THE MYOTOMAL MUSCLE OF LABRIFORM SWIMMING FISH IS NOT DESIGNED FOR HIGH SPEED SUSTAINED SWIMMING

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ABSTRACT

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Two species of labriform swimming fish, *Pseudolabrus celidotus* and *P. fucicola* were exercised in a swimming tunnel. Both species had similar modes of swimming, with the pectoral fins being used for propulsion at all speeds up to the maximum sustainable. Myotomal muscle was only used at the fastest speeds and this led to rapid fatigue. Small amounts of lactate built up in the pectoral fin muscles but not in the myotome. This lack of anaerobic capacity is discussed in relation to the swimming characteristics and way of life of the fish.

KEYWORDS: *Pseudolabrus* - labriform locomotion - lactate - myotome.

INTRODUCTION

Swimming and exercise in fish has been the subject of intensive study, with the production of many papers, several major reviews and even books devoted to the topic (Blake 1983a, Hoar & Randall 1978, Johnston 1981, Webb & Weihs 1983). A major reason for this large volume of work is the fact that fish muscle is arranged in discrete blocks such that the red cruising muscle is essentially separated from the white sprint muscle (Johnston 1981). This makes the muscle ideal to work with, as all of the 'higher' vertebrate muscle is found as a complex mosaic of at least 3 fibre types, with the features of any particular muscle being determined by the dominant fibre type (Dudley *et al.* 1982). Although the literature is large, the number of fish species which have been investigated is quite small. These fish tend to be those which will swim readily, in particular the salmonids and pelagic marine fish. Benthic fish tend not to swim and so are not used (Davison 1985), although work has been carried out on several species of flatfish (Duthie 1982, Milligan & Wood 1987a, b, Wardle 1978). In addition, those fish which have been exercised have tended to be 'typical' fish in that they use their myotomal muscles for both low and high speed swimming (carangiform locomotion). In these fish the bulk of the myotome is composed of white sprint muscle with a small amount of red cruising muscle located just under the skin (Johnston 1981).

Many teleosts, however, do not use their myotomes for low speed swimming, but instead have developed their fins for this function, allowing great manoeuvrability (Webb 1984). In theory, these fish should be ideal animals for the study of muscle function, as the muscle types are not just arranged into discrete blocks within the myotome, but are physically separated, with the slow speed red muscle located in the working fin and the fast white muscle in the myotome (Davison 1987, Davison & Macdonald 1985, Harrison *et al.* 1987). Work on fish which use their fins for low speed swimming, however, has been very limited. Blake (1983b) has reviewed some of the work. Recently, Johnston (1987) and Dunn & Johnston (1986) working on species of fish collected from the Antarctic Peninsula discovered that these fish were incapable of maintaining a high swimming speed once the

myotomal muscle took over from the pectoral fins. This appeared to be due to low levels of activity of enzymes involved in the glycolytic pathway, so that although the fish possessed large amounts of white muscle, which has traditionally been regarded as a sprint muscle, the muscle seemed to be inadequately equipped for its role. Other recent work on swimming in the Antarctic fish *Pagothenia borchgrevinki* has supported these findings (Davison *et al.* 1988, Forster *et al.* 1987).

Antarctic fish are specialist labriform swimmers using their pectoral fins for low speed swimming while their sprint capacity seems to have been compromised. The question remains, however, as to whether this low anaerobic capability is a consequence of the low environmental temperature and a lack of thermal compensation of the enzymes of the glycolytic pathway (Holeton 1974), or whether it is a result of the switch from myotomal based slow speed swimming to pectoral fin based swimming. The present work attempts to answer this question by examining the swimming performance of two species of teleost fish of the genus *Pseudolabrus*, both temperate water labriform swimmers.

MATERIALS AND METHODS

Spotties (*Pseudolabrus celidotus*) and banded wrasse (*P. fucicola*) were collected using handlines in shallow water around the Kaikoura Peninsula, New Zealand. They were transported to the Edward Percival Field Station at Kaikoura where they were held in aquaria with running seawater at environmental temperature and a natural photoperiod. The fish were kept for at least 48 h and up to one week before any experimentation and they were not fed during this period. Fish were selected so that within each species all fish were of approximately equal length.

Fish were exercised in a large version of the Blazka-type respirometer described in Davison (1985), with the front half of the tunnel covered with a cloth to encourage the fish to remain in this section. An animal was introduced into the central tunnel and left to swim against a low water current (approx. 0.5 body lengths per second (bl s^{-1})) for 30 min. The water speed was then increased to 1.5 bl s^{-1} and the fish were exercised for 15 min. Following this, the water speed was increased each 15 min by approximately 0.2 bl s^{-1} until the fish became exhausted and could not swim off the lower restraining grid. Maximum sustainable swimming speed (U-crit) as defined by Brett (1964) was determined for each fish.

