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Pericardial and vascular pressures and blood flow in the albacore tuna, *Thunnus alalunga*

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Summary. Pericardial, ventricular, and dorsal aortic pressures, and blood flow were measured in tabled, anesthetized albacore tuna, *Thunnus alalunga* (7.8–10.7 kg) captured at sea off Monterey, California (USA) during August 1985. Mean pericardial pressure was $-10.0/-2.6$ cm H_2O (Systolic/Diastolic, [S/D]) and mean pericardial pulse pressure was 7.5. Heart rate averaged 87 beats per minute. Mean ventricular pressure was 97.0/12.9 cm H_2O [S/D] and mean dorsal aortic pressure was 64. High ventricular and dorsal aortic pressures of albacore reflect the perfusion requirement of its metabolically active tissues and compensate for the energy losses resulting from blood flow through the gills to arterial heat exchanger to capillaries and again back to the venous heat exchanger. As in elasmobranchs, the remarkably high pericardial pulse pressure, large pericardial volume, and negative pericardial pressure in the albacore suggest that its pericardium is more rigid than that of most teleosts and thus facilitates cardiac filling. Published cardiac output values for most non-tunas, when corrected for body size differences, are less than the mean weight specific cardiac output of albacore (29.4 ml/kg per min, range 12.9–51.9).

Key words: *Thunnus alalunga* – Tuna – Vascular pressures – Cardiac output

Introduction

Tunas (family Scombridae) are highly specialized pelagic fishes renowned for their continuous swimming and transoceanic migrations. They possess numerous adaptations that enable them to sustain high cruising speeds for extended periods (Beamish 1978). Included among these are a streamlined body shape and a high aspect ratio lunate tail which reduce drag and increase swimming efficiency (Magnuson 1978). Tunas also maintain an elevated body temperature which positively affects the metabolic efficiency of their red and white swimming musculature (Stevens and Neill 1978). Metabolic heat generated by their swimming muscles is conserved in the vascular counter-current heat exchangers *(retia mirabilia)*. Vascular supply to these exchangers is via cutaneous arteries and veins that are best developed in the family Scombridae (Graham 1975; Graham and Diener 1978).

The high metabolic activity of a swimming tuna requires the support of a circulatory system capable of delivering high volumes of blood and large quantities of oxygen. Correspondingly, tunas relative to other fishes have greater blood hemoglobin concentrations (Klawe et al. 1963), a larger blood volume (Laurs et al. 1978), and larger gill surface area (Muir and Hughes 1969). A tuna's heart, unlike other teleosts, must additionally pump blood at sufficient pressures to compensate for the energy losses incurred circulating blood from the gills to the heat exchanger to capillaries and then again back through the exchanger (Graham 1975; Graham and Diener 1978). Tunas have large hearts (Graham et al. 1983) and ultrastructural and histochemical analyses (Tota 1978, 1983; Breisch et al. 1983) suggest that this organ can sustain high levels of physiological performance. Moreover, the vascular pressure and heart rate reported for the albacore tuna by Breisch et al. (1983) exceed those of most other fishes.

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Tunas are exceedingly difficult to capture and maintain in captivity, which precludes their use in most experimental studies. By working at sea with freshly captured albacore we were able to partially surmount these limitations. The objectives of our study were to measure the pericardial and vascular pressures and the cardiac output of freshly captured, anesthetized, restrained, and ventilated albacore (*Thunnus alalunga* Bonnaterre).

Materials and methods

All studies were conducted off Monterey, California (USA) aboard the NOAA RV *David Starr Jordan* in August 1985. Thirty-three albacore were captured using feathered jigs trolled just beneath the surface at 5 knots. Immediately following a jig strike the ship was slowed and the fish was brought along side by a hydraulic hoist and lifted to the deck by hand, usually within 1 min. The hook was immediately removed from its mouth and its gills irrigated with running seawater. It was then immobilized with either unbuffered gallamine triethiodide (3–4 mg injected into the lateral cutaneous vessel) or by postcranial spinalectomy. The fish was rushed to the laboratory where it was placed supine on a V-board and ventilated with oxygenated seawater (15.8°–17.0 °C, $\bar{x}$ = 16.5 °C, 1.98 l/min) containing 0.1 g/l of tricaine methane sulphonate (MS222). Depending upon each specimen's reponse level anesthetic was intermittently added to ventilation water. Because of uncertainties about fish condition, experimental protocols were in most cases done in the following succession: pericardial pressure, ventricular pressure, blood flow, and dorsal aortic pressure.

