

SOME ASPECTS OF GAS EXCHANGE IN TUNA*

By E. D. STEVENS

Department of Zoology, University of Hawaii, Honolulu, Hi 96822

(Received 6 December 1971)

INTRODUCTION

In a recent paper Brown & Muir (1970) analysed the function of tuna gills from a theoretical viewpoint. Their analysis was based on Muir's work on the anatomy of tuna gills (Muir, 1969; Muir & Hughes, 1969; Muir & Kendall, 1968), and some assumptions on the physiology of tuna. In the present paper an attempt is made to relate some measurements of the variables affecting respiration to the theoretical analysis by Brown and Muir. I have measured the amount of water passing over the gills, the fraction of oxygen removed from the water, and the drop in hydrostatic pressure as water passes over the gills. These data were used to calculate oxygen uptake and the resistance the gills offer to water flow. In addition, I have measured the partial pressure of oxygen in blood afferent and efferent to the gills and have used this information to calculate effectiveness of gas transfer using the equations derived by Randall, Holeton & Stevens (1967).

SYMBOLS

- \dot{V}_{O_2} = oxygen uptake;
 \dot{V}_g = quantity of water perfusing the gills, ventilation volume;
 U = utilization, fraction of oxygen removed from the water;
 R = resistance to water flow offered by the gills and the opercular slit;
 HL = head loss, drop in water pressure between entry and exit at the gills;
 C_t = concentration of oxygen in water entering gills;
 C_e = concentration of oxygen in water leaving gills;
 P_a = partial pressure of oxygen in arterial blood;
 P_v = partial pressure of oxygen in venous blood;
 P_t = partial pressure of oxygen in water entering gills;
 P_e = partial pressure of oxygen in water leaving the gills.

The above variables are related in the following ways:

$$U = (C_t - C_e)/C_t, \quad (1)$$

$$\dot{V}_{O_2} = \dot{V}_g (C_t - C_e). \quad (2)$$

Equations (1) and (2) can be combined to show the relationship between oxygen uptake, gill water flow, and utilization:

$$\dot{V}_{O_2} = \dot{V}_g U C_t. \quad (3)$$

Thus, oxygen uptake may be increased by increasing either gill water flow or utilization, provided that utilization is less than 1.0. Experimentally, C_t is usually maintained near saturation.

* Supported by PHS Grant No. HE 12608.

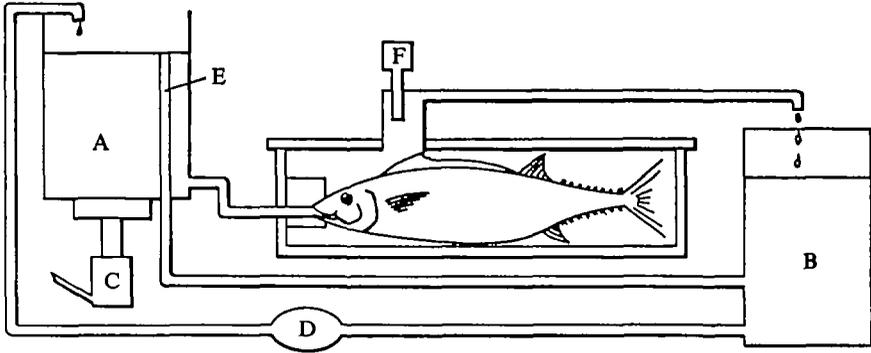


Fig. 1. The apparatus used to measure oxygen uptake and utilization in tuna. (A) Input reservoir; (B) return reservoir; (C) hydraulic jack to change level of input reservoir; (D) pump to return water to input reservoir; (E) overflow drain; (F) oxygen electrode.

A discussion of water flow is greatly facilitated by use of the concept of 'resistance to flow'. This is simply the ratio of the driving force, that is the pressure drop across the gills, to the flow rate across the gills. The relationship is more useful if stated in the following form:

$$\dot{V}_o = HL/R. \quad (4)$$

In these experiments resistance is the sum of the resistance to flow offered by the gills and that offered by the opercular slit. The fish are perfused in such a way that they cannot adjust the resistance by changing the gape of the mouth. The contribution of kinetic energy to HL is negligible at the velocities with which we are concerned (Brown & Muir, 1970). Thus, changes in gill water flow are going to be associated with changes in the pressure drop across the gills, or changes in resistance, or both. Simultaneous measurements of gill water flow and head loss permit the calculation of resistance. Thus, we should be able to answer these questions: can tuna change the resistance to water flow; if so, under what conditions will they change it, and what effects will the change in resistance have on oxygen uptake and utilization?

MATERIALS AND METHODS

Skipjack tuna (*Katsuwonus pelamis*) and kawakawa tuna (*Euthynnus affinis*) were caught in Hawaiian waters by barbless hook and pole while 'chumming' with live bait after the fashion used by commercial fishermen. Fish were placed in 600-gallon transfer tanks and then into large holding tanks (24 ft diameter) at the Kewalo Basin Laboratory of the National Marine Fisheries Service. The methods of capture and handling have been described elsewhere (Nakamura, 1962). Captive tuna were fed on frozen herring twice daily.

A. Restrained tuna

In order to measure oxygen uptake and utilization a fish was placed in a box which allowed perfusion of the gills and at the same time permitted separation of incoming and exhaled water by a rubber membrane (Fig. 1). Perfusion pressure could be changed by changing the level of the input reservoir. Water flow was measured with a graduated cylinder and a stopwatch. The system was a recirculating one of 40 l capacity and contained a very low concentration of MS 222 (1:30,000) to reduce

struggling. The water in the reservoir was vigorously aerated so that P_{O_2} of the inhaled water was always greater than 120 mmHg. Water temperature varied from 23 to 25 °C between experiments, but did not vary more than 0.3 °C in any one trial.

