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AEROBIC AND ANAEROBIC SCALING IN FISH

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CONTENTS

I. INTRODUCTION

The biology of an organism is influenced by its size at every level of organization. Recent reviews describe how the biochemistry, physiology, morphology and behaviour of an individual or species is affected by its size, and how these characteristics in turn influence population and community structure (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). Because many of these relationships, especially at sub-community levels, are associated with the 'universal' decrease in mass-specific respiration rate which occurs with increased size, the scaling of aerobic metabolism has been the subject of particular theoretical and empirical study (Brody, 1945; Kleiber, 1947; Hemmingsen, 1960; Winberg, 1960; McMahon, 1973; Taylor *et al.*, 1980; Heusner, 1982). In contrast to aerobic metabolism, the potential for generating energy by anaerobic metabolism appears to increase with size in the locomotor muscles of both fish and mammals (Somero & Childress, 1980; Emmett & Hochachka, 1981; Siebenaller, Somero & Haedrich, 1982). These reports attribute this relationship to the increased mass-specific costs of locomotion in larger animals (Pedley, 1977), however it is not clear if there is a 'universal' scaling relationship for anaerobic metabolism as is the case with aerobic metabolism.

The importance of anaerobic metabolism to survival and fitness is greater than its contribution to the total energy budget of an individual or species. For although the amount of energy liberated by anaerobic metabolism may be small relative to daily aerobic metabolism (Bennett, 1982), it is called upon during critical burst and sprint

activity associated with predator–prey interactions (Bennett, 1986; Pough & Andrews, 1985*a*, *b*). Small changes in performance, therefore, can mean the difference between *acquiring* energy and being *acquired* energy (Miller, Sinclair & Hochachka, 1959; Taylor & McPhail, 1985). Since maximum muscle power occurs as a result of anaerobic energy production, anaerobic metabolism will largely define the scaling relationships for both maximum locomotor acceleration and the accompanying structural stresses (Currey, 1977; Seeherman *et al.*, 1981). Differences in burst performance and anaerobic demand, as with aerobic metabolism, will also be associated with particular morphologic, foraging and life history patterns (Webb, 1984; Taylor & McPhail, 1986; Webb & Buffrenil, 1990; Goolish, 1991).

The purpose of this review is to examine the relationship between the scaling of anaerobic metabolism and maximum aerobic metabolism. In particular, I consider the scaling of those factors which are likely to influence the demand for, or supply of, anaerobic metabolism by fish during swimming. Aerobic–anaerobic interactions are important because the power requirements during burst and sprint swimming are partially provided by aerobic metabolism and because the recovery period following an anaerobic episode is also dependent on aerobic metabolism. The maximum mass-specific aerobic metabolism of fish is believed to be unaffected by or to increase with body size (Brett & Glass, 1973; Wieser, 1985). This seems to contradict theoretical expectations based on the scaling of oxygen uptake and delivery (Coulson, Hernandez & Herbert, 1977; Peters, 1983). Therefore, I first re-evaluate the scaling relationship for maximum aerobic metabolism in fish by considering the tissue-specific distribution of aerobic capacity and how it is affected by size.

II. AEROBIC METABOLISM

Scaling relationships are conventionally expressed by the equation $Y = aM^b$ where M is the size of the organism measured as weight (W) or length (L). Negative allometry exists when the weight or length exponents are less than 1·0 and 3·0, respectively. Relationships described by exponents greater than these values are said to display positive allometry. The resting or basal metabolic rate among most animal species increases as $W^{0.75}$ (Kleiber, 1947; Hemmingsen, 1960; Feldman & McMahon, 1983). The basal (=standard) metabolic rate of fish appears to be less affected by size, with values for the allometric weight exponent ranging between 0·8 and 0·9 (Brett & Groves, 1979). Currently debated explanations for the scaling of basal metabolism are usually based on the limits imposed by scaling some physiological, morphological, or mechanical property (e.g. oxygen delivery, surface area or bone stress). It is useful to examine these constraints, but it must be kept in mind that these theoretical considerations pertain to the scaling function for maximum metabolic rate. The use of these hypotheses to account for the scaling of basal metabolism is based on the assumption that maximum metabolic rate is a constant multiple of basal metabolism at all sizes. When maximum aerobic capacity is measured during locomotor activity, this assumption appears to be true for mammals (Taylor *et al.*, 1980) but not for fish (Brett & Glass, 1973).

(1) *The paradox in scaling of active metabolic rate*

The maximum aerobic metabolic rate of an individual or species has usually been assumed to occur during intense but sustainable locomotor activity. This is probably

true for most mammals where highly aerobic (relative to fish) locomotor muscle comprises 40–45 % of their body mass (Munro, 1969). In a typical ectothermic fish, however, the red muscle tissue used in aerobic swimming comprises only about 5 % of body mass (Greer-Walker & Pull, 1975; Love, 1980), and many species have essentially no red muscle, e.g. pike (*Esox lucius*). These tissue proportions suggest that aerobic locomotor activity is much less likely to represent the maximum rate of oxygen consumption for fish than for mammals.

Many of the early and comprehensive studies of fish energetics were done using species with atypically high capacities for aerobic metabolism and locomotor performance, e.g. salmon and trout. Most species of fish are much less well adapted, physiologically and morphologically, for locomotor activity. The North American darters (*Percidae*), for example, comprise approximately one-fifth of the species which occur north of Mexico (Kuehne & Barbour, 1983). These fish are characteristically benthic, have a small proportion of red muscle mass and are very poor sustained swimmers. The conclusions drawn from early studies regarding activity and maximum metabolic rate, therefore, may not be representative of most fish species.

The scaling of the maximum metabolic rate of fish has historically been measured by the rate of oxygen consumption during sustained aerobic swimming and has been defined as the active metabolism. The active metabolic rate is, in fact, not a good (i.e. unbiased) measure of the scaling of maximum aerobic capacity because the relative cost of the 'activity', swimming, is known to be dramatically affected by body size (Webb, 1977). Furthermore, the major tissue contributing to oxygen demand during this activity, red muscle, may actually change in relative mass with increased body size (Graham, Koehrn & Dickson, 1983; Goolish, 1989*a*). The scaling of active metabolic rate has been reported to be either isometric ($b = 1{\cdot}0$) or to show positive allometry (Brett & Glass, 1973; Tarby, 1981; Wieser, 1985). These relationships suggest that larger fish are capable of consuming as much or more oxygen per gram of tissue than small fish. This fact seems to contradict predictions of maximum weight-specific oxygen consumption based on the scaling of those factors involved in oxygen uptake and delivery (Peters, 1983; Schmidt-Nielsen, 1984; but see Jones, 1971).

