

Elevated red myotomal muscle temperatures in the most basal tuna species, *Allothunnus fallai*

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The present study tested the hypothesis that *Allothunnus fallai* can elevate its slow-oxidative red myotomal muscle (RM) temperature. Measurements on 30 *A. fallai* (750–850 mm fork length) captured by hook and line off the coast of southern New Zealand revealed that RM temperatures are elevated by mean \pm s.d. $8.1 \pm 1.3^\circ\text{C}$ (range 6.7–10.0 $^\circ\text{C}$) above the mean \pm s.d. ambient sea surface temperature $15.3 \pm 0.8^\circ\text{C}$ (range 14.3 to 16.4 $^\circ\text{C}$). These data provide evidence that the vascular modifications to the central circulation of *A. fallai* act as a counter-current heat exchanger and that RM heat conservation is a character state present in all extant tuna species.

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Key words: *Allothunnus*; endothermy; muscle; Scombridae; temperature; tuna.

INTRODUCTION

The tunas (tribe Thunnini) comprise a monophyletic group, which possess anatomical and physiological specializations that distinguish them from other members of the family Scombridae (Kishinouye, 1923; Collette & Chao, 1975; Collette, 1978; Graham & Dickson, 2000). Among the distinguishing characteristics of the tuna clade are the more anterior and axial position of the slow-oxidative red myotomal muscle (RM) and the presence of counter-current heat exchangers, which allow the conservation of metabolic heat within the RM, the eye and brain, and, in some species, the viscera (regional endothermy) (Carey & Teal, 1966; Carey *et al.*, 1971, 1984; Linthicum & Carey, 1972; Graham & Dickson, 2000; Sepulveda *et al.*, 2007).

Red muscle heat conservation has been documented for all tuna genera (*Auxis*, *Euthynnus*, *Katsuwonus* and *Thunnus*) except *Allothunnus*, a monotypic

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genus from the Southern Ocean (Serventy, 1948; Dickson & Graham, 2004). The most recent phylogenetic analyses have positioned *Allothunnus* as the most basal member of the tuna clade (Cressey *et al.*, 1983; Graham & Dickson, 2000; Collette *et al.*, 2001, Orrell *et al.*, 2006). Because *Allothunnus* is not commonly caught in present-day fisheries, few studies have focused on this scombrid and most of the published work has been based on morphological analyses of fresh and preserved specimens (Serventy, 1948; Nakamura & Mori, 1966; Collette & Chao, 1975; Collette, 1978; Yatsu, 1995; Graham & Dickson, 2000). Graham & Dickson (2000) found that both the RM morphology and the central circulation of the slender tuna *Allothunnus fallai* Serventy were similar to that of other tunas (*Auxis*, *Euthynnus* and *Katsuwonus*), but they interpreted the smaller quantity of RM, the relatively smaller size of the putative central heat exchanger and the absence of a lateral RM circulation and lateral heat exchangers to indicate a decreased specialization for RM heat conservation. Although recent evidence for cranial heat conservation has been reported for *A. fallai* (Sepulveda *et al.*, 2007), the hypothesis that this species can elevate the temperature of its RM remains untested and was therefore the focus of this investigation.

MATERIALS AND METHODS

All experiments were conducted under the guidelines of the University of Otago Animal Ethics Committee, Dunedin, New Zealand, and the Animal Care and Use Committee of the University of California, San Diego (Protocol # S00080), U.S.A. All experiments were performed following the guidelines of the 2000 Report of the American Veterinarian Medical Association Panel on Euthanasia.

