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AN ASSESSMENT OF THE ROLE OF LACTIC ACID AS A LIMIT TO FISH PERFORMANCE DURING CAPTURE

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INTRODUCTION

Some of the major gaps in our knowledge of swimming performance of common marine teleosts were indicated during the conference on fish behaviour in relation to fishing techniques and tactics 1967. In particular, papers by Blaxter (1969), Hemmings (1969) and Foster (1969) pointed to the absence of adequate knowledge of the physiology of swimming and especially the endurance of the fish commonly caught by the seine net or the trawl. Considering the various advances in the study of swimming physiology during recent years it is now possible to propose a working hypothesis that should make much clearer the relationship between the swimming performance of the fish and the speed and motion of the gear designed to catch the fish.

a) - The two swimming systems

Anatomists and histologists have long recognised that in teleosts there are two types of muscle fibre in the lateral swimming muscles. More recently it has been demonstrated that the so-called red muscle is composed typically of slow type muscle fibres and the white muscle is made up of large diameter fast fibres (Barets 1961, George 1967). The presence of oxidative enzyme systems in the red muscle and their absence from the white muscle (Braekkan 1956, Bone 1966), indicate that the red muscle can perform aerobic respiration while the white muscle must function anaerobically.

b) The anaerobic system

It is now well established that when fish are chased forcibly, the level of glycogen in the white muscle falls rapidly to near zero levels within 10 to 20 minutes of exercise (Dando 1969, Beamish 1968, Burt 1969, Wardle in prep.) and it has been shown that 50% of the glycogen may be lost within two minutes (Black et al., 1962). The drop in glycogen levels leads to an equimolar elevation of lactic acid in the same tissue (Black et al., 1962, Wittenberg and Diacuic 1965, Burt and Stroud 1969, Stevens & Black 1966, Beamish 1968, Dando 1969, Burt 1969). There are up to now no reliable estimates of the distance and speed that this fuel store represents. First estimates (Wardle unpublished) suggest that plaice (30 cm) can swim, using anaerobic bursts of swimming distances around 300 to 500 m only and it is to be expected that other teleosts when forced to do so will be capable of swimming distances around 1000 to 1500 body lengths. However, further measurement of these important distances are required. It seems worthwhile considering the teleost as having a limited number of tail beats or contractions of the white lateral muscles related to the breakdown of the glycogen store to lactic acid.

c) The aerobic system

The idea of an aerobic cruising muscle and its independence from the glycogen to lactate anaerobic system is now accepted. It is a well

known observation that each species of teleost has an upper speed of swimming at which it does not tire. As long as the speed is not increased above this cruising threshold the fish can swim for a relatively long period in speed tests. It has been noted in the literature that the cruising speed is related to the amount of red muscle and that this muscle is serviced by a matching oxygen transport system and gill heart system. In general fish with large amounts of red muscle have higher haematocrits and larger hearts than those fish with little or no red muscle (Blaxter, Wardle, Roberts, 1971). It is possible for fish with only traces of an aerobic system to have nearly no red blood cells and a very much expanded lymph system (Blaxter, Wardle, Roberts, 1971; Wardle, 1971).

The physiological limits to the performance of the aerobic muscle system are (1) the maximum rate at which it can repeat contractions (somewhere between 1 and 5 tail beats per second) and (2) the strength of the contraction which will be related to the number of fibres of aerobic tissue contracting. The speed attained by this system will be a function of the strength perhaps seen as tail beat amplitude or as a matched increase in the driving surface of the caudal fin.

The distance moved during one complete tail beat has been found close to a constant of 0.6 body lengths (Bainbridge, 1958). Now it is suggested by various authors that the aerobic muscle system can sustain swimming speeds of between one and three body lengths per second indicating a contraction cycle of between 2 and 5 tail beats per second maintained indefinitely. /Note: Bainbridge's constant of 0.6 body lengths per tail beat does not allow for the concept of a more powerful thrust at the same frequencies suggested by the greater volume of red muscle in cruising species of teleosts./

d) Preliminary experiments

The following experiments were designed to demonstrate the basic proposal that when fish are made to swim at speeds below the cruising threshold for long periods their anaerobic system remains in a resting condition.