Coulson *et al.* (1977) present a clear explanation of how physical constraints on the rate of oxygen and metabolite delivery operate to limit the rate of aerobic metabolism in larger animals. The 1000-fold difference in metabolic rate between a shrew and whale cannot entirely be accounted for by similar changes in either substrate or enzyme concentration. The rate of oxygen and metabolite delivery does, however, differ by this magnitude. The amount of oxygen that can be picked up at the lungs (or gills) and delivered to the tissues in a given time is an inverse function of blood circulation time. One complete circulation in a resting shrew would require just 1·2 s, but approximately 3567 s would be needed in a resting 700 kg alligator (Coulson & Herbert, 1981). The aerobic metabolism of fish must, of course, also adhere to these limitations, making it highly unlikely that the maximum aerobic metabolic rate of fish actually scales as weight to a power of one or greater.

The issue which needs to be addressed, then, is how does maximum metabolic rate scale in fish and what physiological or behavioural activities are responsible. This problem has been approached in mammals by first assuming that locomotor activity is responsible for maximum metabolic rate, and then deriving a scaling relationship for maximum muscle energy demand (McMahon, 1973; Taylor & Jones, 1987). It does not

seem that this explanation of the scaling of maximum metabolic rate can be generalized to include fish since, for example, some species do not even possess red (aerobic) myotomal muscle. Instead, I propose that the maximum metabolic rate of fish is defined by the rate of supply of oxygen and other metabolites, and that the allocation of this maximum aerobic capacity to various activities will vary with size due to changing requirements during ontogeny.

(2) *Relative aerobic capacity of red and white muscle tissue*

While it is true that smaller fish should be capable of higher rates of mass-specific aerobic energy production, when this potential manifests itself (i.e. during which physiological activities) will depend on the scaling of demand and on the scaling of tissue-specific aerobic capacity. It is necessary, therefore, to know the relative aerobic capacity of individual tissues to understand which physiological activities will result in maximum aerobic metabolic rate.

Goolish & Adelman (1988) used cytochrome *c* oxidase (CCO) activity to describe changes in tissue-specific aerobic potential with incresed size in the common carp (*Cyprinus carpio*). The tissue contributing most to whole-body CCO activity was total muscle tissue, increasing in male carp from 50% at 2 g to almost 80% at 2200 g. However, of this total capacity only that contributed by red muscle is relevant to aerobic swimming metabolism. Based on enzyme profiles (Gordon, 1968; Lin, Dobbs & DeVries, 1974; Goolish, unpublished data) and *in vitro* oxygen consumption rates (Itazawa & Oikawa, 1983), red muscle aerobic capacity is approximately four-fold higher than white muscle. However, since red muscle tissue comprises only about 6% of total muscle mass (Johnston & Goldspink, 1973*a*; Love, 1980), most of the aerobic capacity of the muscle (and body) is found in the characteristically anaerobic white muscle tissue. In male carp, 40–65% of whole-body CCO activity is found in the white muscle, whereas red muscle tissue contributes only 10–15% (Goolish & Adelman, 1988; Fig. 1).

Blood flow distribution data indicate essentially the same proportions for the delivery of metabolites. In a study of the arctic grayling (*Thymallus arcticus*) 49·3 and 13·8% of total blood flow occurred to the white and red muscle, respectively (Cameron, 1975). Values of approximately 55 and 3% have been reported for the rainbow trout, *Salmo gairdneri* (Barron, Tarr & Hayton, 1987). Stevens (1968) measured the distribution of blood flow in the rainbow trout following exercise and observed an even more dramatic difference; 79 and 3% of total blood flow was found in the white and red muscle, respectively. This distribution of aerobic capacity is in sharp contrast to the situation in mammals. For example, 83% of the whole-body cytochrome *c* content of adult humans occurs in the characteristically red skeletal muscles (Drabkin, 1950).

The relatively small contribution of red muscle aerobic capacity to that of the whole body suggests that maximum oxygen consumption rates in fish may be associated with activities other than sustained swimming. This is the situation, for example, following exhaustive exercise by cod when the rate of oxygen consumption (oxygen debt) can actually be greater than the active metabolic rate during aerobic swimming (Soofiani & Priede, 1985; *Gadus morhua*). Much of this increased aerobic demand is the result of the oxidation and/or incorporation into glycogen of the lactate produced during activity. These are processes which appear to occur in the white muscle tissue itself

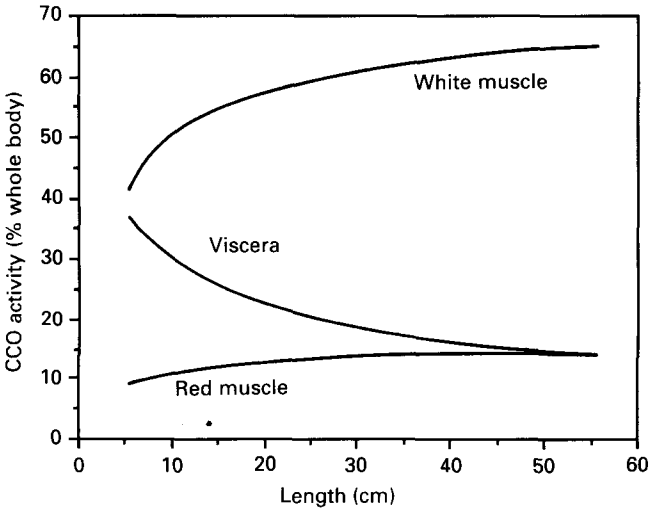

Fig. 1. Effect of size on the tissue-specific distribution of cytochrome *c* oxidase (CCO) activity in male common carp, *Cyprinus carpio*.

(Batty & Wardle, 1979; Milligan & McDonald, 1988). It should not be unexpected, therefore, that the post-exercise elevation in oxygen consumption can exceed active metabolism when one considers the relative amounts of aerobic potential which exists between white and red muscle tissue (Fig. 1). The data of Rao (1968) also demonstrates how arbitrary it is to use active metabolism to represent the maximum metabolic rate of fish. The active rate of oxygen consumption by rainbow trout could be increased 50% and 28% (at 5 and 15 °C, respectively) by swimming in seawater rather than under iso-osmotic conditions. The additional energy-use presumably reflects the aerobic activity of the gills and kidney in ion-osmoregulation.