Pericardial and ventricular pressures

An 18 ga needle was inserted percutaneously into the pericardial space and connected to a Statham P23Db pressure transducer by a catheter filled with teleost saline (Fig. 1). For zero reference on each transducer a second saline-filled catheter was positioned outside the animal's body and at the same level as the pericardial catheter tip. The entire procedure took about 5 min. Pressure recordings were amplified (Honeywell Electronics for Medicine, V2203A) and recorded with a Gould oscillograph (Brush 260). Needle catheters were routinely flushed from a saline-filled syringe reservoir common to the gauge and the catheter (Fig. 1).

Ventricular catheterization was also done percutaneously from the ventral body surface by advancing an 18 ga transducer-connected thin-walled needle filled with heparinized teleost saline into the ventricular lumen (Fig. 1). The position was verified by pressure signal and a zero reference catheter was mounted at the level of the ventricular needle. About 5 min was required for this procedure.

Dorsal aortic pressure

Access to the dorsal aorta was via a cutaneous artery. An incision was made on the mid lateral side of the fish about 2 cm ventral and 5 cm caudal to the pectoral fin (Fig. 1). Removal of the subcutaneous connective tissues revealed the lateral cutaneous vessels and associated fascia. The lateral cutaneous artery was identified and cannulated with PE 90 tubing. To control blood flow during this procedure a silk ligature was passed around the vessel on proximal and distal sides of the cannulation site. The catheter, marked in cm gradations, was advanced 7 to 9 cm anteriorly, depending on the incision site and the size of the fish, to the junction of the cutaneous artery and dorsal aorta, and was secured with a ligature. Pressure measurements and a zero reference were as described above. This procedure required about 20 min.

Ventral aortic flow

An electromagnetic flow probe (Carolina Medical Electronics) was placed on the ventral aorta (Fig. 1). A median incision was made along the gill isthmus and the urohyal bone separated. The ventral aorta was exposed by removing all tissues including those attached to the vessel. A flow probe with a diameter similar to the vessel was attached by gently lifting the vessel away from underlying structures. Once the probe was in place, the incision was closed and held securely by two towel clamps. The flow probe implantation required about 30 min.

At the end of the experiment the fish was sacrificed for in vitro calibration of the flow probe. The portion of the ventral aorta where the probe had been placed was excised and one end was affixed to a three-way stopcock connected to a vertically positioned syringe. The free end of this vessel was opened into a dish of teleost saline. The probe used in the experiment was then mounted on the vessel and known volumes of teleost saline were manually injected through the vessel in a pattern that mimicked the flow records. A Talos X-Y digitizer interfaced to a Tektronix intelligent terminal was used to analyze flow data.

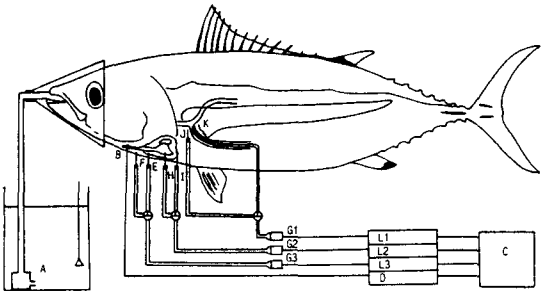

Fig. 1. Recording arrangement for *Thunnus alalunga*. *A* oxygenated reservior; *B* flow probe; *C* Gould oscillograph; *D* flow meter and DC amplifier; *E* pericardial catheter; *F* zero reference for pericardium; *G, I, 2, 3* Statham pressure transducers; *H* ventricular catheter; *I* zero reference for ventricle; *J* zero catheter for dorsal aorta; *K* dorsal aorta catheter; *L, 1, 2, 3* pressure amplifiers

Results

Successful studies were carried out on 19 of the 33 fish tested (Table 1). No differences were found between fish that were immobilized with gallamine triethiodide (n = 13) and those that were spinalectomized (n = 6). Heart rate ranged from 50 to 120 beats per minute (bpm, $\bar{x}$ = 87). Ventricular systolic pressure [S] ranged from 55.0 to 150.0 cm H_2O ($\bar{x}$ = 97.0) and diastolic pressure [D] from −5.0–63.0 cm H_2O ($\bar{x}$ = 12.9).

