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LACTATE PRODUCTION AT HIGH SUSTAINABLE CRUISING SPEEDS IN RAINBOW TROUT (*SALMO GAIRDNERI* RICHARDSON)

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The white myotomal muscle fibres of most teleost fishes are multi-terminally innervated (Bone, 1964). Electro-myographical studies have shown these fibres to be recruited during sustained activity (see Johnston, 1980*a*). The threshold speed for recruitment of the fast motor system differs between species and may be related to the degree of polyneuronal innervation. For example, e.m.g.'s have been recorded from carp white muscle at all speeds above 0·5 body lengths s^{-1} (Bone, Kicenuik & Jones, 1978), but not until 3·2 and 4·5 body lengths s^{-1} respectively in striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*) (Freedman, 1979). The fuels and metabolic pathways utilized by white muscle during sustained swimming are unknown.

Bennett, working with amphibia and reptiles, has used whole body lactate analyses to assess the contribution of anaerobic metabolism to activity (Bennett & Licht, 1972). Measurements of whole-body lactate overcome problems associated with the compartmentalized nature of production and transport of lactate from specific tissues. The present communication reports the first such measurements in fish and investigates the time-course of lactate production in exercise-conditioned rainbow trout (*Salmo gairdneri* Richardson).

Fish (mean ± S.E. length 18·0 ± 0·2 cm, mean weight 49.8 ± 2·5 g) were obtained locally and held in tanks of filtered, fresh water. They were fed to excess daily on a proprietary brand of trout pellets. Swimming experiments were carried out in an open-top flume (150 cm long × 25 cm diameter) described by Johnston & Moon (1980). Temperature in both the holding tanks and exercise chamber were maintained at 9 ± 0·5 °C. Groups of 6-8 fish were introduced to the swimming chamber at least 2 days prior to experiments. During the conditioning period the water flow was maintained at 15 cm s^{-1} (0·9 body lengths s^{-1}). A resting sample was taken from fish swimming steadily at 0·9 body lengths s^{-1}. The water flow was increased to 63 cm s^{-1} (3·5 body lengths s^{-1}) over a period of 25 s and an initial exercised sample taken (Fig. 1). Other groups of fish were allowed to swim for various periods at 3·5 body lengths s^{-1} up to 24 h prior to sampling. Only fish that exhibited steady swimming were taken for lactate analyses. Fish that fell back on to the restraining barrier were immediately removed from the chamber (10-15%) and discarded. Whole fish were freeze-clamped in flasks of liquid nitrogen (—159 °C) to arrest metabolism. To follow the specific changes in the red and white muscle, small samples of these

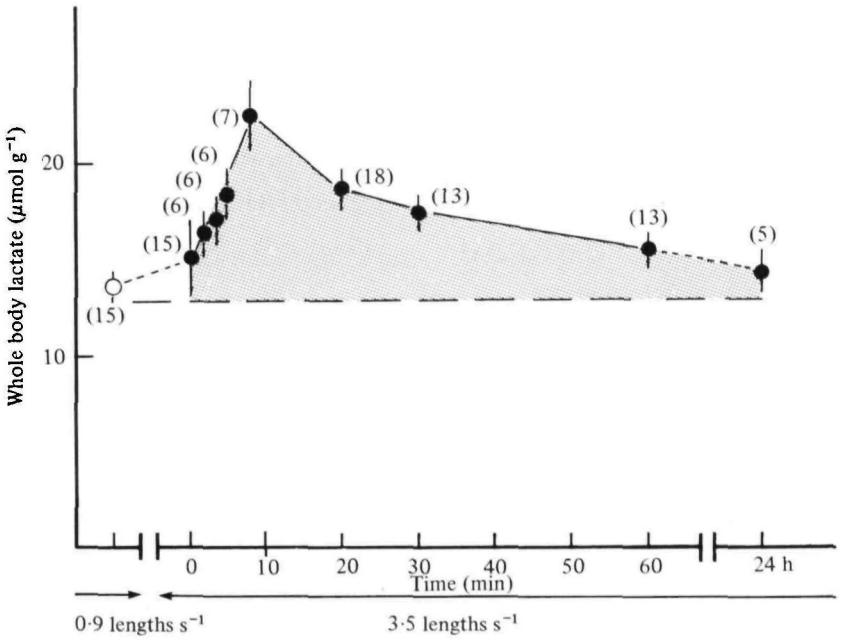

Fig. 1. Changes in whole body lactate (μmoles g wet wt.$^{-1}$) with time in rainbow trout swimming at 3·5 body lengths s^{-1}. Number of fish used shown in parentheses.

tissues (~100 mg) were dissected from the mid-region, immediately beneath the dorsal fin, from the partially thawed carcase (—15 °C). The whole body and muscle samples were homogenized in 0·6 M perchloric acid and extracted for 10 min at +4 °C. Homogenates were centrifuged for 15 min at 6000 *g* and aliquots of the clear supernatant were neutralized with 2 M-K_2HCO_3 in the presence of methyl orange indicator. Lactate concentrations were determined enzymically by the method of Hohorst (1965).

