic temperature was measured by inserting a thermistor, either in the coeliaco-mesenteric artery or the efferent artery of the fourth gill arch, and pushing it into the dorsal aorta. Ventral aortic temperature was measured by inserting a thermistor into a T-shaped polyethylene cannula, and securing this into the ventral aorta. The heater consisted of three resistors in parallel, which were coated (Dow Corning protective sealer 1890) and shaped into a flexible cuff that was fitted around the ventral aorta. Care was taken to avoid cutting the pericardium. Wound closure was achieved with Histoacryl (B. Braun Melsungen, Germany) and sutures. Fish resumed respiratory movements immediately upon return to the water-filled chamber, but were allowed at least 16 h to recover before experimentation. Operative procedures were similar to those described by Saunders & Sutterlin (1971).

Timed heat pulses (5–60 s) were applied through a regulated d.c. power supply (5–25 V, 120 mA). The increases in blood temperature were recorded with a Grass pen-recorder. The amount of heat introduced into the blood in the ventral aorta and the amount remaining in the blood in the dorsal aorta, after passage through the gills, were determined by integrating the area under the temperature curves. Heart
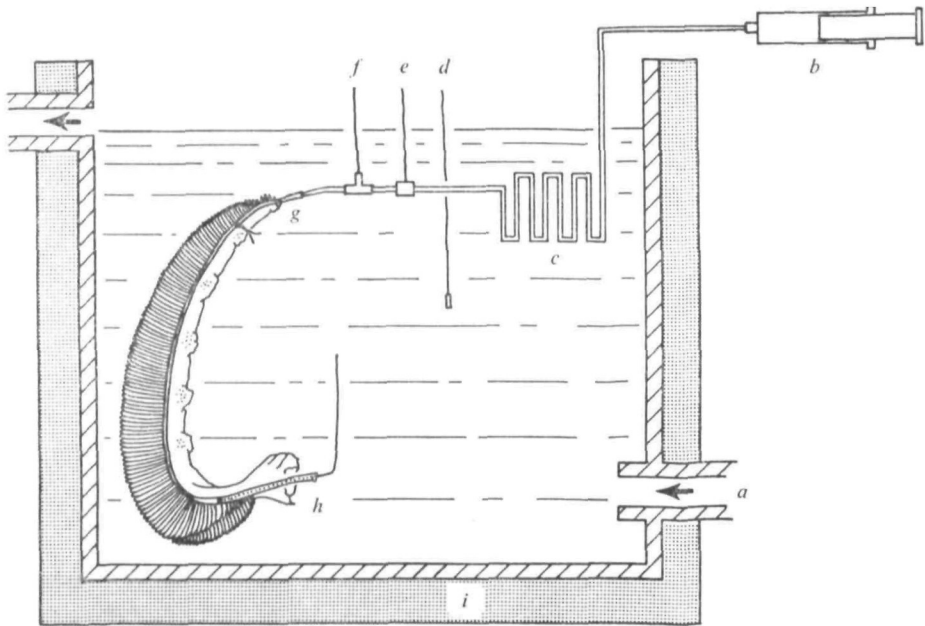
Fig. 2. The apparatus used to measure heat loss from the isolated gill of sea raven or trout. (*a*) input of temperature-regulated ambient water; (*b*) syringe pump to perfuse gill; (*c*) stainless steel heat exchanger to equilibrate blood with ambient water; (*d*) thermistor to measure ambient water temperature; (*e*) heater cuff; (*f*) thermistor to measure heat pulse in; (*g*) polyethylene cannula in afferent branchial artery; (*h*) thermistor in efferent branchial artery.

rate and respiration rate were recorded with suitably placed electrodes. At the end of each experiment, a cannula was secured in the ventricle and cardiac output of the fish during the previous experiment was estimated by perfusing saline with a peristaltic pump at known flow rates and observing the increase in blood temperature in the ventral aorta when heat pulses were applied as before. The stroke rate of a pulsatile pump was adjusted to the same rate as the fish's heart rate during the previous experiment and the size of the heat pulse was determined throughout a range in stroke volumes of the pump.

