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Organ blood flow haemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre)

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Summary. Metabolic haemodynamic, and organ blood flow measurements were made in tabled, partially anaesthetized albacore *Thunnus alalunga*. Heart rates were 115±9 beats/min: blood pressure 98/75 mm Hg (systolic/diastolic): cardiac output 36.1±5 (ml/min/kg): oxygen consumption 3.4±0.7 (ml O_2/min/kg) and cardiac contractility (dP/dt) 6342±822 mm Hg/s. Organ blood flows were measured with radiolabelled microspheres. The red muscle, kidney, and spleen received the highest flows and the white-muscle the least. There was a flow gradient in the white-muscle with the inner portion near the red-muscle receiving the highest flows. Arterial and venous blood gas measurements showed a reverse temperature effect on arterial PO_2 and a P_{50} of 15.9 Torr corrected to 37° C. Red-muscle temperature was 7° C higher than ambient water temperature. These measurements record the albacore's markedly high cardiovascular capability.

Key words: *Thunnus alalunga* – Oxygen consumption – Blood gases – Organ blood flow haemodynamics

Introduction

There is a paucity of cardiovascular data published for tunas and other scombrid fishes. In this paper we report measurements of cardiac output, quantitative organ blood flow, blood pressures, heart rate, oxygen consumption ($\dot{V}O_2$), blood gases, and core body temperatures for the albacore *(Thunnus alalunga)*. Measurements of organ blood flow, haemodynamics and oxygen consumption have rarely been reported for any fish. The organ blood flow data are also notable in that the only other quantitative measurement published for any fish is for rainbow trout (Neumann et al. 1983). Other blood flow determinations were either derived (Cameron 1975) or estimates of relative distribution (Kent et al. 1973; Stevens 1968).

Albacore are endothermic, and by means of a counter current heat exchanger, maintain their deep muscle temperatures up to 10° C warmer than ambient sea water (Carey and Teal 1966; Graham and Dickson 1981). Albacore are also different from most other teleosts in having a high blood volume (Laurs et al. 1978), high haematocrit (Alexander et al. 1980), high metabolic rate (Graham and Laurs 1982), high cardiac performances (Breisch et al. 1983; Lai et al. 1987), specialized haemoglobin-oxygen dissociation characteristics (Cech et al. 1984), and adaptions for continuous fast swimming (Dotson 1976). The present study was undertaken to determine physiological performance levels of albacore.

Materials and methods

Capture, preparation, heart rate, and blood pressure measurements

Studies were conducted at sea on three research cruises aboard the NOAA R/V David Starr Jordan during September 1978, July 1979, and August 1980. Fish were caught by trolling or by rod-and-reel fishing when the ship was stopped. Immediately after a strike the ship was put out of gear and the fish brought along the side of the ship using a hydraulic reel. A dip net was then

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used to bring the fish on board. The time required to land fish caught by trolling was usually about 1 min and to land fish caught by rod-and-reel was 5–15 min. Once aboard, a running sea water hose was placed in the mouth to irrigate the gills while the fish was immobilized by intracardiac injections of gallamine triethiodide (1–2 mg) and immdiately placed in a holding tank. In four fish, tricaine metasulphonate (MS 222) at a concentration of 25 ppm was used to induce anaesthesia, followed by recirculation of MS 222 at 15 ppm for 30 min. No additional anaesthetics were used, so that by the time the first blood pressure and cardiac output measurements were made, some tail movement had returned. Oxygenated sea water was forced past the gills of all experimental fish at a sufficient rate to maintain arterial PO_2 near 60 Torr as determined by measurement of blood gas concentrations with a IL Blood Gas Analyzer, Model 213. The fish were placed in a lateral position during implantation of catheters and flow transducers. Thereafter, the fish were upright in a normal swimming position and submerged in sea water. Organ blood flows and cardiac output were measured in four fish on the 1978 trip. $\dot{V}O_2$ (7 fish), cardiac output (10 fish), haemodynamic parameters, and blood gas levels (18 fish) were measured on the 1979 trip, and effects of temperatures on blood gases (4 fish) and blood P_{50} (4 fish) were measured on the 1980 trip.

Catheters were implanted by removing a small skin flap over the subcutaneous artery and vein just caudal to the pectoral fin. The catheters were passed cephalad, as far as possible, via cutdowns in both the subcutaneous artery and vein. The venous catheter tip was located at the conjecture of the sinus venous and the atrium. The arterial catheter was advanced to the proximal portion of the dorsal aorta (Fig. 1) near the efferent branchial artery. This catheter was used to measure dorsal aortic blood pressure with a Statham P23DB transducer, remove samples for arterial blood gas determinations, inject tracer-labelled microspheres, and withdraw arterial blood samples for determination of cardiac output by dye dilution. The venous catheter was used to obtain samples for blood gas analysis and the injection of dye for cardiac output determination.

