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RAPID TEMPERATURE COMPENSATION OF VOLITIONAL SWIMMING SPEEDS AND LETHAL TEMPERATURES IN TROPICAL TUNAS (SCOMBRIDAE)

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Synopsis

Observations on continuously swimming tunas were used to determine effects of temperature upon volitional locomotory activity and to determine upper and lower lethal temperatures. Experimental subjects were 10 skipjack tuna, *Katsuwonus pelamis*, 9 kawakawa, *Euthynnus affinis*, and 3 yellowfin tuna, *Thunnus albacares.*

Our results: lower and upper lethal temperatures for the euthynnids (*K. pelamis* and *E. affinis*) were 15° and 33° C, respectively. Swimming speed for the euthynnids did not decrease with temperature within most of the zone of thermal tolerance; we observed either temperature independence or increases in speed as the temperature decreased. Yellowfin tuna swam slower as the water temperature decreased, but swimming speed changes lagged behind the water temperature changes. This effect was most certainly due to the large thermal inertia that is a property of tunas. The lag between swim speed and water temperature was eliminated by utilizing an estimate of red muscle temperature, rather than water temperature, as a covariate. Yellowfin tuna swim speed was best correlated with red muscle temperature rather than ambient water or brain temperatures.

Introduction

Most animals respond to temperature change with changed rates of respiration and activity. In general, Q_{10}'s range from 2 to 3 (Prosser & Brown 1961). Yet, for animals that live in heterothermal environments, processes that vary more than twofold for every 10° change should be disadvantageous. Homeotherms have circumvented the problem by controlling temperature of their tissues. Poikilotherms can avoid temperature fluctuations by behavioral thermoregulation, compensate for temperature changes at some level of integration (subcellular to behavioral) or tolerate thermally induced variations in metabolism and activity.

Within their zone of thermal tolerance, tunas apparently have the ability to compensate for rapid temperature fluctuations so that locomotory activity and routine metabolism are independent of temperature. Stevens & Fry (1972) observed that routine swimming speed of two skipjack tuna, *Katsuwonus pelamis*, was relatively constant during rapid temperature change of 10° C. Chang, Ito & Neill (MS)* demonstrated that activity and respiratory rate of skipjack tuna were the same at three temperatures (20°, 24°, and 28° C). Because fish were held 4 h at test temperatures before oxygen measurements were made, some acclimation was possible. Earlier, Gordon (1968) had found that in vitro metabolism of red and

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white tuna muscles was almost constant over a large temperature range (5°–35° C).

In the present paper, we first report upper and lower lethal temperatures for skipjack tuna and kawakawa, *Euthynnus affinis*. For both these and a third species, yellowfin tuna, *Thunnus albacares*, we then present experiments that relate volitional swimming speed to the level and rate of change of environmental temperatures.

Lethal temperatures

Upper and lower lethal temperatures were estimated for skipjack tuna (30–36 cm FL (fork length)) and kawakawa (44–50 cm FL) by increasing or decreasing water temperature 1° C day^{-1}. Initially, water temperatures were about 24° C in three test tanks. One fish was transferred into each test tank from large holding tanks at a similar temperature at least three days before testing began. Then temperature was raised in one tank, lowered in another, and held constant in the third. Animals and treatments were allocated randomly to the tanks with the restriction that each run would have an increasing, a decreasing, and a constant temperature. A run was completed when death temperatures had been reached for the warmed and the cooled fish. Fish were offered thawed smelt daily, and the temperature at which they last took food was also recorded.

Test tanks were 0.6 m deep, 2.4 m in diameter, and were continuously replenished with 120 liters h^{-1} of new water. Sources of heat (quartz glass-sheathed immersion heaters) and cooling (epoxy-coated, stainless steel coils) were located in a vertical cylinder attached to and open at top and bottom to the test tank. The cylinder functioned as an air lift pump, pulling water from the bottom of the test tank, lifting it across the heating and cooling elements, and returning it to the tank at the surface. Mercury contact thermometers and relays controlled heaters and circulation of coolant.

The fish continued to eat some offered food until temperatures were within 1° and 2° C of lethal levels (Table 1). Lower tolerance limits were about 15° C and upper tolerance limits were 33° C. They were essentially the same for both species, and variations among individuals were small.

