Effect of temperature on isotonic twitch of white muscle and predicted maximum swimming speeds of skipjack tuna, *Katsuwonus pelamis*

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Synopsis

Latent period, rise time, contraction time, and half relaxation time from isotonic contractions of isolated white muscle samples from skipjack tuna, *Katsuwonus pelamis*, were determined at 20°, 27°, and 34° C. These parameters were found to be inversely proportional to temperature (Q_{10} = 1.47, 1.67, 1.62, and 1.72, respectively). The data show that contraction time and the effect of temperature on contraction time of skipjack tuna white muscle are not unique when compared to other equal-sized teleosts. Based on contraction time, maximum swimming speeds at each muscle temperature were calculated and found not significantly to exceed the maximum speeds of other equal-sized teleosts, when comparisons are made at the same white muscle temperatures.

Introduction

Descriptions of the specialized vascular anatomy (the countercurrent heat exchangers or so-called 'rete mirabile') of tuna have been available for over 50 years (Kishinouye 1923). In spite of numerous measurements of muscle temperatures and thermal profiles (reviewed in Stevens & Neill 1978), the biological significance of tuna's specialized vascular anatomy and resultant elevated muscle temperatures has not yet been empirically defined nor quantified.

Temperature has multiple effects on muscle contraction. Higher temperature causes a higher rate of T

tubule inward transmission, increased rate and possibly amount of Ca^{+2} release from the terminal cisternae, faster Ca^{+2} diffusion to the actin and myosin overlap zone (A band), and increased rate of Ca^{+2} uptake by the sarcoplasmic reticulum. The higher levels of Ca^{+2} cause more actin sites to become available for combination with myosin (i.e., more actin-myosin cross bridges), and higher rates of cross bridge cycling (reviewed by Fuchs 1974). Therefore, the overall effects of higher muscle temperature are shorter latent period, increased speed of contraction at a given load, increased intensity of active state, decreased duration of the active state plateau, and faster tension decay (Truong et al. 1964, Close & Hoh 1968, Gabel et al. 1968, Podolsky 1968).

Power is defined as force times velocity. Higher muscle temperatures cause increased speed of contraction, hence (assuming force stays constant with increasing speed), increased power output per contraction (Binkhorst et al. 1977). Higher muscle temperatures also permit higher frequencies of contraction, and hence, increased average power output during repeated contractions (such as swimming).

It is, therefore, reasonable to conclude that tuna evolved their specialized circulatory system and elevated muscle temperatures to increase muscle power output (as suggested by Carey et al. 1971). Carey (1973) and Graham (1975) have specifically argued that the elevated muscle temperatures and external morphological adaptations of tuna evolved to increase maximum swimming speeds (see also Walters 1962) and that tuna are capable of exceptional maximum speeds. Yet Walters & Fierstine

(1964) have shown that the maximum speed of wahoo, *Acanthocybium solandri*, is nearly identical to the maximum speed of equal-sized yellowfin tuna, *Thunnus albacares*, even though the former species does not have the specialized circulatory system required to maintain muscle temperature significantly above ambient temperature (Collette 1978). Furthermore, Blaxter & Dickson (1959) and Brett (1964) reported that the measured maximum swimming speeds of several teleost species are temperature independent. However, their data are hard to reconcile with evidence that the average power available from isolated teleost muscle samples (and, therefore, predicted maximum swimming speed) is indeed inversely proportional to temperature (Wardle 1975, 1977).

For the following reasons, we feel it is an open question whether tuna are unique with respect to their maximum swimming speeds, and whether their specialized vascular anatomy evolved to permit higher maximum speeds. First, widely different techniques have been employed to measure the maximum swimming speeds of different species (Blaxter 1969). Second, fish size and water temperature are often either not reported, or not known with certainty. Third, the definition of maximum (or burst) speed is not consistent throughout the literature. Bainbridge (1958) defines burst speed as the highest swimming speed maintained for at least one minute. But the maximum speeds of yellowfin tuna and wahoo, given by Walters & Fierstine (1964) were maintained for less than one second. Moreover, the measurements of tuna's burst speeds were taken in water at 24—27° C. The maximum swimming speeds of other teleosts are generally measured in water 10—20° C (Blaxter 1969).