Heat exchange in isolated gills

Studies similar to the above were performed on isolated gills of sea ravens and a rainbow trout (*Salmo gairdneri*). The sea ravens weighed 1·3–2·3 kg, and the trout 430 g. After an injection of an anticoagulent (sodium citrate) into the ventral aorta, the third gill arch was excised and placed in cold saline. Temperature of blood leaving the gills was measured by inserting a thermistor 2 cm into the efferent artery within the gill arch. The heat pulse was applied and measured by methods similar to those used in the intact fish, except that blood was perfused at a variety of flow rates with a syringe pump. The gill was perfused with blood either from the same fish or from donor fish; occasionally the blood was diluted 50 % with saline. Resistance to blood flow was monitored by measuring input pressure with a Statham transducer. The drop in blood pressure as blood flowed through the isolated gill was similar to

that reported for measurements *in vivo* in other fish (Randall, 1970) and similar to measurements in the intact sea raven (Saunders & Sutterlin, 1971); however, the absolute pressures are less because outflow pressure was atmospheric pressure. Water flow in the perfusion chamber was in a circular pattern and the gill was positioned relative to the water flow so that blood and water moved countercurrent to each other (Fig. 2). Acetylcholine and epinephrine were added to the perfusate by means of a by-pass circuit. The volume added was always 0·4 ml and passed through the gill in less than 1 min.

Excess body temperature

The excess temperature (the difference between body and water temperature) in the muscle adjacent to the spinal column was measured with a needle-mounted thermistor while the fish was in a constant temperature bath at 4 °C.

Rate of change of core temperature: k

The rate of exchange of heat between the fish and surrounding water was estimated in a manner similar to that described by Stevens & Fry (1974). The rate of change of core body temperature (in the muscle adjacent to the spinal column) was measured with a needle-mounted thermistor before and after transfer between two tanks with a 5 °C temperature difference. The rate of heat exchange is expressed as k (°C/min °C) determined as the reciprocal of the time taken for the core temperature to change 63·2 % of the driving gradient. That is,

$$k = -\frac{1}{t}\ln\left[\frac{Te - Tb}{Te - Tb_0}\right]$$

$$= -\frac{1}{t}\ln\,(1-0·632) = -\frac{1}{t}\ln\,(0·368) = \frac{1}{t}, \tag{1}$$

where k = coefficient of temperature change, °C/min °C, t = time in minutes for tissue temperature to decrease from Tb_0 to Tb, Tb_0 = tissue temperature at steady state in warm tank (i.e. at t = 0), Tb = tissue temperature t minutes after being in cold tank, Te = tissue temperature at steady state in cold tank.

This equation is an approximation. Time-dependent solutions to the appropriate differential equations, taken at the centre of any regular geometry, generally give an infinite series of terms exponential with respect to time. For large times (i.e. $t_{\frac{1}{2}}$ and greater), the series can be chosen to converge rapidly so that all but the first term can be ignored, and the process looks approximately first order (i.e. exponential in time); equation (1) then follows. Furthermore, to the extent that this approximation holds, the time-constant thus measured will also apply to steady-state conditions, so that heat production at the point of measurement can be correctly estimated. However, it must be pointed out that this estimate of heat production applies only at the point of measurement near the centre of the fish, and not to the fish as a whole.

Aerobic heat production

Aerobic heat production was estimated indirectly by measuring oxygen uptake and applying the oxycalorific value of 3·20 cal/mg oxygen (Brafield & Solomon, 1972).
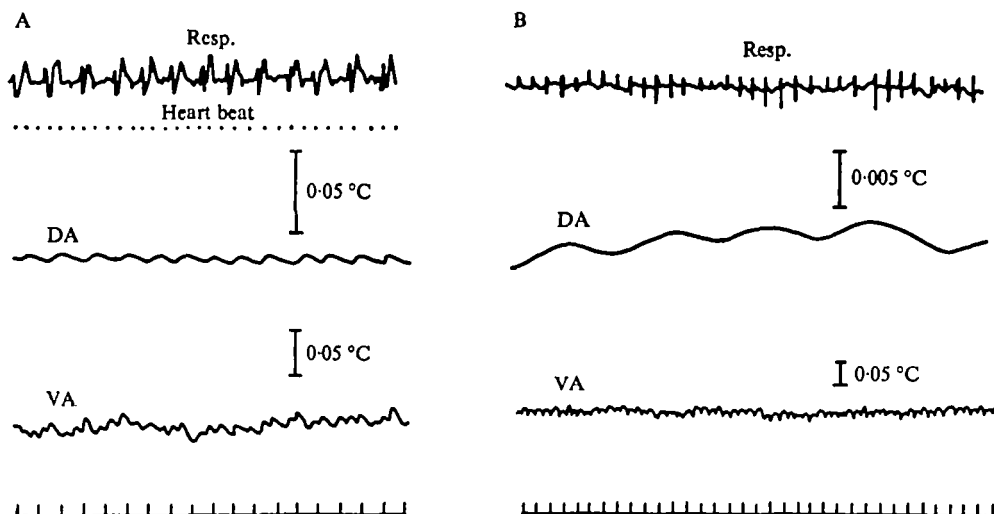
Fig. 3. Record of temperature variations in dorsal and ventral aorta of sea raven in steady state conditions. (RESP) electromyogram from respiratory muscles; (DA) dorsal aortic temperature; (VA) ventral aortic temperature – small pulses occur with each heartbeat. Time marker 5 s. (A) Cyclic variations in dorsal aortic temperature occur with each respiratory cycle. (B) Cyclic variations in dorsal aortic temperature are in phase with the cyclic pattern of respiration with a period of 8 to 10 respiratory movements.