The difference in the proportion of aerobic locomotor muscle between fish and mammals suggests that activities other than locomotion are much more likely to determine maximum aerobic capacity for fish than for mammals. However, situations where activities other than locomotion are responsible for maximum aerobic metabolism do not seem to be restricted to fish. The metabolic rate of the small anuran, *Hyla versicolor*, during physical exercise is only 62% of that during vocalization (Taigen & Wells, 1985). This observation could also have been predicted by a tissue-specific analysis of aerobic capacity. Although the male trunk muscles (used in calling) and leg muscles are of similar mass in this genera, the activity of citrate synthase is six-fold higher in the trunk musculature (Taigen, Wells & Marsh, 1985). Because of the increasing costs of locomotion with increased size, examples such as this should be most common among small species.

(3) *Food processing, growth rate and the scaling of maximum metabolic rate*

Studies on the scaling of active metabolism in fish have usually involved intraspecific comparisons. Therefore, not only is size a variable, but individual fish are compared at different stages in ontogeny when they have vastly different energy distribution patterns. In particular, small fish must allocate a greater proportion of energy to

processing food and allow for a much larger scope for growth if they are to grow rapidly (see Goolish & Adelman, 1988 for discussion). In juvenile bass, *Micropterus salmoides*, high feeding and growth rates (but not size) increase the contribution of gastrointestinal CCO activity from 13 to 30% of whole-body activity (Goolish & Adelman, 1987). In the common carp, a large proportion of total aerobic capacity is also observed in the visceral tissues (Fig. 1), i.e. in those tissues associated with food processing. In small fish the contribution of visceral CCO activity to that of the whole body is approximately four-fold higher than that of the red muscle tissue, whereas in large fish each of these components contribute about equally. Similar results have been reported by measuring *in vitro* oxygen consumption rates of the tissues of carp (Itazawa & Oikawa, 1983; Oikawa & Itazawa, 1984).

The aerobic potential of the visceral tissues of fish should be realized following the ingestion of a large meal, contributing to the postprandial increase in metabolic rate known as Specific Dynamic Action (SDA; Jobling, 1981). It has now been shown that the maximum rate of oxygen consumption following a meal can equal the active metabolic rate in some species, e.g. cod, *Gadus morhua* (Soofiani & Hawkins, 1982). The scaling of tissue-specific aerobic capacity, feeding and growth rate suggests that the SDA response should be relatively larger in small, i.e. fast-growing, fish. This type of relationship has been observed by Tandler & Beamish (1981) who described the scaling of SDA in largemouth bass, *Micropterus salmoides*. The maximum rate of oxygen consumption following satiation exceeded the active metabolic rate for fish less than 100 g but decreased to less than 50% of active metabolism in fish weighing 250 g (Fig. 2). This relationship indicates that the swimming metabolic rate of small fish used to estimate the scaling of active metabolism does not reflect their maximum metabolic rate. If the higher postprandial values of small fish were taken as their maximum metabolic rate, then the slope of the allometric relationship would be lower (Fig. 2, inset). The maximum metabolic rate of fish would then scale according to a mass exponent less than 1·0, i.e. in accord with theoretical expectations based on oxygen uptake and delivery.

How then does maximum metabolic rate scale in fish and what physiological or behavioural activities are responsible? The available information indicates that the activity which contributes most to maximum whole-body metabolic rate will vary with the size of the fish. Because of this, it does not seem that the scaling of maximum metabolic rate in fish (and perhaps other groups) can be explained on the basis of the energy demands for any single activity, such as the historical use of swimming activity. Functional or mechanical features which set locomotor energy demands, therefore, will not necessarily limit maximum metabolic rate. If aerobic locomotor energy demands are less than maximum whole-body oxygen delivery rates, as they appear to be in many situations, it will mean only that this aerobic scope can be exploited through other processes. It is likely that some of the constraints which have been proposed to explain metabolic scaling operate over a certain size range while others operate at other sizes, depending on which physiological activity is responsible for maximum metabolic rate.

The preceding discussion suggests that the scaling of both the basal and maximum metabolic rate of fish may adhere to the general relationship of negative allometry (i.e. $b < 1{\cdot}0$), while only the energy requirements during aerobic swimming scale with $b \geqslant 1$. The significance of this is that the sustained swimming of small fish seems not to be

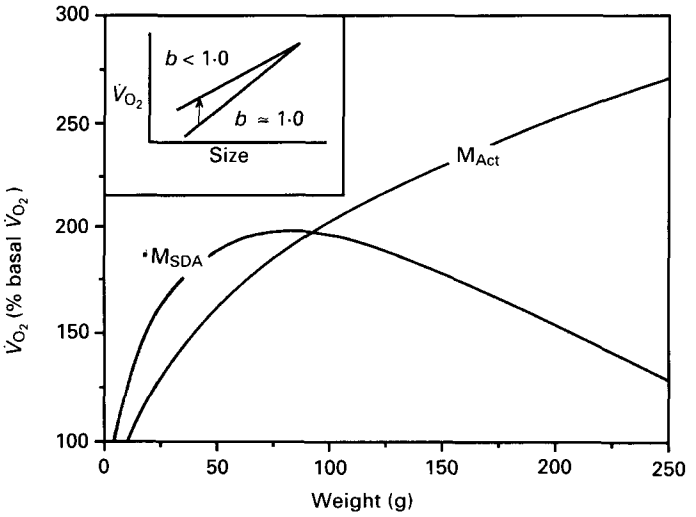

Fig. 2. Effect of size on the relative increase in metabolic rate of largemouth bass, *Micropterus salmoides*, during maximum sustained swimming (M_{Act}) and following the ingestion of a meal (M_{SDA}). Modified from Tandler & Beamish (1981). Inset illustrates how the use of the postprandial metabolic rate of small fish would decrease the mass exponent b in the scaling of maximum metabolic rate.

limited by aerobic respiration, but rather by some other factors. This is important for the scaling of anaerobic metabolism because the additional aerobic scope available to small fish may result in them showing less reliance on anaerobic energy production during burst or sprint swimming. Also, since both basal and maximum metabolism display negative allometry, the ability of fish to recover from an anaerobic swimming episode will decrease with increased size.