Swimming speed

Materials and methods

Fish were chosen from stocks maintained in large

Table 1. Lethal temperatures of skipjack tuna and kawakawa exposed to progressive temperature change of 1° C day^{-1}. Values are temperature at which they were alive and the last temperature at which they ate.

Species	Temperature (° C)			
	Lowest		Highest	
	Alive	Feeding	Feeding	Alive
Skipjack tuna	16	17	33	33
	16	17	34	34
	14	*15*	*33*	*33*
Medians	16	17	33	33
Kawakawa	15	16	33	34
	14	16	30	32
	15	–	–	*33*
Medians	15	16	31.5	33
Grand medians	15	16	33	33

Table 2. Outline of treatments during which locomotory activity was measured as a function of water temperature.

Species	Rate of temperature change					
	5° C h^{-1}			1° C day^{-1}		
	n	Fork length (cm)	Temperatures (° C)	n	Fork length (cm)	Temperatures (° C)
Skipjack tuna	4	45–47	27 → 18	3	30–36	24 → 34
				3	30–33	24 → 14
Kawakawa	3	41–45	29 → 18	3	40–50	24 → 34
				3	45–47	24 → 14
Yellowfin tuna	3	41–56	31 → 20	–	–	–
	1	41	21 → 29	–	–	–

tanks at the Kewalo Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, Hawaii. They were caught by angling with a barbless hook and then transferred in a plastic bag partially filled with seawater. On occasion, fish handled this way have fed immediately. After a test, fork length was measured.

Fish were tested with two rates of temperature change: a treatment comparable to Stevens & Fry (1972) in which temperature changed at 5° C h^{-1}, and a treatment in which temperature was changed much slower – 1° C day^{-1}. Table 2 summarizes treatments and subjects.

1° C per day

Data were collected in the course of the lethal-temperature experiment. Fish were placed in three tanks (described above), one of which served as a control. Swimming performance of the fish in treatment tanks (increasing temperature 1° C day^{-1} or decreasing temperature 1° C day^{-1}) was measured relative to the control. Activity was estimated once before dawn and again at midday prior to feeding them. The number of seconds elapsing during 10 tail beats was recorded at least three times at each observation. The median was converted to tail beats per minute, the control value was subtracted, and this difference was averaged for the two times of observation. The last result, tail beats per second for treatment minus control, gave a number to associate with water temperature. Thermostats were advanced at the end of each light period and tanks reached their new temperatures 8 to 10 h prior to the next observation period.

Attempts to use a 16 mm cine camera to measure swimming speed were successful only for skipjack tuna. Speeds were extracted through frame-by-frame analyses of films spaced throughout the light period prior to feeding time. Results were calculated in terms of body length per second, the simplest and most useful method of comparing swim speeds (Webb 1974).

5° C per hour

Tests were performed in a large ring-shaped tank in which a tuna swam laps that were timed with photocells to give swimming speed. The fiber glass tank had two concentric walls, one at 6 m diameter and the second at 4.5 m diameter. The resulting circular channel was 0.75 m wide and 0.5 m deep – six laps equalled 100 m. To cool the tank, water was removed from the channel, chilled in transit through a stainless steel heat exchanger, and pumped back at the rate of 19 liters sec^{-1} (1 volume every 4.5 h).

Passage of the fish was sensed at four photocell stations (six photocells per station) at 90° intervals around the periphery of the channel. Information from the photocells was translated into minutes per lap by digital logic equipment and printed every six laps.

Swimming speeds were measured for 100 min prior to lowering temperature. The temperature was then lowered to about 20° C, the chiller was shut down and tank temperature allowed to rise overnight.