Once a fish had become exhausted it was removed from the respirometer and killed by a blow to the head. Whole pectoral fin muscles (musculus adductor profundus) and samples from the deep part of the myotome immediately below the dorsal fin were dissected from the animal and plunged into liquid nitrogen. Samples of liver were collected from the banded wrasse. Tissue samples were freeze ground under liquid nitrogen, denatured with perchloric acid and assayed for lactate using a commercial test kit (Boehringer Mannheim, kit no 139084). Control fish were captured and removed from their holding tanks without struggling and killed by a blow to the head. Tissue samples were acquired and dealt with as above.

RESULTS

Each fish swam readily in the tunnel respirometer, maintaining station at the anterior end of the tunnel, beneath the shaded portion. Increasing the swimming speed caused the fish initially to lose its position in the tunnel, but this was quickly regained and the fish settled rapidly to the new water speed. Swimming at the lower speeds was accomplished entirely by pectoral fin locomotion. Each time the water speed was increased, the fish utilised its myotomal muscle for a few tail beats before resuming swimming with the pectoral fins. Towards U-crit, fish clearly had difficulty maintaining station by using only the pectoral fins and only at this point did myotomal muscle become important for locomotion. Typically the fish would swim using its pectoral fins, while losing station, drifting back towards the rear grid, as the water speed was too great for the amount of thrust available from the pectoral fin muscles. The fish would then regain station using several beats of the tail and the process would begin again. At U-crit, the myotomal muscle was used extensively. Swimming

	CONTROL			EXERCISE		
	Mean	*s.d.*	Range	Mean	*s.d.*	Range
U-crit (bl s^{-1})						
banded wrasse (n = 5)				2.98	0.13	2.81-3.11
spotty (n = 6)				3.64	0.08	3.58-3.7
Lactate (µmol g^{-1})						
banded wrasse (n = 5)						
Pectoral fin	18.34	9.00	9.88-27.8	15.13	9.36	8.89-28.96
Myotome	10.22	1.69	8.9-12.13	12.73	7.60	6.33-23.40
Liver	1.45	0.53	0.85-1.88	2.37	1.17	1.08-3.62
spotty (n = 6)						
Pectoral fin	5.20	1.57	3.70-7.74	7.69	6.17	2.73-19.55
Myotome	7.96	0.71	7.32-9.02	5.92	1.33	4.27-8.18

Table 1. Values of critical swimming speed (U-crit) and lactate concentrations in the muscles of banded wrasse and spotties.

was maintained for a few minutes and then the fish fell back onto the lower restraining grid, and was unable to remove itself from it. U-crit for banded wrasse was 2.98 bl s^{-1} for fish 271 mm total length (223 g). A single small banded wrasse (120 mm total length) had a U-crit of 3.96 bl s^{-1}. Maximum sustainable swimming speed for spotties was 3.64 bl s^{-1} for fish with an average total length of 158 mm (58 g) (Table 1).

Tissue lactate concentrations can be seen in Table 1. Control values from spotty muscle were 5.20 and 7.97 µmol g^{-1} for pectoral fin and myotome respectively. After exercise lactate levels in the pectoral fin increased to 7.69 µmol g^{-1} while levels in the myotomal muscle decreased to 5.92 µmol g^{-1}. These values were not significantly different from the controls. Pectoral fin muscle from control banded wrasse had high levels of lactate (18.34 µmol g^{-1}), with moderate levels in the myotome (10.22 µmol g^{-1}). Levels in the liver were very low. Exercise in these fish produced a decrease in lactate in the pectoral fin and an increase in the myotome (new levels 15.13 and 12.73 µmol g^{-1} for pectoral fin and myotome respectively). However, there was a great deal of variability in lactate levels in the pectoral muscle of both control and exercised fish and also in the myotome of the exercised fish, and none of the changes were significantly different. Lactate levels in the liver doubled with exercise, but again, this was a non-significant change (Table 1).

DISCUSSION

The two species of *Pseudolabrus* examined in the present study are typical members of the group in that they are diurnal reef dwelling fish usually found during the day actively swimming in mid-water. This swimming is labriform, with the pectoral fins carrying out all of the low speed work. The tail and myotomal muscle is used for fast swimming, but observations of these fish in the wild indicate that the tail is not used for extended periods of swimming, but only for a few tail beats, giving a short period of rapid acceleration. This is probably the usual mode of utilisation of the myotomal muscle for most reef dwelling fish, as they rely on the topography of the reef and associated weeds for protection, rather than the ability to outswim any predator (Webb 1984). Certainly the vast majority of reef dwelling teleosts have abandoned the myotome as a cruising muscle and use their fins for locomotion, perhaps as a prerequisite for life around a reef where manoeuvrability is more

important than speed.