III. ANAEROBIC METABOLISM

(1) *Enzymatic and metabolite evidence of anaerobic scaling*

Interspecific scaling studies of fish have reported that the glycolytic enzyme activity of white muscle tissue increases with size (Somero & Childress, 1980; Sullivan & Somero, 1983; Fig. 3). Average values for the allometric weight exponent b were 0·35 and 0·21, respectively, for weight-specific lactate dehydrogenase (LDH) and pyruvate kinase (PK) activity. The authors report close agreement between the magnitude of scaling for total muscle enzyme activity and predicted power requirements during burst swimming. A recent study of the rainbow trout, *Salmo gairdneri*, has demonstrated that the increased enzyme potential of large fish results in a higher rate of lactate production ('anaerobic scope'; *sensu* Bennett & Licht, 1972) in white muscle during maximal burst-type activity (Goolish, 1989*a*). Furthermore, the maximum white muscle lactate concentration following exhaustive activity (i.e. total anaerobic capacity) also increased with body size, scaling as $W^{1{\cdot}2}$ ($=L^{3{\cdot}6}$).

In addition to these intraspecific examples of metabolic allometry in fish, other available information suggests that the interspecific scaling of anaerobic metabolism also displays positive allometry. Most of the studies which have been done on the

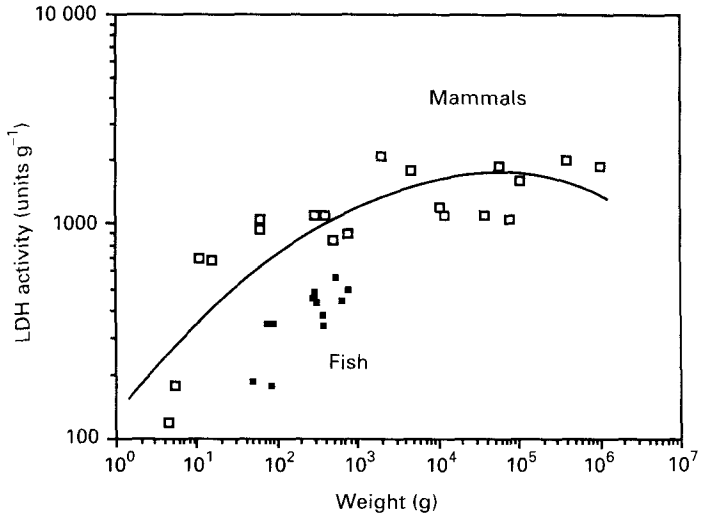

Fig. 3. Scaling of weight-specific lactate dehydrogenase (LDH) activity in the locomotor muscle of mammals (□) and the white muscle tissue of fish (■). The fitted polynomial function represents only the data for mammals. Interspecific mammalian data is from Emmett & Hochachka (1981); data for fish are pooled from *Paralabrax clathratus* and *P. nebulifer* (Somero & Childress, 1980).

anaerobic metabolism of fish during activity have involved fish of intermediate size (20–30 cm). These studies report maximum white muscle lactate concentrations following exhaustion of approximately 40–50 μmol g^{-1} (see, e.g. Stevens & Black, 1966; Turner, Wood & Clark, 1983; Schwalme & Mackay, 1985). Higher anaerobic scope in large fish was suggested by the data of Connor *et al.* (1964) who sampled very large salmonids (1·2–5·3 kg) and found control lactate concentrations as high as those typically observed following exhaustion. These high baseline values, however, may have been the result of struggling prior to sampling.

The few studies which have examined small fish following activity report lactate concentrations considerably lower than those observed for larger fish. Muscle lactate concentrations of *Fundulus heteroclitus* (8·0 cm) following swimming to fatigue were between 17 and 24 μmol g^{-1} (DiMichele & Powers, 1982). The concentration of lactate in the muscle of small (10–40 g) roach, *Rutilus rutilus*, following exhaustive exercise ranged from approximately 7 to 16 μmol g^{-1}, depending on temperature (Wieser *et al.*, 1986). The whole-body concentration of lactate in untrained 2 g chub, *Leuciscus cephalus*, following exhaustive chasing was 6·3 μmol g^{-1} (Lackner *et al.*, 1988), or about 13 μmol g^{-1} of white muscle. Finally, Wieser, Platzer & Hinterleitner (1985) analysed very small rainbow trout (80–1000 mg) following one minute of activity (electrical stimulation) and observed whole-body lactate concentrations of just 2·2 μmol g^{-1}, or approximately 4 μmol g^{-1} of white muscle tissue. It is also worth noting here the data obtained for larvae of the anuran, *Rana catesbeiana*. Lactate concentrations in the tails of these tadpoles after 30 seconds of intense activity reached only 2·2 μmol g^{-1}, and were not significantly higher than resting values (Gatten, Caldwell & Stockard, 1984).

An interesting exception to the pattern of anaerobic scaling is the low glycolytic potential and anaerobic capacity of the white muscle of adult common carp (Driedzic

& Hochachka, 1975; Johnston, 1977), an unusually large member of the characteristically small minnow family (Cyprinidae). The taxonomic position of the carp suggests its anaerobic potential may be constrained by its phylogeny, however additional species will need to be studied to demonstrate this.

An interspecific, ecologically based correlation has been observed between the glycolytic potential of fish locomotor muscle and muscle buffering capacity (Castellini & Somero, 1981). This relationship suggests that the intraspecific positive allometry in anaerobic metabolism may be similarly accompanied by differences in muscle or blood buffering capacity. A recent study of perch (*Perca flavescens*) reports not the expected increase but rather a decrease in white muscle buffering capacity with increased size (Nelson & Magnuson, 1987). This pattern varied seasonally, however, which may mean that compositional changes associated with reproduction were responsible for the decline. The absence of intraspecific allometry in buffering capacity would be in agreement with the general observation that mortalities associated with exhaustive activity are more common in larger individuals (Bennett *et al.*, 1985).

Information obtained in the past decade indicates that the potential for anaerobic energy production during locomotor activity also increases with size for groups of animals other than fish. This has been demonstrated in mammals by the positive allometry of weight-specific glycolytic enzyme activity in the muscle tissue of different species (Emmett & Hochachka, 1981; Fig. 3). Among the reptiles, an intraspecific example of positive allometry in muscle LDH activity has been reported for the lizard, *Ctenosaura similis* (Garland, 1984). A recent study of the salt-water crocodile (*Crocodylus porosus*) found higher levels of lactate in the blood of larger individuals following exhaustion (Bennett *et al.*, 1985). Positive allometry in anaerobic capacity has also been observed in two species of snake (Pough, 1977, 1978).

