

BLUEFIN TUNA WARM THEIR VISCERA DURING DIGESTION

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SUMMARY

Acoustic telemetry showed that stomach temperature from large bluefin tuna, *Thunnus thynnus*, held in an impoundment, changes markedly during feeding. The stomach cools rapidly on ingesting cold food. It then warms to a maximum of 10–15 °C above water temperature over a period of 12–20 h. Temperature decreases slowly over the next 20–30 h to a final state where it remains 3–6 °C above water temperature. The viscera are thermally isolated. Conductive heat losses are reduced by an overlying gas bladder and by the thick fatty muscle of the body wall. Convective heat losses are prevented by heat exchangers in the circulation. The temperature rise can be accounted for by heat released in the hydrolytic processes of digestion and by an increase in metabolic rate. The elevated temperatures should speed digestion and allow the tuna to feed frequently when food is abundant.

INTRODUCTION

Because of heat losses involved in aquatic respiration, the bodies of most fish are at water temperature. Bluefin tuna and certain other fishes are unusual in being warm. Their elevated body temperatures are made possible by a high rate of metabolic heat production and by an elaborate system of countercurrent heat exchangers that minimize convective heat loss through the circulatory system. The maximum temperature elevation (T_m) in red muscle of the bluefin varies in a predictable fashion with water temperature (T_w) from +2 °C in 30 °C water to +20 °C in 7 °C water:

$$T_m = 0.25 \times T_w + 25,$$

(Carey & Teal, 1969). The visceral organs of bluefin are also warm, but visceral temperatures show wide variation, ranging from as warm as the warmest muscle to just a few degrees above water temperature. In some previous acoustic telemetry

experiments where temperature was transmitted from free-ranging bluefin tuna stomach temperatures were held at several degrees above water temperature for periods of days. During the course of one such experiment stomach temperature increased from 3 to 10°C above water temperature during an 18-h period (Carey & Lawson, 1973). This warming was initiated after an event which suggested that the fish was feeding. It appeared that feeding could change the stomach temperature of the bluefin.

The establishment of a bluefin tuna ranching operation in St Margaret's Bay, Nova Scotia, Canada, provided an unusual opportunity to continue investigations of stomach temperature in these fish. St Margaret's Bay is a deep fjord-like bay just south of Halifax. Numbers of bluefin tuna come there for a brief period in early summer and are taken in mackerel traps (weirs). These tuna have just migrated from their spawning area in the Gulf of Mexico and are emaciated and of little commercial value when they arrive. By late summer the fish are fat and in prime condition for the Japanese market, but few are caught in St Margaret's Bay at that time. In the late 1970's a ranching operation developed in which tuna trapped early in the season were transferred to holding pounds and fed until the fall when they were fat enough to be sold on the fresh fish market in Japan. The pounds were about 50 m across, 15 m deep and made of heavy netting suspended on floats. During 1977 and 1978, each pound contained about 30 tuna, with a maximum of 98 in one larger pound. The existence of this commercial tuna holding operation gave dependable access to bluefin in a semi-natural situation and provided a unique opportunity to study them. It is important to appreciate, however, that the fish were owned by the fishermen and were very valuable. This limited our experiments to non-invasive techniques that would not injure or disturb the fish. Most of our measurements were made by feeding the tuna transmitters which broadcast their stomach temperature. Although we had no control over the fish or the water temperature, the situation enabled us to obtain continuous, accurate records of fish temperatures by telemetry and frequent measurements of water temperature. The results of these experiments allow a detailed description of the temperature variation with feeding in the bluefin.

MATERIALS AND METHODS

Water temperature

Surface water temperature at the pound was measured several times daily with a mercury thermometer. The location of the thermocline and deep water temperatures were determined by daily lowerings of a bathythermograph (Spilhaus, 1938). Water temperature selected by the fish was noted during frequent observations by divers. In one experiment an externally attached temperature transmitter provided an 8-day record of water temperature selected by the tuna.

Acute measurements of tissue temperatures

At harvest time in the fall it was possible to measure temperatures of internal organs in freshly killed tuna. The period of several hours between death and landing of the fish was too great for meaningful temperatures to be obtained after they were brought

shore. It was therefore necessary to work at the pound with the tuna still in the water tied to the side of our boat. The difficulty in reaching the various organs and the occasional entry of cold water into the body cavity caused problems with these measurements.

Telemetry of stomach temperatures

The acoustic transmitters sensed temperature with a thermistor and broadcast this information coded as a variable repetition rate of sound pulses (Kanwisher, Lawson & Sundnes, 1974; Carey & Lawson, 1973). The transmitters operated at one of three different frequencies, 32.7, 40 and 50 kHz. They were powered by replaceable lithium batteries and were cast in epoxy resin as a package 12 cm long, 3 cm diameter, and weighing 140 g in air, 53 g in water. The transmitter circuit was stable to voltage fluctuations and the calibration could be repeated to within 0.1 °C after an instrument had been in a tuna for 2 weeks.

The cylindrical listening hydrophones were mounted in 90° reflector cones which gave them a high sensitivity in one direction. They were held on the bottom about 100 m away from the pound so as not to interfere with the fishing gear. This signal was amplified some 200× by a pre-amplifier at the hydrophone and then led ashore through an armoured steel multiconductor cable which in some cases was as long as 600 m. A shelter on shore contained the receivers, recorder and power supply battery.

A three-channel receiver used tuned circuits to separate the 32.7, 40 and 50 kHz telemetry signals so that three different transmitters could be operated simultaneously in the same pound. The signal pulse was detected by a phase lock loop circuit. The output from the phase lock loop drove a tachometer circuit which produced a voltage proportional to the pulse rate. This analogue voltage was recorded on a strip chart recorder. Overall accuracy of the telemetry system was about ±0.2 °C but resolution was considerably greater. Further details are available from the authors.

Stomach contractions

Our limitation to non-invasive techniques and the ease with which transmitters could be placed in the stomachs of the tuna prompted us to develop a stomach contraction transmitter to monitor muscular activity of the stomach. A mechanical device was used rather than a pressure sensor for stomach contractions because the large hydrostatic pressure changes as the fish changed depth (1 atmosphere per 10 m) would mask the small pressure changes expected from stomach contractions. The contraction transmitter had a spring-loaded 12 cm long lever attached to one end so as to form an acute angle of about 25° with the case. The lever was mounted on the shaft of a potentiometer and when squeezed toward the body of the transmitter caused an increase in pulse rate. An increase in force from 20 g to 200 g on the end of the lever caused a linear increase in pulse rate from 33–46 min⁻¹. A force of 500 g just closed the lever and increased pulse rate to 50 min⁻¹. The transmitter spanned 8.5 cm with the lever open and 3.5 cm with it fully closed. For an experiment the contraction transmitter and a temperature transmitter were placed in mackerel which were tied together so that both could be fed to the same fish.

Feeding

The tuna were fed daily by the fishermen who owned the pounds. Large volumes of mackerel (*Scomber scomber*) and herring (*Clupea harengus* and *Pomolobus pseudoharengus*) were removed from freezers and partially thawed for feeding. The tuna became excited when the feed boat entered the pound and made the water boil as they were fed. The food was shovelled in rapidly at first, then more slowly as the tuna fed less readily. The feeding usually took less than 15 min. Weather permitting, the tuna were fed 6 days per week, usually between 10.00 and 16.00 h. The fishermen kept records of the number of tuna and amount of food fed in each pound.

RESULTS

Water temperature

St Margaret's Bay is a sheltered, deep water bay (average depth 70 m) which receives fresh water from a number of small rivers. The bottom water is cold even in July, but a warm surface layer develops in the summer. The surface layer is stabilized by a salinity gradient and is separated from the bottom water by a sharp thermocline. The surface layer above the thermocline was usually 12–17°C (Fig. 1). Below the thermocline water temperature fell to 6°C near the bottom in August 1977 and to 2°C in July 1978. Thermocline depth was typically about 7 m, but varied markedly from day to day as the wind blew the warm surface water away or piled it up. During the summer a wide range of water temperature was usually available to the tuna in the pounds. Near the end of August 1977 and 1978 strong winds mixed the water and the bay was isothermal from surface to bottom (Fig. 1).