Individual sea ravens were left in cylindrical plexiglass chambers with flowing sea water overnight to become accustomed to the situation. Oxygen uptake was determined by measuring the change in oxygen concentration for a known time interval, but the oxygen concentration did not fall below 70 % air saturation. The water samples were forced from the chamber by inflating a balloon with water within the chamber.

RESULTS

Gill heat exchange in situ

Small changes in temperature (about 0·025 °C) of blood in the ventral aorta were observed with each heartbeat as blood, warmed by metabolism, was pumped into the ventral aorta (Fig. 3). These changes were occasionally used to monitor heartbeat rate.

Smaller changes in temperature (about 0·005 °C) of blood in the dorsal aorta were also evident. Usually these were in phase with respiration (Fig. 3A); occasionally there were cycles associated with cycles in the pattern of respiration with a period of about 35 s or ten breaths (Fig. 3B). Sometimes there were changes in the temperature of the blood in the dorsal aorta in phase with heart rate rather than respiration, even though the blood takes about four heartbeats to pass through the gills (Fig. 4).

Fig. 4 shows an exemplary response of the application of a heat pulse to the ventral aorta, its measurement in the ventral aorta and the remainder of the heat pulse in the dorsal aorta after passage through the gills. These curves were used to estimate the fraction of heat lost at the gills.

The maximum temperature change in the blood in the ventral aorta caused by the heat pulse was always less than 0·5 °C and did not affect heart rate or the pattern of
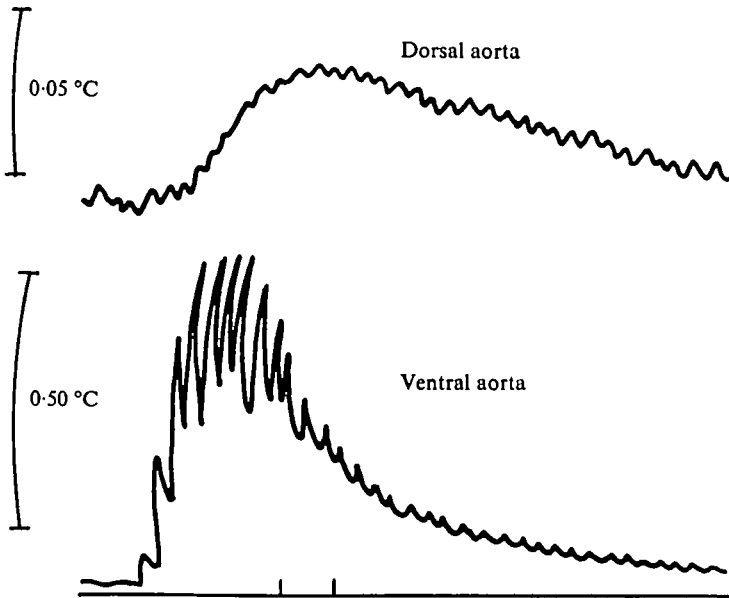
Fig. 4. Exemplary record of blood temperatures from both sides of the gills of a sea raven
after application of a 15 s heat pulse to blood in the ventral aorta.

Table 1. *Circulatory parameters for resting sea raven in sea water at 5–7 °C*

| | | | | Time for heat pulse to appear in dorsal aorta | | | | |
| | | | | Pulse onset to onset | | | Pulse peak to peak | | |
Body weight (kg)	Cardiac output (ml/min.fish)	Heart rate (beats/min)	Stroke volume (ml/stroke)	(s)	n (heartbeats)		(s)	n	(heartbeats)
1.	2·6	10	24	0·42	11·4	5	4·6	14·6	20	5·8
2.	1·6	9·7	29	0·33	8·0	6	3·8	—		
3.	1·2	2·5	30	0·08	7·7	9	3·8	13·2	6	6·6

respiration. Although most of the heat was lost to the water as the blood passed through the gills, in all cases it was possible to detect a small amount that remained in blood sampled in the dorsal aorta.

Fish 4 served as a control for the effects of inserting the thermistor in the ventral aorta. Even though no sensor was placed in the ventral aorta, the heat pulse was evident in the dorsal aorta and was similar in amplitude, duration, and latency to other fish. The absence of the ventral aorta sensor precluded calculation of the amount of heat and cardiac output for this fish.