(2) *The scaling of anaerobic demand*

The generation of energy via anaerobic metabolism is an inefficient process. Instead of the 38 ATPs which result from aerobic metabolism, the mobilization of one glucosyl unit (from glycogen) to lactate produces just 2 ATP molecules; 7 ATP molecules are required to resynthesize the glycogen (Atkinson, 1977). Selection can be expected to operate, therefore, towards a system where anaerobic metabolism is not invoked unless absolutely necessary, i.e. only when the energy demands cannot be met through aerobic metabolism. Such situations may be related to environmental hypoxia (Hochachka & Somero, 1984) or to intense locomotor activity, the focus of this review. The latter is a more universal necessity for anaerobic metabolism to provide energy in fitness critical situations at rates greater than is possible through aerobic metabolism. Hence, to understand when and to what extent anaerobic metabolism will be employed during swimming, it is also necessary to consider maximum aerobic metabolism as it will define limits above which anaerobic metabolism is required.

The scaling of aerobic and anaerobic energy metabolism during locomotor activity is perhaps best studied in fish where red (aerobic) and white (largely anaerobic) muscle tissue are well differentiated. This arrangement allows for more accurate measurement of the mass of each type of muscle, their metabolite production, and electromyographic activity (Wittenberger, Coprean & Morar, 1975; Johnston, 1977; Bone, Kiceniuk & Jones, 1978; Black & Love, 1986). These studies indicate, as suggested earlier, that

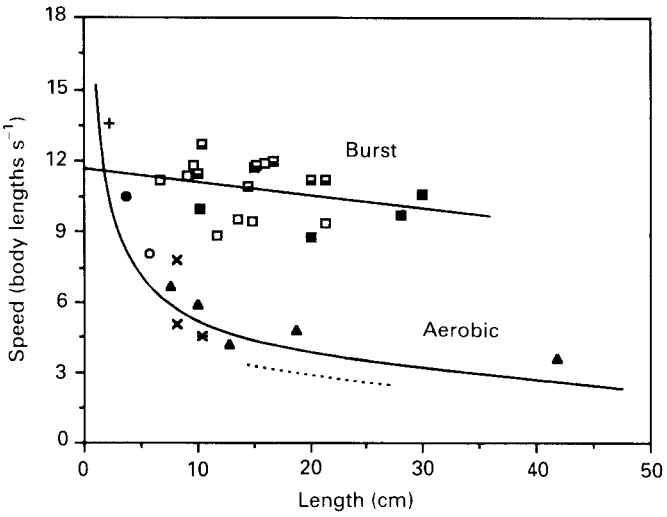

Fig. 4. Scaling relationships for length-specific burst (initial 1 s) and sustained aerobic swimming speed in fish. Burst speeds are described by least squares regression (L s^{-1} = 11·68 − 0·056L). Relationship for aerobic speeds is fitted by eye. Data on burst speeds are for rainbow trout (*Salmo irideus*, ■), dace (*Leuciscus leuciscus*, ⬓) and goldfish (*Carassius auratus*, □); Bainbridge, 1960. Aerobic swimming data are for largemouth bass (*Micropterus salmoides*), Beamish, 1970 (- - - -), Dahlberg *et al.* 1968 (×), Hocutt, 1973 (○), Farlinger & Beamish, 1977 (*); smallmouth bass (*M. dolomieui*), Larimore & Duever, 1968 (+); sockeye salmon (*Oncorhynchus nerka*), Brett & Glass, 1973 (▲); and chinook salmon (*O. tshawytscha*), Kerr, 1953 (●).

anaerobic metabolism is only invoked when the energy demand cannot be supplied by aerobic means. This is the case with regard to swimming velocity, where aerobic energy production by red muscle tissue is predominant at slow speeds but at higher speeds anaerobic metabolism by white muscle tissue is initiated (Johnston & Goldspink, 1973*b*; Freadman, 1979). Rather than a simple two-geared system, however, the shift from aerobic to anaerobic energy production appears to be one of gradually transition (Smit *et al.*, 1971; Greer-Walker & Pull, 1973; Johnston, Davison & Goldspink, 1977; Duthie, 1982). Most importantly, it has been shown that when the aerobic potential of muscle is reduced (by cold temperatures), then the anaerobic white muscle tissue is recruited at a slower swimming speed (Rome, Loughna & Goldspink, 1984, 1985). This suggests that when aerobic potential is reduced by other factors, such as increased body size, that anaerobic metabolism will similarly be invoked sooner and relied upon more heavily.

(*a*) *Aerobic and anaerobic swimming performance*

The scaling of anaerobic demand can therefore be defined more precisely as the difference between the energy required to overcome drag at burst or sprint speeds and the energy contributed by aerobic metabolism. A first approximation of this difference can be seen by comparing the scaling relationships for burst (anaerobic) and prolonged, aerobic swimming performance. Figure 4 presents data for bass (*Micropterus* spp.) and salmon (*Oncorhynchus* spp.) which illustrate the effect of body size on the aerobic swimming performance of fish. The increasing energy demands required by larger fish must be supplied by muscle tissue and whole body mass having decreasing weight-

specific aerobic capacity, hence aerobic swimming performance displays severe negative allometry ($=L^{0.5}$; Beamish, 1978). Burst swimming, at least initially, is not under the energetic constraints of aerobic metabolism and therefore is much less affected by body size. A velocity of 10 body lengths per second ($=L^{1.0}$) has been considered by some to be representative of most streamlined fish less than one meter in length (Wu, 1977). The actual scaling relationship may be closer to $L^{0.9}$ (Blaxter & Dickson, 1959; Bainbridge, 1960; Somero & Childress, 1980), depending on the duration over which performance is measured. Figure 4 also includes data which show the effect of size on the initial (1 s) burst performance of rainbow trout, goldfish and dace (Bainbridge, 1960). The scaling function for this relationship is $L^{0.92}$.

The swimming performance data of Bainbridge (1960), often referred to in the literature, is in possible error because of limitations in his experimental apparatus. The fish were forced to swim in circular tanks and therefore had to expend energy to produce the centripetal force required for motion in a curved path. Corrected speeds were calculated following Weihs (1981), assuming that the centripetal power requirements were used for thrust. The effects on absolute speeds and the scaling relationship for burst speed were found to be negligible, in part because of the relatively large diameter of the tank used (228 cm). Tanks of smaller diameter may result in significant effects on swimming performance.

Because of the different mechanisms which limit aerobic and anaerobic swimming performance, the differential between characteristically aerobic and burst (i.e. anaerobic) swimming speed increases with larger body size (Fig. 4). The aerobic swimming speed of a 30 cm fish, for example, is approximately one-third of its anaerobic burst speed, whereas the aerobic speed of small fish (less than 5 cm) nearly approaches the observed burst swimming speeds. It appears from these comparisons that aerobic metabolism contributes a greater proportion of energy requirements to high-speed swimming in small fish. Thus, the data on swimming performance demonstrates, at the organismic level, the positive allometry in anaerobic demand which is predicted by enzymatic and metabolite studies. If the relationships presented in Fig. 4 are extrapolated to very large sizes, however, the performance curves for sustained and burst swimming would seem to converge.

