THE RELATION BETWEEN EXERCISE AND BIOCHEMICAL CHANGES IN RED AND WHITE MUSCLE AND LIVER IN THE JACK MACKEREL, *Trachurus symmetricus*

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ABSTRACT

Glycogen, lactic acid, and fat concentration in red and white muscle and glycogen in the liver of jack mackerel, *Trachurus symmetricus*, were measured after periods of forced swimming by *Trachurus* at speeds above, below, and at the sustained speed threshold. Failure to swim at any speed was associated with an almost complete depletion of glycogen in the white muscle only. The trend of glycogen use in the red muscle closely followed that of the liver and was not correlated with failure to swim. Reduction of glycogen levels in red muscle and liver were associated with extended periods of swim- Lipid use was slow and not correlated with fatigured muscle and was insignificant in white muscle. ming. High lipid content was characteristic of e. A decline in lipid concentration after exercise occurred only in the red muscle and only after a swimming period of 6 hr at a subthreshold speed. High lactate levels were characteristic of both muscle types and did not appear to be related to fatigue at any swimming speed.

The high lactate levels in white muscle, the almost complete depletion of glycogen in the white muscle of exhausted fish, and the parallel pattern of glycogen depletion in red muscle and liver suggested that white muscle was the primary locomotor organ near and above the threshold for sustained speed. At these speeds red muscle like the liver may provide nutrients to the white muscle, provided time for mobilization is sufficient. At speeds below the sustained speed threshold our analysis indicated that both the red and white muscle systems were used but the relative significance of the locomotory role played by each system could not be evaluated.

The lateral musculature of many fishes may be readily segregated by color into red and white portions. Typically in active fishes the red muscle makes up from 10 to 20% of the total musculature and is arranged in a thin lateral sheet just beneath the skin whereas the white muscle makes up the underlying mass of the myotome. The two muscle types also differ in the diameter of their muscle fibers, speed of contraction, blood supply, mitochondrial content, patterns of innervation, and glycogen and fat content (Bone, 1966).

The accepted view of the function of red and white muscle tissues in fishes was outlined by Bone (1966). He concluded from his own work on dogfish and from an extensive literature review that the two muscle fibers represent two separate motor systems which operate independently, utilize different metabolites, and serve different locomotory functions, viz., the red muscle is used for slow cruising speeds and functions by aerobic metabolism of fat whereas the white muscle is used for rapid bursts of swimming and is driven by anaerobic glycolysis. Bone's conclusions have subsequently been supported by measurements of oxygen uptake in red and white muscle by Gordon (1968) and by electrophysiological studies on oceanic skipjack, *Katsuwonus pelamis*, by Rayner and Keenan (1967). On the other hand, Braekkan (1956) and Wittenberger (1967) believe the red muscle has no independent locomotor role and functions as a metabolic organ for the white muscle. Electrode recordings from the red muscle (Bone, 1966; Rayner and Keenan, 1967) have provided irrefutable evidence for an independent locomotor function of red muscle at certain slow speeds, but the metabolic independence of the two muscle systems and their metabolic and locomotor function at higher speeds is still open

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to question. Although the roles assigned to the two muscle systems are dependent on swimming speed, no studies have been made on the function of the muscle systems using normally swimming intact animals at known speeds. The objective of this study was to re-examine the metabolic and locomotor roles of red and white muscle by measurement of glycogen, lactate, and fat levels in the muscle and glycogen levels in the liver in fish exposed to various velocity treatments of known strength and duration. Juvenile jack mackerel, *Trachurus symmetricus*, were used in this study because the maximum sustained speed threshold for 6 hr of continuous swimming had already been established for this species (Hunter, 1971), and consequently we were able to relate all of our chemical measurements to known levels of swimming performance.