Whole-body lactate concentrations (13·9 μmol/g) of fish swimming steadily at 0·9 body lengths $^{-1}$ are comparable to resting values for amphibia and reptiles (Bennett & Licht, 1972: Bennett, 1978). Whole-body lactate increased by 3·12 μmol g^{-1} or around 16% during the 25 s acceleration from 0·9 to 3·5 body lengths $^{-1}$ (Fig. 1). A proportion of the initial lactate production may be associated with a stress reaction. Initially the fish were seen to swim unsteadily in a series of flick-glide manoeuvres which may result in a higher lactate production than that found after 1-2 min of steady swimming. Nevertheless, it is clear from Fig. 1 that initially a large proportion of total energy needs are met anaerobically. At 3·5 body lengths $^{-1}$ whole body lactate concentrations increase almost linearly for around 8 min (Fig. 1). This is equivalent to 0·62 μmol lactate production g body weight^{-1} min^{-1}, which represents an anaerobic energy production of 54 mmol ATP kg^{-1} h^{-1} assuming an ATP yield of 0·016 mmol ATP per mg lactate (Bennett & Licht, 1972).

The maximum energy obtainable from aerobic sources is known to vary with body size (Brett, 1972; Bennett, 1978). For small rainbow trout a maximal oxygen uptake of around 500 mg O_2 kg^{-1} h^{-1} would seem reasonable (see Jones & Randall, 1978)

Table 1. *Lactate concentrations in red and white myotomal muscles*

Time from start of exercise (min)	No. of fish	Lactate (μmol g wet wt.$^{-1}$)	
		Red muscle	White muscle
0	15	44·2 ±5·8	28·3 ±1·6
2 min	15	94·8 ±27·1	40·1 ±7·9
20 min	15	113·7 ±7·4	56·8 ±6·4
40 min	12	93·2 ±26·9	52·4 ±6·6
24 h	5	30·3 ±4·8	33·3 ±4·7

This is equivalent to on ATP production of 90 mmol kg^{-1} h^{-1} assuming an aerobic scope of 450 mg O_2 kg^{-1} h^{-1} and that 1 mg O_2 yields 0·20 mmol ATP (Bennett & Licht, 1972). Literature values for the critical swimming speeds of small salmonids vary from around 2 to 4 body lengths s^{-1} (Webb, 1971). The percentage of maximum oxygen uptake at 3·5 body lengths s^{-1} is likely to be in the range 60-100% or an ATP equivalent from aerobic sources of 54-90 mmol ATP kg^{-1} h^{-1}. Thus total energy expenditure for a 50 g fish at this swimming speed can be calculated to be in the range of 108-144 mmol ATP kg^{-1} h^{-1}. The initial anaerobic contribution is thus likely to be at least 38%.

The fall in whole body lactate after 8 min indicates a significant catabolism of lactate and may indicate a decreased reliance on anaerobic metabolism as the fish settle down to a more economical type of swimming (Fig. 1). Following 24 h swimming at 3·5 body lengths s^{-1}, whole body lactate has dropped to a concentration not significantly different from the 'rested' fish (Fig. 1).

Preliminary experiments have shown that 60% of 50 g rainbow trout could swim for more than 4 h at 5 body lengths s^{-1}. The whole-body lactate levels rose from 16·3 to 28·8 μmol g^{-1} over this period, indicating that lactate production now exceeds its maximum rat of catabolism.

Lactate increase 110% in red and 85% in white muscles after 40 min swimming (Table 1). The threshold swimming speed for recruitment of white muscle in rainbow trout (26-34 cm) has been estimated as 1·2-1·5 body lengths s^{-1} by Hudson (1973) and as 2-2·5 body lengths s^{-1} by Bone *et al.* (1978) (17-30 cm fish). Thus in our 18 cm fish it is likely that both red and white muscle are contributing to the power output at 3·5 body lengths s^{-1}. As only a proportion of white fibres are recruited at this speed net lactate accumulation may be higher per active mass of muscle than these figures indicate Table 1). Following 40 min swimming both red and white muscle lactate remains high in the region sampled even though there has been a net catabolism of lactate from the body (Fig. 1).

Hudson (1973) has suggested that the sustained operation of anaerobically supported contractions is achieved by a rotation of recruitment of white fibre motor units. A variety of mechanisms for maintaining redox balance within white muscle have been proposed including the transfer of lactate to other tissues such as red muscle, gills, kidney and liver for subsequent oxidation to pyruvate (Bone, 1975). An interesting possibility is that lactate constitutes a major substrate for aerobic metabolism by red muscle. The rise in red muscle lactate (Table 1) and the rapid catabolism of the initial lactate load produced at 3·5 body lengths s^{-1} (Fig. 1) is at least consistent with this idea.

Although anaerobic metabolism is an inefficient means of producing ATP for sustained swimming, it is likely that for short periods of activity this is compensated for by increasing the range of speeds at which the fish is able to swim.

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