When the tuna were not distracted, divers usually observed them steadily circling around the pound, swimming at the bottom of the warm surface layer just above the steep thermal gradient of the thermocline. They would readily pass through the thermocline when offered food by divers located in the cold water or when in pursuit

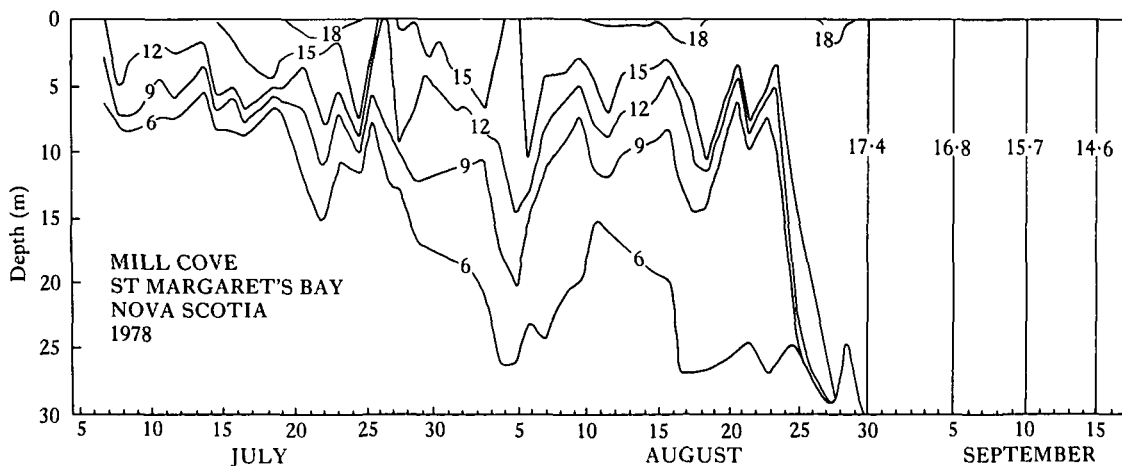


Fig. 1. Isotherm depth diagram from July to September 1978. 3°C isotherms were constructed from daily bathythermograph lowerings.

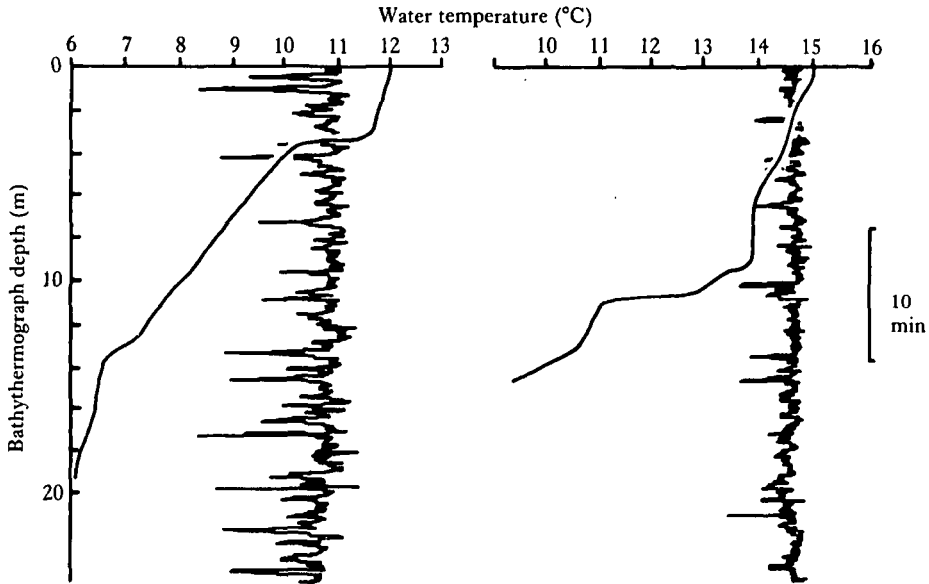


Fig. 2. Water temperature was telemetered from a bluefin tuna for an 8-day period. Portions of the telemetry record are shown here with superimposed bathythermograph traces to indicate the water temperatures available to the fish. On the left, a 40-min segment of the record starting at 19.20 h, 27 August 1977, shows that the tuna was usually in the thermocline. At the right, during a 40-min period starting at 11.30 h, 28 August 1977, the tuna was usually in the warm surface water.

of food shovelled in from the surface. An 8-day long telemetry experiment in which a temperature transmitter was attached to the skin of a tuna showed that it frequented the surface layer down to a position in the thermocline where the water temperature was several degrees below surface temperature (Fig. 2). This tuna preferred to swim in 13 to 14°C water (Fig. 3). Previous telemetry experiments with free-swimming bluefin tuna on the continental shelf off Nova Scotia showed a preference for location in the thermal gradient at the bottom of the surface mixed layer (Carey & Lawson, 1973; Carey & Olson, 1982).

Acute measurements of visceral temperatures

Our most successful attempt to measure temperatures of visceral organs in freshly killed tuna was on 14 October 1977. Twenty-four tuna were crowded into a seine where they struggled for 5–10 min. Then, at intervals of several minutes each in turn was seized with a gaff, and shot in the head with a shotgun. The heart and large surface vessels were opened to bleed them and the belly was slit to begin the cooling process. We held the tuna in the water alongside the boat and measured temperatures by reaching an arm's-length up into the body cavity with a thermistor probe. Temperature measurements on six tuna were made at times varying from 5–40 min after death (Table 1). The organs were identified by feel: the fibrous consistency of the caecum, the fragile texture of the liver, etc. The empty stomach was difficult to identify by touch, resulting in few measurements of its temperature. The tuna had been fed the previous day and while the stomach was empty, the caecal mass was full of fluid.

In another set of three fish we measured temperatures in the body wall. The wall

Table 1. *Temperatures in viscera of freshly killed tuna*

	Caecum	Stomach	Liver	
			Proximal	Distal
	26.4	—	20.1	23.5
	30.0	29.0	23.7	26.6
	28.1	26.5	—	24.6
	31.2	25.4	28.6*	23.7
	27.0	—	20.4	24.4
	27.3	—	21.7	23.7
\bar{X}	28.3 ± 1.9	26.9 ± 1.8	21.5 ± 1.4	24.3 ± 1.0
$\bar{X} \Delta t$	15.7	14.3	8.9	11.7

Water temperature 12.6°C
 *This is probably a caecal, not a liver temperature, and was omitted from the average.

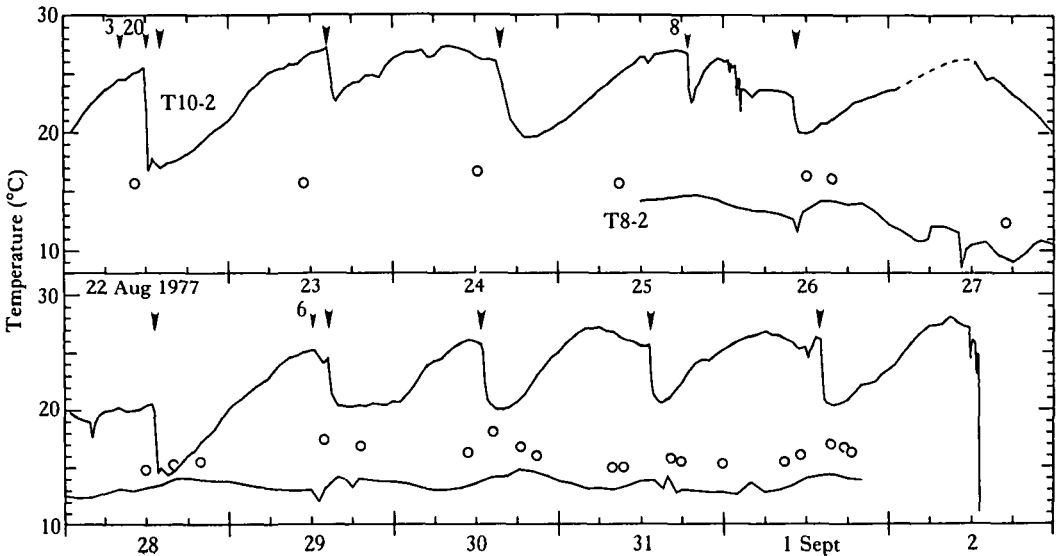


Fig. 3. Stomach temperature (T10-2) and water temperature (T8-2) from two different bluefin tuna. Stomach temperature drops on feeding, rises to a maximum after 12–18 h then slowly decreases. Preferred water temperature was usually several degrees cooler than surface water temperature. Small arrowheads with numerals indicate small feedings of known quantities (kg). Large arrowheads indicate large feedings. Open circles, (O) indicate surface water temperature. Time ticks at 6-h intervals.