The pressure drop across the gills was measured with a Sanborn differential pressure transducer (model 268B) and recorded on a Sanborn pen recorder (model 321). The transducer was calibrated with a water column. The pressure cannulae were polyethylene tubing (Clay-Adams 240). One cannula was placed in the perfusion tube going into the mouth, the other was placed in the box adjacent to the operculum at the same level.

In some cases, heart rate and relative blood flow were measured by placing a transcutaneous doppler flowmeter (Parks Electronics, model 803) over the ventral aorta.

In a separate group of eight fish the partial pressure of oxygen in the blood was measured. A fish was placed in the box described above but the system was left open so that blood samples could be taken by syringe from the heart (mixed venous blood), coronary artery, and dorsal aorta. The partial pressure of oxygen was measured on small blood samples polarographically with a Radiometer blood-gas analyser.

B. *Free-swimming tuna*

In a separate experiment utilization was measured in 11 small (about 1 kg) free-swimming tuna. A fish was caught from the large holding tank, a cannula was inserted through one opercular opening, and then the fish was placed in a 600-gallon transfer tank. The operation took about 1 min, and the gills were perfused with sea water during that time. The cannula was polyethylene (Clay-Adams, PE 240) and 1 m long. Samples of exhaled water were periodically taken by slowly drawing water into a syringe from the free end of the cannula while the tuna was swimming freely in the tank. The partial pressure of oxygen was determined with an oxygen electrode (Radiometer, model PHM 71). Water temperature was 23.8 °C.

In both experiments the oxygen concentration or partial pressure was measured in the ambient water between every measurement of exhaled water.

RESULTS

A. *Restrained tuna*

Perfusion rate, head loss, resistance to water flow, oxygen uptake, and utilization data for seven tuna appear in Table 1. The number of measurements and the duration between measurements varied for each fish. The mean value is not weighted for the number of observations on each fish, but rather is the mean of the mean values for each fish. Note especially that the resistance to gill water flow was not constant for any one fish, but varied depending on other conditions. Under the conditions of the present experiment, changes in resistance to water flow appeared to be due solely to changes in the opercular slit.

A plot of the changes in these variables with time for two tuna is shown in Fig. 2. In fish S2 gill flow tended to remain constant whereas in S3 it was quite variable. In spite of the relative constancy of gill flow in S2, oxygen uptake and utilization both fluctuated markedly. Because changes in gill flow were small, changes in oxygen uptake and utilization tended to be similar both in direction and magnitude. In con-

Table 1. *Perfusion rate of gills, head loss, resistance to water flow offered by the gills (calculated), oxygen uptake, and utilization (calculated) for seven skipjack tuna and one kawakawa tuna (S4)*

Fish	Weight kg	<i>n</i>	\dot{V}_g, \bar{x} (range) (l/min.kg)	HL, \bar{x} (cm water)	R, \bar{x} (range) (cm water.min.kg/l)	\dot{V}_{O_2}, \bar{x} (range) (mg/h.kg)	Utilization \bar{x} (range)
S1	1.60	2	3.05 (3.00-3.09)	2.3	0.77 (0.75-0.77)	1005 (990-1020)	0.82 (0.82-0.82)
S2	1.53	8	3.27 (3.08-3.48)	2.2	0.68 (0.60-0.78)	563 (327-683)	0.47 (0.26-0.64)
S3	1.51	11	2.45 (1.89-3.18)	1.3	0.54 (0.24-0.84)	695 (556-888)	0.84 (0.79-0.91)
S5	1.47	8	2.76 (2.44-3.14)	2.1	0.76 (0.63-0.95)	534 (396-613)	0.54 (0.44-0.67)
S6	1.55	7	2.70 (2.22-2.70)	1.3	0.49 (0.34-0.77)	587 (493-665)	0.65 (0.53-0.85)
S7	1.74	6	2.54 (1.95-2.54)	2.0	0.80 (0.73-1.03)	767 (514-879)	0.94 (0.83-1.00)
Av.			2.80	1.9	0.67	692	0.71
S4	2.26	3	1.77 (1.55-1.88)	1.8	1.03 (0.90-1.29)	503 (400-643)	0.79 (0.69-0.95)