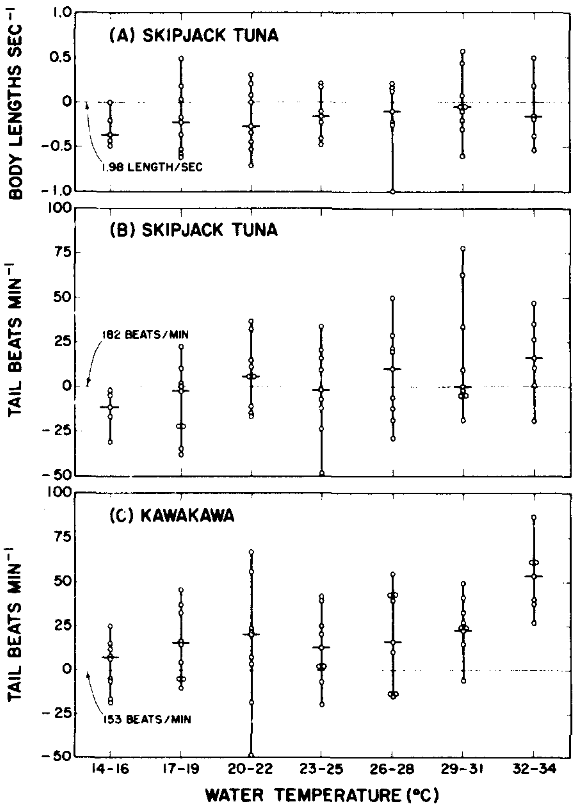

Fig. 1. Influence of temperature changing at 1° C day^{-1} from 24° C on the locomotory activity of skipjack tuna and kawakawa. Controls were held at 24° C; activities are plotted as differences from mean activities of controls. Short horizontal bars are grand medians of the experimental subjects.

Fish were subjected to two or three periods of declining temperatures on consecutive days. For one yellowfin tuna, temperature was kept low all night and data were collected during the recovery period the next morning.

Speed in minutes per lap was converted to body lengths per second. Red muscle and brain temperatures were estimated by the method of Neill & Stevens (1974) using parameters determined by Neill, Chang & Dizon (1976). $\log_{10}$ speeds were regressed on either water temperature or red muscle temperature.

Results

1° C per day

For both skipjack tuna and kawakawa, swimming speed from lower to upper lethal temperatures appeared remarkably unrelated to water temperature changing at 1° C day^{-1} (Fig. 1). For skipjack tuna none of the differences for tail beats or swim speed were significant among temperatures grouped by 3° C (Kruskal-Wallis 1-way AOV). But differences in tail beat frequencies among temperature treatments for kawakawa were significant ($P \leq 0.05$, Kruskal-Wallis 1-way AOV). A multiple comparison test of the kawakawa data (Hollander & Wolfe 1973, p. 125) indicated that the only significant difference was between the two extreme temperature groups, i.e., tail beat rate at 14°–16°C was less than that at 32°–34°C.

Linear regressions of tail beat differences from control on temperature (not grouped by 3° C) were similar for skipjack tuna and kawakawa. Standard errors of the estimate were reduced by using a log transformation of the tail beats per minute difference from control. The regression model thus obtained was $\log_{10}(A + 100) = 1.84327 + 0.006687T + \text{error}$ ($n = 57$, $r = 0.36$, $P \leq 0.05$) for skipjack tuna and $\log_{10}(A + 100) = 1.89401 + 0.007137T + \text{error}$ ($n = 61$, $r = 0.43$, $P \leq 0.01$) for kawakawa. A is tail beats per minute difference from control and T is Celsius degrees. For control fish, tail beats per minute were 182 min^{-1} for skipjack tuna and 153 min^{-1} for kawakawa. Thus, at a rate of change of 1° C day^{-1}, the volitional swimming activities of skipjack tuna and kawakawa were almost unresponsive to temperature. Both rising and falling temperatures produced similar results.

5° C per hour

These experiments provide a rate of temperature change almost the same as used by Stevens & Fry (1972). Because responses of *Euthynnus*-type* species (skipjack tuna and kawakawa) and the yellowfin tuna (*Thunnus*) were markedly different, results are presented separately.

Euthynnids. Regression relationships of log swim speed versus temperature were determined seven times for four skipjack tuna and six times for three kawakawa (Table 3; Figs. 2 and 3). As with 1° C day^{-1} data, standard errors of the estimates were reduced using the log transformation of the swim speed. Each estimate was based on 22–84 laps (every 6th lap is automatically sampled). Values ranged from