of the body cavity was 7–9 cm thick and had a linear temperature gradient of $0.8^{\circ}\text{C cm}^{-1}$ from the 12°C water temperature at the skin to visceral temperatures of $18\text{--}20^{\circ}\text{C}$ at the peritoneal surface.

Telemetry experiments with stomach temperature

The tuna readily swallowed transmitters which had been tucked into mackerel and offered to them by divers. Continuous recordings of stomach temperature were obtained from nine tuna in 1977 and from six tuna in 1978 (Fig. 3). The longest record was from a 450-kg fish that retained a transmitter for 13 days in 1977 (record T10-2, Fig. 3). This fish was easily recognized by patches of damaged skin on its jaw and

prehead. It was a calm animal that would swim slowly by the boat and take fish from the hand. On one occasion we fed it 58 mackerel (20 kg) in the space of 1 h.

The stomach temperature recordings showed a repetitive pattern of cooling and warming. Stomach temperature drops sharply when cold food is ingested. It then starts to warm and temperature continues to rise over a 12- to 20-h period. After a maximum temperature is reached, the stomach starts to cool slowly, but the decline is usually broken by the sharp temperature drop of the next feeding.

The temperature decrease on feeding was rapid, with stomach temperature dropping 4–20°C over a 5- to 30-min period. The temperature decrease then slowed, reflecting a decreasing rate of ingestion and finally the end of feeding. Stomach temperatures recorded by the transmitter would sometimes drop to several degrees below water temperature when the tuna ingested frozen food. The extent of the temperature decrease depended on the food temperature and the amount of food eaten. Some extreme examples are shown in Fig. 4. In 1977 much of the food was still frozen solid when fed, whereas in 1978 it was usually thawed, the degree of thawing depending on the weather and the time of day that tuna in a particular pound were fed.

At the end of feeding, stomach temperature sometimes slowly continued to decrease for an hour or so (Fig. 3), and sometimes started to warm immediately (Fig. 4). Records kept by fishermen showed that the tuna regularly ate 20 kg of fish or more at a feeding. The observed temperature changes were probably influenced by the changing position of the transmitter in the mass of cold food. The telemetry records show a smooth increase in temperature continuing over a 12- to 20-h period. Early in the warming process, when the rate of temperature increase was fairly linear with

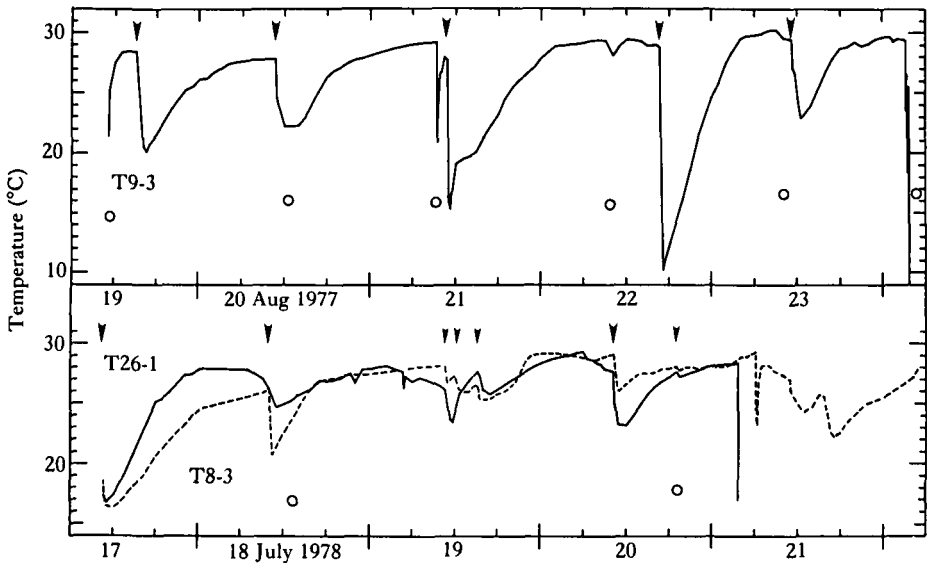


Fig. 4. Three telemetry records showing stomach temperature change on feeding. The upper panel shows stomach temperature excursions as great as 20°C when the tuna was fed large amounts of frozen food. The lower panel shows simultaneous records for two fish in the same impoundment. Temperature excursions were smaller in these tuna which were fed smaller amounts of thawed food. Large arrowheads indicate large feedings; small arrowheads indicate small feedings. Open circles (O) are surface water temperature. Time tics at 6-h intervals.

time, the stomach warmed $1.0 \pm 0.3^\circ\text{C h}^{-1}$ (eight individuals, 22 feedings). The average time required for temperature to rise to 63.2% of the value before feeding was 8.3 h (range 2–13 h). There was no obvious difference between warming rates for experiments early in the season in July, when the tuna were lean, or later in the season in August and October when they were fat. Inferring the size of the ration from the amount of food the fishermen placed in the pound and from the magnitude of the stomach temperature decrease, it appears that the rate of stomach temperature increase was greater after a large feeding than after small ones. The maximum temperature achieved varied from day to day and from individual to individual. Maximum temperature values of 15°C above surface water temperature occurred on two occasions. Temperature elevations of 14°C were common and the average maximum temperature was 13°C above surface water temperature. The actual temperature elevation was probably several degrees greater as the tuna were often in water cooler than surface temperature (Figs 2, 3).

After reaching a maximum temperature the stomach slowly cooled. The cooling phase of the temperature cycle was usually broken by the next feeding and is best seen in records for days when the tuna were not fed (Fig. 5). Cooling proceeded slowly and rather irregularly. By 36–48 h after the feeding the stomach temperature had reached a value of about 22°C or about 6°C above surface water temperature. About 1.5–2 days were required to complete the cycle of stomach temperature changes initiated by feeding.

Stomach contractions

Simultaneous recordings of stomach temperature and stomach contractions made on two tuna over the course of eight feedings showed that the amplitude of the stomach contractions varied during the feeding cycle (Fig. 6). There was usually a marked

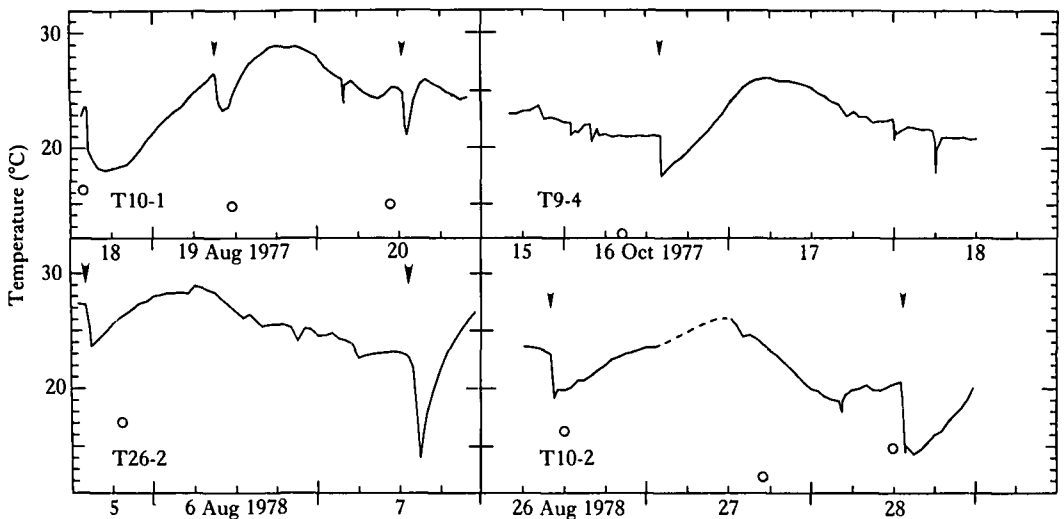


Fig. 5. Stomach temperature records showing the gradual cooling which occurs when the fish are not fed. Large arrowheads indicate large feedings; small arrowheads indicate small feedings. Open circles (○) are surface water temperature. Time ticks at 6-h intervals.