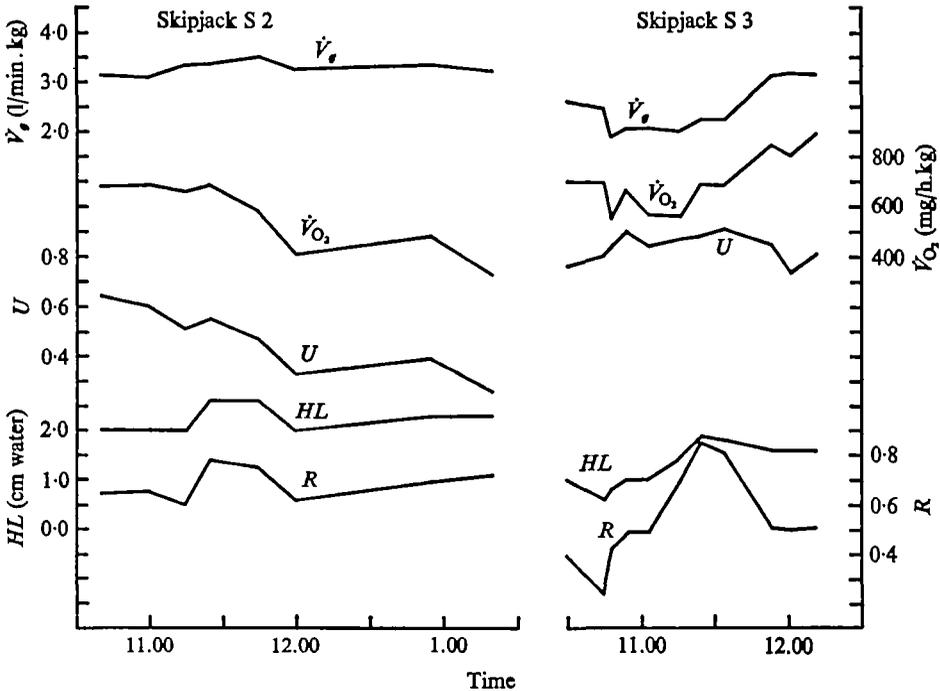


Fig. 2. Changes in perfusion rate, oxygen uptake, utilization, head loss, and resistance to water flow in two tuna while in the perfusion apparatus. Scales are the same for both fish.

trast, fish S3 showed changes in oxygen uptake in the same direction as those of gill flow, but changes in utilization were small and in either direction. The data from these two fish serve to illustrate the fact that there is much variation in the five variables between individual fish, and that the relationship between changes in the variables is different in different individuals.

Table 2. A correlation matrix of the levels of the five variables

(Data is from 41 observations on six skipjack tuna. $t_{0.5} = 0.30$; $t_{0.1} = 0.39$. (** indicates significant correlation).)

	\dot{V}_g	\dot{V}_{O_2}	U	HL	R
\dot{V}_g	1	0.13	-0.58**	0.46**	-0.12
\dot{V}_{O_2}	—	1	0.67**	0.06	0.02
U	—	—	1	-0.30	0.03
HL	—	—	—	1	0.82**
R	—	—	—	—	1

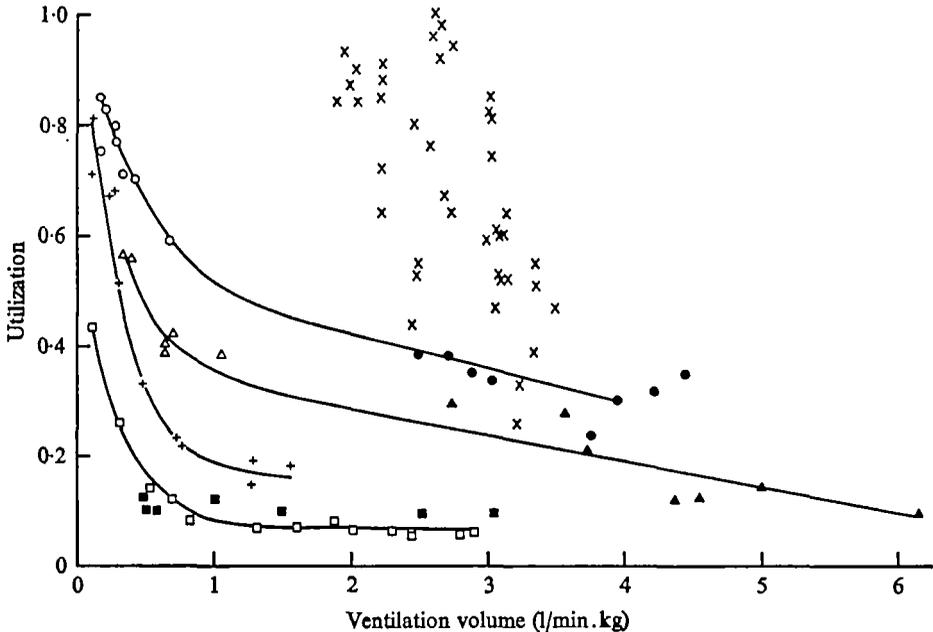


Fig. 3. Relationship between utilization and gill flow rate in several teleosts. x, Tuna perfused in the present study; □, trout perfused (Davis & Cameron, 1970); ■, trout during forced swimming activity (Stevens & Randall, 1967); ○, carp during hypoxia; ●, carp during forced swimming activity; △, sucker during hypoxia; ▲, sucker during forced swimming activity (Saunders, 1962); +, dogfish perfused (Hughes & Umezawa, 1968a).

(1) Relationships between perfusion rate, head loss, resistance to water flow, oxygen uptake, and utilization

The results of a correlation analysis between the five variables appear in Table 2. The highest correlation coefficient occurs between resistance and head loss. This indicates a relationship between fish and not within fish. Because mean gill flow is about the same from fish to fish, then in fish with a high head loss resistance to water flow must also be high, and in fish with a low head loss the resistance to water flow must be low (see equation (4)). Similarly, oxygen uptake and utilization are positively correlated. This also is due in part to the relationship between fish. That is, because mean gill flow is about the same from fish to fish, then in fish with a high oxygen uptake there is positive correlation between utilization and oxygen uptake within five out of six fish tested, as well as between individual fish. Fish S2 in Fig. 2 illustrates the relationship, fish S3 was the exception to the rule.

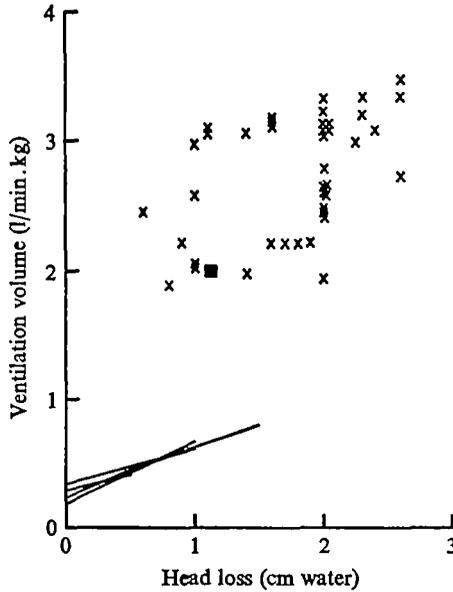


Fig. 4. Relationship between ventilation volume and pressure head loss. \times , Tuna perfused in the present study, lines are data for the dragonet (Hughes & Umezawa, 1968b); \blacksquare , value assumed by Brown & Muir (1970) in their analysis.