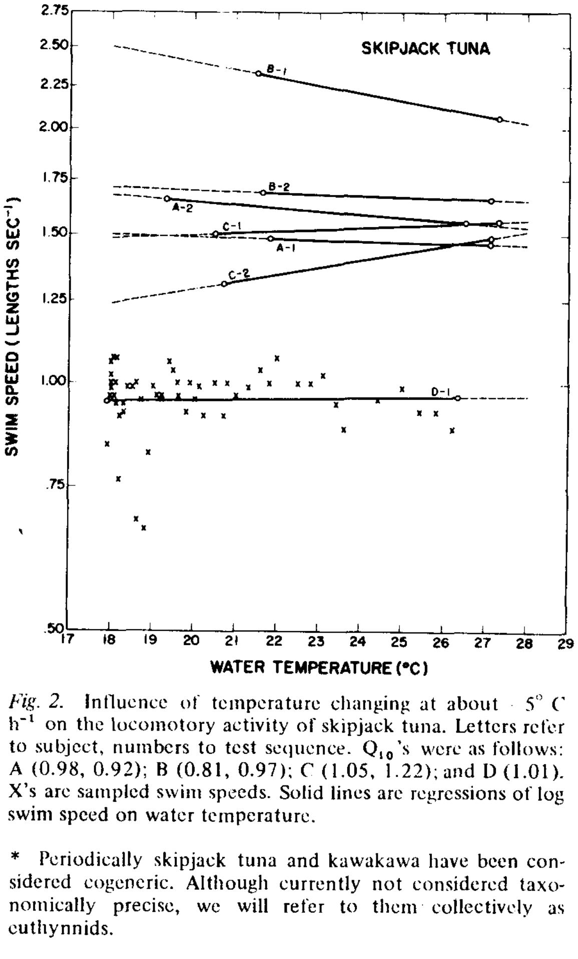

Fig. 2. Influence of temperature changing at about 5° C h^{-1} on the locomotory activity of skipjack tuna. Letters refer to subject, numbers to test sequence. Q_{10}'s were as follows: A (0.98, 0.92); B (0.81, 0.97); C (1.05, 1.22); and D (1.01). X's are sampled swim speeds. Solid lines are regressions of log swim speed on water temperature.

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* Periodically skipjack tuna and kawakawa have been considered cogeneric. Although currently not considered taxonomically precise, we will refer to them collectively as euthynnids.

Table 3. Regression statistics for log swim speed as a function of either ambient temperature (skipjack tuna – SJ or kawakawa – KK) or estimated red muscle temperature (yellowfin tuna – YF). Small letters refer to individuals, numbers to test.

Fish	Fork length (cm)	n	Mean log swim speed (lengths per sec)	Standard deviation	Min. log swim speed (lengths per sec)	Max. log swim speed (lengths per sec)	Regression coefficients			Temperature range (° C)
							a	b	r	
SJa–1	45.5	27	0.167	0.00859	0.161	0.185	0.18977	–0.00092	0.1753	21.8–27.1
–2		42	0.204	0.03282	0.173	0.338	0.28737	–0.00369	0.2569	19.3–26.5
SJb–1	45.0	40	0.340	0.05957	0.233	0.449	0.56119	–0.00906	0.2791	21.5–27.3
–2		30	0.221	0.03251	0.146	0.286	0.25182	–0.00129	0.0700	21.6–27.1
SJc–1	46.5	69	0.181	0.03573	0.086	0.258	0.13096	0.00219	0.1203	20.5–27.3
–2		54	0.135	0.04354	0.000	0.233	–0.06269	0.00866	0.3788**	20.7–27.1
SJd–1	47.0	54	–0.002	0.04093	–0.174	0.029	–0.03370	0.00067	0.0380	17.9–26.2
KKa–1	40.7	33	0.314	0.02255	0.279	0.371	0.32599	–0.00057	0.0275	20.9–26.7
–2		45	0.207	0.10221	0.033	0.358	0.97239	–0.03422	0.4855**	20.9–26.5
KKb–1	42.2	39	0.349	0.06122	0.250	0.539	0.76260	–0.01787	0.4681**	21.4–27.4
KKc–1	45.3	57	0.156	0.02698	0.076	0.210	0.29338	–0.00634	0.4451**	19.7–26.0
–2		22	0.072	0.02402	0.025	0.100	0.29423	–0.00958	0.5561**	21.2–25.7
–3		84	0.159	0.02198	0.090	0.223	0.05198	0.00502	0.6261**	17.5–29.0
YFa–1	40.6	28	0.043	0.05537	–0.101	0.160	–0.37285	0.01600	0.7740**	22.1–30.7
–2		37	–0.001	0.08774	–0.102	0.179	–0.84377	0.03330	0.8895**	22.0–28.9
–3		62	0.022	0.10177	–0.103	0.223	–0.84196	0.03592	0.9610**	21.4–28.9
YFb–1	43.4	28	–0.125	0.10472	–0.301	0.031	–1.17840	0.04139	0.8320**	22.0–28.9
–2		33	–0.048	0.08444	–0.210	0.092	–0.98192	0.03650	0.8624**	23.1–28.9
–3		21	0.146	0.07633	–0.091	0.240	–0.27147	0.01646	0.3933	23.0–30.7
YFc–1	56.0	69	–0.012	0.06808	–0.190	0.180	–0.65590	0.02560	0.8832**	20.7–28.9
–2		39	0.024	0.09250	–0.188	0.169	–0.62685	0.02555	0.9293**	20.0–29.0
–3		42	0.070	0.10395	–0.149	0.181	–0.78534	0.03140	0.9313**	20.4–30.9