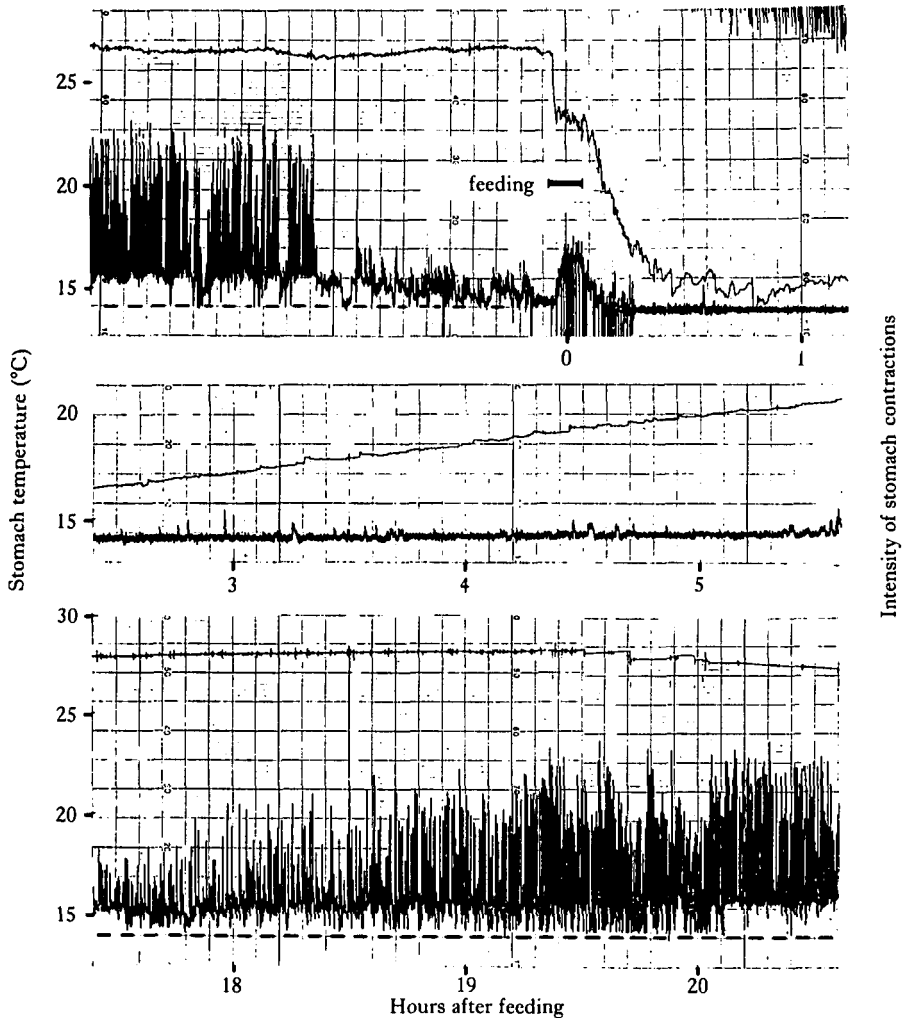


Fig. 6. Telemetry records showing stomach temperature (upper trace) and stomach contractions (lower trace). Strong contractions occur at the beginning of the record just before feeding. After feeding the stomach is quiet for a number of hours until small contractions begin. The contractions increase in amplitude and reach a maximum at about the time of the temperature maximum. During the strong contractions, the baseline rises, indicating that the stomach walls press in on the lever of the transmitter and prevent it from extending completely.

decrease in amplitude immediately after ingestion of food. The contractions remained small for a while, but slowly increased in size as stomach temperature rose. Large contractions were recorded after the stomach temperature had reached a maximum. At about this time the baseline of the record would often rise, indicating that the stomach had reduced enough in diameter (less than 8.5 cm) to prevent the lever from opening fully. During the first half of the feeding cycle when stomach temperature was rising the duration of the contractions was about 5–10 s and they came with a frequency that was more or less constant at 1–3 min⁻¹. During the latter half of the cycle, when maximum temperature had been reached and the contractions were large

Table 2. *Change in size of visceral organs relative to the change in weight and length of bluefin tuna during the 1978 fishing season*

Visceral organ	Early season 14 July–9 Aug	Late season 23 Sept–22 Oct	Increase (%)	Student's 't'
Liver (kg)	4.53 ± 0.34	7.79 ± 0.43	72	5.94
Stomach (kg)	3.31 ± 0.27	3.53 ± 0.10	6	0.75
Caecum (kg)	2.83 ± 0.18	7.25 ± 0.36	156	11.1
Gonad (kg)	2.90 ± 0.27	7.94 ± 0.48	174	9.20
Liver + stomach + caecum (kg)	10.7 ± 0.63	18.6 ± 0.72	74	8.28
Body (kg)	348 ± 9.05	452 ± 8.78	30	8.25
Total length (cm)	268 ± 2.97	267 ± 3.39	0	0.25

Sample size is 14 in both cases.
Values are means ± standard errors.

in amplitude, the pattern would sometimes change to slower, more prolonged contractions lasting 30–60 s.

Weights of visceral organs

The tuna were lean when they arrived in St Margaret's Bay, but gained about 30 % of their body weight during the time they were held in the pounds (Table 2). The weight increase was largely due to the accumulation of fat and there was no detectable increase in length of the fish. The visceral organs increased in size, with the combined weight of the stomach, liver and caecum increasing by 1.7 times. The stomach weight remained almost constant over the season, the liver weight increased by 1.7 times and the caecum weight increased by 2.5 times.

DISCUSSION

Variation in stomach temperature

This section presents estimates of magnitude for several sources of stomach temperature variance. The analysis was carried out by considering only the temperatures at times 00.00, 04.00, 08.00, 12.00, 16.00 and 20.00 h. Data for both years and for all fish were included.

Variation between years

Mean stomach temperature was $24.5 \pm 0.26^\circ\text{C}$ (s.e.) ($N = 171$) in 1977 and was slightly higher ($25.4 \pm 0.23^\circ\text{C}$, $N = 172$) in 1978. The grand mean for all data from all fish for both years is 25.0°C .