Fishing operations and temperature measurement protocols have been previously described (Sepulveda *et al.*, 2007). Briefly, 30 *A. fallai* were caught by hook and line while they were foraging at the surface off South Island New Zealand from March to May 2001. Moderate tackle (18 kg monofilament) was used to reduce the time spent struggling on the line. For all specimens, the time from initial hook-set to the landing of the fish did not exceed 4 min in duration. The methods employed in this study follow those of previous postcapture thermal studies on other scombrid species (Barrett & Hester, 1964; Carey *et al.*, 1971; Schaefer, 1985; Dickson, 1994; Sepulveda *et al.*, 2007). Once landed, the fish were immediately pithed using a rigid thermocouple penetration probe (Barnant model 600; Barrington, IL, U.S.A.) to instantaneously sever the central nervous system. Simultaneous cranial (Sepulveda *et al.*, 2007) and red muscle temperature (T_{RM}) measurements were taken using two independent digital thermocouple thermometers (Barnant model 600). All T_{RM} measurements were taken at the same body position, with the probe introduction point in the dorsal musculature below the insertion of the first dorsal fin and along the body midline. This site corresponds to the position of maximum RM in *A. fallai* (Graham & Dickson, 2000). After the highest RM temperature reading was recorded, the seawater surface temperature (T_{SS}) was also measured using the same thermocouple (all fish were caught at the surface). The difference between T_{RM} and T_{SS} provided the excess RM temperature ($T_{XRM} = T_{RM} - T_{SS}$). For all experiments, air temperatures were lower than the T_{SS} . After each field experiment, thermocouple calibration was verified in the laboratory with a standard mercury thermometer.

RESULTS

Postcapture T_{RM} data were obtained for 30 *A. fallai* ranging in size from 755 to 850 mm fork length (L_F) and 5.6 to 10.6 kg (Table I). All specimens had

TABLE I. Body size, postcapture red muscle temperature (T_{RM}) and sea surface temperature (T_{SS}) data for *Allothunnus fallai*

L_F (mm)	Mass (kg)	T_{RM} ($^{\circ}$ C)	T_{SS} ($^{\circ}$ C)	T_{XRM} ($^{\circ}$ C)
710	5.6	23.7	14.3	9.4
740	8.2	21.6	14.8	6.8
750	4.9	23.8	14.3	9.5
760	7.0	23.2	14.7	8.5
760	7.5	22.7	14.6	8.1
760	7.5	22.2	14.9	7.3
760	5.5	21.7	14.9	6.8
780	6.9	21.6	14.9	6.7
780	6.4	24.0	14.9	9.1
790	8.0	24.7	16.4	8.3
790	8.2	23.2	15.8	7.4
790	9.3	24.1	16.0	8.1
790	8.2	23.6	14.3	9.3
800	8.0	24.3	15.0	9.3
800	8.0	23.3	16.3	7.0
800	8.0	24.6	16.4	8.2
800	9.0	24.8	16.2	8.6
800	7.3	22.3	14.3	8.0
810	9.0	25.8	15.8	10.0
810	9.3	23.4	16.3	7.1
810	7.8	23.0	15.9	7.1
820	8.5	21.9	14.8	7.1
820	7.9	23.4	14.6	8.8
820	8.2	23.5	16.0	7.5
840	9.5	24.7	16.3	8.4
840	8.5	22.4	14.9	7.5
850	10.6	24.7	16.4	8.3
850	9.8	23.9	14.6	9.3
850	9.0	24.3	14.6	9.7
870	10.3	24.0	14.9	9.1
Mean \pm s.d.				
800 \pm 35	8.1 \pm 1.3	23.5 \pm 1.1	15.3 \pm 0.8	8.2 \pm 1.0

L_F , fork length; T_{XRM} , T_{RM} - T_{SS} .

a T_{RM} that was higher than T_{SS} (Fig. 1). The mean \pm s.d. T_{RM} was $23.5 \pm 1.1^{\circ}$ C taken in surface waters ranging from 14.3 to 16.4° C (mean \pm s.d., $15.3 \pm 0.8^{\circ}$ C). The T_{XRM} values ranged from 6.7 to 10.0° C with a mean \pm s.d. of $8.2 \pm 1.0^{\circ}$ C (Fig. 2).