** = Significant at 0.01.

−0.00906 to 0.00866 (median −0.00906) for skipjack tuna and −0.03422 to 0.00502 (median −0.00958) for kawakawa (Figs. 2 and 3). The slopes were significantly greater than zero for only one of seven skipjack tuna estimates and significantly less than zero for four of the six kawakawa estimates. The results vary greatly among fish and for the same fish among days. Not only did the slopes differ, but swimming speeds at a given temperature varied by a factor greater than two for each species. Regardless of variation, swimming activity did not increase two to three times for a 10° C increase as observed in other species (Prosser & Brown 1961). Rather speed appeared to be constant for skipjack tuna and increased with decreasing temperature for kawakawa.

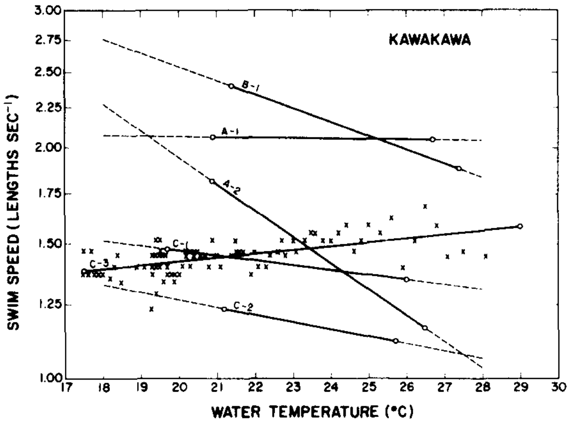


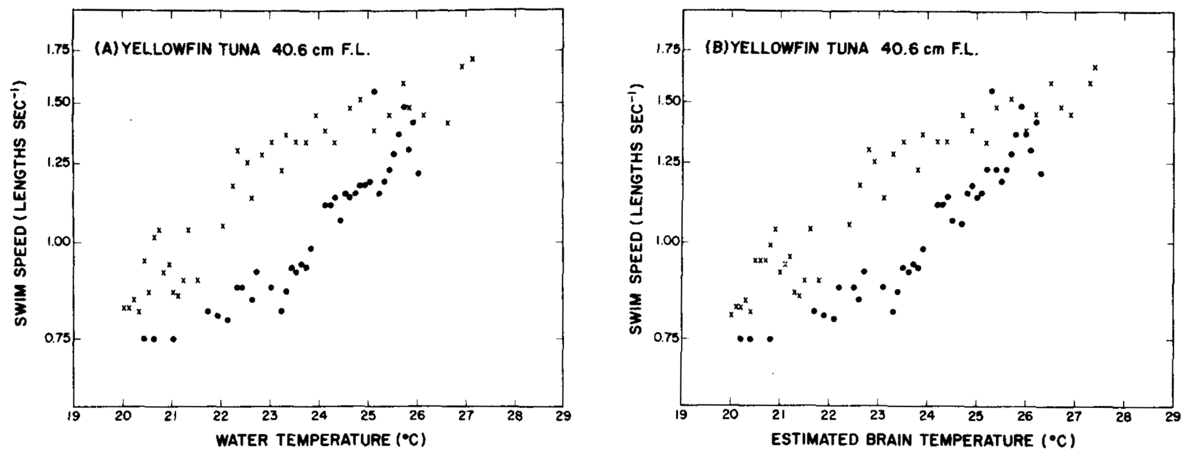
Fig. 3. Influence of temperature changing at about −5°C h^{-1} in locomotory activity of kawakawa. Letters refer to subject, numbers to test sequence. Q_{10}'s were as follows: A (0.98, 0.45); B (0.66); and C (0.86, 0.80, 1.12). X's are sampled swim speeds Solid lines are regressions of log swim speed on water temperature.