Our study was undertaken to determine the effect of temperature on several parameters of the isotonic twitch of white muscle samples from skipjack tuna, *Katsuwonus pelamis*. Using a technique presented by Wardle (1975), we use our results to predict maximum swimming speeds at various muscle temperatures, and in this way, quantify the relationship between muscle temperature and predicted maximum swimming speed.

Materials and methods

Skipjack tuna, purchased from local fishermen, were maintained at the Kewalo Research Facility of the National Marine Fisheries Service. Nakamura (1972) provides details on capture and handling.

200

Five fish were used; each was removed from its holding tank, brought into the laboratory, and placed in a plexiglass trough lined with foam rubber. A hose with running seawater (24° C) was inserted into the fish's mouth. The spinal cord was cut immediately behind the skull, and the wound packed with Gel-Foam (Upjohn Pharmacueticals)[3] to minimize bleeding. The animal was then rested for 1 hour before muscle samples were removed.

Samples consisted of muscle blocks approximately 2 x 1 x 1 cm. (The long axis of the block corresponded to the anterior-posterior axis of the fish.) The muscle blocks were impaled on two stainless steel stimulating electrodes mounted on a micromanipulator. The stationary electrode was fashioned from the barrel of a 15-gage hypodermic needle, the second (movable) electrode was a solid stainless steel needle (0.1 mm maximum diameter). The distance between the electrodes was slightly adjusted as required to fit the length of the muscle blocks. Both electrodes were insulated to the tip. Square wave, direct current pulses (10—100 V, 1 ms duration) were used to stimulate the muscle.

The movable electrode was connected by a short length of nylon thread to an isotonic, photoelectric force transducer (Myograph A, #705—001, Narco Biosystems, Houston, TX). Transducer output was displayed on a storage oscilloscope and photographed with a 35 mm camera. The photographs were analyzed on a microfilm reader.

During testing, muscle blocks were immersed in a temperature regulated bath containing tuna muscle Ringer's solution.[4] Test temperatures were 20°, 27°, and 34° C (± 0.2° C), which approximately span skipjack tuna's thermal habitat (Blackburn 1965). To change temperature, the bath was drained and refilled with fresh Ringer's solution at the appropriate

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[3] Reference to trade names does not imply endorsement of the product by the National Marine Fisheries Service, NOAA.

[4] The Ringer's solution used in this study was based on Saither and Rogers (1967) and Hudson (1968). Ion concentrations approximate tuna plasma.

Salt	Weight (g)
NaCl	10.85
KCl	0.382
CaCl$_2$. 2H$_2$O	0.556
MgCl$_2$. 6H$_2$O	0.226
NaHCO$_3$	1.26
NaH$_2$PO$_4$. H$_2$O	0.413
Glucose	1.00

Distilled H$_2$O to 1 liter

temperature. The muscle block was left for 2–3 minutes at the new temperature before testing was resumed. Temperature sequence was randomized. Five to seven twitches were recorded at each temperature, and muscle blocks were discarded after being tested at all three temperatures. No more than 10 muscle samples were taken from any one fish.

Results

Effect of temperature on the isotonic twitch

Four measurements were taken from each oscilloscope tracing of a single twitch: (1) the time from stimulation to the maximum height of contraction (contraction time); (2) the time from stimulation to the onset of contraction (latent period); (3) the time from the onset of contraction to maximum height of contraction (rise time) (note, contraction time = latent period + rise time); and (4) the time from maximum height of contraction to one-half maxi-

mum height of contraction (half relaxation time).

Increased temperature caused reduced contraction times because of a significant reduction in both latent period and rise time (Fig. 1). The causes of the significant interfish differences in contraction time, within each test temperature, are not known. These differences are not, as might be expected, due to fish size (Hill 1956). The skipjack tuna used in this study ranged from only 36.6 to 42.9 cm fork length and are numbered in order of decreasing size (Table 1).