The amount of heat introduced into the ventral aorta per pulse was estimated from the temperature records by multiplying the area under the temperature curve (Table 2) by the heat capacity of the blood (0·92 cal/g) and the cardiac output (Table 1). The fraction of heat loss at the gills tended to be constant within each particular fish independent of changes in the amount of heat introduced (Table 2). This is not surprising as the major function of the gills is gas exchange, not heat exchange, so that compensatory adjustments in respiration and circulation are not expected, especially for heat loads as-small as those used. The amount of heat not lost at the gills (i.e. the amount measured in the dorsal aorta) is plotted as a function of the amount of heat

Table 2. *The amount of heat put into the ventral aorta during the 15 s heat pulse, the amount remaining in the dorsal aorta expressed as heat not lost at the gills, and the fraction not lost expressed as a percentage (means ± standard errors)*

| Fish	Heat applied to heater (W)	n	Heat in ventral aorta (cal)	Heat out dorsal aorta (cal)	Heat retained (%) $\dfrac{\text{Dorsal aorta} \times 100}{\text{Ventral aorta}}$
1	3·0	5	2·87 ±0·0527	0·407 ±0·0552	12·9±2·00
2	3·0	5	2·53 ±0·107	0·514 ±0·0284	20·4±1·63
	2·4	5	1·66 ±0·0521	0·363 ±0·0509	22·0±3·20
	1·8	5	0·944±0·0388	0·230 ±0·0197	24·6±2·25
	1·2	5	0·388±0·00951	0·0425±0·00419	11·0±1·19
3	3·0	5	1·14 ±0·0558	0·116 ±0·00262	10·2±0·54
	2·4	5	0·778±0·0351	0·0723±0·0103	9·2±1·16
	1·8	5	0·423±0·0196	0·0341±0·00731	8·2±1·86
	1·2	1	0·233		
5	3·0	9	1·13 ±0·0676	0·104 ±0·0101	9·3±0·89
	2·4	8	0·598±0·0140	0·0531±0·00375	9·0±0·77
	1·8	3	0·320±0·0267	0·0226±0·00578	7·5±2·49
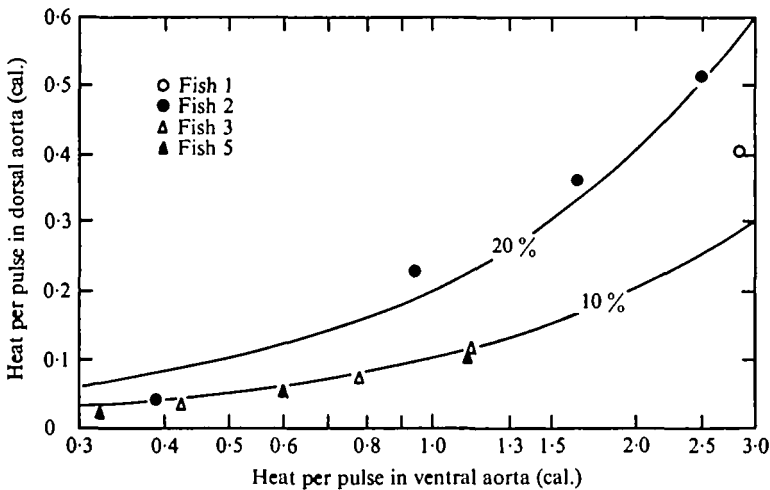
Fig. 5. The amount of heat not lost at the gills (i.e. the amount remaining in the dorsal aorta) as a function of the amount of heat put into the blood before it passes through the gills. The solid construction lines (10 and 20%) indicate when 90 and 80%, respectively, of the heat per pulse would be lost as blood passes through the gills. Logarithmic scale on abscissa is for clarification only.

in the blood entering the gills in Fig. 5. For resting sea raven at 5–7 °C, about 80–90 % of the heat in venous blood is lost as it passes through the gills.