Blood pressure measurements were also made in the ventricle and bulbus arteriosus percutaneously with a 19 gauge needle connected to a Statham P23DB transducer. Heart rates were determined from phasic blood pressure measurements in the ventricle, dorsal aorta, and bulbus arteriosus for periods of up to 2 h after instrumentation. A measure of myocardial contractile function, dP/dt (mm Hg/s) of the heart was measured from the slope of the ventricular pressure traces at paper speeds of 100 mm/s.

Cardiac output measurements

Cardiac output measurements were made with an electromagnetic flowmeter (Biotronix, Model 610) in six fish, by dye dilution in four albacore, and with both methods simultaneously in one fish. Dye dilution was used to measure cardiac output in four fish where organ blood flow was determined. The flow transducers were placed around the ventral aorta which was dissected free just anterior to the bulbus arteriosus. In order to avoid occlusion of the coronary artery, which runs along the ventral aorta, the flow transducer (usually 4 mm internal diameter) was fitted around the vessel with the open key slot over the coronary artery. The dye dilution technique was similar to that used by Murdaugh et al. (1965).

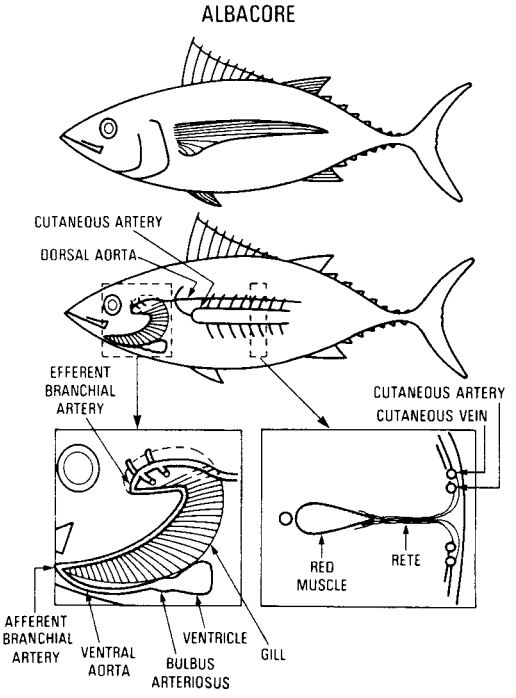

Fig. 1. Relative positions of the cutaneous arteries, veins, retia, heart, dorsal aortic and gills in *Thunnus alalunga*. The *left insert* shows the position of the efferent branchial artery where the tip of the arterial catheter would be positioned. The *right insert* shows the relative position of the red muscle, rete and cutaneous arteries and veins

The dye was injected into the subcutaneous vein and blood was withdrawn from the dorsal aorta. The electromagnetic flow meter technique in fish has been previously described by Johansen (1962).

Organ blood flow measurements

Organ blood flows were determined using tracer-labelled microspheres (^{141}Ce) injected into the dorsal aorta in four albacore showing spontaneous tail movement. Microspheres (15 ± 1 μm in diameter, New England Nuclear, Boston, Mass, USA) were suspended in 10% dextran with a small amount of Tween-80 detergent (0.05%) added to reduce clumping. The accuracy of blood flow measurements determined by microspheres is dependent on having a minimum of several hundred spheres per sample (Heymann et al. 1977). Neumann et al. (1983) found that fish white-muscle is sparsely perfused. We thus injected 2×10^6 microspheres into each albacore to be sure that white-muscle flow estimations could be made.

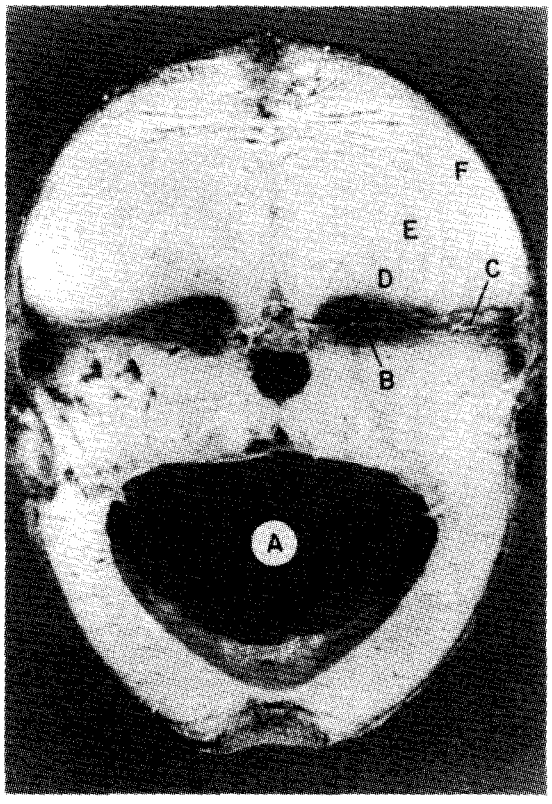

Fig. 2. Relative positions of white- and red-muscle from the midsection of the albacore tuna. *A* body cavity; *B* red-muscle; *C* rete; *D* inner white-muscle; *E* middle white-muscle; *F* outer white-muscle. *D*, *E* and *F* indicate sites of white-muscle sampling for blood flow measurements