The equivalent comparison of performance for mammals would be maximum running speed (anaerobic) and maximum aerobic running speed. For mammals less than 300 kg (Garland, 1983), maximum running speed and maximum aerobic running speed scale as $W^{0.225}$ and $W^{0.15}$, respectively. These allometric relationships indicate, similarly to fish, an increasing disparity with increased size between the power requirements at maximum speed and the contribution made from aerobic metabolism (i.e. increasing anaerobic scope).

(*b*) *Red muscle contribution to power requirements*

A more quantitative picture of the scaling of anaerobic demand in fish can be obtained by comparing the absolute drag forces which must be overcome at burst speeds with the power development by the red muscle tissue. The burst speeds predicted by the relationship in Fig. 4 are used here together with the following Newtonian drag equation (Bainbridge, 1961; Webb, 1975):

$$P_b = 0{\cdot}5\rho A V^3 C_d\, k,$$

where P_b is the thrust power required to swim at velocity V, ρ is the density of water and A is the surface area of the fish. The reference drag coefficient (C_d) for a flat plate with turbulent flow is $0{\cdot}072R^{-0{\cdot}2}$. The Reynolds number ($R$) is equal to LV ν^{-1}, where ν is the kinematic viscosity. An additional factor (k) is included to account for the increased drag which is produced by the oscillating body of fish. Numerous studies have shown that the actual drag of a swimming fish is from two to five times higher than theoretical drag (Kliashtorin, 1973; Webb, 1975; Alexander, 1977; Videler, 1981). Here k is taken to be 3, as reported for rainbow trout (Webb *et al.*, 1984). The scaling relationship which results from these calculations indicates that the power necessary to swim at the observed burst speeds increases as $L^{4{\cdot}38}$ ($=W^{1{\cdot}46}$); larger fish have higher weight-specific energy demands during burst swimming (Webb, 1975; Somero & Childress, 1980).

The aerobic contribution to this power demand is provided by red muscle tissue which comprises approximately 6% of the muscle mass in a typical active fish (Greer-Walker & Pull, 1975; Love, 1980), or about 3% of total body weight. Recent estimates of maximum power output by the red muscle of blue marlin (*Makaira nigricans*) are near 10 W kg^{-1} (Johnston & Salamonski, 1984). The blue marlin is an atypically powerful swimmer, however, so the slightly lower value of 8·5 W kg^{-1} (Johnston, Sidell & Dridezic, 1985) for the common carp, *Cyprinus carpio*, is used in the present calculation. The value has been halved on the assumption that only one-half of the musculature is active at any instant.

The scaling relationship for total red muscle power output (P_m) is shown in Fig. 5 together with the estimated power demands at burst swimming speeds (P_b). It is evident from this comparison, as with whole-body performance, that the difference between aerobic energy production and the energy demands during burst swimming increases with larger body size. This difference represents the demand for anaerobic energy production, or anaerobic scope, at each size. The anaerobic scope can, in fact, be expected to increase even faster than shown since the mass-specific aerobic energy output of red muscle tissue should decline according to the general allometric relationship for aerobic metabolism (i.e. as $W^{0{\cdot}75} = L^{2{\cdot}25}$).

As with swimming performance (Fig. 4), the relationships for burst power demands and aerobic muscle power suggest that these values may converge at very small sizes, i.e. that the energy demands at maximum swimming speeds may be met without anaerobic metabolism. That such a threshold might exist for anaerobic metabolism is also indicated by enzymatic data (Hinterleitner, Platzer & Wieser, 1986; El-Fiky & Wieser, 1988). The deeper muscle mass ('white') of newly hatched larvae shows very high CCO activity which decreases after 35 days and by 90 days is nearly absent. The activity of glycolytic enzymes, on the other hand, increase during this period (Fig. 6; Forstner *et al.*, 1983), perhaps in conjunction with the transition from the use of the superficial red layer to the branchial gills as the major respiratory system. The relative occurrence of various LDH isoenzymes also indicates a transition to anaerobic metabolism, with the aerobic H_4 form dominant after hatching but being superceded by the anaerobic M_4 form after approximately 2 weeks (El-Fiky, Hinterleitner & Wieser, 1987). These studies suggest that the swimming of early larvae is almost entirely aerobic, and powered by the characteristically 'white' deep layers of muscle fibres. With increased size, however, weight-specific aerobic capacity declines (due to

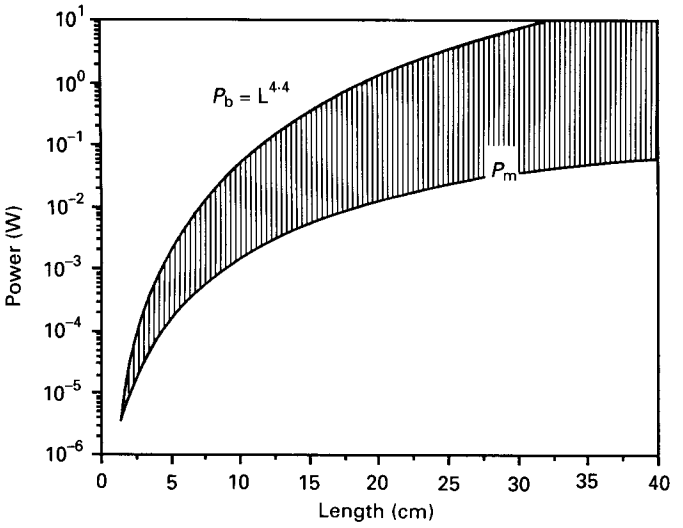

Fig. 5. A comparison of the power required to overcome drag during burst swimming (P_b) and the maximum power output from the red muscle tissue of a typical fish (P_m). See text for details.