Table 3a. Relationship between changes in variables associated with either an increased or decreased gill flow

(+ denotes an increase, - a decrease. Data taken from six skipjack tuna. For example, in the first line an increase in \dot{V}_g was associated with an increase in both HL and R, but HL increased more than did R.)

Relative change in the ratio	No. of cases observed	
	HL/R	\dot{V}_{O_2}/UC_t
Associated with an increase in \dot{V}_g		
+/+	5	5
+/o	o	1
+/-	o	1
o/-	6	o
-/-	3	7
Associated with a decrease in \dot{V}_g		
-/-	3	5
-/o	o	o
-/+	o	4
o/+	6	1
+/+	2	2

Table 3b. Relationship between changes in variables when there was no change in gill water flow

(The other four possible combinations of changes did not occur.)

HL/R	\dot{V}_{O_2}/UC_t	No. of cases
+/+	+/+	2
o/o	+/+	2
-/-	-/-	2
o/o	-/-	4

Of more biological significance is the observation that head loss and utilization were negatively correlated, and that gill water flow and utilization were negatively correlated (Fig. 3). That is, high utilizations tended to be associated with low gill flow levels but high oxygen uptake levels, and low utilizations tended to be associated with high gill flow levels but low oxygen uptake levels. A high negative correlation between gill flow and utilization was found only in two skipjack (S₃ and S₆).

(2) *Relationships between changes in perfusion rate, head loss, resistance to water flow, oxygen uptake, and utilization*

In an attempt to elucidate causal relationships between the variables, relationships between changes in the variables were plotted. It is obvious from equation (3) that changes in gill flow may be associated with either changes in head loss, changes in resistance, or changes in both; and from equation (4) that they may also be associated with changes in oxygen uptake, utilization, or both. Each of the possible changes and the number of times that they occurred is summarized in Table 3.

An increased gill flow was more often due to a decrease in resistance than an increase in head loss. A decreased gill flow was more often due to an increase in resistance than a decrease in head loss. That is, there was a tendency for resistance to change and for head loss to remain constant during changes in gill perfusion rate.

An increased gill flow was associated with an increased oxygen uptake just as many times as it was associated with a decreased utilization. A decreased gill flow was associated with an increased oxygen uptake almost as often as it was associated with a decreased utilization. That is, there was no tendency for either oxygen uptake or utilization to remain constant during changes in gill perfusion rate.

Often the ratios of HL/R and \dot{V}_{O_2}/UC_t would change in the same direction and magnitude, that is, the changes were not associated with any change in gill flow (see Table 3*b*). In these situations an increased ratio of HL/R was always associated with an increased ratio of \dot{V}_{O_2}/UC_t . However, the ratio of \dot{V}_{O_2}/UC_t increased or decreased six times with no change in the ratio HL/R or in gill flow.

(3) *Relationships between resistance and utilization*

Intuitively one might expect to find relationships between changes in resistance to water flow and in utilization. That is, the fish might reduce the size of the opercular slit to decrease water velocity and thus increase utilization.

There was no relationship between resistance and utilization between the different fish. That is, the correlation coefficient was not significant using mean values from each fish. However, there was a significant positive correlation between resistance and utilization within three individual fish (S₃, S₅, S₆) but no correlation for three fish (S₂, S₄, S₇).

The relationship between changes in resistance and changes in utilization seem appropriate only in some cases. Changes in the two variables were in the same direction (i.e. both increase or both decrease) in fish S₂ (6 out of 7 times), S₃ (8 out of 10), and S₆ (4 out of 6). The four cases in which resistance and utilization did not change in the same direction in the above fish were all associated with changes during a decrease in gill water flow, never an increase. In the other tuna, the relationship did not hold: S₅ (3 out of 7) and S₇ (1 out of 5).

Table 4. *Heart rate of tuna immediately after being placed in perfusion apparatus, and during the experiment*

Fish	Initial decrease	During experiment after initial decrease	
		\bar{x}	(n)
S1	None measured	58	2
S2	168 to 92 in 30 min	80	5
S3	131 to 46 in 30 min	46	11
S4	None measured	51	2
S5	None measured	142	3
S6	None measured	63	2
S7	93 to 56 in 15 min	50	2
Mean		70	—

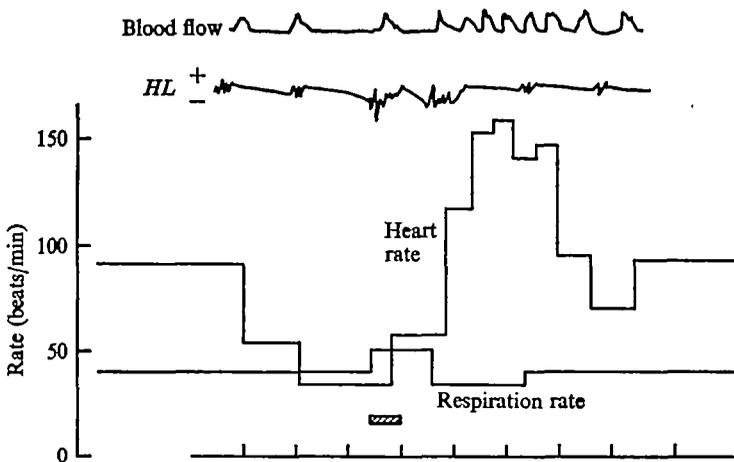


Fig. 5. Changes in heart rate and respiration rate in a tuna during a 'cough'. The shaded bar indicates the 'cough'. The upper trace is the blood velocity in the ventral aorta, the lower trace is head loss or differential water pressure across the gills. Time marks are one second apart. Heart rate and respiratory rate were calculated from beat-to-beat intervals.