The cardiac output and organ blood flow studies were carried out between 30 min and 1 h after the initial instrumentation. At the end of the experiments, the fish were sacrificed and tissue samples of about 20 g were taken from each organ. These were blotted and weighed, minced, immersed in formalin, and allowed to dry for several days. The pieces were then packed into counting tubes and assayed in a Packard Autogamma Spectrometer (5912A) by standard techniques (Heymann et al. 1977). Blood flow was determined to the red- and white-muscle in samples collected from the side of the fish contralateral to catheter placement. White-muscle samples were taken from the cephalic and caudal sections of the fish and each sample was divided into outer, middle and inner sections (Fig. 2). Red-muscle samples were then taken from the cephalic and caudal areas about the midline of the fish. The entire gill structure was also measured for radioactivity to determine if microspheres had lodged in this tissue. To ensure equal distribution of microspheres to organs of the viscera, the dorsal aortic catheter was inserted as far toward the head as possible (see Fig. 1). At the end of each experiment the position of this catheter was verified. The external diameter of the catheter was 1.0 mm while the internal diameter of the dorsal aorta at this site was about 2.0 mm. Thus sufficient blood flow for normal distribution was available.

The total activity of the microsphere suspension injected into each fish was calculated and regional blood flow was determined as follows:

Tissue flow = (Q × tissue cpm)/(injected cpm) where Q = cardiac output (ml/min), tissue cpm = counts per min in tissue samples, and injected cpm = counts per min of the injected microsphere suspension. Blood flow, expressed as ml/min/g, was computed by dividing tissue flow by the weight of each sample.

Temperature measurements

Needle thermistors were inserted into or near the centres of the red- and white-muscle mass of six fish within 5 min of capture. Temperatures were measured with a Yellow Springs Instrument (YSI), No. 513, thermistor probe and read on a YSI Model 41 Tele Thermometer.

Blood gas measurements were made in 18 fish, 7 of which were also used in $\dot{V}O_2$ studies. The effect of temperature on blood gases was determined by using two gas analysers set at the upper and lower temperature extremes experienced by

albacore blood. One instrument (Instrumentation Laboratories, Model 213) was maintained at 22° C (ambient water temperature), while a second (Radiometer Model BMS-3) was set at 32° C, the highest red-muscle temperature likely to be encountered. Blood gas results, used in the $\dot{V}O_2$ calculations, were taken from one machine set at 25° C.

$\dot{V}O_2$ was calculated from the product of cardiac output and arterial-venous O_2 content difference. O_2 contents were calculated as the sum of dissolved plus haemoglobin-bound oxygen. The dissolved O_2 was calculated assuming a blood temperature of 25° C, and a plasma solubility given by the following relationship:

Solubility = 0.00595−0.0001266*T + 0.0000013*T2

where T is the temperature in ° C.

The haemoglobin-bound component was calculated using a standard relationship between tension and partial pressure (Kelman 1966), and using a measured haemoglobin P_{50}. Haemoglobin concentration was measured using the cyanomethaemoglobin technique. To avoid inaccuracies due to interference from erythrocyte nuclei, samples were centrifuged prior to measuring optical absorbance at 540 mn. Haemoglobin P_{50} was measured using a modification of the technique described by Neville (1974). Briefly, 0.1 ml of fresh blood was suspended in 1.6 ml of a yeast-buffer-glucose solution (tris-[hydroxymethyl] aminomethanebuffer, 310 mOsm, pH 7.5) and measured by tonometer to a PO_2 of 300–400 Torr. This mixture was injected into a heated cuvette which included a Clark microelectrode fitted with a 0.8 mil polyethylene membrane to improve the response at low levels of PO_2. The mixture was warmed and the fall in PO_2 with time was recorded. The pH of the reacting suspension was measured anaerobically with a glass pH electrode (Radiometer). The P_{50} of the red cells was calculated from the rate of fall in PO_2 with time, and corrected to a pH of 7.4 using a blood gas slide rule (Severinghaus 1966).

Measured and calculated values for all parameters are presented as mean ± standard error of the mean. The student *t*-test was used to determine significance of the mean values between two groups. Differences were considered significant at $P < 0.05$.

Results

Heart rate

Heart rates, calculated from blood pressure measurements, were relatively stable over the 90 min periods of experimentation for each fish (Table 1), but varied considerably among the fishes, (69–150 beats/min). In five albacore a marked drop in heart rate, from 107±3 beats/min to 13±2 beats/min, was noted within 2 min of hypoxia (cessation of ventilation).