Variation between fish

There are clear individual differences in average stomach temperatures (Table 3). While the stomach temperatures in the simultaneous experiments in Fig. 4 are similar, the variation between individuals was often as large as that observed for maximum muscle temperatures (Carey & Teal, 1969) and is further evidence that this speci-

Table 3. Variation in mean stomach temperature of bluefin tuna

Year	Fish No.	Stomach temperature			Date of record
		X	S.E.	N	
1977	T10-1	27.49 ± 0.910		11	19-20 Aug
	T7-2	27.26 ± 0.680		14	14-17 Aug
	T9-2	26.29 ± 0.799		8	17-18 Aug
	T9-3	26.24 ± 0.642		28	19-24 Aug
	T7-3	26.17 ± 0.762		3	17 Aug
	T9-1	25.79 ± 0.489		15	14-16 Aug
	T7-1	23.38 ± 0.988		3	13 Aug
	T10-2	22.92 ± 0.362		71	21 Aug-2 Sept
	T9-4	22.38 ± 0.482		18	15-18 Oct
	Total	24.54 ± 0.257		171	
1978	T26-3	27.86 ± 1.042		12	24-27 Aug
	T26-4	26.60 ± 0.798		10	28-30 Aug
	T26-1	26.59 ± 0.481		28	16-21 July
	T10-3	25.83 ± 0.515		9	17-19 Aug
	T8-2	24.78 ± 0.342		71	15-29 July
	T26-2	24.58 ± 0.503		41	2-9 Aug
	Total	25.37 ± 0.234		172	
1977 and 1978	Total	24.96 ± 0.175		343	

Temperatures at 00.00, 04.00, 08.00, 12.00, 16.00 and 20.00 h were averaged for each fish.

does not maintain a narrowly controlled body temperature. In both 1977 and 1978, the warmest tuna stomachs were about 27°C. The coolest in 1977 was about 22°C and in 1978 it was about 25°C.

Variation during the day

The introduction of cold food on a regular feeding schedule generated a daily temperature cycle which persists even after averaging all the records. In both 1977 and 1978 the highest stomach temperature was observed at 08.00 and the lowest at 16.00. The feeding schedule of one large meal per day which drove this temperature cycle is probably an unnatural one. Normally the fish feed opportunistically and probably over a prolonged time each day. The temperature changes in wild bluefin tuna would not show the large and rapid temperature decrease from ingesting frozen food that is seen in experiment T9-3, Fig. 4. The natural temperature fluctuations are probably closer to those in experiments T26-1 and T8-3 in that figure. The viscera of wild fish do get as warm as the captive ones however (F. G. Carey, unpublished observations).

Variation during the season

There was no seasonal trend in the temperature elevation in the stomach during the season (Fig. 7, Table 3). The difference between maximum stomach temperature during the day and maximum surface water temperature gives only a conservative estimate of the ability of the tuna to raise its stomach temperature, since the tuna were

usually swimming in water several degrees cooler than the surface water (Fig. 2). The average excess temperature was 11.0°C (all data, $N = 74$) and did not change over the season. When the season was divided into 5-day periods and the average temperature for each period plotted, the variations generally reflected changes in water temperature. In 1977 there was a consistent decrease in stomach temperature during August with the September–October values being significantly ($P = 0.01$) lower than those in August. In 1978, the stomach temperature tended to increase slightly from mid-July to August, but the differences are small.

Variation with the weights of the visceral organs

The tuna are lean when they arrive in Nova Scotia, but they gain about 100 kg or 30% of the body weight during the time they are in the pounds. Much of this increase is due to fat deposited in the muscle and under the skin, but the visceral organs also increase in weight. An index of organ weights – obtained by dividing the weight of liver, stomach and caecal mass by the length of the fish to remove variation between fish – increased throughout the season (Fig. 7). This clear increase in weight of the digestive organs contrasts with the constancy of the temperature elevation and shows that the magnitude of the temperature rise is not related to the size of the viscera.

Anatomical considerations

Most of the organ systems of the bluefin tuna are supplied with blood through a rete mirabile, a mass of parallel, closely packed arteries and veins. The retia act as heat

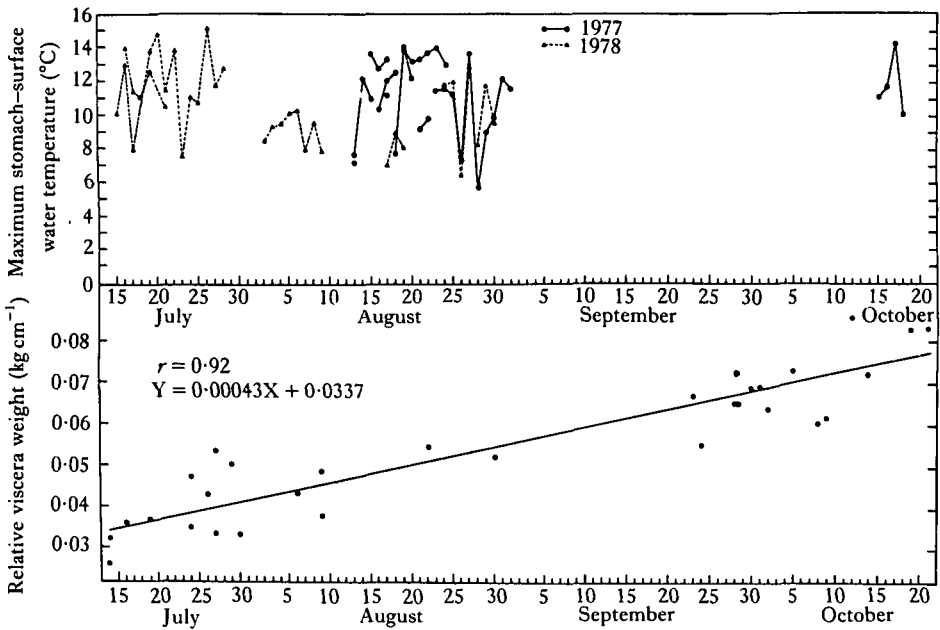


Fig. 7. The excess temperature, calculated as the difference between the maximum stomach temperature and surface water temperature each day, shows no seasonal trend, although the viscera grow in size. The ratio of visceral organ weight to total body length shows a clear increase during the season. Lines link records from individual fish.

Exchangers which transfer metabolic heat from the venous to the arterial blood, returning it to the tissues where its accumulation raises the temperature. Large retia are found in the circulation to the swimming muscles (Kishinouye, 1923) and certain of the visceral organs (Eschricht & Müller, 1835). No heat exchangers are apparent in the coronary circulation to the heart, or in the coeliac and renal arteries supplying oesophagus, liver or kidney. After giving rise to the hepatic arteries, the coeliac artery divides into masses of small parallel arteries which, with the accompanying veins, form a series of large retia on the posterior surface of the liver. These retia are illustrated in Fig. 8 and shown in cross section in Fig. 9. The small vessels coalesce on the distal side of the retia to form trunks that supply the stomach, caecum, intestine and spleen. Warm venous blood from these organs passes through the retia where its excess heat content is transferred to the cool, incoming arterial blood. The venous blood on the cardiac side of the heat exchangers is near water temperature as it enters the liver and the blood pumped by the heart is also cold. The retia constitute an array of individual thermal barriers arranged as shown diagrammatically in Fig. 10. Blood on the proximal or cardiac side of the heat exchangers is cold. The system makes an important contribution to the thermal isolation of the digestive organs and eliminates convective heat transfer from one organ system to another. Warm blood generated in the muscle for instance cannot be used to warm the stomach.

The digestive organs are also insulated against conductive heat transfer. The gas bladder is a flattened sac which covers the concave upper surface of the body cavity. An X-ray image of this structure was published by Magnuson (1973) and it appears in cross section in Fig. 9. This gas-filled space greatly reduces conductive heat transfer between the viscera and the warm hypaxial muscle. The wall of the visceral cavity is 7–9 cm thick. The large amount of fat within the muscle of the body wall gives this tissue a distinctly lighter appearance than the swimming muscle (Fig. 9). In a well-fed fish there is also a layer of fat just under the skin. The fatty body wall provides a thick mass of inactive tissue which reduces conductive heat transfer between the viscera and the water.