(4) *Respiratory rhythm and heart rate*

Under the conditions of the present experiment four of the tuna exhibited a respiratory rhythm in that there were rhythmic changes in head loss. From visual observations it was apparent that these changes were due to rhythmic movements of the opercula. The rate in skipjack tuna varied from 52 to 63/min (S1), from 41 to 46/min (S2), and from 21 to 27/min (S7). In the kawakawa tuna the rate was 10–11/min with relatively large excursions in head loss (1.1–2.3 cm water). Rhythmic fluctuations in head loss were not observed in the other fish (S3, S5, S6).

Results of heart-rate measurements appear in Table 4. Heart rate was extremely elevated immediately after a fish was placed in the apparatus but decreased to a constant level in about 30 min. Thereafter heart rate tended to remain constant throughout the experiment in spite of changes in the other variables. In some cases the experiment was terminated because of an irregular heart rate. If the oxygen content in the inhaled water was decreased, a marked bradycardia rapidly ensued; heart rate returned to previous levels when the oxygen level was restored. The bradycardia reflex was also

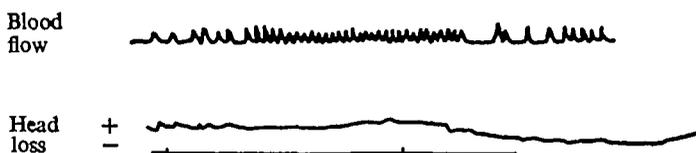


Fig. 6. Relationship between blood flow in the ventral aorta and slow waves in head loss. Time marks are 15 sec apart.

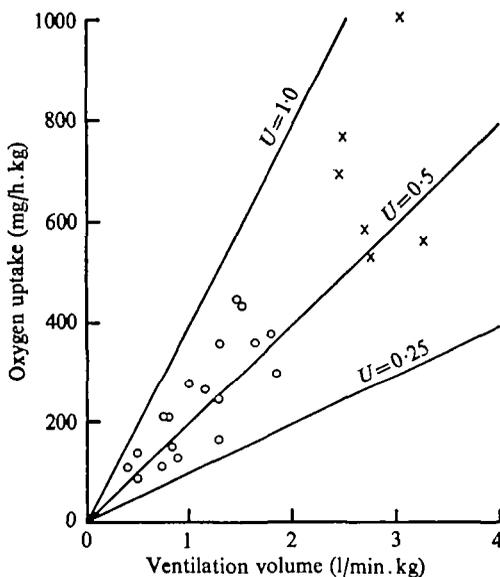


Fig. 7. Relationship between oxygen uptake and ventilation volume in perfused tuna. Three utilizations lines are drawn: 1.0, 0.5, and 0.25. x, Mean values taken from Table 1; o, individual values taken from eight skipjack tuna; these animals did not survive long, presumably because the perfusion rate was too low.

Table 5. Utilization in 11 free-swimming skipjack tuna

Fish	n	Utilization	
		\bar{x}	Range
Q2	1	0.43	—
Q3	4	0.74	0.70-0.78
Q4	5	0.64	0.54-0.76
Q5	4	0.48	0.45-0.51
Q6	5	0.46	0.42-0.53
Q7	4	0.45	0.40-0.53
Q9	4	0.52	0.45-0.60
Q11	5	0.59	0.57-0.62
Q12	5	0.55	0.38-0.69
Q13	2	0.57	0.47-0.67
Q14	5	0.75	0.71-0.78
Mean		0.56	0.50-0.63

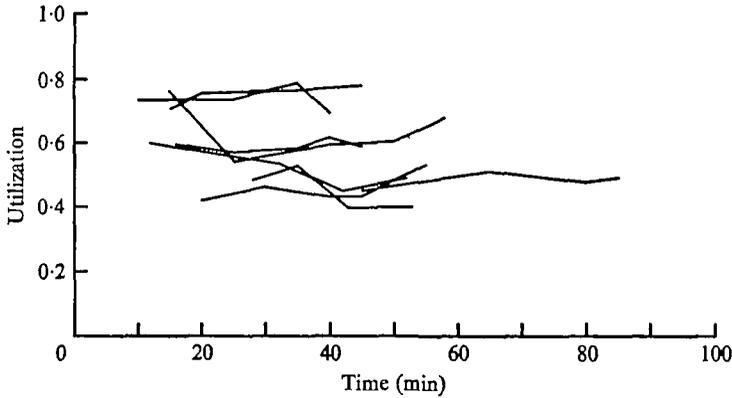


Fig. 8. Oxygen utilization in free-swimming skipjack tuna.

initiated if gill water flow was inadvertently decreased too much. In two skipjack there was often synchrony between heart rate and respiratory rate. In tuna S₁ the relationship was 1 heart beat : 1 respiratory movement, but in S₂ it was 2 : 1. Head loss tended to decrease rapidly during the decrease in blood velocity in the ventral aorta, and then gradually to increase as the blood flowed through the gills. All fish occasionally showed a change in the head-loss level which is usually referred to as a cough. Heart rate tended to decrease immediately before a cough and then to increase for a short period after (Fig. 5).