Thunnus. Regression analysis was performed on nine tests with three yellowfin tuna. Each estimate was based on 21–69 laps (every 6th lap is sampled) (Table 4). These estimates were based on red muscle temperature rather than water temperature because tissue temperatures of the yellowfin tuna lag markedly behind water temperature changes if the latter changes sufficiently fast. Red muscle temperature was estimated by methods outlined in Neill et al. (1976). The importance of this approach can be seen in Figure 4. In Figure 4 log swimming speed is plotted against water temperature of a yellowfin tuna first cooled to about 19° C and then rewarmed the following day. Because swim speed did not decrease as fast as water temperature decreased, the slope of the relationship of the two covariates is initially close to zero. After a delay proportional to the coefficient of temperature change (k, Neill et al. 1976), the slope became steeper. The same is observed during the warming on the next day. The resultant hysteresis is obvious. Brain temperature changes slower than changes in the water temperature (Neill et al. 1976) and when speed is plotted against calculated brain temperatures (Fig. 4b) the hysteresis is slightly re-

Table 4. Summary of Q_{10} values estimated for scombrids.

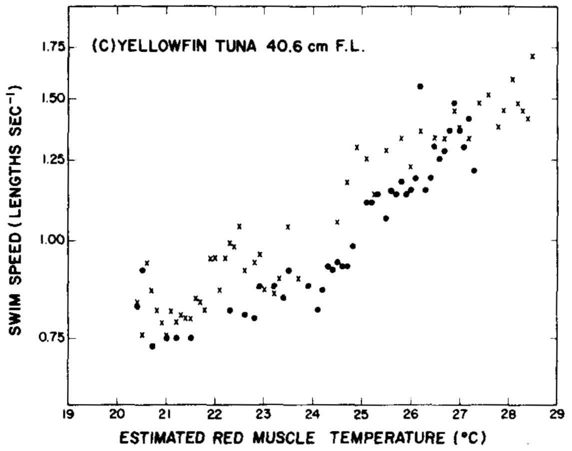
Species	Locomotory activity			Tissue metabolism	Whole animal metabolism
	Rate of temperature change				
	4° C h^{-1}	5° C h^{-1}	1° C day^{-1}		
Euthynnus					
Skipjack tuna	[1] 1.04 (0.96–1.11)	0.98 (0.81–1.22)	1.09	[2] 1.0–1.2	[3] 1.0–1.1
Kawakawa	–	0.85 (0.45–1.12)	1.12	–	–
Thunnus					
Yellowfin tuna	–	2.15 (1.44–2.59)	–	–	–
Bigeye tuna	–	–	–	[2] 1.0–1.2	–

[1] Estimated by us from figure in Stevens & Fry (1972).
[2] Gordon (1968).
[3] Chang, Ito & Neill (see text footnote p. 83).



a

b



c

Fig. 4. Effect of choice of covariate on hysteresis and linearity of temperature-log swim speed plot. X's are swim speeds during cooling. 0's are swim speeds during warming. See text.

duced. But when speed is plotted against calculated red muscle temperature the hysteresis is almost eliminated (Fig. 4c). The relation between speed and temperature observed for yellowfin tuna is mediated apparently by muscle temperature (or some structure that cools and warms at the same rate) rather than by brain temperature or directly by water temperature acting on surface temperature receptors.

It is also apparent from the above that swim speed of yellowfin tuna, in contrast to the euthynnids, is dependent on temperature (Fig. 5). Slopes ranged from 0.01646 to 0.04139 with a median of 0.03140. The slopes of eight of the nine regressions were significantly greater than zero at $P \leq 0.01$.