Table 1. Heart rate (n = 19), ventricular (n = 17), and pericardial pressures (n = 15) of *Thunnus alalunga*

Albacore No.	Fork length (mm)	Body weight[a] (kg)	Heart rate (bpm)	Ventricular pressure			Pericardial pressure		
				Systole	Diastole (cm H_2O)	Pulse	Systole	Diastole (cm H_2O)	Pulse
2	777	9.2	102	120.0	50.0	70.0	−15.0	−14.0	1.0
3	775	9.1	102	85.0	−5.0	90.0	−9.5	−9.0	0.5
4	800	9.9	108	56.0	30.0	26.0	−6.9	−5.8	1.1
5	780	9.3	100	120.0	10.0	110.0	−5.0	−4.0	1.0
7	750	8.3	60	85.0	−5.0	90.0	−6.0	−5.0	1.0
9	760	8.6	75	74.0	63.0	11.0	−18.0	−8.9	9.1
12	750	8.3	50	95.0	5.0	90.0	−19.8	6.6	26.4
13	780	9.3	120	125.0	0	125.0	−20.0	0	20.0
16	820	10.7	100	140.0	50.0	90.0	0	3.3	3.3
17	790	9.6	120	–	–	–	−6.6	−3.3	3.3
22	810	10.3	106	57.0	0	57.0	–	–	–
23	795	9.8	83	131.0	5.7	125.3	−8.3	13.2	21.5
25	760	8.6	107	103.0	5.7	97.3	−9.9	0	9.9
26	770	9.0	79	150.0	10.0	140.0	−16.5	−9.9	6.6
27	740	7.9	50	–	–	–	–	–	–
28	800	9.9	107	120.0	0	120.0	–	–	–
31	770	9.0	51	55.0	0	55.0	−4.0	−1.0	3.0
32	760	8.6	71	60.0	0	60.0	−5.2	−0.7	4.5
33	735	7.8	59	73.0	0	73.0	–	–	–
Mean	–	–	87	97.0	12.9	84.1	−10.0	−2.6	7.5
Standard error	–	–	±6	±7.7	±5.2	±8.6	±1.6	±1.8	±2.2

[a] Estimated by regression, $M = 4.514 \times 10^{-5} L^{2.8746}$ (Dotson 1976), where M is mass in grams and L is fork length in mm

Table 2. Simultaneous ventricular and dorsal aortic pressures of *Thunnus alalunga* (n = 5) showing the transbranchial pressure drop. See Table 1 for body size data

Albacore No.	Ventricular pressure (cm H_2O)	Dorsal aortic pressure (cm H_2O)	Transbranchial pressure drop (cm H_2O)	Percent drop
13	125	90	35	28
25	103	73	30	29
26	150	30	120	80
28	120	96	24	20
32	60	30	30	50
Mean	112	64	48	41
Standard error	±15	±14	±18	±11

Table 3. Cardiac output (n = 5) of *Thunnus alalunga*. See Table 1 for body size

Albacore No.	Heart rate (bpm)	Stroke volume (ml/stroke)	Cardiac output (ml/min)	Weight-specific cardiac output (ml/kg per min)
25	107	2.5	267.5	31.1
27	107	1.7	181.9	23.0
28	107	4.8	513.6	51.9
32	71	3.4	241.4	28.1
33	59	1.7	100.3	12.9
Mean	90	2.8	260.9	29.4
Standard error	±10	±0.6	±69.4	±6.4

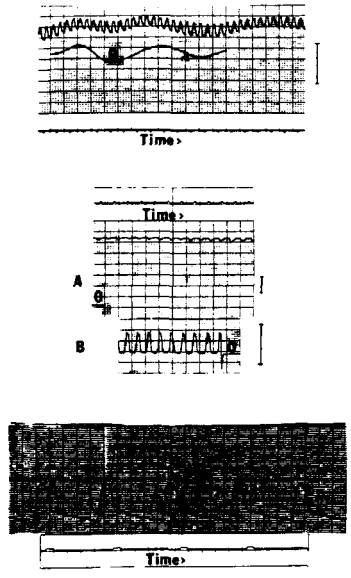

Fig. 2. *Top* Recording of ventricular pressures in *Thunnus alalunga* showing the effect of ship roll. Lower trace is the zero reference. Vertical scale = 200 cm H_2O. Time marks are 1 s. *Middle* Recordings of dorsal aorta (A) and ventricular (B) pressures in *Thunnus alalunga*. Zeroes are marked on the tracings. Vertical scales: A = 20 cm H_2O, B = 200 cm H_2O. Time marks are 1 s. *Bottom* Ventral aorta blood flow in *Thunnus alalunga*. Upper trace is a record for 3 ml saline passed through the same probe. Time marks are 1 s