Maximum sustainable swimming speed is dependent on the species of fish and also the size of fish used. Fish such as the salmonids have high U-crits reflecting the life style of the animal, while fish which do not swim continuously have much lower maximum swimming speeds (Beamish 1978). U-crit is determined by the shape of the fish (Webb 1984) and the training history, as training produces an increase in this parameter (Besner & Smith 1983, Nahhas *et al.* 1982). However, the genetic history is also important as Duthie (1987) has recently shown that inbreeding of rainbow trout at a fish farm in the U.K. has produced a strain of fish with particularly poor swimming characteristics. The data presented in the present work show that spotties and banded wrasse (closely related fish with similar lifestyles) have similar values for U-crit and that this is related to size. The value of 2.98 bl s^{-1} for banded wrasse is below that for the spotties, but the former were much bigger fish. The small banded wrasse which was exercised had a U-crit greater than both groups of fish, showing quite nicely the effect of size. Values of U-crit of between 3 and 4 bl s^{-1} for fish of the size used compares well with other fish species (Beamish 1978) and is similar to the 3.9 bl s^{-1} recorded for the surfperch *Cymatogaster aggregata*, a labriform swimmer examined by Webb (1973).

Swimming did not produce significant changes in the lactate concentrations of either the pectoral fin or myotomal muscles in either species of fish. The pectoral fin muscle of these fish, although predominantly a red muscle used for slow speed cruising, also contains populations of fast twitch red and white fibres (Starling 1985, Davison unpubl. data). After exercise, the pectoral fin muscles had higher values of lactate than the myotomal muscle and it is probably the fast twitch fibres which have produced it. Observations of the fish in the swimming tunnel certainly indicated that they did not use the myotome until it was absolutely necessary, so at high speeds the pectoral fin muscle was working very hard. Even so, lactate concentrations were not high after exercise in either species indicating that this muscle is not primarily an anaerobic muscle (Davison *et al.* 1988). An obvious feature of the pectoral fin lactate values shown in Table 1. is the great variability between animals. This is probably due to differences in utilisation of the fast twitch fibres at high speed, and perhaps genetic differences in the number of white fibres present in the muscle. In addition, banded wrasse control fins showed a large range of values. Although great care was taken to minimise struggling during handling of these animals it is likely that these differences were caused by handling prior to sacrifice. The low values of lactate in the liver suggests that lactate was not high in the muscles prior to removal from the holding tanks.

The myotomal muscle did not show the large increases in lactate usually expected in this tissue following exercise (Fraser *et al.* 1966, Wokoma & Johnston 1981). Similar findings were reported by Davison *et al.* (1988) working with the Antarctic fish *Pagothenia borchgrevinki*, while the work of Dunn & Johnston (1986) and Johnston (1987) suggests that the white muscle in these cold water labriform swimmers simply does not possess the glycolytic capacity to produce this metabolic end product. Data from labriform swimmers from temperate or tropical waters are not available, although Whoriskey & Wootton (1987), working on the three-spined stickleback reported that the change from labriform to myotomal swimming produced very rapid fatigue. The present work indicates that although there may be some capacity for anaerobiosis in the pectoral fin muscle, fish using labriform locomotion do not develop the capacity for rapid production of lactate in the myotome. This in turn must limit the ability of these animals to maintain a high sustained swimming speed using the tail for propulsion.

Webb (1984) has suggested that fish can be classified into three swimming groups which he terms accelerators, cruisers and manoeuvrers. As labriform swimmers the Pseudolabrids would fit into the latter group. Webb states that the body form required for manoeuvrability leads to a shape which is particularly unsuited for high speed carangiform style swimming and as a result, this capability has not been well developed. Weibel *et al.* (1981), although working on scaling effects on the oxidative capabilities of mammalian tissues, have suggested that cellular sys-

tems are balanced with the needs of the body and that there is no 'spare' capacity. For example, oxidative capacity in a mammalian muscle is determined by the level of activity of that muscle at that time. An increase in activity due to training requires a corresponding increase in the oxidative capacity by changes in mitochondrial content to reach a new balance. Extending this to the *Pseudolabrus* situation, it is feasible that this lack of ability to generate large concentrations of lactate is a consequence of the lack of sustained high speed carangiform swimming in these animals in the wild. The system is well adapted for short bursts of swimming using the myotome by utilising the existing stores of high energy compounds such as ATP and creatine phosphate (Dunn & Johnston 1986), but this only allows a few tail beats. Recovery from this would utilise the existing cellular mechanisms without the requirement for extensive glycolytic capacity. The implication from this is that training of the white myotomal muscle would lead to increased levels of glycolytic enzyme activities, however, as these fish do not use their myotome until absolutely necessary, in practice it would be almost impossible to carry out the training work. The present work thus indicates that labriform swimming fish have myotomal muscle which is not designed for high speed sustained swimming.

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