In addition, we determined the time it took for the heat pulse to pass through the gills. Fastest gill time (i.e. time from onset of the pulse in the ventral aorta to its first appearance in the dorsal aorta) was about 8 s or 4 heartbeats (Table 1). Mean gill time (i.e. time from the peak of the pulse in the ventral aorta to the peak of the pulse in the dorsal aorta) was about 14 s or 7 heartbeats (Table 1). Cardiac output for sea ravens in sea water at 4 °C was 2 to 6 ml/min.kg body weight; heart rate was 24–30 beats/ min (Table 1).
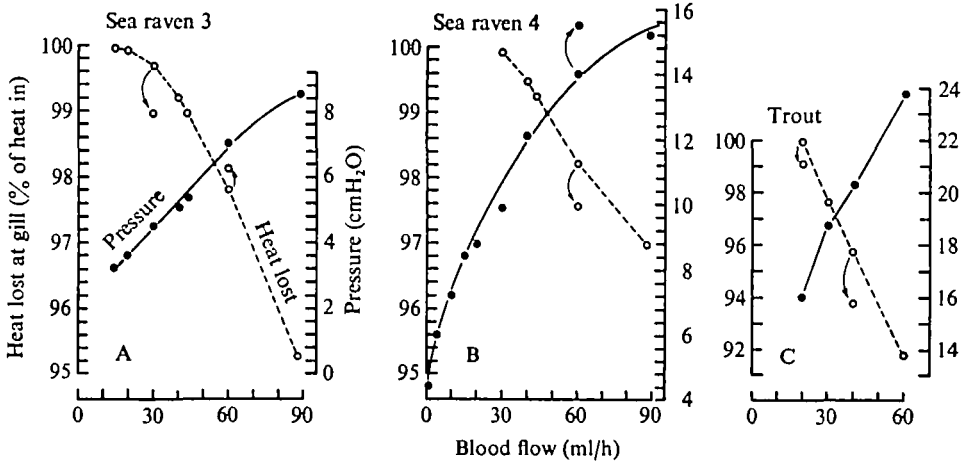
Fig. 6. Amount of heat lost and pressure drop across the isolated gill as a function of perfusion flow rate; A and B, sea raven; C, rainbow trout; O, heat loss; ●, pressure drop across gill. In panel A the decrease in heat loss shown by the arrow was due to acetylcholine, the increase shown by the arrow due to epinephrine. In panel B the decrease in heat loss and increase in pressure were due to reversing the direction of water flow. In panel C the decrease in heat loss at a blood flow rate of 20 ml/h was due to stopping water flow, the decrease at a blood flow rate of 40 ml/h was due to increasing ambient temperature to 13 °C.

Heat exchange in isolated gills

Heat exchange was more nearly complete in isolated gill preparations than in the intact fish, but the amount of heat lost was very sensitive to the rate at which the gill was perfused with blood. In addition, the preparations were extremely consistent from trial to trial with respect to the amount of heat loss. Fig. 6 illustrates the relationship between blood flow rate and the amount of heat loss as blood is perfused through an isolated gill. At least 95 % of the heat pulse was lost in each of eighty-one trials carried out on preparations from five sea ravens. When blood flow through the gill was 0·5 ml/min or less, then 99 % of the heat pulse was lost. The pressure drop across the gills increased in a curvilinear fashion with increased flow rates (Fig. 6). The pressure drop across the gills was 7–15 cm H_2O at flow rates similar to those occurring in the intact fish.

Acetylcholine (10^{-4} M) in the blood slightly decreased and epinephrine (10^{-4} M) slightly increased heat transfer at the gills. The typical effect of acetylcholine and epinephrine was consistent, but very small (Fig. 6A). Both drugs caused the expected changes in vascular resistance: acetylcholine caused vasoconstriction (pressure drop across the gills increased from 15 to 24 cm H_2O) and epinephrine caused vasodilation. Although the drugs were perfused through the preparation within 30 s, the change in vascular resistance took 1 min to develop and lasted for 6–8 min.

Reversing the direction of water flow across the gills so that blood and water flowed in the same direction (co-current flows) caused a small decrease in the ability of the gill to transfer heat, and also a small increase in resistance to blood flow (Fig. 6 B).

Eighty-one trials were carried out on a gill from a rainbow trout with similar results (Fig. 6C). 91–100 % of heat was lost as blood passed through the gill. Stopping water flow over the gill, or increasing ambient water temperature, caused small decreases in the ability of the isolated gill to transfer heat.
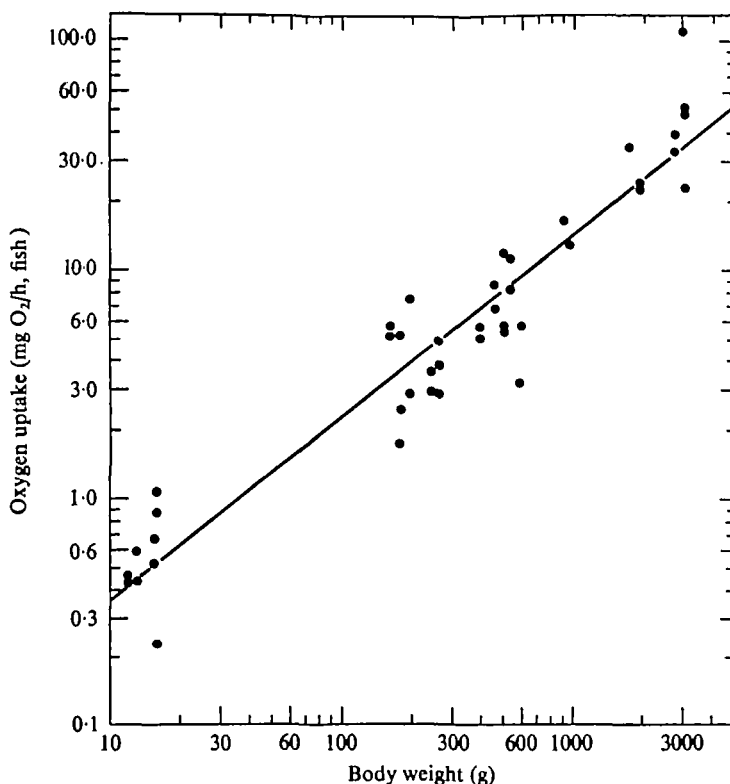
Fig. 7. Oxygen uptake of sea raven acclimated and tested in sea water at 4 °C. Both scales are logarithmic. $\dot{V}_{O_2} = 0.05639 \times \text{weight}^{0.8496}$.