METHODS

Cod, Gadus morhua; saithe, Gadus virens and haddock, Melanogrammus aeglefinus, were caught in shallow water (7-10 m) off Girdleness, Aberdeen. They were placed in the centre area of a 10 m diameter circular gantry tank, Fig. 1, in sea water maintained at 12°C and 90% oxygen saturation until feeding was established (5-10 days). Groups of 20-30 fish were herded into the test channel (Fig. 1) through a gate and the fish were adapted to low light intensity. The fish were made to move by projecting light patterns from the gantry (Fig. 1). The gantry has a variable speed of rotation around the perimeter of the tank being pivoted at the centre. A successful arrangement was evolved where the tank room was in darkness and the fish swam in an area of speckled illumination in front of the gantry and were reluctant to fall back into an area of bright illumination behind the gantry. Fish were sampled from the channel by opening a gate in the outer wall of the channel which lead individuals between two stainless steel electrode grids 100 cm apart. When the fish was exactly between the electrodes an alternating current (20 volts 40 amps) was applied for 10 seconds and the stunned fish removed. The head of the fish was cut from the body and muscle samples one from each side were frozen in liquid nitrogen. The two samples from each fish were analysed for lactate (Hohorst 1963) and glycogen, (Handel 1965) blood samples were collected from the renal portal vein and analysed for lactic acid as described in Wardle (1971).

RESULTS

The levels of muscle, glycogen and lactic acid in fish adapted to the tank and stunned electrically without exercise are shown in Table 1. A group of similar fish was exercised by constant chasing and their low muscle glycogen and high muscle lactic acid levels are shown in Table 2.

A group of the same batch of fish was made to swim at a speed of 36.7 cm per second for seven hours per day for 21 days. At this speed a proportion of these fish repeatedly dropped back behind the moving gantry and missed revolutions. The muscle glycogen of those that dropped behind was found to be depleted (Table 3). All but one (C19) of the fish which had kept swimming for 194.0 km at 36.7 cm/sec showed resting levels of glycogen and lactate when sampled after their final seven hours of swimming (Table 4).

Another group of cod, haddock and saithe were made to swim at 36.7 cm/sec continuously for 102 hours (134.64 km). The muscle of these fish showed a resting state of high glycogen and low lactate levels (Table 5).

The experimental treatments and their effect on the muscle glycogen and lactate are summarised in the diagram (Fig. 2).

DISCUSSION

The formation or non-formation of lactic acid in the muscle is clearly critical at all stages of capture by trawl or seine net. When fish first encounter the fishing gear they will normally be in a rested condition. As long as the fish are moved only slowly by the gear they could remain in this rested condition possibly swimming at speeds up to 1-3 body lengths per second without significant production of muscle lactic acid. For example, when the bridle warps of the seine net sweep the bottom they herd fish to the centre (Hemmings 1969). As the rope moves in, the apparent movement inwards is a small vector of the forward hauling speed on the rope. The reactions of haddock, cod and saithe to the warps have not yet been observed but it is thought likely that the roundfish will swim away from the rope at a slow steady speed until they arrive between the wings. Once between the wings haddock maintain station swimming with the forward moving wings for some minutes before turning back into the tunnel of the net. The speed here is likely to be of the order of 100-200 cm/sec (2-4 knots) and the fish would have to be 100-200 cm long in order to avoid using their anaerobic muscle. The lactic acid production in the smaller fish may at a certain stage become critical and decide the time of dropping back into the net.

The state of exhaustion of the fish seen landed on the deck of the catching ship is clearly not the same as the state of the fish when it dropped back in the mouth of the net. Observation of the cod-end by divers during a haul shows that the confinements of the netting cause the fish to struggle violently. The period of this confinement is up to 20 minutes while the net is hauled to the surface, giving adequate time for the complete exhaustion of the muscle glycogen as has been recorded by Beamish (1966), Dando (1969), Wardle (in prep.).

Lactate as a lethal factor in fish capture was discussed by Black (1958), Jonas (1962), Beamish (1966). Recent observations (Wardle in prep.) have suggested that the high levels of lactate in the blood of fish after capture is not due to a normal release of lactate from exhausted muscle but is probably due to the weakening of the animals' metabolism by some other feature, for example, oxygen lack. This damage weakens an

active metabolic process which holds lactic acid in the muscle cells. The lactic acid then released contributes to a spiral of non-recovery. This is of importance here only in that fish taken from the cod-end will have this potential for self-destruction if the metabolism is weakened. Exhaustion of this sort will play no part during the swimming of the fish in front of the gear.