Figure 2 shows that half relaxation time is also inversely proportional to temperature.

The Q_{10} values, based on measurements made at 20° and 34° C are listed in Table 1. Apparently temperature has a smaller effect on latent period than on the other parameters. The Q_{10} for contraction time (and, therefore, predicted maximum swimming speed) was 1.62.

Predicted maximum swimming speeds

Contraction time is used to predict maximum swimming speed based on the following assumptions: (1) white muscle is used for high speed swimming (Bone 1975); (2) tail beat amplitude is independent of swimming speed; skipjack tuna, therefore, move a constant fraction of their body length per tail beat cycle (Bainbridge 1958, Hunter & Zwiefel 1971,
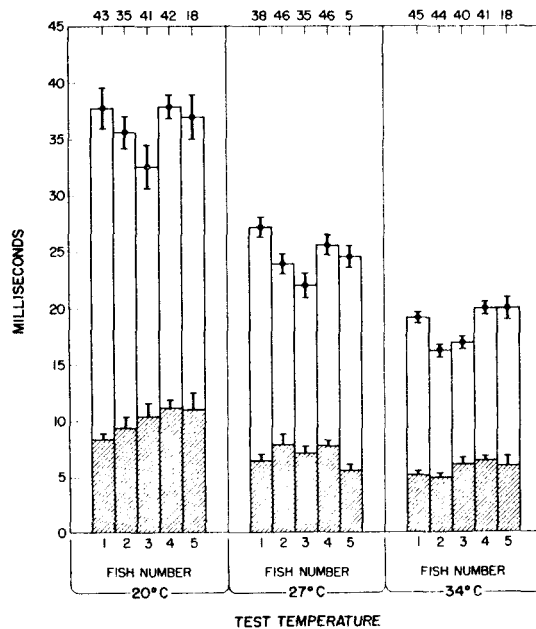

Fig. 1. Mean contraction times and mean latent periods (shaded area) at each test temperature. Vertical lines indicate 95% confidence limits, and numbers above each bar are total number of twitches used to determine each mean. (The film record for fish no. 5 was damaged during processing.)
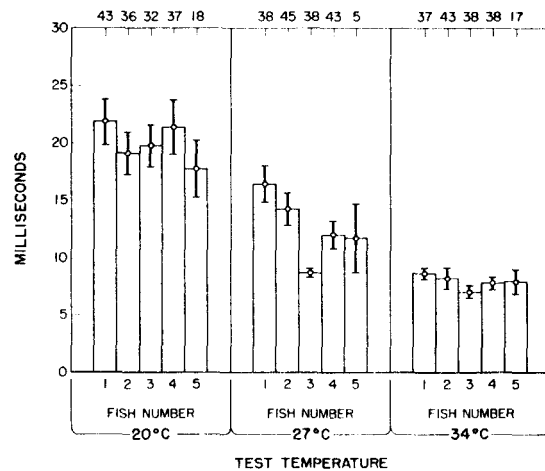

Fig. 2. Mean half relaxation times at each test temperature. Vertical lines indicate 95% confidence limits, and numbers above each bar are total number of twitches used to determine each mean.

201

Hudson 1973, Brill & Dizon MS[5]) at all swimming speeds; (3) maximum swimming speed is limited by maximum tail beat frequency (Wardle 1975); and (4) tail beat frequency is limited by the isotonic contraction times of two sets of laterally opposed muscles (Wardle 1975).

Maximum swimming speed (U_{max} in body lengths per second) is therefore predicted by:

$$U_{max} = A / (2 \cdot C_t) \tag{1}$$

where A is the stride length coefficient (i.e., the fraction of fork length traveled per complete tail beat cycle) and C_t is contraction time, in seconds.