Excess body temperature

Excess core body temperature in steady-state conditions at water temperature of 4 °C was 0·066 °C (range 0·049–0·087 °C for 12 individuals) and was not significantly related to body weight.

Rate of change of core temperature: k

The rate of cooling from 7·5 to 3.5 °C for fish acclimated to 4 °C was related to body weight, smaller fish coming to a new steady state more quickly than larger ones. The relationship is described by the following equation determined for 24 individuals weighing 12–3178 g; k in °C/min.°C gradient:

$$k = 3.32 \times W^{-0.536} \quad \text{(standard error of estimate} = 0.0934; \ W \text{ in g).}$$

Aerobic heat production

The rate of oxygen uptake of sea ravens acclimated and tested at 4 °C in sea water (Fig. 7) is described by the following equation determined for 42 individuals weighing 12–2948 g; $\dot{V}_{O_2}$ in mg/h.fish; W in g. Equation fitted by least square sregression on logarithmic transformed data.

$$\dot{V}_{O_2} = 0.0564 \times W^{0.805} \quad \text{(standard error of the estimate } 0.194).$$

DISCUSSION

The observation that 80–90% of heat is lost as blood passes through the gills is not surprising. Perhaps what is surprising is that any heat remains after blood passes through the gills because of the high heat capacity of blood and water, the large area available for transfer and the high rate of water flow. Furthermore, recent evidence indicates that all blood passes through the flat lacunar secondary lamellae and that there are no non-respiratory filamental shunts in teleost gills (Morgan & Tovell, 1973; Gannon, Campbell & Randall, 1973). The lack of complete transfer of the heat pulse to the water seems possible only if some fraction of the blood passing through the gills is not available for heat exchange. Another, and more likely, explanation is that the heat is transferred before reaching the secondary lamellae by direct transfer from the afferent artery to the efferent artery in the gill bar.

Despite the usual effects on vascular resistance the smallness of drug effects on the amount of heat transferred also supports our contention that heat transfer occurs prior to blood reaching the secondary lamellae. Bergman, Olson & Fromm (1974) observed large effects of drugs on the ability of rainbow trout gills to transfer urea. In their preparation epinephrine (10^{-5} M) increased urea transport (that is, respiratory exchange area) 500% over control values, and acetylcholine (10^{-6} M) decreased respiratory exchange area to 20% of control values. Our data, obtained from a rainbow trout prepared in the same manner as theirs, indicate that the effect of these drugs on heat transfer is at least two orders of magnitude less than that on respiratory exchange area. These data also support the idea that some heat is conserved in the gill bar before blood gets to the respiratory exchange area.

The measurements of cardiac output, stroke volume and heart rate agree with values for other fish of similar habits (Randall, 1970). The cardiac output values are low but similar to that of the ling cod (Stevens et al. 1972). There are very few measurements of gill circulation time (Randall, 1970). Mott (1950) observed that blood took 5·6 s to pass through the gills of an eel. Circulation time can be estimated by dividing blood volume by blood flow. Values calculated in this way are much larger than those measured radiographically by Mott. For example, Davis (1970) measured total circulation time of 64 s in a trout, and using a gill blood volume of 6·7 ml/kg (Stevens, 1968), then the calculated gill circulation time is 22 s at 8–10 °C. The time between the pulse appearance in the ventral aorta and its appearance in the dorsal aorta reported here for the sea raven is lower than blood circulation times through the gills because the heat pulse passes through the gill bar rather than through the secondary lamellae. The small drug effects that were observed may have been due to changes in tone in the afferent and/or efferent branchial arteries. Homgren & Nilsson (1974) have shown that these drugs alter the tone of isolated artery strips of teleosts.