Source of heat

The temperature increase during digestion must be in part due to the heat released during hydrolysis of the food. The bluefin tuna in the holding pounds of St Margaret's Bay ate an average of 20 kg of food at each feeding. The food was mostly herring and mackerel, oily fishes with an approximate composition of 20 % protein, 15 % fat and very little carbohydrate (Mannan, Fraser & Dyer, 1961). The meal thus included 4 kg protein and 3 kg fat. The average formula weight per ester bond for a C^{18} triglyceride is 297 g and the heat of hydrolysis is $2.5 \text{ kcal mol}^{-1}$ of ester bond. The 3 kg fat will thus yield 25 kcal on hydrolysis. With an average formula weight per amino acid residue of 114 g the 4 kg of protein contains approximately 35 mol of peptide bonds. At 3 kcal mol^{-1} of peptide bond, 105 kcal will be released on hydrolysis of protein. Complete hydrolysis during digestion of the fat and protein in the 20 kg of mackerel should yield 130 kcal. This heat will raise the temperature of the visceral organs and their contents. If the effect is confined to the stomach, caeca and intestine, the 20 kg ration and the 11.7 kg of digestive organs will be warmed 5.1°C (assuming a specific heat of $1.8 \text{ cal }^\circ\text{C}^{-1}$). If losses to the exterior are neglected, the heat released during hydrolysis

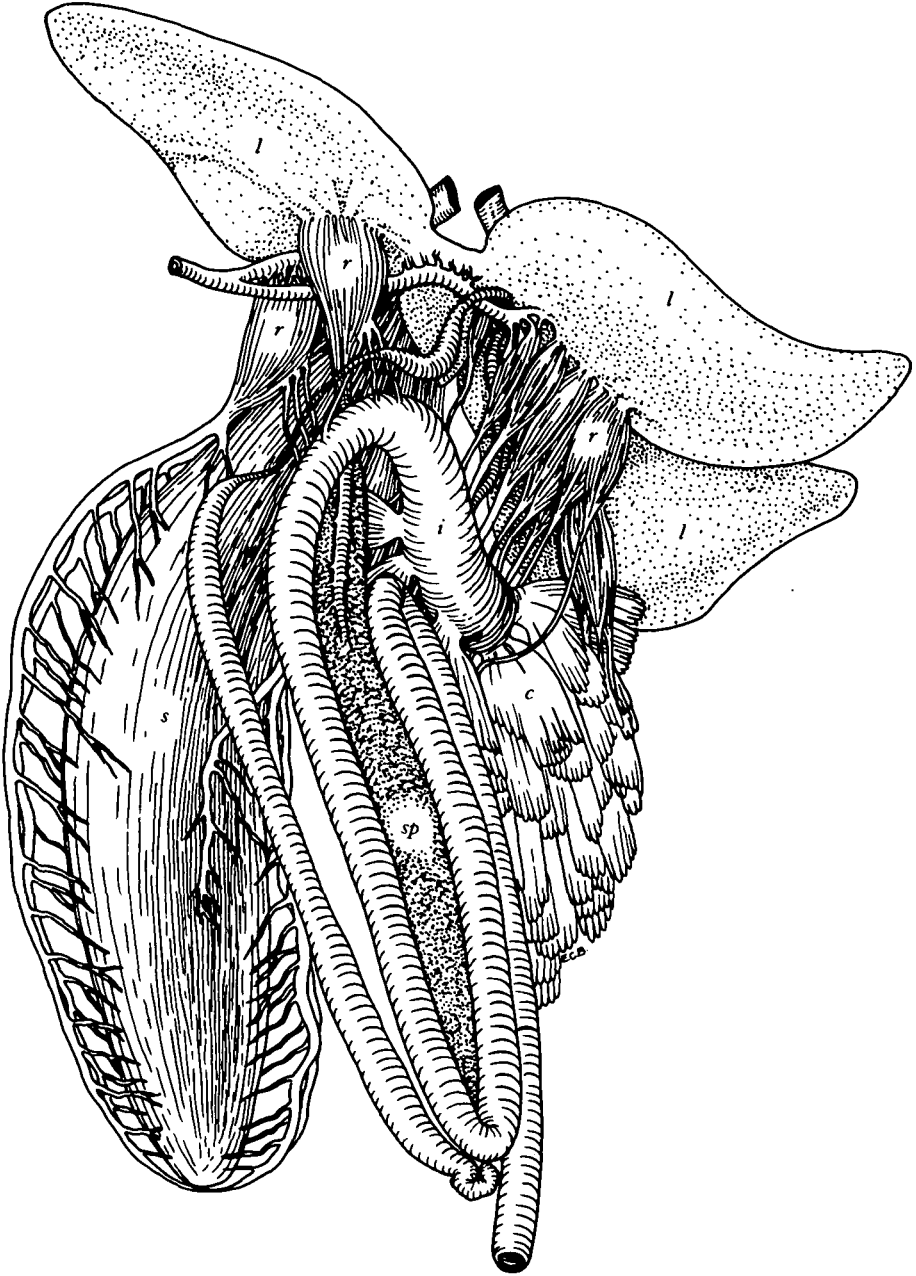


Fig. 8. Digestive organs and retia from a bluefin tuna redrawn from Eschricht & Müller, 1835. The large retia (*r*) behind the liver (*l*) supply blood to the stomach (*s*), intestine (*i*), spleen (*sp*) and pyloric caeca (*c*).

of ester and peptide bonds can account for between one-third and one-half of the observed temperature increase. Since there must be heat loss to the exterior, heat production by hydrolysis probably only accounts for a fraction of the rise in visceral temperature.

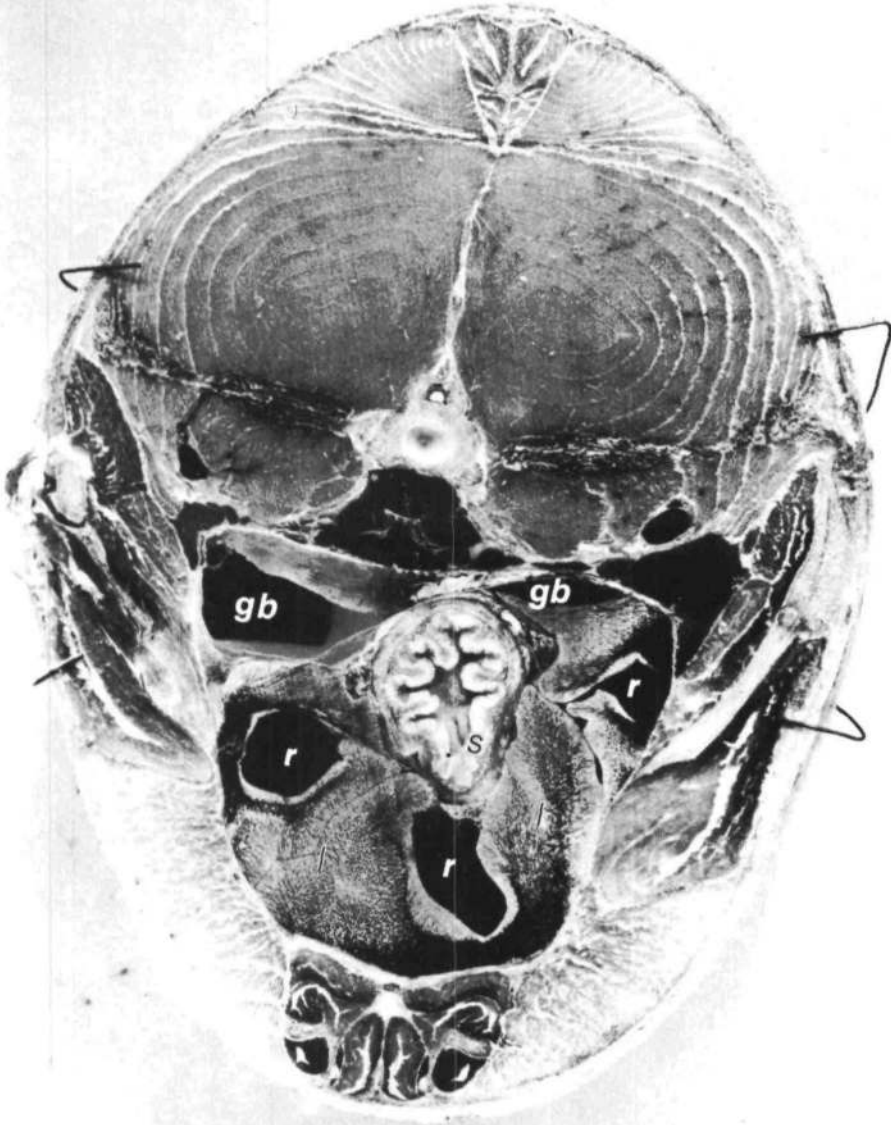


Fig. 9. Cross-section of a bluefin tuna just anterior to the origin of the pectoral fins. The viscera slumped to the right side as the tuna was frozen and the gas bladder (*gb*) which should extend evenly over the top of the body cavity, was pushed to the left side. The viscera are insulated from the warm swimming muscles by the gas bladder and from the cold water by the thick fatty muscle of the body wall. Blood is supplied to the visceral organs through a system of retia mirabilia (*r*) which are in three main groups on the back of the liver (*l*). The stomach (*s*) is thermally isolated in the centre of the fish.