DISCUSSION

The finding of elevated RM temperatures for *A. fallai* confirms that the small vascular plexus within the haemal arch described by Graham & Dickson (2000) functions as a central counter-current heat exchanger and identifies RM heat

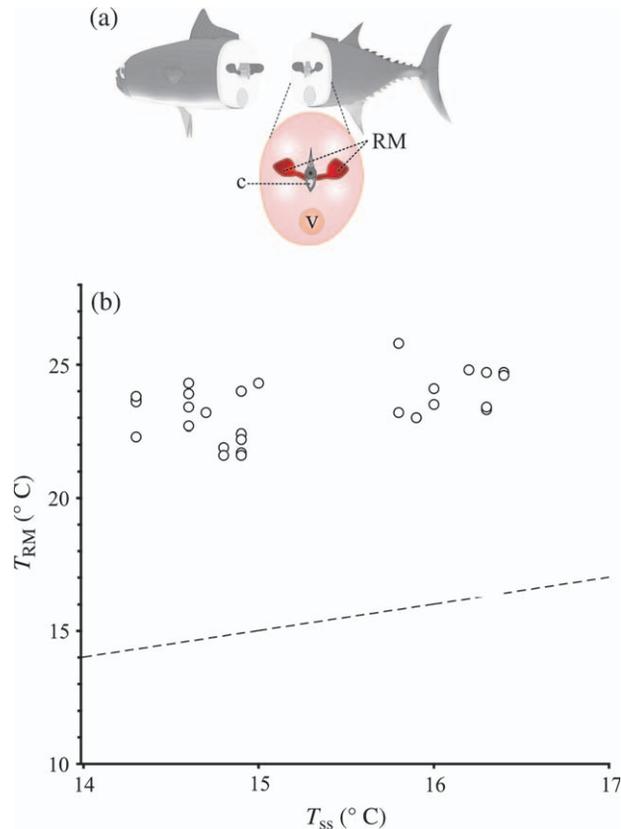


FIG. 1. (a) Three-dimensional image of *Allothunnus fallai* sectioned at 50% fork length (L_F). Transverse section shows the position of the red muscle (RM), the central rete (C) and viscera (V). (b) Mean \pm s.d. postcapture RM temperature (T_{RM}) for 30 *A. fallai* (○) (8.1 ± 1.3 kg body mass) collected at a mean \pm s.d. sea surface temperature (T_{SS}) of $15.3 \pm 0.8^\circ\text{C}$ (-----, the line of equality).

conservation as a shared, derived trait of the Thunnini. These findings, coupled with the presence of cranial heat conservation in this species (Sepulveda *et al.*, 2007), suggest that regional endothermy is an adaptation to the cool ambient conditions experienced throughout the southerly range of this species (Block & Finnerty, 1994; Yatsu, 1995).

Studies on the morphology of the heat exchanger of *A. fallai* suggested that its capacity for heat conservation should be less than that of the other tunas because of its small size and lower mean artery:vein ratio and larger vessel diameters (Graham & Dickson, 2000). Unlike the other tuna genera, which possess either cutaneous (lateral) retia [*Thunnus thynnus* (L.), *Thunnus obesus* (Lowe) and *Thunnus alalunga* (Bonnaterre)] or a combination of cutaneous and central retia [*Auxis* sp., *Euthynnus alletteratus* (Rafinesque), *Katsuwonus pelamis* (L.), *Thunnus albacares* (Bonnaterre), *Thunnus atlanticus* (Lesson) and *Thunnus tonggol* (Bleeker)], *A. fallai* only has a small central rete (Graham & Dickson, 2000, 2004; Orrell *et al.*, 2006). Other *A. fallai* characteristics that are also suggestive of a reduced capacity for RM heat conservation include