Fish S₄ showed unusual slow changes in head loss with a period of about 1 min which did not resemble a cough. Heart rate increased markedly (to about 140/min) when head loss increased, and decreased (to about 80/min) when head loss decreased (Fig. 6).

(5) *Partial pressure of oxygen in blood*

The partial pressure of oxygen in ventral aortic blood was 31.8 ± 2.08 mmHg (mean + s.e.). The partial pressure of oxygen in dorsal aortic blood was 90.0 ± 11.17 mmHg. The blood in the coronary artery was sampled in three fish only; the average partial pressure of oxygen was 50 mmHg. Haematocrits were determined for six samples and were $41.0 \pm 3.45\%$ cells.

B. *Utilization in free-swimming tuna*

Utilization values for 11 skipjack tuna are given in Table 5. Mean utilization was 0.56 compared to 0.71 for the perfused fish. Utilization tended to remain relatively constant throughout the observation period (Fig. 8). The tuna appeared well able to tolerate the operative procedure and the cannula; most survived when returned to the holding tanks.

DISCUSSION

At the outset of this experiment it was hoped that some insight into the regulation of the respiratory system of tuna might be gained by changing one or more variables and observing how the others change in response to the controlled variable. However, it appears that the fish can change gill resistance and thus effect changes in gill flow in spite of the experimenter's changes in input pressure; and in addition it can

Table 6. *A comparison of the data collected in the present experiment on perfused tuna with the theoretical predictions of Brown & Muir (1970)*

Fish	\dot{V}_g (ml/sec.kg)	Head loss (dynes/cm ²)	Resistance (dynes sec/cm ²)
S1	50.8	2351	46.3
S2	54.5	2250	41.3
S3	40.8	1312	32.2
S5	40.6	2109	51.9
S6	45.0	1271	28.2
S7	42.3	2018	47.7
Average	45.7	1885	41.3
Brown & Muir	33.5	1100	32.8
Kawakawa	29.5	1816	61.6

change utilization and oxygen uptake. If the input pressure is lowered then gill flow and oxygen uptake are reduced. Under these conditions it is possible to demonstrate a positive correlation between gill flow and oxygen uptake (Fig. 7). However, tuna die quickly at reduced gill flow rates. None of the fish in Fig. 7 with gill flows less than 2 l/min.kg survived an hour, whereas those with higher gill flow rates were still alive (i.e. heart rate and oxygen uptake unchanged) after being perfused for 4 h. A positive correlation between oxygen uptake and ventilation volume has been demonstrated in many other fish, especially during activity.

The absolute value for gill flow is very high when compared to that of other workers for fish under similar conditions. Recent reviews (Shelton, 1970; Davis & Cameron, 1970) list only three values higher than those observed in the present study, and those three were elicited either by an increase in oxygen demand (forced activity) or by a decrease in oxygen supply, both of which stimulate ventilation markedly.

What is much more striking is the fact that tuna are able to maintain a high utilization even at very high gill flow rates (Fig. 3). Tuna can extract 50% of the oxygen from the water at gill flow rates about four times as high as other fishes. It is likely that utilization is even higher under natural conditions since the perfusion tube alters the flow pattern of the water during entry (Davis & Cameron, 1970). The structure of the tuna gill is suited to high utilization levels at high flow rates. The area of the gills is much greater than that of other teleosts and approaches the lung area of terrestrial mammals (Muir, 1969). The total gill areas for the fish used in Fig. 3 were extrapolated from Muir (1969) for fish weighing 1 kg; the relative areas are: skipjack tuna 18,000, trout 2200, carp 1200, and sucker 600 cm². Trout have a lower utilization at any particular gill flow rate than either carp or sucker in spite of the fact that trout have the larger gill area. In addition to their large surface area, tuna gills have the secondary lamellae of adjacent gill filaments fused. This fusion prevents the filaments from being forced apart at high flow rates and thus permits a high utilization. It is likely that the high utilization is also associated with adaptations in the circulatory side of the system, for example a high cardiac output and a high blood oxygen capacity.

The head loss as water passes through the gills is 70% higher than predicted by Brown & Muir (Table 6). It varied considerably between fish but none had a mean level as low as that predicted. That is, the gills offer more resistance to water flow than expected on theoretical grounds alone. This difference is due largely to the fact

that the flow rates in the present study were higher than those used by Brown & Muir. However, substituting the average value of flow rate observed in the present study into their theoretical equations yields a value for head loss of 1833 dynes/cm², which is almost identical to that observed in the present study (1885 dynes/cm²). The discrepancy is small compared to the large difference in resistance values of other fish. The resistance to flow in the dragonet is almost four times that of the tuna (Fig. 4). One is even more impressed when one realizes that the exchange area of the tuna gill is about 17 times that of the dragonet (Muir, 1969). Variations in the resistance to gill water flow have been reported for other fishes (Hughes & Shelton, 1958, 1962; Hughes & Umezawa, 1968).

The absolute value of oxygen uptake is much higher than in any other resting or perfused fish. It is more than twice as high as standard oxygen uptake of man, and is higher than most values of oxygen uptake during maximum sustained swimming in other fish at the same temperature (Brett, 1964; Beamish & Moorkherji, 1964). Clearly it is not a 'resting' oxygen uptake. However, it was found that in order to keep the animal alive it was necessary to perfuse at high gill flow rates and that high gill flow rates either caused or were associated with high oxygen uptake values.

There was tendency for gill perfusion rate to change due to changes in resistance so that changes in head loss were minimized. Visual observations confirmed that under the conditions of the present study changes in resistance were effected by changes in the size of the opercular slit. Measurements of changes in the size of the opercular slit have not been reported for free-swimming tuna and will be forthcoming only when observations can be made on tuna swimming in a tube or trough. However, mackerel progressively increase mouth gape and opercular slit while maintaining approximately the same swimming speed when the oxygen content of the water is reduced (Brown & Muir, 1970). It may be that scombrids regulate gill water flow by changing mouth gape or the size of the opercular slit under different conditions.