METHODS AND PROCEDURES

SWIMMING TESTS

Jack mackerel were maintained at a regulated seawater temperature of 18.5° C in a plastic swimming pool 4.57 m diameter and fed an abundant ration of brine shrimp, *Artemia*, and chopped fish and squid each day. The fish were not fed for 20 hr prior to testing. Jack mackerel were tested in an activity chamber patterned after that of Beamish (1968) and described in detail by Hunter and Zweifel (1971). The swimming compartment of the apparatus consisted of a tube 230 cm long and 41 cm in diameter through which seawater could be moved at speeds ranging from 12 to 212 cm/sec. Fish were placed in the tube and forced to swim at a water speed for certain periods varying from 8 min to 6 hr. At the end of the swimming period they were removed and dropped immediately into liquid nitrogen and the frozen fish were stored at —30° C until used for chemical analysis. The time required for removal and freezing did not exceed 1 min.

Speed treatments for the experiments were chosen relative to the 50% endurance threshold for jack mackerel at 22 $L^{0.6}$/sec for 6 hr of swimming where L is total length (Hunter, 1971). Five jack mackerel, mean length 14.6 cm, were tested at the subthreshold speed of 19.6 $L^{0.6}$/sec (98 cm/sec); 14 jack mackerel, mean length 16.3 cm, were tested at the near threshold speed of 21.1 $L^{0.6}$/sec (113 cm/sec); and 10 jack mackerel, mean length 14.7 cm, were tested at the superthreshold speed of 27.7 $L^{0.6}$/sec (139 cm/sec). Fish tested at the subthreshold speed swam continuously for 6 hr and were sampled at the end of that period. Fish tested at the threshold speed were divided into two groups: seven fish that were sampled after 6 hr of continuous swimming; and seven fish that fell from exhaustion at some time during the 6-hr period. The latter group of seven fish were quickly removed from the apparatus and frozen as soon as they fell against the rear screen. Fish tested at the superthreshold speed were also divided into two groups: those that swam successfully for 8 min; and those that failed after 8 or less minutes of swimming.

Ten jack mackerel, mean length 14.5 cm, were used as controls. Five of the control animals were removed from the holding tank, placed in the apparatus, allowed to swim for 30 min at the slow speed of 6.2 $L^{0.6}$/sec (30 cm/sec), removed, and frozen. The other five control fish were removed from the holding tank and immediately frozen. The data from these two control groups were later combined because no difference between them was detected.

CHEMICAL ANALYSES

White and red muscle were dissected from the frozen fish while still frozen. One lateral strip of red muscle was used for fat analysis and the other divided into two equal portions for lactate and glycogen analysis respectively. About 1 g of white muscle from the dorsal portion of the myotome was used for glycogen determinations, 0.5 g for lactate, and 0.5 g for fat measurements. Fish were returned to the freezer and liver samples (0.1-0.2 g) were analyzed for glycogen about a month after the muscle determinations.

For lactate measurements muscle was quickly cut into small pieces, weighed, and homogenized in 10% trichloroacetic acid in prechilled tubes. Proteins and cellular debris were spun down in a clinical centrifuge. Aliquots of the protein-free supernatant fluid were analyzed for lactate enzymatically using the test reagents supplied by SIGMA Chemical Company.[3] The test is based on the conversion of nicotine adenine nucleotide (NAD) to the reduced form (NADH) as lactate is converted to pyruvate by lactate dehydrogenase. All readings were made at 340 mμ on a Beckman DU spectrophotometer. Results are expressed as mg of lactic acid per 100 g wet weight muscle tissue.

Muscle and liver samples for glycogen determinations were dropped into preweighed graduated centrifuge tubes containing 3 ml of 30% potassium hydroxide. Glycogen was precipitated with alcohol and determined according to the method of Montgomery (1957). All readings were made at 490 mμ on a Beckman DU spectrophotometer. Results are expressed as mg glycogen (as glucose) per 100 g wet weight in the case of muscle, and as percent glycogen in the case of liver.

Muscle tissue was dried in an oven at 60° C to constant weight for fat analysis. Fat was removed by a soxhlet extraction with chloroform-methanol (2:1, v:v). After the extraction the solvent in the tissue was evaporated and the difference in weight of the tissue recorded (Krvarić and Mužinić, 1950).