Table 1. Heart rate and blood pressure in *Thunnus alalunga*

HR		Ventricular (S/D) (mm Hg)		Bulbus (S/D) (mm Hg)		Dorsal aortic (S/D) (mm Hg)	
		Time (min)					
30′	90′	30′	90′	30′	90′	30′	90′
135	133	100/7	55/6	98/75	55/40	78/72	40/38
136	142	112/5	89/4	110/93	75/60	89/85	60/58
76	73	90/8	60/4	90/65	60/36	71/68	45/42
69	73	107/3	105/8	105/80	100/80	96/90	76/72
150	130	90/2	73/5	88/70	70/50	–	–
133	136	100/6	88/5	98/75	–	–	–
120	120	–	89/7	–	–	–	–
136	130	120/10	–	–	–	112/108	70/67
125	95	–	–	–	–	90/84	85/82
136	–	–	–	–	–	68/60	–
120	–	–	–	–	–	–	62/53
142	–	–	–	–	–	77/72	–
$\bar{x}$ 115	115	103/6	79*/6	98/78	72*/53*	84/78	57*/59*
± 5	5	3/1	7/0.05	3/4	8/8	5/5	10/6

S/D Systolic/Diastolic; ± ±SEM (standard error of mean); * Significant $P < 0.05$ compared to 30′; Pressures are given as mm Hg

Table 2. Cardiac output and stroke volume in *Thunnus alalunga*

Fish	Mass (kg)	CO (ml/min)	CO^1 (ml/min/kg)	HR (beats/min)	SV (ml)	Method
1	11.2	320	28.6	99	3.2	DD
2	9.8	340	34.7	120	2.8	DD
3	10.1	362	35.8	142	2.5	DD
4	9.9	280	28.3	79	3.5	DD
4	9.9	273	27.5	82	3.3	EM
5	7.8	374	47.9	104	3.6	EM
6	8.1	194	24.0	89	2.2	EM
7	7.4	458	61.9	77	5.9	EM
$\bar{x}$	9.3	325	36.1	99	3.4	
±SEM (Standard error of mean)	0.5	30	5	8	0.4	

CO Cardiac output; *HR* heart rate at the time of cardiac output measurement; *SV* stroke volume, calculated as $\frac{CO}{HR}$;

DD dye dilution; *EM* electromagnetic flow transducer; CO^1 normalized cardiac output $\frac{CO\ (ml/min)}{Mass\ (kg)}$

Blood pressures

Systolic and diastolic blood pressures measured in the ventricle, bulbus arteriosus, and dorsal aorta at 30 min and 90 min after the fish were prepared for experimentation, are presented in Table 1. Highest blood pressures were measured in the ventricle during systole, mean 103±3 mm Hg ($n=7$). During diastole there was a marked drop in pressure in the ventricle, mean 6±0.05 mm Hg ($n=7$). Systolic pressures in the bulbus arteriosus, mean 98±3 mm Hg ($n=6$), were almost identical to those in the ventricle, suggesting little pressure drop across the valve. However, bulbus diastolic pressures, mean 78±4 mm Hg ($n=6$), were higher than in the ventricle as would be expected: the former is the true diastolic pressure in the arterial system while the latter is a measure of preload in the ventricle. The mean systolic pressure in the dorsal aorta was 84±5 mm Hg ($n=8$), which represents an approximate 14% drop in pressure across the gills. During diastole only slight decreases in pressures were recorded in the dorsal aorta, mean 78±5 mm Hg ($n=8$), which is identical to the mean diastolic pressure measured in the bulbus arteriosus.

There was a gradual, but marked decrease in systolic pressures during the experimental period. At 90 min the mean systolic pressures in the ventricle ($n=7$), bulbus arteriosus ($n=5$) and dorsal aorta ($n=7$) were 79±7, 72±8 and 57±10 mm Hg, respectively. These values are significantly lower ($P<0.05$) than those recorded at 30 min. Diastolic pressures in the bulbus arteriosus and dorsal aorta decreased to 53±8 and 59±6 mm Hg, respectively, at 90 min, which are significantly lower ($P<0.05$) than at 30 min. The contractile force of the heart, dP/dt (mm Hg/s), was measured in four albacore at 6342±822 mm Hg/sec.

Cardiac output

Cardiac output data from seven fish are given in Table 2. Fishes 1–4 had cardiac output determined by dye dilution. Electromagnetic flow-transduced cardiac output measurements were made in fish 4–7. Both measurements were made in fish 4 and are in good agreement. Stroke volume showed some variation among fish which could not be accounted for by differences in body mass or heart rate, although there was generally an inverse relationship between heart rate and stroke volume. Cardiac output varied greatly between fish of nearly equal mass, due to differences in heart rate and stroke volume. The mean cardiac output was 36.1±5 (ml/min/kg).