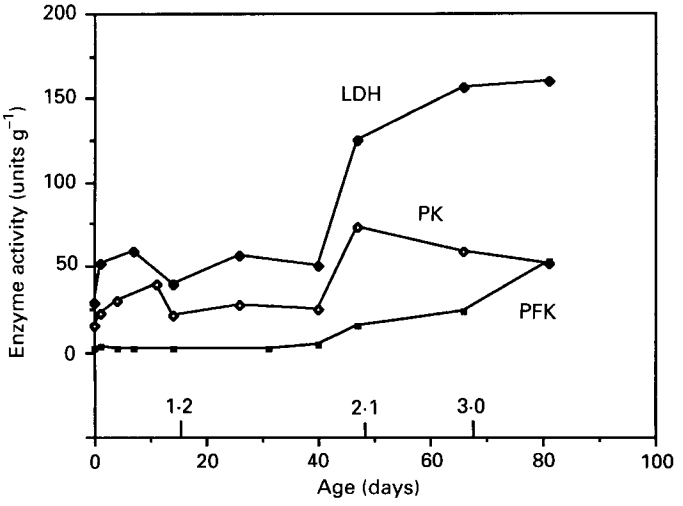

Fig. 6. Changes in weight-specific glycolytic enzyme activity during the growth of *Coregonus* sp. larvae (from Forstner *et al.*, 1983). Lengths in cm, calculated from the coregonid length–weight relationship of Dabrowski (1986), are also indicated. LDH, lactate dehydrogenase; PK, pyruvate kinase; PFK, phosphofructose kinase.

decreased surface area, increased blood circulation time, etc.) and the result is an increased need for anaerobic energy production. The contribution to energy production by anaerobic metabolism appears to become important at approximately 1–3 cm, although the particular behaviour of the species also seems to be an important factor.

(3) *Upper limits to anaerobic metabolism*

From the preceding discussion it appears that the anaerobic scope of fish during locomotion begins at a small size (< 3 cm), and that it displays positive allometry with further increase in size. There are, however, several reasons why such an increase in anaerobic scope cannot continue indefinitely and why it may not be possible to describe the scaling of anaerobic metabolism with a single allometric function.

(*a*) *The scaling of glycogen reserves*

Firstly, there are limits imposed by the scaling function for total muscle glycogen, the fuel reserve for anaerobic metabolism. Maximum white muscle glycogen concentrations are relatively constant in fish at approximately 1 % of muscle weight (Love, 1980). This means that for large fish which mobilize their glycogen reserves completely, anaerobic capacity will scale approximately as the volume of muscle mass, i.e. as L^3. The power requirements during burst swimming, however, scale according to length raised to an exponent between 4 and 5 (Fig. 4; Somero & Childress, 1980). With larger size, therefore, there is an increasing differential between the energy requirements at maximum speed and the anaerobic energy provided by the available glycogen reserves. An evaluation of these interactions for rainbow trout (Goolish, 1989*a*) suggests that, even over the relatively small size range of 5–50 cm, large declines in burst swimming velocity and stamina should occur with increased size.

(*b*) *Aerobic constraints on anaerobic recovery*

More importantly, practical reliance on anaerobic energy production (including how often it can be utilized) will also be limited by the rates at which lactate can be metabolized and the glycogen reserves restored. These rates are largely dependent on the aerobic capacity of the species or individual under consideration. In humans, for example, it requires approximately 1 h for arterial lactate concentrations to return to pre-exercise levels (Harris *et al.*, 1968) while in young alligators nearly 5 h are needed (Coulson, 1987). The time required for blood lactate levels to return to normal in fish is even longer, with 12 h being needed for a 300 g rainbow trout, *Salmo gairdneri* (Turner *et al.*, 1983). The relationship between aerobic metabolic capacity and anaerobic recovery also applies among animals of different size. This is evidenced by the much shorter time required, just 2 h for lactate concentrations to return to normal in the small (2 g) chub, *Leuciscus cephalus* (Lackner *et al.*, 1988). The post-exercise elevation in oxygen consumption following exhaustive swimming is also of shorter duration in small (8 cm) compared to large (33 cm) fish (Goolish, 1989*b*).

The same pattern following exhaustion is observed between aerobic metabolism and the rate of glycogen restoration, and Coulson (1987) has applied this relationship to predict glycogen restoration times for large mammals and reptiles. Although such estimates are only approximate they can still prove very instructive. Coulson (1987) estimates, for example, that it would require 9 days for a large dinosaur to restore muscle glycogen if it had typical reptilian metabolism – a seemingly prohibitive length of time. To evaluate its role as a limiting factor in fish, similar estimates of glycogen restoration times can be made by applying the appropriate scaling function to the characteristically low metabolic rate of fish. The rate of glycogen restoration by fish

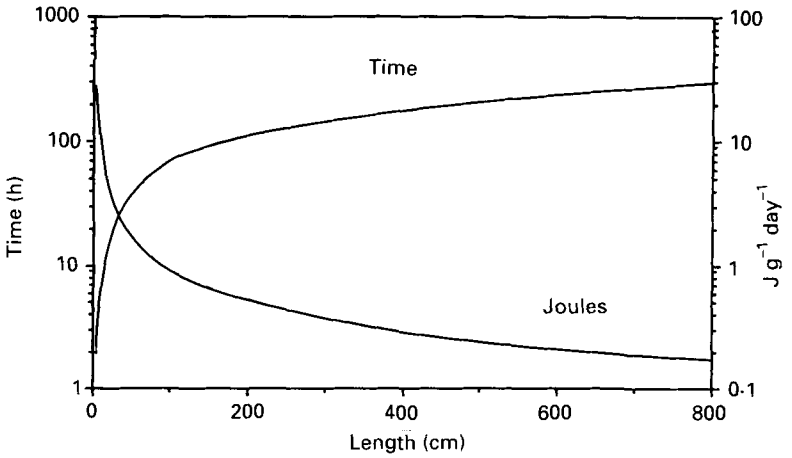

Fig. 7. Estimated time required by fish of different size to restore white muscle glycogen following anaerobic activity. Also shown is the scaling relationship for daily anaerobic energy production, per gram of white muscle, based on glycogen restoration times.

appears to be considerably slower than the rate of lactate removal (Schwalme & Mackay, 1985). The available information is largely from fish of intermediate size (approximately 30 cm) and indicates that the resynthesis of mobilized glycogen requires nearly 24 h (Wardle, 1978; Milligan & Wood, 1986). Glycogen restoration times can be estimated for fish of other sizes by assuming proportionality with metabolic rate, i.e. a doubling of metabolism will reduce the time required by one-half.

A scaling relationship for glycogen restoration times in fish is presented in Fig. 7 which is based on the general metabolic allometry function of $W^{0.75}$. The estimated time which would be required for glycogen restoration in small fish (approximately 4 cm) is on the order of 1–3 h. Glycogen restoration times become extremely long, however, for very large fish. At 800 cm, the length of a relatively small whale shark (*Rhiniodon typus*; Compagno, 1984), the estimated time for glycogen restoration would be approximately 300 h, or over 10 days. Restoration times of this length suggest that anaerobic metabolism is not nearly as practical as an energy source for large fish, and that these energetic constraints may, in fact, play a role in limiting the ultimate size of fish. The replacement of the fish design with its largely anaerobic white muscle mass with the aerobic muscle of mammals may explain why fish are, by far, not the largest aquatic vertebrates.