Also, maximum tail beat frequency (F_t) is predicted by:

$$F_t = 1 / (2 \cdot C_t) . \tag{2}$$

By substituting maximum tail beat frequency into an empirically determined regression equation relating swimming speed to tail beat frequency in skipjack tuna (Yuen 1966), we were able to arrive at a second estimate for maximum swimming speed. Figure 3 gives predicted maximum speeds at each test temperature based both on a stride length coefficient of 0.7 (Bainbridge 1978, Brill & Dizon MS, see footnote 5) and the Yuen (1966) regression equation.

Table 1. Fork lengths, weights, and Q_{10} relationships.

Fish No.	Fork length (cm)	Weight (g)	Latent period	Rise time	Contraction time	Half relaxation time
					Q_{10} [a]	
1	42.9	1,040	1.41	1.69	1.62	1.72
2	40.6	749	1.57	1.83	1.75	1.64
3	39.9	752	1.46	1.71	1.60	1.84
4	39.1	713	1.48	1.63	1.58	1.80
5	36.3	778	1.55	1.50	1.55	1.60
		Mean	1.49	1.67	1.62	1.72
	Standard deviation		0.07	0.12	0.08	0.10

a. The Q_{10} values were calculated as follows:

$$Q_{10} = \left(\frac{P_{20°}}{P_{34°}}\right)^{10°/34°-20°} \quad \text{where: } P_{20°} = \text{latent period, rise}$$

time, contraction time or half relaxation time measured at 20° C, in msec, $P_{34°}$ = latent period, rise time, contraction time, or half relaxation time measured at 34° C, in msec.

[5] Brill, R. W. & A. E. Dizon. Red and white muscle fiber activity in swimming skipjack tuna, *Katsuwonus pelamis* (Linnaeus). Manuscript in preparation.

202

Discussion

We chose the standard parameters of latent period, rise time, contraction time, and half relaxation time to characterize the effect of temperature on our isolated muscle samples, rather than maximum twitch tension (force), for the following reason: The maximum force developed during a twitch is a function of both the intensity and duration of active state (Gabel et al. 1968). Because the physiological processes affecting these two parameters may have widely different Q_{10} relationships, the effect of temperature on maximum twitch tension is a complex phenomenon. Maximum twitch tension is, therefore, not a uniquely suitable measure to characterize the influence of temperature on muscle contraction (Hill 1951, Truong et al. 1964). Furthermore, we chose to use an isotonic (rather than an isometric) system to make our results directly comparable to the data presented by Wardle (1975, 1977).
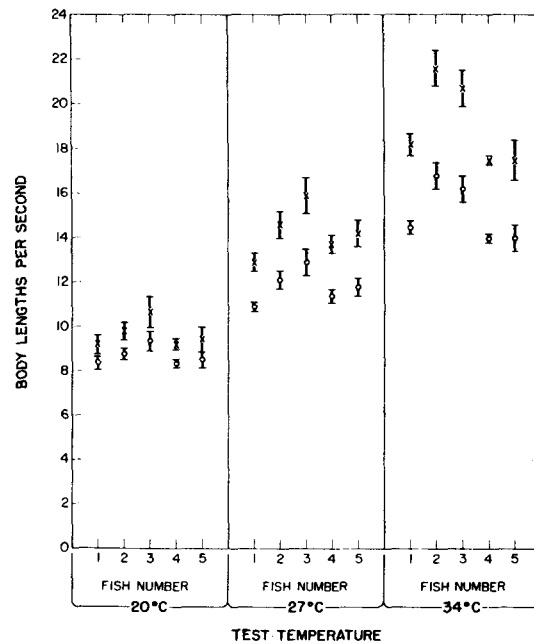

Fig. 3. Predicted maximum swimming speeds versus muscle temperatures. Open circles (o) represent maximum swimming speeds based on tail beat frequency versus swimming speed regression equation presented by Yuen (1966); crosses (x) are based on a stride length coefficient of 0.7. Vertical bars are based on 95% confidence intervals of contraction times.