Organ blood flow

Microsphere measurements showed considerable differences in blood flow rates (ml/min/g) to different organs of the body (Table 3). The highest flow was to the kidneys, 0.42±0.07 ml/min/g, and the smallest was to the white-muscle, 0.01±0.005 ml/min/g and to the skin, 0.01±0.005 ml/min/g. Blood flow to white-muscle ranged from 0.029±0.04 ml/min/g (in the inner portion of the fish) to 0.006 ml/min/g (in the midregion of the tail) (Table 4 and Fig. 2). Blood flow measurements as low as 0.003 ml/min/g represent negligible flow and are within the permitted error of the method. Blood flow to red-muscle

Table 3. Organ blood flow in *Thunnus alalunga*

Tissue	Organ Mass (g)	% CO	Flow (ml/min/g)
Red-muscle	452 ± 30	36.2	0.22 ± 0.04
White-muscle	5950 ± 290	27.5	0.013 ± 0.005
Stomach	136 ± 8	2.8	0.057 ± 0.007
Intestine	28.7 ± 2	1.8	0.17 ± 0.06
Spleen	17.5 ± 0.5	1.4	0.22 ± 0.06
Kidney	45 ± 5	6.7	0.42 ± 0.07
Liver	243 ± 16	13.0	0.15 ± 0.02
Skin	65 ± 2.1	0.2	0.01 ± 0.005

Mean ± SEM (standard error of mean); $N = 4$; Mean body mass = 9.8 ± 0.34 kg; *CO*, cardiac output

Table 4. Regional flow in the white-muscle of *Thunnus alalunga*

	Cephalic	Caudal
Inner	0.029 ± 0.04	0.004** ± 0.0003
Mid	0.009* ± 0.003	0.0006** ± 0.0002
Outer	0.004* ± 0.006	0.003** ± 0.0005

Mean ± SEM (standard error of mean); Flow in ml/min/g; * Significant $P < 0.05$ compared to inner; ** Significant $P < 0.05$ compared to cephalic

and spleen were relatively high and identical 0.22 ± 0.04 ml/min/g. Lesser flow rates were recorded to the intestine, 0.17 ± 0.06 ml/min/g, and liver, 0.15 ± 0.02 ml/min/g. A relatively low rate of flow was measured in the stomach, 0.06 ± 0.007 ml/min/g.

Blood gases, oxygen consumption, and body temperature

Blood gas data are contained in Table 5. Arterial PO_2 was 62.0 ± 2.9 Torr and decreased to 14.3 ± 1.2 in venous blood. The arterial blood was significantly more alkaline than the venous blood. Haemoglobin volumes were 15.8 ± 0.1 which is equivalent to a haematocrit of 47.5. Arterial-venous oxygen content difference and oxygen consumptions are given in Table 6. The mean oxygen consumption was 3.4 ± 7 (ml O_2/min/kg). The effects of temperature on blood gases are given in Table 7. Arterial and venous blood samples from each fish were run at different temperatures in separate blood gas machines. Both arterial and venous blood, had PO_2's which were higher in cooler blood. There was no temperature effect on CO_2 tension but the blood was more alkaline at lower temperatures in both arterial and venous blood. The average P_{50} was 15.9 Torr at a temperature of 37° C and pH of 7.4.

Temperature measurements in red-muscles were made at three time periods: 10–15 min after landing, 30 min, and 90 min. The initial red-mus-

Table 6. Oxygen consumption of *Thunnus alalunga*

Fish	Arterial-venous difference (ml O_2/dl)	$\dot{V}O_2$ (ml O_2/min/kg)
1	9.4	2.7
2	12.0	4.2
3	5.6	2.0
4	6.6	1.9
5	9.8	4.7
6	8.4	2.0
7	10.8	6.7
$\bar{x}$	8.9	3.4
±SEM (Standard error of mean)	0.9	0.7

Same fish as Table 2; $\dot{V}O_2$ calculated as: (cardiac output x arterial-venous difference); $\dot{V}O_2$ = oxygen consumption

Table 5. Blood gases and O_2 content in *Thunnus alalunga*

Fish	Arterial						Venous				
	PO_2 (Torr)	PCO_2 (Torr)	pH	O_2 Cont (ml O_2/dl)	SAT (%)	Hb (g/dl)	PO_2 (Torr)	PCO_2 (Torr)	pH	O_2 Cont (ml O_2/dl)	SAT (%)
1	68.1	5.6	7.846	21.9	99.4	16.0	14.5	10.5	7.479	12.5	56.9
2	57.5	4.9	7.533	21.7	98.6	15.5	12.1	10.0	7.444	9.7	44.4
3	56.2	3.5	8.038	21.9	99.4	15.4	18.2	6.5	7.522	16.3	74.5
4	70.0	3.8	7.850	22.0	99.5	16.1	17.9	11.9	7.498	15.4	70.4
5	50.5	3.2	7.944	21.4	99.2	15.4	11.3	7.6	7.690	11.6	54.4
6	70.6	3.0	7.807	21.5	99.5	15.7	16.0	10.0	7.440	13.1	60.7
7	61.4	5.0	7.964	21.5	99.4	16.2	9.8	6.6	7.748	10.7	49.9
$\bar{x}$	62.0	4.1	7.855	21.7	99.3	15.8	14.3	9.0	7.546	12.8	58.7
±SEM (standard error of mean)	2.9	0.4	0.62	0.1	0.1	0.1	1.2*	0.8*	0.046*	0.9*	4.1*