To my knowledge there are no other published measurements of heart rate on tuna. In the present experiment three of six tuna showed a marked decrease (25–65%) in heart rate within 30 min after being placed in the apparatus; the heart rate then became stabilized and remained constant. In three other tuna there was no initial decrease in rate, two had low rates to begin with and the other rate remained high throughout the experiment. The high initial heart rates are the highest recorded for any fish of any size under any condition. The heart rate of teleosts is influenced most by the level of vagal tone and temperature. The large variation in heart rates between fish during the experiment (46–142 beats/min) probably is due to differences in vagal tone. The mean heart rate during the experiment was 70 beats/min; this too is very high compared to heart rates of other teleosts. The very high oxygen uptake levels of tuna require that the circulatory system have a high oxygen transport capacity in order to extract oxygen from the water. The high heart rates of tuna in the perfusion apparatus are probably indicative of a high cardiac output relative to other teleosts. Experiments in which other teleosts have been perfused did not elevate heart rate above that of free-swimming fish when they were restrained (Davis & Cameron, 1970; Hughes & Umezawa, 1968b).

The bradycardia which occurs after a decrease in the ambient oxygen level is similar to that described for other teleosts. Heart rate gradually decreases as oxygen

Concentration in the inhaled water decreases, and returns to normal very quickly after the oxygen level returns to normal. The bradycardia is due to a marked increase in vagal tone (Randall, 1970). The oxygen-sensitive receptor may be located in either the buccal cavity or on the gills (Randall & Smith, 1967; Hughes & Umezawa, 1968*b*) or in the arterial blood stream (Laurent, 1967). Since in the present experiments the bradycardia occurred in response to decreased gill flow rates as well as to hypoxia, it is likely that at least in tuna the oxygen receptor is in the arterial blood stream.

Synchrony occurred in two of the six skipjack in which heart rate was examined. Thus, as in all other teleosts examined, there is coupling between the circulatory and respiratory systems. It has been suggested for other fish that this coupling facilitates oxygen transfer (Satchell, 1961). It is possible that tuna alter the flow pattern of water across the gills rhythmically and that this is coordinated with the blood flow through the gills under certain environmental conditions in order to facilitate gas transfer. Cardiorespiratory coupling was evident in all tuna examined when they 'coughed' (Fig. 5). The decrease in heart rate always occurred prior to the cough and may facilitate flushing of the gills by reducing the hydrostatic blood pressure within them. The increase in heart rate following the cough indicates the possible influence of an oxygen receptor in the arterial blood stream responding to the decreased blood flow.

The partial pressure of oxygen in the blood of tuna is similar to values reported for other fish (for references see Randall, 1970). These data were used to calculate the effectiveness of oxygen removal from the water:

$$\text{effectiveness of O}_2 \text{ removal} = U [P_i / (P_i - P_v)] = 90\% \text{ for tuna.} \quad (5)$$

Values for other fish from the literature range from 10 to 30% (Randall, 1970); the value for man is about 33%. The very high value for tuna stresses the great efficiency of the tuna gill in removing oxygen from the water.

The transfer factor is the most suitable estimate of the capacity of the gills to transfer oxygen (Randall, 1970). It is a measure of the ability of the gas-exchange apparatus to transfer gas per unit gradient:

$$T_{O_2} = \dot{V}_{O_2} / [\frac{1}{2}(P_i + P_e) - \frac{1}{2}(P_a + P_v)]. \quad (6)$$

The transfer factor of oxygen for tuna is 0.12 ml/min.kg.mmHg. This value is compared to that for other fish and mammals in Table 7. The transfer factor of oxygen in tuna is much greater than that for other fish, it is about twice that for resting man, but is slightly less than that of mammals of equivalent weight. The extraordinary high transfer factor for oxygen suggests that there probably is a high transfer factor for water and ions also. It is likely that tuna also have an especially well-developed system to handle the osmotic and ionic stresses imposed by the large transfer factor.

Saito (1953) related haematocrit values to haemoglobin concentrations for skipjack tuna blood. The haematocrit determined in the present study (41% cells) is equivalent to 11.93 g haemoglobin/100 ml blood, which is equivalent to an oxygen capacity of 16 vol%. Although the actual blood-gas contents were not determined in the present study, it is likely that the arterial blood was saturated with oxygen, based on dissociation curves for other tunas (F. Carey, personal communication). Calculation of cardiac output by the Fick principle reveals that the minimum cardiac output of skipjack tuna in the present experiments is 50 ml/min.kg (i.e. assuming complete

Table 7. Calculation of transfer factor for oxygen and comparison of tuna data with those of other fish and mammals (trout and man, Randall, Holeton & Stevens 1967; dogfish, Püper & Baumgarten-Schumann 1968)

	Resting trout	Swimming trout	Dogfish	Tuna	Cat	Man
\dot{V}_{O_2} (ml/min.kg)	0.425	2.18	0.67	8.07	10	3.57
P_{i,O_2} (mmHg)	134	134	149	153	—	159
P_{e,O_2}	121	121	57	109	—	120
P_{a,O_2}	85	78	49	90	—	95
P_{v,O_2}	19	16	10	32	—	40
Gradient (mmHg)	75.5	80.5	73.5	70	75	72
T_{O_2} (ml/min.kg.mmHg)	0.0056	0.027	0.009	0.115	0.13	0.05

oxygen extraction), and that a realistic figure is 80 ml/min.kg or about the same as that of resting man.