[3] P.O. Box 14508, St. Louis, Mo. 63178. Reference to commercial products does not imply endorsement.

RESULTS

Fish that swam continuously for 6 hr at the subthreshold speed of 98 cm/sec and at the threshold speed showed no difference in the glycogen content of the white muscle from the controls (Table 1). On the other hand, in fish

TABLE 1.—Glycogen in red and white muscle, and liver of jack mackerel following various forced swimming conditions. Red and white muscle glycogen in mg per 100 g wet weight; liver glycogen is percent of wet weight. -- indicates measurement was lost during analysis.

	Controls			19 $L^{0.6}$ Subthreshold speed			21 $L^{0.6}$ Threshold speed successes		
	Red	White	Liver	Red	White	Liver	Red	White	Liver
	76.6	85.9	6.42	15.23	53.90	0.125	26.71	204.3	0.043
	102.8	--	9.49	52.80	143.2	4.36	33.33	159.4	1.63
	176.3	--	22.74	192.5	76.69	.317	37.59	80.74	1.85
	277.8	276.8	8.75	145.2	316.2	8.31	95.93	492.8	.125
	562.0	142.6	18.59	147.6	102.6	3.16	152.4	223.2	3.42
	706.0	157.9	18.17				191.7	638.0	3.19
	1075	267.8	10.26				475.1	216.3	1.38
	1394	72.9	17.00						
	1417	71.1	11.82						
	1706	216.5	24.24						
Mean	749.4	161.4	14.75	[1]110.7	138.5	[1]3.25	[1]144.7	287.8	[1]1.66

	21 $L^{0.6}$ Threshold speed fatigued			28 $L^{0.6}$ Superthreshold speed-individually fatigued			28 $L^{0.6}$ Superthreshold speed, 8-min test		
	Red	White	Liver	Red	White	Liver	Red	White	Liver
	11.5	26.50	.078	--	--	0.546	--	39.93	10.00
	16.00	4.51	.034	149.6	8.02	4.73	298.6	141.9	10.00
	17.10	20.63	3.30	215.0	19.56	3.83	473.3	25.44	3.16
	40.55	27.77	5.04	490.4	6.76	13.23	533.1	141.0	10.94
	104.8	--	11.96	654.5	18.49	5.81	553.9	57.22	11.31
	151.8	11.15	.820						
	241.5	50.2	12.50						
Mean	[1]83.27	[1]23.46	[1]4.82	377.4	[1]13.21	[1]5.63	464.7	[1]81.1	9.08

[1] Differed from the controls, $P \leq 0.05$, Mann Whitney U test (Siegel, 1956).

that failed to swim the full 6 hr at the same speed the glycogen levels in the white muscle were lower and were different from the controls ($P = 0.001$ Mann Whitney U test, Siegel, 1956). Glycogen levels in white muscle of all fish tested at the superthreshold velocity were also much lower and statistically different from the controls ($P = 0.05$). The lowest glycogen levels of all were in fish that failed from exhaustion at superthreshold speeds. The values in these exhausted fish were statistically different from those of fish that swam at the same speed but which were removed after 8 min of swimming before they could fall from exhaustion. In sum, strenuous exercise and exhaustion regardless of speed were associated with a marked depletion of glycogen reserves in the white muscle, whereas successful swimming for 6 hr at subthreshold or threshold speed produced no. significant change in white muscle glycogen.

The glycogen content of the liver and red muscle were lower and different from the controls in fish tested at threshold and subthreshold speeds ($P = 0.05$). At superthreshold speed, on the other hand, the glycogen content of the red muscle was not different from the controls and that of the liver was different only in fish that failed from exhaustion ($P = 0.02$).