Temperature 25° C; O_2 Content in ml O_2 per deciliter of blood; *SAT* saturation in %; *Hb* haemoglobin in grams per deciliter; Gas tension in Torr; * Significant $P < 0.05$ venous compared to arterial values

Table 7. Effects of temperature °C on blood gases of *Thunnus alalunga*

Fish	PO_2 (Torr)				PCO_2 (Torr)				pH			
	A		V		A		V		A		V	
	32°	22°	32°	22°	32°	22°	32°	22°	32°	22°	32°	22°
1	39.5	52.6	17.2	18.7	3.0	3.0	5.6	5.6	7.73	8.03	7.55	7.84
2	60.0	67.6	12.2	13.2	2.6	2.6	4.5	8.8	7.55	7.86	7.29	7.49
3	40.0	58.7	6.0	8.1	4.4	4.4	3.2	5.0	7.65	8.02	7.76	7.96
4	26.0	30.1	7.3	7.6	3.3	3.3	10.0	5.8	7.57	7.85	7.57	7.85
$\bar{x}$	41.4	52.3	10.7	11.9	3.3	3.3	5.8	6.3	7.63	7.94	7.54	7.79
±SEM (standard error of mean)	7.0	8.0*	2.6	2.6*	0.4	0.4	1.4	0.9	0.04	0.05*	0.10	0.10*

* Significant $P < 0.05$ 22°C vs. 32°C paired *t*-test; *A* arterial; *V* venous; the temperature (°C) of blood gas machine 1 was 22°C and bloodgas machine 2 was 32°C

cle temperature was 28.9° ± 0.8° C, at 30 min, 26.9° ± 0.7° C and at 90 min, 24.7° ± 0.9° C. The water temperature of the holding tank was 21.9° ± 0.1° C and the surface sea water temperature was 21.3° ± 0.1° C.

Discussion

Heart rate and blood pressure

Reported heart rates in fishes usually range from 25–70 beats/min (Randall 1970). The heart rate of swimming salmon has been measured as high as 100 beats/min (Smith et al. 1967). Heart rates in our study had a very wide range (69–150 beats/min), but the albacore, in which only heart rates and blood pressures were measured (Table 1), had mean heart rates of 115 ± 9 beats/min. These heart rates remained relatively constant over several hours despite decreasing red-muscle temperatures and decreasing blood pressures. Temperature, vagal tone and hypoxia all may have a marked influence on the heart rate of fishes (Randall 1970; Stevens 1972). Hypoxia was probably not a major factor in heart rate measurements in most of the albacore because arterial PO_2 was maintained higher than 60 Torr. As in other species, induced acute hypoxia caused bradycardia in five albacore. The heart rates seen in this study are higher than those reported by Stevens (1972) of 70 beats/min in the restrained skipjack tuna. But Stevens also reported a large variation in heart rate during the experiments (46–142 beats/min) which he attributed to differences in vagal tone. Brill (1987) reported heart rates in skipjack and kawakawa of over 200 beats/min under experimental conditions similar to this study.

Our recordings of ventricular pressures of 98 ± 3 mm Hg are higher than that reported in other teleosts (Randall 1970). Randall et al. (1965) reported ventricular pressures in freshwater fish of approximately 40–45 mm Hg, and in the Pacific salmon Robertson et al. (1966) reported ventral aortic pressures of approximately 80 mm Hg. We observed a systolic pressure drop (20 mm Hg) across the gill which is similar to that reported by other investigators (Hanson 1967; Holeton and Randall 1967; Lai et al. 1987). The high heart rates and blood pressures are physiologic evidence of high cardiac performance. The data from this study showed a relatively high contractile force in the heart (over 6000 mm Hg/s). This high contractile force combined with the filling pressure of 6 mm Hg, can take advantage of the Starling effect which would dictate a relatively high stroke volume. It has been shown that increased filling pressure combined with the increased contractile force of the heart contributes to higher stroke volume (White et al. 1987). Normal mammalian measurements of dP/dt in pigs (White et al. 1987) are 2000 mm Hg/s, which increase to about 8000 mm Hg/s during intense exercise. It appears that the albacore ventricular contractile force is equivalent to that of mammals. Breisch et al. (1983) showed that the albacore myocardium is composed of 82% spongy mass and 18% compact myocardium. It is unlikely that only 18% of the myocardium is responsible for the relatively high amount of cardiac work seen in this fish. Therefore, it is probable that the spongy myocardium provides a considerable force for the ejection of blood and the generation of high ventricular pressures. Further investigations of the force generated by the spongy myocardium are needed to understand fish ventricular mechanics.