The effects of stopping or reversing the direction of water flow over the isolated gill are probably due to a decrease in the effective convective loss of heat from the afferent and efferent arteries within the gill bar. The locations of these arteries within the gill bar are such that direct heat transfer from the afferent to the efferent artery will be favoured when water flow is opposite to the normal direction (Datta Munshi & Singh, 1968).

The rate of change of core temperature, k, for the sea raven in sea water at 4 °C

Table 3. *Oxygen uptake of fishes at low temperature and activity levels*

(For some species it was necessary to extrapolate to estimate rate at 1 kg body weight. SW, salt water; FW, fresh water.)

Species	Activity level	Temperature (°C)	Oxygen uptake (mg/h. fish) (W in g)	Oxygen uptake at $W = 1$ kg	Reference
Cod (*Gadus morhua*)	Routine	12 SW	$0\cdot245 \times W^{0.83}$	71	Edwards *et al.* (1972)
Cod (*G. callarias*)	Routine	— SW	$1\cdot17 \times W^{0.41}$	85	Sundnes (1957)
Cod (*G. morhua*)	Routine	3 SW	$0\cdot183 \times W^{0.78}$	43	Saunders (1963)
Cod (*Ophiodon elongatus*)	Routine	12 SW	$0\cdot286 \times W^{0.78}$	63	Pritchard *et al.* (1958)
Sculpin (*Myoxocephalus scorpius*)	Routine	−1·5 SW	$0\cdot432 \times W^{0.91}$	23	Holeton (1974)
Carp	Standard	10 FW	$0\cdot184 \times W^{0.88}$	16	Beamish (1964)
Goldfish	Standard	10 FW	$0\cdot270 \times W^{0.85}$	12	Beamish & Mookherjii (1964)
Zoarcid (*Gymnelis viridis*)	Standard	−1·5 SW	$0\cdot360 \times W^{0.83}$	10	Holeton (1974)
Sea raven (*Hemitripterus americanus*)	Standard	4 SW	$0\cdot564 \times W^{0.80}$	14	present study

$(3\cdot3 \times W^{-0\cdot54})$ is in close agreement with values for the common white sucker i fresh water at 17 °C $(3\cdot7 \times W^{-0\cdot57})$ (Stevens & Fry, 1974). The core temperature of sea ravens changes slightly more quickly and this is probably because of their very large, well vascularized fins. For example, the core temperature of sea ravens changes about 15 % more rapidly than a sucker per degree driving gradient for body weights of 1–2 kg ($k = 0\cdot082$ °C/min °C for sea raven, $0\cdot070$ °C/min °C for sucker at body weight of 1 kg). The excess body temperature of sea ravens at ambient water temperature of 4 °C is about $0\cdot07$ °C or about an order of magnitude less than values reported for other fishes of a similar body weight (Stevens & Fry, 1970, 1974). We are confident of the accuracy of the measurements of the present study; the low values are probably due to very low metabolic rates at low ambient temperatures.

The level of aerobic heat production as determined by the rate of oxygen uptake is low when compared to other reported values (Table 3). The levels arel ow because of low ambient temperature and because of the sedentary nature of the species used. Values for cod at 10–12 °C are four to six times greater than those observed for sea raven; even those determined at 3 °C are three times greater than those observed for sea raven. This difference occurs because the sea raven, unlike most other fish, will lie motionless in the respiration chamber for days. The values for carp and goldfish were obtained by extrapolating to zero activity and these values compare favourably with those observed in the present study.

Aerobic heat production was estimated from oxygen uptake values using an oxycalorific equivalent of $3\cdot20$ cal/mg O_2 (Table 3). It is also possible to calculate the rate of muscle metabolism using data from the rate of cooling and the excess temperature at the same point in the muscle. That is, heat must be produced at some rate to account for the measured excess temperature at the known rate of cooling, k, when ambient temperature is not changing. Given that heat production is aerobic and that heat capacity of fish muscle is $0\cdot8$ cal/g °C (Slavin, 1964; Charm & Moody, 1966), then oxygen uptake of 1 g of muscle for a 1 kg sea raven is:

$$\dot{V}O_2 = \frac{60\ \text{min}}{\text{h}} \times \frac{\text{mgO}_2}{3\cdot20\ \text{cal}} \times \frac{0\cdot8\ \text{cal}}{\text{g muscle}.°C} \times \frac{0\cdot0819\ °C}{\text{min}\ °C} \times 0\cdot066\ °C$$