Thus, the trends in the levels of red muscle and liver glycogen in relation to swimming speed were nearly the reverse of that for white muscle glycogen. Low levels of glycogen in red muscle and liver were associated with slow speeds that could be sustained for extended periods. These results suggest that glycogen from red muscle and liver provide energy to the white muscle at nearly all swimming speeds. We believe that no drop occurred in red muscle glycogen in fish fatigued at high speeds because the time was too short for the white muscle to mobilize significant amounts of glycogen. This view is supported by the negative correlation between the level of glycogen in the red muscle and swimming time to fatigue at threshold speed. This is illustrated in the following table:

Threshold speed = 21 $L^{0.6}$

Time to fatigue (*min*)	Glycogen in red muscle (*mg per 100 g wet weight*)
282	11.5
110	16.0
131	17.1
79	40.6
15	104.
38	241.

($r_s = -0.857$, $P < 0.05$)

In fish exercised at the superthreshold speed the lactic acid content of the red and white muscle was considerably above that of the controls and statistically different from them ($P = 0.05$) (Table 2). At threshold and subthreshold speeds, the lactic acid concentration in red and white muscle formed no distinct pattern. At threshold speed the lactate levels of red and white muscle were about the same as the controls and did not differ from them except for one case where the values were actually lower

TABLE 2.—Concentration of lactic acid in red and white muscle of jack mackerel following various forced swimming conditions. Values given are mg lactic acid per 100 g wet weight.

Controls		19 $L^{0.6}$ Subthreshold speed		21 $L^{0.6}$ Threshold speed successes	
Red	White	Red	White	Red	White
40.49	233.0	94.6	520.9	20.60	310.4
59.29	425.3	97.6	596.6	22.83	344.5
71.58	387.5	99.2	521.9	26.79	385.3
77.46	521.0	117.1	630.3	45.66	464.8
79.53	570.3	156.8	762.3	56.94	403.1
82.19	341.5			82.19	345.2
86.76	390.6			83.87	410.2
86.76	319.0				
86.76	553.4				
95.44	589.6				
Mean 76.63	433.1	[1]113.1	606.4	[1]48.41	380.5

21 $L^{0.6}$ Threshold speed fatigued		28 $L^{0.6}$ Superthreshold speed - individually fatigued		28 $L^{0.6}$ Superthreshold speed, 8-min test	
Red	White	Red	White	Red	White
26.23	564.6	101.2	422.9	124.2	724.1
39.61	545.3	108.4	538.6	132.3	668.9
56.58	404.4	120.4	723.1	189.0	799.9
66.6	499.2	151.9	745.8	202.8	807.4
86.76	489.7	230.5	800.6	237.4	733.5
122.5	486.2				
205.5	646.1				
Mean 86.25	519.4	[1]142.5	[1]646.2	[1]177.1	[1]746.8

[1] Differed from the controls, $P \leq 0.05$, Mann Whitney U test (Siegel, 1956).

than the controls; at this subthreshold speed lactate levels of red and white muscle were higher than the controls and differed statistically ($P = 0.02$). We have no explanation for these differences except to suggest that the high muscle lactate concentration in the control animals may have obscured changes resulting from moderate exercise. A larger sample size may be required to obtain reliable measurements of differences in lactic acid concentration caused by moderate exercise.

Muscle lactate level did not appear to be related to fatigue at any swimming speed. Lactate levels in fish that fatigued at the threshold speed were not different from the controls. Fish that failed at superthreshold speeds had a higher muscle lactate level than did the controls but the level did not differ from that of fish that swam at the same speed but were removed before they became exhausted. These results suggest that high lactic acid concentration in muscle was not the principal cause of exhaustion.

Red muscle contained considerably more fat per unit weight than white muscle. Indeed, white muscle fat levels were almost undetectable in many cases (Table 3). White muscle fat levels did not differ from the control at any speed level. Red muscle fat did not differ from the controls at threshold and superthreshold speeds but at the subthreshold speed the mean level of fat in the red muscle was lower than the controls and differed statistically from them ($P = 0.02$). Thus only when the fish swam for at least 6 hr at subthreshold speed was there evidence of fat utilization in the red muscle.[4] The reduction in fat in the red muscle suggests that the red muscle system may have been used at the subthreshold velocity. On the other hand, presence of high muscle lactate in both red and white muscle and the drop in red muscle and liver glycogen at subthreshold speeds implies that the white muscle was also active.