Cardiac output and oxygen consumption

Both methods of measurement used in this study, dye dilution and the electromagnetic flow transducer, have been used in fish previously. In our experiments, both methods seem comparable: however the dye technique was simpler to use, and the effects of opening the pericardium in order to implant the electromagnetic flow probe around the ventral aorta, could have a deleterious effect on cardiac function (Lai et al. 1987). Resting cardiac outputs have been measured in a number of fish species. Values in the trout range from 18 ml/min/kg (Kiceniuk and Jones 1977) to 45 ml/min/kg (Neumann et al. 1983). Using the electromagnetic flow probe, Johansen (1962) measured a cardiac output of 9.3 ml/min/kg in the cod. Murdaugh et al. (1965), using dye techniques, measured a cardiac output of 26.7 ml/min/kg in *Squalus acanthias*. Our measurements of about 34 ml/min/kg appear to be not unusual for a teleost and are very similar to that reported in the albacore by Lai et al. (1987). But we must be cautious on any interpretation of the cardiac output in a partially anaesthesized and traumatized fish compared to one that is free swimming. $\dot{V}O_2$ data given in this paper are similar to that given by Graham and Laurs (1982) for albacore swimming in a respirometer.

Organ blood flow

The microsphere method allowed several observations to be made about organ blood flow in the albacore. However, this method was limited because of the unavailability of a suitable catheter location to distribute microspheres to the heart and brain. Since both the heart and brain are perfused by arteries coming from the efferent branchial arteries, no microspheres reached these organs. The relative and absolute blood flows to various organs are similar to those reported in the Arctic grayling (Cameron 1975), although the kidney and the spleen flows are somewhat lower and higher respectively. White-muscle blood is sparse but there is a heterogenous flow of blood to this organ. We found that white-muscle blood flow was highest nearest the red-muscle and decreased to near zero in the caudal direction. This is in agreement with the finding of Cameron (1975) that the highest white-muscle flows were in the cephalic direction. These data may support the concept that tuna white-muscle possesses a greater potential for aerobic metabolism, particularly in the region where temperatures are elevated. Graham et al. (1983) suggested that white-muscle activity partiall assumes red-muscle function where the temperatures are elevated. Our finding that the inner white-muscle has increased blood flow further supports the concept of a mixed function and morphology for albacore white-muscle.

Red-muscle received the highest percentage of the total cardiac output, approximately 36%, although this organ represents less than 5% of the fish mass. The rate of blood flow to the white-muscle was quite low, but due to its large mass, occupying more than 60% of the total mass of the fish, the white-muscle received almost 28% of the cardiac output. The liver, which accounts for 2.5% of the total body weight, received 13% of the cardiac output. The kidney, while comprising only 0.5% of the total body weight, received 6.7% of the cardiac output. The stomach received less than 3% of the cardiac output, the intestine and spleen each received less than 2% and the skin less than 0.2%. Our measurements account for 89.6% of the cardiac output. Microspheres in the gills account for another 5% of the total injected. We asume that the remainder, approximately 4.5%, found its way to tissues that were not assayed (bone, heart, brain, and other organs). These tissue blood flows are similar to those found in mammals.

Blood gas measurements

The blood gas measurements presented here are markedly similar to those of Jones et al. (1986) in the free swimming tuna, *Euthynnus affinis* (kawakawa). Cech et al. (1984) clearly showed a reverse temperature effect of lowering arterial PO_2 with warming in the albacore, while Jones et al. (1986) showed a positive temperature effect in the kawakawa. Our data confirm the reverse temperature effect on PO_2 in albacore and show a decrease in pH with increasing temperature. However, we could not see marked temperature effects on CO_2, perhaps because of the narrow range of CO_2 values in the blood. Our P_{50} value of 15.9 Torr is lower than that reported by either Cech et al. (1984) or Jones et al. (1986). However, this value is not unreasonable given that the average venous PO_2 we observed (Table 5) was 14.3 Torr at 25° C

In conclusion these data show that the albacore tuna is capable of relatively high cardiovascular performances and blood flows which are similar to those in mammals.