Mean utilization was 0.56 for the free-swimming fish compared to 0.71 for the perfused tuna. In a similar study on trout (Davis & Cameron, 1970), mean utilization was 0.46 for free-swimming trout and 0.44 for the perfused fish. Davis & Watters (1970) have criticized the opercular catheterization method and have shown that it yields values which are much more variable than those obtained by direct methods and tend to yield slightly lower values. It is possible that my measurements of utilization in free-swimming tuna are underestimates of actual utilization. If this is the case then one cannot be but even more impressed with the ability of these animals to extract oxygen from the water at high gill flow rates.

SUMMARY

1. Some aspects of gas exchange in restrained skipjack tuna were analysed.
2. The average rate at which water flowed over the gills was 2.8 l/min.kg.
3. The concentration of oxygen in water entering and leaving the gills was measured and used to calculate oxygen uptake (692 mg/h.kg) and utilization (0.71).
4. The drop in hydrostatic pressure as water flowed over the gills was 1.9 cm water and agrees favourably with theoretical predictions.
5. The partial pressure of oxygen was measured in blood afferent and efferent to the gills and used to calculate effectiveness of oxygen removal from the water (90%) and the transfer factor for oxygen (0.12 ml/min.kg.mmHg).
6. The average utilization measured in free-swimming tuna was 0.56.
7. The extraordinary ability of tuna to efficiently extract oxygen from the water at high gill water flow rates is discussed.

This study could not have been carried out without the continued assistance of the staff of the National Marine Fisheries Service in obtaining and maintaining tuna at their Kewalo Basin Laboratory. I would like especially to thank Dr Frank Hester and Mr Reg Gooding of N.M.F.S. Drs B. S. Muir, D. J. Randall, J. C. Davis, and Jim Cameron gave many useful criticisms of the manuscript.

REFERENCES

- BEAMISH, F. W. H. & MOORKHERJII, P. S. (1964). Respiration of fishes with special emphasis on standard oxygen consumption. *Can. J. Zool.* **42**, 161-75.
- BRETT, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Can.* **21**, 1183-226.
- BROWN, C. E. & MUIR, B. S. (1970). Analysis of ram ventilation of fish gills with application to skipjack tuna (*Katsuwonus pelamis*). *J. Fish. Res. Bd. Can.* **27**, 1637-52.
- DAVIS, J. C. & CAMERON, J. N. (1970). Water flow and gas exchange at the gills of rainbow trout, *Salmo gairdneri*. *J. exp. Biol.* **54**, 1-18.
- DAVIS, J. C. & WATTERS, K. (1970). Evaluation of opercular catheterization as a method of sampling water expired by fish. *J. Fish. Res. Bd. Can.* **27**, 1627-35.
- HUGHES, G. M. & SHELTON, G. (1958). The mechanism of gill ventilation in three fresh-water teleosts. *J. exp. Biol.* **35**, 807-23.
- HUGHES, G. M. & SHELTON, G. (1962). Respiratory mechanisms and their nervous control in fish. *Adv. Comp. Physiol. Biochem.* **1**, 275-364.
- HUGHES, G. M. & UMEZAWA, S. (1968a). Oxygen consumption and gill water flow in the dogfish *Scyliorhinus canicula*. *J. exp. Biol.* **49**, 557-64.
- HUGHES, G. M. & UMEZAWA, S. (1968b). On respiration in the dragonet *Callionymus lyra*. *J. exp. Biol.* **49**, 565-82.
- LAURENT, P. (1967). La pseudobranchie des téléostéens. *C. r. hebd. Séanc. Acad. Sci., Paris* **264**, 1879-82.
- MUIR, B. S. (1969). Gill dimensions as a function of fish size. *J. Fish. Res. Bd. Can.* **26**, 165-70.
- MUIR, B. S. & HUGHES, G. M. (1969). Gill dimensions for three species of tunny. *J. exp. Biol.* **51**, 271-85.
- MUIR, B. S. & KENDALL, J. I. (1968). Structural modifications in the gills of tunas and some other oceanic fishes. *Copeia* **1968**, 388-98.
- NAKAMURA, E. (1962). Observations on the behavior of skipjack tuna, *Euthymnus pelamis*, in captivity. *Copeia* **1962**, 499-505.
- PIIPER, J. & BAUMGARTEN-SCHUMANN, D. (1968). The effectiveness of O₂ and CO₂ exchange in the gills of the dogfish. *Resp. Physiol.* **5**, 338-49.
- RANDALL, D. J. (1970). Gas exchange in fish. In *Fish Physiology* (eds. W. S. Hoar and D. J. Randall). New York: Academic Press.
- RANDALL, D. J. & SMITH, J. C. (1967). The regulation of cardiac activity of fish in a hypoxic environment. *Physiol. Zool.* **40**, 104-13.
- RANDALL, D. J., HOLETON, G. F. & STEVENS, E. D. (1967). The exchange of oxygen and carbon dioxide across the gills of rainbow trout. *J. Exp. Biol.* **46**, 339-48.
- SAITO, K. (1953). Biochemical studies on fish blood. *Mem. Fac. Fish. Kagoshima Univ.* **3** (1), 132-40.
- SATCHELL, G. H. (1960). The reflex coordination of the heart beat with respiration of the dogfish. *J. exp. Biol.* **37**, 719-31.
- SAUNDERS, R. L. (1962). The irrigation of gills in fishes. *Can. J. Zool.* **40**, 817-62.
- SHELTON, G. (1970). The regulation of breathing. In *Fish Physiology* (eds. W. S. Hoar and D. J. Randall). New York: Academic Press.