$$= 0\cdot081\ \text{mg/h}.\text{g muscle}.$$

Thus, the value for whole fish determined by oxygen uptake is about $\frac{1}{5}$th of the value for muscle near the centre of the fish estimated from k and excess muscle temperature. Similar comparisons for common white sucker and *Tilapia* appear in Table 4. For all three non-tunas the estimate of metabolic rate calculated from heat loss is about 5 times greater than that obtained by direct measurements of oxygen uptake on the whole fish. It is likely that estimates using heat loss are high because the fish must be disturbed by the procedures to make the measurements, and that the disturbance elevates metabolic rate. It is unlikely that muscle metabolic rate greatly exceeds the metabolic rate of the animal as a whole, since it forms such a large part of the body mass. Errors for the other terms in the equation (oxycalorific equivalent and specific heat) are unlikely to exceed 10 %, and certainly cannot account for a fivefold discrepancy. The equation used assumes a lumped model (i.e. temperature within the fish is uniform). This model becomes more sensitive to the lack of uniformity of muscle temperature when the excess muscle temperatures become very small. The values for

Table 4. *Muscle metabolic rate calculated from rate of heat loss from the muscle and excess temperature at the same point in the muscle compared with metabolic rates determined for the whole fish (All values determined for fish weighing 1 kg.)*

Fish	k (°C/min·°C)	Excess (°C)	Metabolic rate (mg/hg)		Ratio Muscle/ Whole fish
			At muscle point	Whole fish	
Sea raven	0·0819	0·066	0·081	0·014	5·8
Common white sucker	0·07[1]	0·34	0·357	0·065[2]	5·5
Tilapia	0·0713	0·44	0·469	0·086[4]	5·4
Tuna red muscle	0·044[5]	1·45	0·957	0·692[6]	1·4
Tuna white muscle	0·048[5]	1·29	0·923	—	—

References: [1]Stevens & Fry (1974); [2]Beamish (1964); [3]Stevens & Fry (1970); [4]Job (1969); [5]Neill *et al.* (1975); [6]Stevens (1972).

Table 5. *Total heat loss and fraction of heat lost at gills of sea raven in sea water at 5 °C when ambient temperature is not changing*

Fish	Weight (kg)	Heat fraction lost at gills	Gill blood flow (ml/min)	Excess temp. venous blood (°C)	Heat lost at gills (cal/min)	Total heat lost (cal/min)	% of heat loss at gills
1	2·6	0·87	10	0·050	0·400	1·80	22
2	1·55	0·80	9·7	0·048	0·343	1·19	29
3	1·22	0·91	2·5	0·055	0·115	0·978	12
4	2·72	0·91	3·9	0·045	0·147	1·86	8

tuna are in closer agreement and this is because both heat exchange and oxygen uptake were obtained from fish restrained in a similar manner and because of the higher excess temperatures.

Proportion of heat transfer by the gills

It is often stated that one of the reasons for fish not having high excess temperatures is because they use water for their respiratory medium and because of their pattern of circulation lose most of their metabolic heat at the gills. By combining the data on heat loss at the gills and metabolic rate, it is possible to estimate what fraction of aerobic metabolic heat produced is lost through the gills (Table 5). In steady-state conditions heat gain must equal heat loss. Assuming that during routine activity all heat is produced aerobically, then total heat loss was calculated from oxygen uptake using an oxycalorific equivalent of 3·20 cal/mg O_2. Heat lost at the gills was calculated by the following:

$$HL \text{ (gills)} = f \times s \times \dot{Q} \times Tx,$$

where f = fraction of heat lost as blood passes through the gills, s = heat capacity of blood = 0·92 cal/ml (Mendlowitz, 1948), $\dot{Q}$ = cardiac output = gill blood flow (ml/min), and Tx = measured excess temperature in ventral aorta. These calculations are summarized in Table 5. In the sea raven only 8–29 % of heat loss was via the gills, the balance was lost through the body wall and fins. It is clear, then, that most of the heat lost through the body wall and fins. One might thus reasonably ask why fish have not evolved an insulative layer of fat under the skin as have marine mammals to

decrease heat loss and increase body temperature. Insulation of this type wouldᶜ however, be of little advantage, because an elevated body temperature would only increase the driving gradient and result in a larger amount of heat lost at the gills (see equation 1). The data for the sea raven (Table 5), shows that if the excess temperature of the venous blood increased to only 0·6 °C then it would be enough to account for all heat loss. The few fish that are warm-bodied (some tunas and pelagic sharks) reduce heat loss by elaborating massive vascular counter-current heat exchangers that reduce the temperature excess of the blood in the ventral aorta, and not with subcutaneous fat insulation (Stevens, Lam & Kendall, 1974; Carey, 1973).

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