References

Alexander N, Laurs RM, McIntosh A, Russell SW (1980) Haematological characteristics of albacore, *Thunnus alalunga* (Bonnaterre) and Skipjack, Katsuwonus pelamis (Linnaeus). J Fish Biol 16: 383–395

Breisch EA, White FC, Jones MH, Laurs RM (1983) Ultrastructural morphometry of the myocardium of *Thunnus alalunga*. Cell Tissue Res 233: 427–438

Brill RW (1987) On the standard metabolism rates of tropical tunas, including the effect of body size and acute temperature change. Fish Bull 85: 25–35

Cameron JN (1975) Blood flow distribution as indicated by tracer microspheres in resting and hypoxic grayling *(Thymallus arcticus)*. Comp Biochem Physiol 52A: 441–444

Carey FG, Teal JM (1966) Heat conservation in tuna fish muscle. Proc Natl Acad Sci USA 56: 191–195

Cech JJ, Laurs RM, Graham JB (1984) Temperature-induced changes in blood gas equilibria in the albacore, *Thunnus alalunga*, a warm-bodied tuna. J Exp Biol 109: 21–34

Dotson RG (1976) Minimum swimming speed of albacore *Thunnus alalunga*. Fish Bull US 74: 955–960

Graham JB, Dickson KA (1981) Physiological thermoregulation in the albacore *Thunnus alalunga*. Physiol Zool 54: 470–486

Graham JB, Laurs RM (1982) Metabolic rate of the albacore tuna *Thunnus alalunga*. Mar Biol 72: 1–6

Graham JB, Koehrn FJ, Dickson KA (1983) Distribution and relative proportions of red muscle in scombrid fish: consequences of body size and relationship to locomotion and endothermy. Can J Zool 61: 2087–2097

Hanson D (1967) Cardiovascular dynamics and aspects of gas exchange in Chondrichthyes. Ph D thesis, University of Washington, Seattle

Heymann MA, Payne BD, Hoffman JIE, Rudolph AM (1977) Blood flow measurements with radionuclide labeled particles. Prog Cardiovasc Dis 20: 55–79

Holeton GF, Randall DJ (1967) Changes in blood pressure in the rainbow trout during hypoxia. J Exp Biol 46: 297–305

Johansen K (1962) Cardiac output and pulsatile aortic flow in the teleost *Gadus morhua*. Comp Biochem Physiol 7: 169–174

Jones DR, Brill RW, Mense DC (1986) The influence of blood gas properties on gas tension and pH of ventral and dorsal aortic blood in free swimming tuna, *Ethynnus affinis*. J Exp Biol 120: 201–213

Kelman GR (1966) Digital computer subroutine for conversion of oxygen tension into saturation. J Appl Physiol 21: 1375–1376

Kent BB, Pierce ED, Bever CT (1973) Distribution of blood flow in *Squalus acanthias*. Fed Proc Fed Am Soc Exp Biol 32: 396

Kiceniuk JW, Jones DR (1977) The oxygen transport system in trout *(Salmo gairdneri)* during sustained exercise. J Exp Biol 69: 247–260

Lai NC, Graham JB, Lowell WR, Laurs RM (1987) Pericardial and vascular pressure and blood flow in albacore tuna *Thunnus alalunga*. Exp Biol 46: 187–192

Laurs RM, Ulevitch RJ, Morrison DC (1978) Estimates of blood volume in the albacore tuna. In: Sharp GD, Dizon AE (eds) The physiological ecology of tunas. Academic Press, New York, pp 135–140

Murdaugh HV, Robin ED, Millen JE, Drewry WF (1965) Cardiac output determinations by the dye dilution method in *Squalus acanthias*. Am J Physiol 209: 723–726

Neumann P, Holeton GF, Heisler N (1983) Cardiac output and regional blood flow in gills and muscles after exhaustive exercise in rainbow trout *Salmo gairdneri*. J Exp Biol 105: 1–14

Neville JR (1974) Hemoglobin oxygen affinity measurements using biotonometry. J Appl Physiol 37: 967–971

Randall DJ (1970) The circulatory system. In: Hoar WS, Randall DJ (eds) Fish physiology, vol 4. Academic Press, New York, pp 133–168

Randall DJ, Smith LS, Brett JR (1965) Dorsal aortic blood pressure recorded from rainbow trout *(Salmo gairdneri)*. Can J Zool 43: 263–877

Robertson OH, Krupp MA, Thompson SF, Hane S (1966) Blood pressure and heart weight in immature and spawning Pacific salmon. Am J Physiol 256: 957–964

Severinghaus JW (1966) Blood gas calculator. J Appl Physiol 21: 1108–1116

Smith LS, Brett JR, Davis JC (1967) Cardiovascular dynamics in swimming adult sockeye salmon. J Fish Res Board Can 24: 1775–1790

Stevens ED (1968) The effect of exercise on the distribution of blood to various organs in rainbow trout. Comp Biochem Physiol 25: 615–625

Stevens ED (1972) some aspects of gas exchange in tuna. J Exp Biol 56: 809–823

White FC, McKirnan D, Breisch E, Guth BD, Liu Y, Bloor CM (1987) Adaptation of the left ventricle to exercise induced hypertrophy. J Appl Physiol 62: 1097–1110

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