Pericardial systolic pressure was successfully measured in 15 albacore and in all cases was either negative or zero (Table 1). Mean pericardial pressure during systole was -10.0 cm H_2O and during diastole was -2.6 cm H_2O. The mean pericardial pulse pressure (the difference between the mean D and S pressures) was 7.5 cm H_2O. Dorsal aortic pressure (Table 2, Fig. 2) ranged from 30 to 96 cm H_2O ($\bar{x} = 64$). In cases where both were measured in the same fish, ventricular pressure always exceeded that in the dorsal aorta.

A typical electromagnetic flow output is shown in Fig. 2. Stroke volume ranged from 1.7 to 4.8 ml and increased with body size (Table 3). Mean cardiac output was 260.9 ml/min. The weight-specific cardiac output also increased with fish size ($\bar{x} = 29.4$ ml/kg per min, range 12.9–51.9).

Discussion

There have been few studies reporting teleostean pericardial pressures. Freadman (1983) measured this in swimming bluefish (*Pomatomus saltatrix*, $-6.4/-2.6$ cm H_2O [S/D]) and tautogs (*Tautoga onitis*, $-2.6/0.7$ cm H_2O [S/D]. The pericardial pulse pressures of these fishes are much less than that of tabled albacore (Table 1).

How might large negative pressure affect albacore heart function? In elasmobranchs a negative pericardial pressure facilitates aspiration of blood for cardiac filling (Johansen 1965; Sudak 1965; Shabetai et al. 1985). Yet, the pericardial pulse pressures reported by Shabetai et al. (1985) for active pelagic species (blue shark 3.9 cm H_2O, bat ray 2.9, mako shark 1.9, and the great white shark 3.2) are much less than in albacore (7.5). Features of elasmobranch anatomy that relate to its cardiac filling mechanism are the semi-rigid pericardium and the large ratio of pericardial to cardiac volume, the mean ratio is 3.8 for all species studied by Shabetai et al. (1985). Teleosts are generally regarded as having a more compliant pericardium than elasmobranchs (Satchell 1970, 1971) but comparative biomechanical studies are lacking. Preliminary studies in our laboratory do reveal that pericardial compliancy of albacore is similar to that measured for the transverse septum of elasmobranchs. Also, measurements (using self-leveling silastic rubber) in two 9 kg albacore yielded pericardial volumes of about 50 ml and thus a ratio of pericardial to cardiac volume of 2. Thus, our preliminary compliancy and volume studies together with the measured high pulse pressures lead us to speculate that the albacore may have a more rigid pericardium than other teleosts and that this, as in elasmobranchs, facilitates cardiac filling.

Tunas, swordfish, and elasmobranchs exhibit a high level of cardiac organization (Tota 1978, 1983; Briesch et al. 1983; Emery 1985). The well developed compact myocardium of tuna heart resembles the homeotherm ventricle in having high capillary density (Tota 1983) and is capable of generating high pressure. The mean systolic ventricular pressure (97.0 cm H_2O, Table 1) of albacore is higher than reported for all other fishes (Johansen 1962; Johansen et al. 1966; Stevens et al. 1972; Shabetai et al. 1985). The heart rate, pericardial, ventricular, and dorsal aortic pressures reported here are variable, which could be attributed to factors such as the effects of capture, handling, MS222, and the length of time required to conduct the experiments. Variability of the dorsal aortic pressure is further attributable to a decline in viability of specimens late in the experimental protocol (e.g., fish 26 and 32, Table 2). High dorsal aortic pressures (maximum 96 cm H_2O), however, were recorded in several instances. These are similar to values reported by

Briesch et al. (1983, 107 cm H_2O) and are also higher than values reported for most fishes, (e.g., *Onchorhynchus tschawytscha* 64 cm H_2O, Robertson et al. 1966; *Onchorhynchus nerka* 56, Smith et al. 1967; *Salmo gairdneri* 35, Stevens and Randall 1967; *Squalus acanthias* 39, Burger and Bradley 1951).