Comparing Figure 1 with the data presented in Wardle (1977) indicates that, at 20° C, contraction times of muscle samples from skipjack tuna are equal to or longer than the contraction time of muscle samples from other teleosts of equal fork length. As for the effect of temperature, Q_{10} values were calculated based on measurements taken at 20° and 34° C, so as to estimate the effect of temperature over the approximate operating temperature range of skipjack tuna white muscle (Stevens & Neill 1978). The Q_{10} for contraction time of skipjack tuna white muscle (Q_{10} = 1.67) is only slightly higher than that for other teleosts (Q_{10} = 1.4, Wardle 1977, estimated from measurements taken at 14° and 20° C).

Therefore, in spite of other adaptations for high speed swimming (Fierstine & Walters 1967, Magnuson 1978), skipjack tuna white muscle appears not to be physiologically unique, in comparison with other teleosts, with respect to contraction time, or the effect of temperature on contraction time.

There are apparently no data in the literature concerning the effect of temperature on latent period, rise time or half relaxation time in fish muscle. Therefore, no comparisons can be made.

Accuracy of predicted maximum swimming speeds

Owing to the complex orientation of teleost myomeres (Fierstine & Walters 1967, Alexander 1969), it is almost impossible to isolate muscle samples with parallel fibers. Absolute values for maximum force development or maximum speed of contraction cannot be measured. However, contraction time (the parameter of interest with respect to predicting maximum swimming speed) is supposedly independent of after load, muscle sample size, and fiber orientation (Wardle 1975).

The 0.7 stride length coefficient (Bainbridge 1958) was originally assumed to be appropriate for skipjack tuna, at all swimming speeds. Electromyographic (EMG) recordings from swimming skipjack tuna (Brill & Dizon MS, see footnote 5) have recently confirmed that: (1) swimming speed is indeed linearly proportional to tail beat frequency, and (2) a stride length coefficient of 0.7 is appropriate; at least over a swimming speed range of approximately 1.5 to 5.5 body lengths per second (bl s⁻¹). Whether skipjack tuna maintain a linear tail beat frequency — swimming speed relationship and a stride length coefficient of 0.7 at speeds up to 10 to 20 bl s⁻¹ still await direct

confirmation. However, Watanabe (1942) and Yuen (1966) measured the maximum swimming speeds of skipjack tuna (in water of 25–27° C) as approximately 14–15 bl s⁻¹. Mean predicted maximum swimming speed at 27° C, based on a stride length coefficient of 0.7 is 14.3 bl s⁻¹. The agreement of predicted and observed values indicates the suitability of our techniques. The Yuen linear regression equation predicts maximum swimming speeds lower than those observed by Watanabe (1942) and Yuen (1966).

The mean predicted maximum swimming speed at 20° C (based on the 0.7 stride length coefficient) is 9.7 bl s⁻¹, a value equal to or less than the measured maximum swimming speeds of 40 cm salmonids in 19° C water (Weaver 1963, Blaxter 1969). Skipjack tuna are apparently not capable of exceptionally high maximum swimming speeds when compared to other teleosts of equal fork length and similar muscle temperatures.

The data presented here clearly show that increased white muscle temperature will increase maximum swimming speeds of skipjack tuna. However, skipjack tuna white muscle appears to be only slightly more temperature sensitive than white muscle of other teleosts. The maximum sustainable 1–2° C temperature difference between skipjack tuna white muscle temperature and water temperature (Dizon et al. 1978) is unlikely to have a significant effect on the maximum swimming speed of this species.

Summary

1. Latent period, rise time, contraction time, and half relaxation time from isotonic contractions of isolated white muscle samples from skipjack tuna were determined at 20°, 27°, and 34° C, and were found to be inversely proportional to temperature (Q_{10} = 1.47, 1.67, 1.62, 1.72, respectively).
2. The data show that the contraction time and the effect of temperature on contraction time of skipjack tuna white muscle are not unique when compared to other equal-sized teleosts.
3. Based on contraction time, maximum swimming speeds at each test temperature were calculated and found not significantly to exceed the maximum speeds of other equal-sized teleosts when comparisons are made at equal white muscle temperatures.

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