It was noted by Black (1958a) and Black et al. (1961) that trout exercised by chasing showed a change in behaviour at a certain stage during exhaustion described as a change from "run" to "seek shelter". This would seem to present a protective mechanism so that the anaerobic system is not voluntarily, completely depleted. The change in behaviour is repeatedly seen in fish that are made to swim for some time at speeds above true cruising and it may be of some significance in the reaction of fish to gear used to capture them.

Whether the reason for drop back in the mouth of the net be exhaustion or a simple feed back effect of lactic acid build up in muscle or blood on behaviour, it is clear that those parts of the net herding fish should not induce the dropping back reaction, whereas fish in the region of the mouth of the net should be induced to drop back as rapidly as possible. It is also clear that a critical point is whether or not the induced swimming involves the anaerobic muscle system.

In conclusion, further knowledge is required on the true cruising rate, i.e. the maximum speed at which the fish is not using its anaerobic system. We must know the distance a fish can swim using its anaerobic fuel store and at what speeds. The change in behaviour of the fish as the anaerobic store is used up must be analysed. The speed at which fish swim at different stages during the capture process and the physiological state at these different stages must be investigated.

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Table 1

Muscle glycogen and lactate levels of resting fish sampled by electric shock

Species* No.	Muscle Glycogen mg/100g	Muscle Lactate mg/100g	Muscle Total G+L mg/100g	Length (cm)	Weight (gm)
C1	105.4	156.3	261.7	29	263
C2	113.1	100.9	214.0	34	417
C3	207.1	65.3	272.4	29	257
C4	15.3	81.1	96.4	31	279
C5	36.9	97.7	134.6	37	568
C6	147.2	50.2	197.4	34	356
S1	566.4	89.9	646.3	36	546
H1	74.4	187.6	262.0	26	148

*C = cod S = saithe H = haddock

Table 2

Muscle glycogen and lactate levels of five rested fish exercised to exhaustion during 15 minutes

Species* No.	Muscle Glycogen mg/100g	Muscle Lactate mg/100g	Muscle Total G+L mg/100g	Length (cm)	Weight (gm)
C7	4.6	269.4	274.0	33	330
C8	2.5	154.5	157.0	30	241
C9	10.0	157.7	167.7	27	191
C10	5.1	209.2	214.3	31	268
S2	22.5	124.3	146.8	38	503

*C = cod S = saithe

Table 3

Muscle glycogen and lactate levels of five cod which dropped behind during cruising experiment (see Table 4)

Species No.	Muscle Glycogen mg/100g	Muscle Lactate mg/100g	Muscle Total G+L mg/100g	Length (cm)	Weight (gm)
C20	10.8	113.6	124.4	29	241
C21	11.2	63.9	75.1	22	86
C22	14.3	68.0	82.3	28	198
C23	4.1	110.6	114.7	27	169
C24	2.9	90.3	93.2	31	265

Table 4

Muscle of glycogen and lactate levels of cod cruising 7 hours a day for 21 days, sampled by electric shock

Species No.	Muscle Glycogen mg/100g	Muscle Lactate mg/100g	Muscle Total G+L mg/100g	Length (cm)	Weight (gm)	Blood Lactate mg/100g
C11	197.2	94.8	292.0	33	415	5.0
C12	227.0	198.3	425.3	54	1400	13.1
C13	133.5	79.1	212.6	39	637	3.0
C14	122.0	83.0	205.0	32	352	4.9
C15	248.0	92.1	340.1	30	319	4.1
C16	105.0	77.4	182.4	29	259	7.0
C17	109.5	88.8	198.3	27	206	7.8
C18	135.9	76.2	212.1	32	383	7.6
C19	15.9	254.2	270.1	34	390	58.3

Table 5

Muscle glycogen and lactate levels of twenty fish cruising continuously for 102 hours at 36.7 cm/sec total distance swum 134.64 kilometres