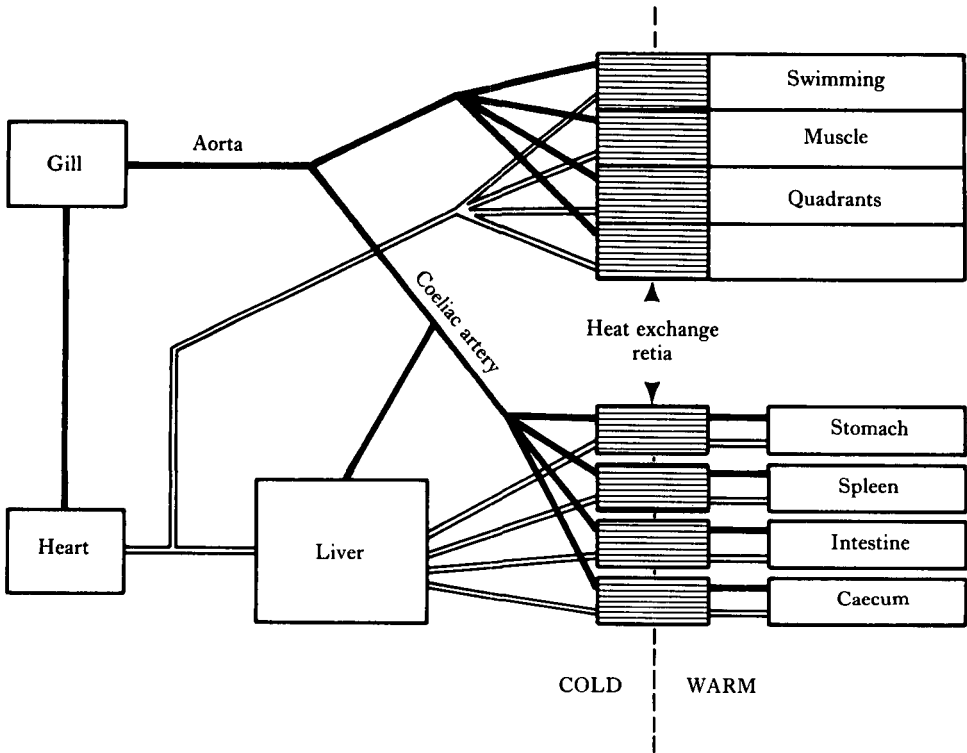


Fig. 10. Diagram of the circulatory system of a bluefin tuna. The heat exchange retia form a thermal barrier which prevents the blood from carrying heat away from the warm organs to be lost in the gills. Blood and tissue on the distal side of the rete is warm, that on the cardiac side is cool. Note that the heart and liver are on the cold side of the heat exchangers. Arteries, black; veins, white.

Heat increment and cardiac output

Oxygen consumption and metabolic heat production in animals often show a distinct increase after feeding. This phenomenon, variously termed calorogenic effect, heat increment or specific dynamic action, is common in fish. After feeding, oxygen consumption and metabolic heat production increase abruptly, rise to a maximum, then decrease slowly. The cycle may take from half a day to several days and the extent and duration varies from species to species. The effect is influenced by water temperature, is proportional to the quantity of food ingested, and is affected by food quality, with protein usually having the greatest effect (Muir & Niimi, 1972; Beamish, 1974; Smith, 1973; Smith, Rumsey & Scott, 1978; Brett & Groves, 1979). There may also be a behavioural component (Brett & Zala, 1975). The mechanical energy needed to process a meal also contributes some heat, but experiments with inert artificial diets show that this is a minor fraction of the effect (Tandler & Beamish, 1979). In fish the heat increment ranges from 4–40 % of the caloric value of the food ingested and is commonly 10–15 % (Brett & Groves, 1979).

The heat increment probably contributes to the post feeding temperature rise in the bluefin stomach. Because of the large size of the ration – 20 kg containing about 40 000 kcal – the 10–15 % heat increment commonly observed in fish represents a

great increase in metabolism. For a 5% effect, 2000 kcal would be released. This heat increment of 2000 kcal is enough to produce a 15°C temperature rise in 170 kg of tissue, assuming a specific heat of 0.8 cal °C⁻¹ and neglecting heat losses. This is much more than the mass of the viscera (11.7 kg) and the meal (20 kg).

A different estimate of metabolic heat production can be obtained by assuming that the viscera are a calorimeter. To the degree that the visceral organs are thermally isolated by heat exchangers, gas bladder and fatty body wall, the temperature rise can be viewed as the integral of metabolic activity (Carey *et al.* 1982). The initial warming of the stomach was more or less linear with time at a rate of 1.0°C h⁻¹. This requires a heat production of 0.8 kcal kg⁻¹ h⁻¹. Some of the heat is contributed by the heat of hydrolysis of peptide and ester bonds during digestion; 130 kcal generated in 31.7 kg of viscera and ration during a period of 16 h gives 0.26 kcal kg⁻¹ h⁻¹. The remaining 0.54 kcal kg⁻¹ h⁻¹ must be generated by aerobic metabolism and this would require a respiration rate of 108 ml O₂ kg⁻¹ h⁻¹. The viscera must be a rather poor calorimeter at best and significant amounts of heat which are lost to the environment by conduction through the tissues and by inefficiencies in heat exchange (Brill, Guernsey & Stevens, 1978; Neill, Chang & Dizon, 1976; Carey & Gibson, 1983) do not contribute to the rise in temperature. Because of such losses, the actual rate of respiration would probably have to be larger, perhaps 200 ml O₂ kg⁻¹ h⁻¹. To supply this oxygen from blood containing 0.18 ml O₂ ml⁻¹ blood requires a blood flow of 1.1 litre kg⁻¹ h⁻¹ passing through the viscera with a high efficiency of heat exchange. An oxygen utilization coefficient of 100% has been assumed here. With a more realistic coefficient or with a greater conductive heat loss, the respiration and blood flow required would be proportionately larger, but still within a reasonable range.

Site of heat generation

The pyloric caecum is the warmest visceral organ in tuna killed the day after feeding (Table 1). It is the largest digestive organ, contains enzymes of protein and fat digestion, and is active in fat absorption (Greene, 1913). The caeca were filled with a cloudy, viscous, yellow fluid and appeared to be still active at the time of maximum temperature, while the stomach appeared to be empty. The timing of the temperature increase implicates the caecum as a source of heat. Heat is probably also generated in the stomach itself. It has large blood vessels, a thick, active muscular coat and a heavy mucosal layer. The presence of heat exchangers would prevent the circulatory system from transferring heat from the caecum to the stomach. The organs are intimately associated however and in contact over a large area (Fig. 9) so that conductive heat transfer could occur between them.