Although the increase in surface area of the *rete* reduces vascular resistance, the albacore still needs to conserve a high vascular pressure to compensate for the energy loss imposed by the gills and heat exchanger and ensure perfusion of its metabolically active tissues. Data for fish 13, 25, and 28 (Table 2) show that blood flow across the gills resulted in an average pressure drop of 30 cm H_2O (26%), which is low relative to that recorded for most fishes. From data summarized for seven species by Satchell (1971), we estimated pressure drops of from 22 to 79%. We do not know how factors such as anesthesia, oxygenated water, and the supine, emergent position of the albacore may have affected branchial resistance.

The mean transbranchial pressure drop we recorded for fish 13, 25, and 28 (30 cm H_2O) is, however, higher than the colloidal osmotic pressure values reported by Hargens (1971) for active temperate zone fishes (range 18–23 cm H_2O). Saltwater teleosts are hyposmotic and constantly face problems of water loss. Vascular pressure has been shown to increase transbranchial water loss in trout (Davie and Daxboek 1982). Our data suggest that the high vascular pressures in tunas would have the same effect. Thus, albacore may need to maintain higher colloidal osmotic pressures or have a specialized gill epithelia to mitigate water loss.

Estimates of cardiac output differ among species. They vary with activity state and temperature, and are also dependent upon the measurement techniques used (Metcalfe and Butler 1982). Size is also important (Schmidt-Nielsen 1984) and values for weight-specific cardiac output have been mostly obtained for fishes weighing less than 1 kg. Our cardiac output estimate for an 8.6 kg albacore (Table 3) is similar to that measured for this species by White et al. (in preparation, 33.8 ml/kg per min). However, for reasons given above, direct comparison of our data with other fish species is not easy. For example, the highest known cardiac output values are for restrained skipjack tuna (*Katsuwonus pelamis*, mean weight 1.6 kg, Stevens 1972). These were calculated by the Fick method and ranged from 50–80 ml/kg per min at 23–25 °C. In the case of resting non-tunas, values for rainbow trout (*Salmo gairdneri*, 0.2–0.4 kg, 15–30 ml/kg per min at 4–8 °C; Stevens and Randall 1967) and cod (*Gadus morhua*, 0.4–1.0 kg, 29.1 ml/kg per min at 10 °C; Pettersson and Nilsson 1980) are among the highest reported. Since weight-specific cardiac output declines with increased body size (Schmidt-Nielsen 1984) the above values decline when extrapolated to 8.6 kg. The metabolic rates of fishes are generally an order of magnitude lower than mammals yet the relationship between metabolic rate and body size in these two groups remains the same (Schmidt-Nielsen 1975) and it can be reasonably assumed that cardiac output and oxygen consumption are correlated (Schmidt-Nielsen 1984). Stahl (1967) worked out the mammalian relationship between cardiac output ($\dot{Q}_h$, in ml/min) and body weight (M_b, in kg) as

$$\dot{Q}_h = 187 M_b^{0.81}$$

Assuming that fish follow a similar relationship we calculated that the weight-specific cardiac output values for rainbow trout and cod would be 10 and 18 ml/kg per min respectively at 8.6 kg. That for a skipjack would be 43 ml/kg per min. Thus at comparable body sizes cardiac outputs of the two non-tunas are less whereas the cardiac output of the skipjack remains higher than albacore. The high cardiac output of skipjack may reflect errors inherent in the Fick calculation (Stevens 1972; Metcalfe and Butler 1982). It may also relate to the skipjack's higher metabolic rate (discussed in Graham and Laurs 1982). When the above equation is used to compare cardiac outputs of elasmobranchs at 8.6 kg (all weighing between 0.5 and 7 kg, Murdaugh et al. 1965; Metcalfe and Butler 1982), the values are lower than the albacore.

High heart rate, pericardial pulse pressure, and ventricular pressure are all indicative of high cardiac performance in the albacore. We are uncertain about the extent that restraint and anesthesia affect cardiac function. Thus, further work on free swimming albacore is needed to define the scope of its cardiac function.

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