Discussion

Scombrids can be credited with three compensatory mechanisms with respect to temperature: 1) physiological thermoregulation in which tissue temperatures are maintained at a more or less constant level in spite of variation in external temperature (Barrett & Hester 1964, Cary & Teal 1969, Carey et al. 1971, Stevens & Fry 1971, Graham 1975); 2) behavioral thermoregulation mechanisms, in which the fish can occupy preferred and presumably optional habitat temperatures (Dizon et al. 1974, Dizon, Byles & Stevens 1976, Steffel et al. 1976, Laurs, Yuen & Johnson MS*); and 3) molecular mechanisms of rate-process compensation.

The last category is subdivided by Hazel & Prosser (1974) into a) instantaneous temperature compensa-

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* Laurs, R. M., H. S. H. Yuen & J. H. Johnson. Study of the small-scale movements of albacore tuna, *Thunnus alalunga* (Bonnaterre) using ultrasonic tracking techniques. Manuscript in preparation. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

tion, b) thermal compensation requiring a period of acclimation, and c) compensation over evolutionary time. At the moment, there exists no experimental evidence that individual scombrids possess the ability to acclimate to new temperature environments. Considering their zone of thermal tolerance, there is no reason to suggest that they cannot. Evolutionary thermal compensation has certainly occurred considering the adaptive radiation of tuna species and subspecies through temperate and tropical oceans (Blackburn 1965). Q_{10}'s taken from our study and the literature (Table 4) indicate that euthynnid scombrids do compensate rapidly for changes in temperature. Compensation seems more rapid than in typical temperature acclimation and therefore resembles instantaneous temperature compensation. As a consequence, locomotory activity and metabolism tend to be relatively constant in the face of rapidly changing temperatures. Molecular compensation must be occurring with the observed temperature-independent metabolism (Gordon 1968, Chang et al., see footnote p. 83) and temperature-independent activity is observed for rates of temperature change of 4° C h^{-1}, 5° C h^{-1}, and 1° C day^{-1}; for increasing and decreasing temperatures, and over the entire temperature range (15°–34° C) found to be tolerated by euthynnids. Several exceptions to these statements may be important and should be highlighted.

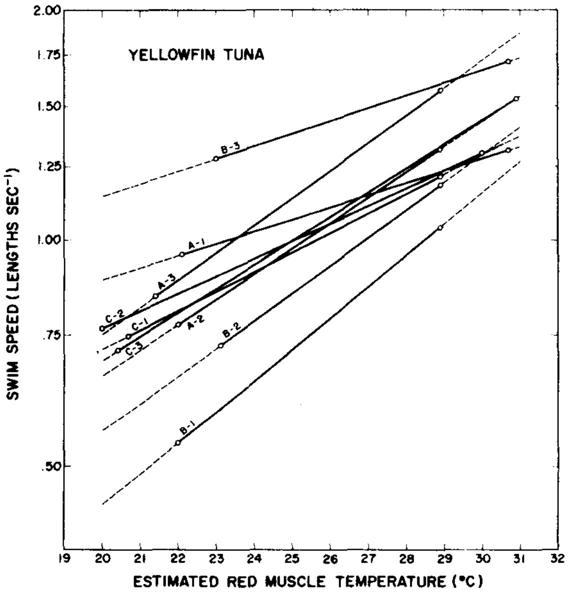

Fig. 5. Influence of temperature changing at about −5°C h^{-1} on the locomotory activity of yellowfin tuna. Letters refer to subject, numbers to test sequence. Q_{10} are as follows: A (1.44, 2.15, 2.24); B (2.59, 2.32, 1.46); and C (1.80, 2.06). Solid lines are regressions of log swim speeds on estimated red muscle temperatures.

First, yellowfin tuna, in contrast to the *Euthynnus* species and to the tissue metabolism of another *Thunnus* (Gordon 1968), have a Q_{10} for locomotory activity similar to nonscombrid fishes (for example *Salmo salar*, see Peterson & Anderson 1969). This is puzzling because they, even more than the *Euthynnus* species, are believed to be fishes of the thermocline and owing to their larger size, could build up higher heat loads with exercise. Both of the above considerations would suggest that yellowfin tuna have greater need for mechanisms of rapid temperature compensation.