The warm temperatures in the liver of dead tuna are surprising because the liver is on the cold side of the heat exchangers where it should be close to water temperature. The blood vascular system of the liver does not have the grossly obvious retia mirabilia found in the circulation to the caecal mass, stomach and intestine. In the dead tuna, the liver anterior to the pyloric caecum had a temperature elevation of 9°C while the liver lobes, which extend posteriorly between the body wall and other organs were warmer – 11°C above water temperature. In *Thunnus thynnus* and in *T. obesus* and *T. alalunga* the ventral surface of the liver shows a remarkable pattern of striations (Eschricht & Müller, 1835; Godsil & Beyers, 1944; Kishinouye, 1923).

formed by an array of parallel venous spaces. The anatomical connections of these veins have not been determined, but their number and arrangement suggest heat exchange. Unless some such undescribed system is operating in the liver however, it seems likely that in life the large volume of cool portal blood flowing from the heat exchangers serving the other visceral organs would keep the liver close to water temperature. The warm liver temperatures we measured might be a *post mortem* artefact caused by heat conducted from other visceral organs after death.

A second important aspect of our uncertainty about liver temperatures concerns the heat increment. In mammals, the heat increment produced by protein is closely associated with the liver (Buttery & Annison, 1973). In tuna, the stomach, pyloric caecum and intestine are warmer than the liver. This implies that the liver cannot be the major source of the heat that caused the temperature rise observed in these organs. The heat increment is probably generated in the caecal mass or the stomach itself, a situation quite different from that in mammals.

Temperature control

The stomach temperature cycle results from varying rates of heat production and heat loss. Our calculations indicate that a major fraction of heat production must be from aerobic metabolism with a smaller share from heat released by hydrolysis of fat and protein during digestion. The production of metabolic heat requires oxygen and is closely linked to heat loss. In the process of obtaining oxygen by aquatic respiration, the blood convectively transports metabolic heat to the gills where it is lost to the water. The tight linkage between the heat-generating processes of aerobic metabolism and the heat loss in obtaining oxygen by aquatic respiration minimizes the effects of metabolic rate on temperature. The heat increment with feeding is clearly an increase in heat production, but because supplying the extra oxygen required must involve a proportional increase in heat loss, it will not *necessarily* result in a temperature increase.

There are circumstances where increased metabolic heat production can result in an increase in temperature. More oxygen can be obtained without increased heat loss by increasing the fraction of oxygen extracted from the blood rather than increasing blood flow. This effect is limited to the usual range of oxygen utilization coefficients of about 0.5 in resting tissue to 0.8 in active tissues, but should allow a significant increase in temperature.

A change in balance between routes of heat loss can result in a rise in temperature with increasing metabolic rate. In a warm fish the two processes transferring heat to the environment are convection by the blood and conduction through the tissues. (There is no heat transfer by radiation or evaporation and we ignore the transfer of mechanical energy to the environment in swimming.) Convective heat losses occur when inefficiencies in the heat exchange process allow some heat to be lost to the water in the gills. The remaining heat loss is that conducted down a temperature gradient from the warm tissues to the water. Assume that each of these processes accounts for half of the total heat loss. If heat production in a steady state is $1 \text{ kcal kg}^{-1} \text{ h}^{-1}$, 0.5 kcal will be lost through the circulation and 0.5 kcal by conduction. If metabolic rate doubles to $2.0 \text{ kcal kg}^{-1} \text{ h}^{-1}$, heat loss through convection will also approximately double because of increased blood flow, and will rise to 1.0 kcal . Heat loss through

conduction will not change immediately and will remain at 0.5 kcal. The remaining 0.5 kcal of heat produced at the increased rate will be available for increasing tissue temperature. As tissue temperatures rise, the temperature gradient will steepen and conductive heat losses will increase until a new steady state is reached at a higher temperature. Thus when the heat exchangers are operating efficiently enough to maintain elevated tissue temperatures in the face of significant conductive heat losses, an increase in metabolic rate can result in an increase in body temperature.

Increased metabolic rate could also result in a lowering of tissue temperature. The efficiency of countercurrent heat exchangers is inversely proportional to flow. In order to achieve the observed temperatures, the exchangers must be very efficient. A simple calculation shows that for bluefin to maintain a temperature elevation of 15 °C with blood of an oxygen capacity of 0.18 ml O₂ ml⁻¹, a heat exchange efficiency of 93.6 % is required if all the oxygen is utilized and other routes of heat loss are insignificant (Carey & Gibson, 1983). With a more realistic coefficient of oxygen utilization and allowing for conductive heat losses, efficiencies in excess of 97 % are required. In this situation small decreases in efficiency can produce large decreases in temperature. The extra blood flow required to support an increased rate of metabolism might degrade the performance of the heat exchanger and actually decrease tissue temperature. The final effect on body temperature depends on a balance between factors that are difficult to evaluate. Experiments have been reported which illustrate both heating and cooling of tuna after an increase in activity. Skipjack may increase their body temperature when chased around the tank (Stevens & Fry, 1971) and albacore show a greater temperature elevation with increased activity (Graham & Dickson, 1981). Large bluefin tuna on the other hand were found to decrease their body temperature after a prolonged struggle on hook and line (Carey & Teal, 1969). Both an increase in efficiency of heat conservation and an increase in heat production are probably required to explain the temperature increase in the bluefin stomach after feeding.

Stomach contractions

The muscular activity of the stomach, as recorded with the contraction transmitter, showed a pattern that can be related to the feeding cycle (Fig. 6). After a large feeding, the transmitter soon ceased indicating contractions or showed only small ones. Following the rapid ingestion of food, some time would pass before gastric juices and enzymes were secreted in adequate amounts and digestion was well under way. While the stomach was distended with 20 kg of firm, undigested fish, there was little motion in the contents to depress the transmitter lever. After a period of 2–8 h, the instrument began to indicate small contractions. These grew in amplitude until the transmitter lever was being squeezed to the limit of its range at about the time temperature had reached a maximum. The contractions probably reflect the liquefaction of the food and serve to mix the stomach contents and to drive fluid out into the intestine and caeca. The strong contractions around the time of the temperature maximum probably represent the emptying of the remaining fluid into the intestine. Commonly the baseline would rise during this phase, indicating that the lever was never fully extended, but remained partially depressed as the stomach reduced in diameter and the walls pressed in upon the transmitter.

Regurgitation

Eventually the tuna expelled all of the transmitters. This usually happened at a time when the stomach was empty, a day or so after being fed. The tuna stomach is an elongated muscular sac with the intestine attached to the pyloric region near the oesophagus. The opening to the intestine is too small for the transmitter to pass through and the tuna expelled them by regurgitation rather than by defaecation. The first sign that the transmitter was going to come out was a series of cold pulses on the temperature record as seen on 26 August and 2 September in Fig. 3 and 20 August and 18 October in Fig. 4. These were probably caused by the tuna swallowing enough water to lower the stomach temperature briefly. If this persisted for several hours, it was usually followed by the transmitter being spat out. If the tuna was fed a few mackerel the cold pulses would stop and the transmitter would remain in place. The long records, as shown in Fig. 3, were obtained by feeding the fish when necessary to keep the transmitter in. It seems likely that regurgitation is a normal reaction and that tuna wait until their stomachs are empty of food to purge themselves of non-food items such as pieces of wood, seaweed, squid beaks and bones.

Utility of warm viscera

The warm temperatures in the viscera of the bluefin tuna should speed the processes of maceration, digestion, absorption and assimilation. The fishes and squid ingested are more rapidly penetrated by enzymes and soften faster at high temperatures. Stevens & McLeese (1984) have shown that an increase in temperature from 10–25 °C decreases the time for protein digestion with tuna trypsin and chymotrypsin to about one-third. A significant increase in the rates of the various other digestive enzymes can be expected at the 10–15 °C elevation of temperature achieved in the tuna stomach. To a certain extent the giant bluefin tuna appear to partition their yearly migration cycle in a fashion similar to that of the great whales. They spend the winter in tropical waters where they spawn, but feed little so that they are lean when they return to the rich northern waters for the summer. During the warm months they remain in an area where there is an abundance of food and increase rapidly in weight. The high visceral temperatures are probably important in allowing them to take maximum advantage of a food supply which may be only sporadically abundant. When the herring, mackerel, sand eels, etc. are available the tuna can process them rapidly and load enough fat onto their bodies to last them through the next migrations.

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