[4] In an earlier and preliminary experiment, five smaller jack mackerel, mean length 9.2 cm, swam at the subthreshold speed of 12.7 $L^{0.6}$/sec (48 cm/sec) for 48 hr without failure and we recorded a decrease in the mean fat content of red muscle from 23.7% (range, 20.4-28.4%; $n = 5$) to 18.0% (range, 16.2-20.8%; $n = 5$) ($P<0.05$).

TABLE 3.—Fat analyses in red and white muscle of jack mackerel following various forced swimming conditions. Where 0.0% is given for white muscle, only traces of fat were found with the chloroform-methanol extraction. For convenience zeros were used for averaging. Values given as percent dry weight of tissue.

Controls		19 $L^{0.6}$ Subthreshold speed		21 $L^{0.6}$ Threshold speed successes	
Red	White	Red	White	Red	White
20.16	1.98	15.07	0.230	16.91	0.0
21.00	0.0	15.69	2.12	22.45	0.0
21.78	.337	16.19	1.24	23.80	2.19
22.24	1.15	20.54	0.0	24.67	0.0
23.05	1.32	24.63	0.0	24.97	1.54
25.11	0.0			26.43	4.09
25.14	.390			29.37	4.10
25.89	.924				
27.29	2.65				
32.32	2.20				
Mean 24.40	1.10	[1]18.42	.718	24.08	1.70

21 $L^{0.6}$ Threshold speed fatigued		28 $L^{0.6}$ Superthreshold speed - individually fatigued		28 $L^{0.6}$ Superthreshold speed, 8-min test	
Red	White	Red	White	Red	White
21.30	0.0	16.54	0.0	21.96	2.01
21.97	0.0	16.71	0.0	23.08	.04
22.47	0.0	26.47	1.22	24.20	.18
28.70	0.0	28.19	.732	25.57	.50
30.11	2.56	28.70	2.13	29.54	2.26
32.08	1.12				
32.90	6.46				
Mean 27.08	1.45	23.32	.816	24.87	.998

[1] Differed from the controls, $P = 0.02$, Mann Whitney U test (Siegel, 1956).

DISCUSSION

Control levels of jack mackerel white muscle glycogen were similar to those recorded by Canadian workers for mixed red and white muscle in salmonids (Black, Robertson, and Parker, 1961; Black et al., 1962; Connor et al., 1964) and to those from a variety of marine teleosts (Beamish, 1968; Fraser et al., 1966; Wittenberger, 1968; Wittenberger et al., 1969). Red muscle glycogen has not often been separately determined. Our mean control value of 750 mg percent was somewhat higher than the mean of 420 mg percent reported by Wittenberger (1968) for *Trachurus mediterraneus ponticus*, a related species from the Black Sea. Fraser et al. (1966) gave a range of 215 to 279 mg percent for red muscle glycogen of cod, based on analysis of three fish in a relaxed (anesthesized) state. Wittenberger et al. (1969) reported 320

mg percent in a clupeid, *Harengula humeralis*. A much higher level of 1866 mg percent was given by Bone (1966) for dogfish. In most cases, the concentration of glycogen in red muscle was considerably higher than in white muscle.

Liver glycogen controls in jack mackerel were much higher than those reported previously in teleosts. Connor et al. (1964) for example, obtained values of about 1% in chinook and sockeye salmon and steelhead trout, and found that moderate exercise associated with ascending fishways had no effect on liver glycogen levels. Black et al. (1960) reported liver glycogen levels of 0.5-4% in rainbow trout, and Dean and Goodnight (1964) obtained 0.8-3% in four species of warmwater centrachid fishes. Values similar to ours were reported by Wittenberger and Diaciuc (1965) in carp (13.8%) and by Bellamy (1968) in recently fed red piranha (10.3%). Even if a high degree of gluconeogenesis were operative in jack mackerel, it seems unlikely that this could entirely explain the high levels of liver glycogen.