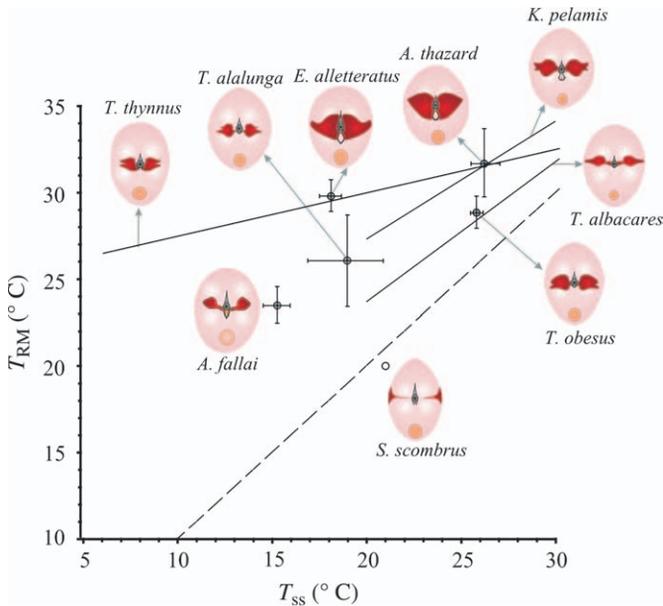


FIG. 2. Postcapture red muscle (T_{RM}) temperature (T_{RM}) data plotted against sea surface temperature (T_{SS}) in selected scombrids. Transverse section for each species shows RM and viscera position at c. 50% fork length (L_F). The T_{RM} data are shown as mean \pm s.d. for slender tuna, *Allothunnus fallai* [$n = 30$, 4.9–10.6 kg body mass (this study)], frigate tuna *Auxis thazard* (Lacepède) [$n = 1$, 0.90 kg body mass (unpubl. data) and $n = 6$, 0.74–0.82 kg body mass (Schaefer, 1985)], little tunny *Euthynnus alletteratus* (Rafinesque) [$n = 16$, 4.5–13.6 kg body mass (Linthicum & Carey, 1972)], albacore tuna, *Thunnus alalunga* (Bonnaterre) [$n = 10$, 4.8–12.3 kg body mass (Graham & Dickson, 1981)], bigeye tuna *Thunnus obesus* (Lowe) [$n = 13$, 6–15 kg body mass (unpubl. data)] and Atlantic mackerel *Scomber scombrus* L. [< 3 kg body mass (Linthicum & Carey, 1972)]. Linear regressions are shown for *Thunnus thynnus* (L.) ($n = 121$, 68–362 kg body mass; $y = 24.94 + 0.25x$) (Carey & Teal, 1969), skipjack tuna *Katsuwonus pelamis* (L.) ($n = 53$, 2.0–3.5 kg body mass; $y = 13.7 + 0.68x$) (Carey & Teal, 1969) and yellowfin tuna *Thunnus albacares* (Bonnaterre) ($n = 62$, 3–14 kg body mass; $y = 7.47 + 0.81x$) (Barrett & Hester, 1964) (-----, the line of equality).

a low relative amount of RM (4.8% of total body mass, one of the lowest values recorded for tunas, which range from 4.1 to 13.0%; Graham *et al.*, 1983; Graham & Dickson, 2000) and a smaller relative heart size (0.28% *v.* 0.33–0.81% body mass; Graham *et al.*, 1983; Graham & Dickson, 2000). Despite these characters, the postcapture T_{RM} data for *A. fallai* was found to be similar to those of other tunas in which T_{RM} (obtained using similar methods) has been shown to range typically between 22 and 30°C (Fig. 2) (Barrett & Hester, 1964; Carey *et al.*, 1971; Stevens & Fry, 1971; Linthicum & Carey, 1972; Graham & Dickson, 1981; Schaefer, 1985; Dickson, 1994).

Explanations for the similar T_{XRM} recorded in *A. fallai* and other tuna species must consider that the T_{RM} data for *A. fallai* were collected at cool ambient conditions (*i.e.* T_{SS} of 14.3–16.4°C), whereas most of the previous data on postcapture tuna muscle temperatures have been recorded for fishes in warmer waters (T_{SS} ranging from 18 to 30°C) (Fig. 2) (Carey *et al.*, 1971; Stevens & Fry, 1971; Linthicum & Carey, 1972; Schaefer, 1985; Dickson, 1994). It has been shown that, when in warmer waters, tunas (including the more derived

members of the clade which possess morphologically more complex heat exchangers) may exhibit a lower T_{XRM} in order to maintain T_{RM} within an optimal operating range (22–30° C; Fig. 2). Support for this comes from *in vivo* studies that have shown tunas to use both behavioural and physiological thermoregulation to control body temperature (Carey & Teal, 1969; Carey & Lawson, 1973; Graham & Dickson, 1981; Holland *et al.*, 1992; Dewar *et al.*, 1994; Stevens *et al.*, 2000; Kitagawa *et al.*, 2001, 2006, 2007; Marcinek *et al.*, 2001; Musyl *et al.*, 2003; Teo *et al.*, 2007). Additional support for this comes from *in vitro* studies on *T. albacares* that show enhanced RM contractile performance (*e.g.* increased power output and higher cycle frequencies) at this temperature range (25–30° C) (Altringham & Block, 1997; Syme & Shadwick, 2002).