Species* No.	Muscle Glycogen mg/100g	Muscle Lactate mg/100g	Muscle Total G+L mg/100g	Blood Lactate mg/100g	Length (cm)	Weight (gm)	Speed Body length/ second
C25	176.1	42.7	216.8	5.4	40	669	0.92
C26	287.9	144.2	432.1	5.8	27	196	1.36
C27	135.8	144.8	280.6	6.3	32	322	1.15
C28	241.2	139.8	381.0	5.7	35	504	1.05
C29	322.3	95.5	417.8	2.1	35	481	1.05
C30	45.1	277.1	322.2	7.5	37	498	0.99
C31	270.8	115.5	386.3	10.4	28	238	1.31
C32	58.1	91.5	149.6	8.9	32	297	1.15
C33	377.5	125.1	502.6	6.6	25	151	1.47
S 3	1256.1	119.3	1375.4	5.3	39	624	0.94
S 4	1442.1	107.1	1549.2	3.3	39	682	0.94
S 5	466.3	159.5	625.8	6.9	40	706	0.92
S 6	376.2	138.5	514.7	3.8	45	1000+	0.81
S 7	1456.6	130.5	1587.1	16.8	37	579	0.99
S 8	188.4	112.1	300.5	1.8	36	423	1.02
S 9	223.7	141.1	364.8	3.9	43	754	0.85
S10	382.9	152.0	534.9	2.4	41	743	0.89
S11	33.8	262.5	296.3	21.1	29	240	1.26
H 2	379.8	228.1	607.9	2.4	34	366	1.08
H 3	474.9	287.1	762.0	8.4	35	457	1.05

*C = cod
S = saithe
H = haddock

FIG. 1. DIAGRAM OF THE GANTRY TANK

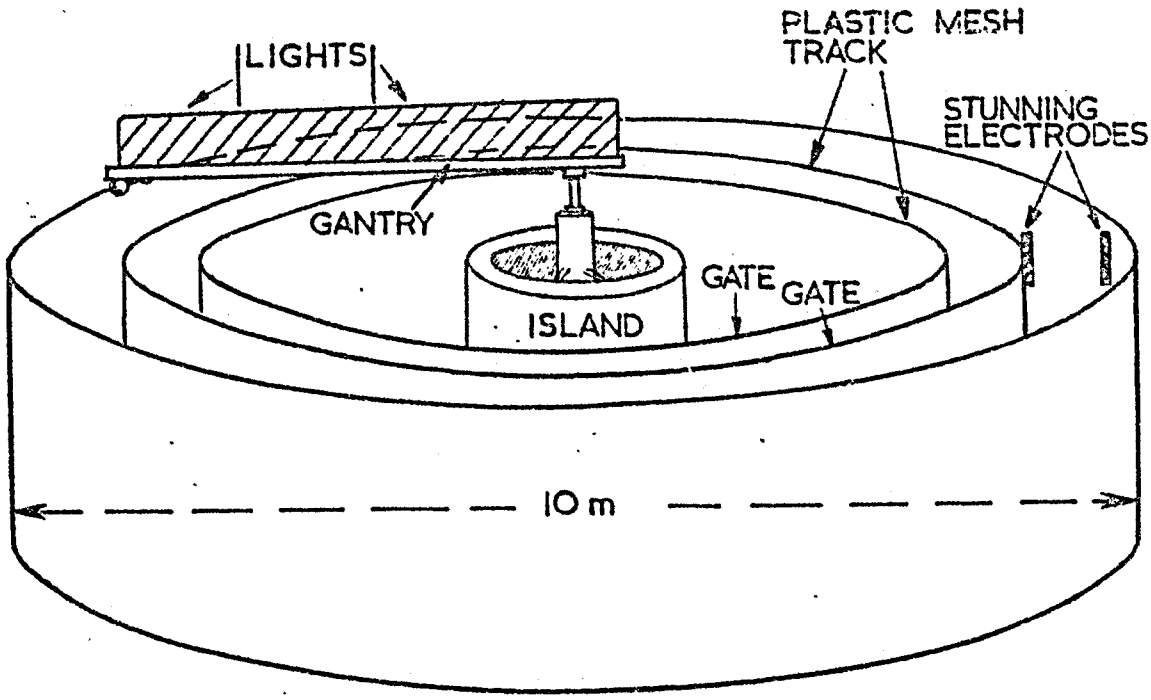

FIG. 2. SHOWING THE TOTAL AND RELATIVE LEVELS OF GLYCOGEN AND LACTIC ACID IN THE ANAEROBIC MUSCLE IN THE CONDITIONS INDICATED.