One possible explanation for the difference between the yellowfin tuna and the two euthynnids is related to factors dictating continuous swimming as a part of their habits. Scombrids are negatively buoyant, and to maintain hydrostatic equilibrium they must swim at speeds and produce lift on their extended pectoral fins that counters their weight in water (Magnuson 1973). Yellowfin tuna have a gas bladder and large pectoral fins that allow slower minimum speeds than is possible in the euthynnids that have small pectoral fins and no gas bladder. Since yellowfin tuna can swim slower, perhaps they can maintain speeds further above their hydrostatic minimum than can euthynnids and thus have more scope to respond to temperature change. Euthynnids on the other hand may be forced for hydrostatic reasons to swim closer to their maximim endurance speed and thus be less able to respond to temperature changes and, therefore, must need some sort of temperature compensation mechanisms.

Speeds observed in the ring-shaped tank were highly variable, and all three species swam for periods faster and slower than their minimum hydrostatic speeds as calculated by Magnuson (1973) for wild fish. We can only test individual fish in the ring-shaped tank. Tunas of this size are always found in schools and the responses of individuals when prevented from schooling are unpredictable. Removal from their school and introduction into a confining test situation produce degrees of excitement that probably vary among individuals and affects swim speed. While an individual tuna can swim with remarkable speed precision for long periods of time, unexplained and abrupt changes in speed are observed. As yet we are unable to relate these shifts in speed to any observable factors save direction of swimming. Upon reversal in swimming direction, an individual will settle to a new average speed and again maintain it with remarkable precision.

Also contributing to interfish variability is that captive fish lose fat mass, becoming less dense, and can then swim at speeds below minimum. Kawakawa held for long periods (Magnuson 1970) were 40% less dense than wild fish. Some were even 60% less dense in respect to the density of seawater (1.025 g cc^{-1}), with densities as low as 1.049g cc^{-1} compared with the 1.086 g cc^{-1} characteristic of wild fish. Such captivity-induced variations in density could significantly decrease speeds required for hydrostatic equilibrium. Scombrids can also vary the lift coefficient of the pectoral fins (Magnuson 1973) to increase lift, and can incline their bodies at an upward angle of attack to increase lift forces. Fortunately, the observed scope in speed in the ring tank allowed us to assume that both the euthynnids and the yellowfin tuna had the flexibility to respond to temperature change if it had been in their nature; the former did not, the latter did. Secondly, four kawakawa exposed to a 5° C h^{-1} decrease in temperature swam significantly faster at cooler temperatures. This suggests an alarm response to temperatures near their lethal temperature. But skipjack tuna at the same rate of temperature change did not increase their speeds near lethal temperatures. Also kawakawa at 1° C day^{-1} decreased speed near lethal temperature as did skipjack tuna in Stevens & Fry's work. An increased speed near lethal temperatures was not consistent, but if real would be quite functional as it would allow the fish to counteract the cool water by generating more metabolic heat and would remove the fish from a suboptimal area.

Rapid temperature compensation by the euthynnids adds growing evidence of a unique niche filled by skipjack tuna. These tuna with their sensory ability to thermoregulate behaviorally (Dizon et al. 1974, 1976, Steffel et al. 1976), with their countercurrent heat exchanger to damp out short-term temperature change (Neill et al. 1976), and with a metabolism and respiration that is rapidly temperature compensated, possess potent mechanisms to deal with a highly heterothermal environment. Yet, the surface mixed layer of the tropical oceans, generally thought to be the habitat of these tunas, is an environment characterized by little temperature variation. Barkley, Neill & Gooding (MS)* have identified three environmental conditions that should determine distribution for the skipjack tuna: 1) a lower temperature limit – about 18° C; 2) a lower oxygen limit – about 3.5 ml O_2 $liter^{-1}$; and 3) an upper temperature limit ranging from about 33° C for the smallest commercially sought fish to 20° C for the oldest and largest. These limits may account for the unusual features of their areal distribution and suggest that the actual habitat of adult skipjack tuna is the upper thermocline. Since much forage for the adult tunas is likely to be in the upper mixed layer, frequent forays into warmer, upper waters must be made. Most animals whose metabolism is instantaneously temperature-compensated live in an environment in which temperature fluctuates dramatically (i.e., intertidal forms, Hazel & Prosser 1974). The habitat of the adult skipjack tuna could be similarly constituted. Consider also that they lack a swim bladder, which frees them from effects of changing pressure. Skipjack tuna are thus well suited to exploit fully the environment extending from the upper thermocline to the surface; rapid movements through extremes of temperature and depth pose no particular problems to these highly adapted animals. Rapid temperature compensation contributes to the ability to fill this niche.

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