While T_{RM} provides the *in situ* operating temperature of the muscle, a critical component for muscle performance studies, T_{XRM} is the value more commonly used to assess and compare endothermic capacity (Stevens & Neill, 1978; Dickson, 1994). Although often a benchmark for comparison, T_{XRM} represents a variable measurement that is dependent upon the ambient conditions, including the immediate diving history of the animal. Even though the T_{XRM} data of this study are from wild-caught fish that underwent a variable degree of struggle before capture, this study reports a relatively narrow T_{XRM} range (6.7–10.0° C) for all specimens tested. Although muscle temperature studies on tunas have shown that acute exercise may increase body temperature (Stevens & Neill, 1978; Dewar *et al.*, 1994; Dickson, 1994), the maximum T_{XRM} reported for exercised ectothermic fishes is only 2.7° C (Dickson, 1994). Hence, although the thermal data presented in this study are from exercised fish and thus may be an overestimate of the steady-state T_{RM} experienced in the wild, the values are on average 5.5° C above the maximum value recorded for any exercised ectothermic species.

The T_{XRM} data from postcapture individuals, like those of this study, are clearly confounded by the act of capture and boat side handling, both of which can significantly affect heat production and retention (Brill *et al.*, 1994). From the present study, it is not possible to fully assess the degree to which *A. fallai* is specialized for RM heat conservation or whether this species is capable of physiological thermoregulation. These data do, however, provide the first evidence for RM heat conservation in this poorly studied species.

TUNA BIOGEOGRAPHY

The geographical distribution and the extent to which fishes are specialized for regional endothermy have been used to support the hypothesis that niche expansion was an important selective force in the evolution of this trait in both the tunas and the lamnid sharks (Carey *et al.*, 1985; Block *et al.*, 1993; Block & Finnerty, 1994). The finding of RM heat conservation for *A. fallai* not only supports the niche expansion hypothesis but also raises additional questions regarding the geographical distribution of *A. fallai* and its phylogenetic placement as the most basal tuna species (Cressey *et al.*, 1983; Graham & Dickson, 2000; Collette *et al.*, 2001; Orrell *et al.*, 2006). Certainly, the ability to elevate T_{RM} could have been selected for in the cold waters of the Southern Ocean, but how the evolution of regional endothermy occurred within the tuna clade

becomes less clear when the very different geographical distribution of *A. fallai* (between 20 and 45° S; Nakamura & Mori, 1966; Yatsu, 1995) is compared to the tropical and sub-tropical distributions of the other tuna genera with similar central heat exchange systems (*Auxis*, *Euthynnus* and *Katsuwonus*). According to hypotheses based on the fossil record, the radiation of the tunas from the tropics would result in the most basal members of the Thunnini having the strongest affinity for low latitudes, whereas only the more derived members of the group would have radiated into colder habitats (Graham & Dickson, 2004). *Allothunnus fallai* larvae occur in relatively cold waters (latitudes between 20 and 30° S; Watanabe *et al.*, 1966), and the adults have not been shown to migrate to warm waters to spawn. Therefore, it seems that *A. fallai* is the only tuna to have broken its ancestral link to warm waters for reproduction.

This study documents RM heat conservation for *A. fallai* and thus strengthens the phylogenetic hypotheses that align *Allothunnus* with the other tunas by identifying an additional character state that can be uniformly used to describe the Thunnini. Although structural differences are present between *A. fallai* and the other tunas in both the RM heat exchange system (reliance solely upon a central circulation) and the cranial heat production and retention mechanisms, the extent to which *A. fallai* elevates both T_{RM} and cranium temperature ($T_{Cranium}$) is comparable to that of the other members of the Thunnini. This study further adds to the understanding of the evolution of regional heat conservation in tunas and also raises new questions concerning the adaptive significance of this specialization.

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