Control levels of glycogen in jack mackerel white muscle appeared to be similar to those in other fishes. However, in the red muscle and especially in the liver, glycogen levels were usually higher than in fishes studied earlier.

The most striking finding of this study was the virtually complete depletion of glycogen in the white muscle of fish that failed from exhaustion. The depletion of glycogen in white muscle occurred in all fish that failed regardless of the speed of swimming or how long they swam. In fish that did not fail at a near threshold speed of 21 $L^{0.6}$/sec (Hunter 1971) the glycogen in the white muscle did not differ from controls, whereas in the fish that failed, glycogen in the white muscle was at nearly the same low level as it was in fish that failed after a few minutes of exertion at a much higher speed. Red muscle glycogen was also depleted at some swimming speeds but the pattern of glycogen depletion in red muscle closely paralleled that of the liver. Red muscle had one-fifth the lactate found in white muscle on a percent basis but only about one-fiftieth on an absolute basis because the mass of white muscle exceeds the red by 10 to 1.

The high lactate levels in the white muscle, the almost complete depletion of glycogen in the white muscle of exhausted fish, and the parallel pattern of glycogen depletion in red muscle and liver all point to the same hypothesis. In jack mackerel at threshold and higher speeds the energy used for swimming was derived primarily from glycolysis in the white muscle which was the principal locomotor organ. Red muscle like the liver may serve as a storage organ whose resources could be used to drive the white muscle, given sufficient time for mobilization. Thus at threshold speeds, red muscle function appeared to be tied to that of the white and it could not be considered as acting independently. No change in red muscle glycogen was detected at the highest test speed, possibly because time was insufficient to mobilize the glycogen reserves other than in the white muscle itself. This time dependency for mobilizing red muscle glycogen under conditions of strenuous exercise could explain why Bone (1966), Wittenberger and Diacuic (1965), Wittenberger (1968), and Fraser et al. (1966) detected no change in red muscle glycogen after strenuous exercise. It must be remembered that in all of these previous studies the strength and the duration of the exercise was unknown, except that it was considered to be extreme.

The decrease in fat content plus the high lactate levels suggest that the red muscle was used for swimming at subthreshold speeds. Bilinski (1969) showed that the rate of oxidation of fatty acids in red muscle of rainbow trout and sockeye salmon exceeded that in the white muscle by one or more orders of magnitude depending on the fatty acid substrate. On the other hand, neither the high oxidative capacity nor the decline in lipid levels in red muscle with moderate exercise are sufficient evidence for an independent locomotor role. In addition, the presence of high lactate levels in white muscle and the drop in the glycogen content of the white muscle indicated that the white muscle was also used at the subthreshold speed of 19 $L^{0.6}$/sec. The electrophysiological evidence for indepen-

dent locomotor activity of the red muscle cannot be ignored. At some speed slower than any used in the present experiment jack mackerel may depend only on red muscle for propulsion and on lipids for fuel. At what velocity red muscle begins to play a major role or how significant this speed may be in the life of the animal are questions that remain to be answered. The most tenable explanation for these data is that both muscle systems were used at the subthreshold speed but we are unable to choose which system played the more significant role.

Jack mackerel appear to be specialized in body form and swimming capabilities for high-speed continuous swimming (Hunter, 1971). Thus the physiological characteristics we have described, namely use of glycolysis in white muscle for swimming, high liver glycogen levels, and tolerance of high muscle lactate levels may represent specializations for high-speed swimming and may not be representative of the general pattern in fishes. On the other hand, *Trachurus* may share these characteristics with other fishes of similar habits, for example other carangids and the scombroid fishes. It seems possible that evolution may have favored the development of these physiological characteristics because severe velocity limits may be set by aerobic lipid metabolism.

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