Also shown in Fig. 7 is the daily anaerobic energy production (per gram of white muscle) which would be possible for each size of fish based on the rates of glycogen restoration at each size. These values of energy production are conservative estimates since all of the glycogen need not be restored to be remobilized (Stevens & Black, 1966). The scaling relationship is clear, however, and the influence of size is large. Daily anaerobic energy production per gram of white muscle should decline from approximately 10 J to just 0·17 J over the size range given above for glycogen restoration (4–800 cm). Unless large fish have evolved some unique physiological or biochemical adaptation for increasing the rate of glycogen synthesis, a dramatic decline in the power available to large fish from anaerobic metabolism appears inescapable.

The higher sustainable rate of anaerobic energy production by small individuals may provide them with metabolic options not available to larger ones. For example, it has been suggested that the vocalization rates of small anurans (8 g) are limited by the reserves of glycogen (Wells & Taigen, 1986). The rapid rates of glycogen synthesis which can be expected for these animals would, unlike larger species, allow them to utilize anaerobic energy production repeatedly during the course of a day.

(4) *Anaerobic metabolism: positive or negative allometry?*

The preceding analysis raises an interesting and fundamental question. Is anaerobic metabolism positively allometric as suggested by enzyme profiles and by the initial rate of lactate production; or is it negatively allometric as suggested, for example, by a daily rate of weight-specific energy production? The answer to this question depends on the time-frame over which observations are made and on the size range of the individuals under observation. If one considers the first seconds after muscular stimulation, then anaerobic metabolism must be considered positively allometric. If expressed in the same way as aerobic metabolism is conventionally expressed, i.e. in terms of an hourly or daily energy budget, then weight-specific energy production by anaerobic metabolism must be considered negatively allometric. The dependence of anaerobic scaling on temporal resolution is, perhaps, really no different than the situation with aerobic metabolism. If, as is generally agreed, the primary limitation on aerobic metabolism is the rate of oxygen uptake and delivery, then oxygen consumption rates measured over the initial seconds following demand may, like anaerobic metabolism, show little dependence on size. In fact, the scaling of myoglobin concentration in mammals displays positive allometry ($=W^{1.3}$; Adolph, 1949; Drabkin, 1950). This suggests that initial rates of aerobic energy production may also be higher in larger animals, as is the case with anaerobic metabolism.

The factors which appear to influence the scaling of anaerobic metabolism in fish are summarized in Fig. 8. As body size increases, the power required to overcome the drag forces encountered at burst or sprint speeds (P_d) increases on a mass-specific basis. At the same time, however, the mass-specific aerobic power output of the locomotor muscle tissue (P_{aer}) is decreasing due to constraints on oxygen uptake and delivery. The result of these relationships is a threshold size at which anaerobic metabolism is required to power maximum speeds, with further increases in size resulting in increased anaerobic scope. Upper limits to anaerobic scope are constrained by (1) the differential in scaling functions for glycogen (L^3) and the power requirements at burst speeds ($L^{4.4}$), and (2) the decreasing aerobic capacity to metabolize lactate and resynthesize glycogen with increased size.

The observation that anaerobic metabolism has both positively allometric (at small sizes and over short periods) and negatively allometric (at larger sizes and on a sustainable basis) characteristics suggests that, from an ecological and behavioural perspective, there may exist an optimal size among fish with regard to the use of anaerobic metabolism during locomotion. This view is consistent with the generally held belief that length-specific burst performance is relatively size-independent for small and medium-sized fish (<1 m; Wu, 1977), but that performance for larger fish is sharply reduced. The available enzymatic data of mammals also suggests that anaerobic potential is limited at large sizes (Fig. 3). The relationship between weight-

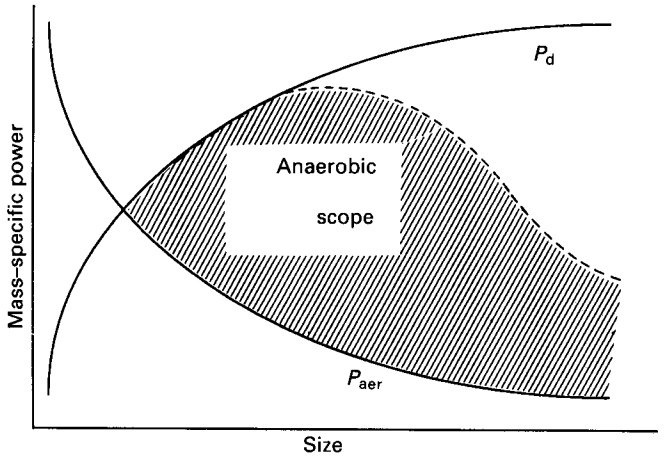

Fig. 8. Summary of factors influencing the scaling of anaerobic scope in fish. Increases in size are accompanied by higher mass-specific power requirements during burst and sprint speeds (P_d) and decreased aerobic muscle power output (P_{aer}). The dashed line illustrates decreased use of anaerobic metabolism in large individuals due to limited glycogen reserves and decreased aerobic capacity during recovery.

specific LDH activity and size (log *vs.* log), originally presented as a linear increase, is more accurately described by a polynomial function ($P < 0{\cdot}05$). The burst and sprint performance of small fish, therefore, appears to be limited much more by muscle mechanics (e.g. contraction time) whereas the performance of larger fish may be energy-limited.

Interspecific comparisons of fish indicate that those species which have high aerobic metabolism also have high anaerobic potential. Lactate dehydrogenase activity and muscle buffering capacity are higher among warm-bodied and active pelagic species compared to deep-sea species and those characterized as sit-and-wait predators (Castellini & Somero, 1981; Torres & Somero, 1988). There is also evidence which suggests that total muscle lactate production is higher in active species (Pritchard, Hunter & Lasker, 1971, *Trachurus symmetricus*; Guppy & Hochachka, 1978, *Euthynnus pelamis*) than in inactive species (Turner, Wood & Hobe, 1983, *Hippoglossoides elassodon*). This positive relationship between aerobic and anaerobic metabolism among species is similar to the negatively allometric character of anaerobic scaling. That is, in both situations increased aerobic capacity allows for higher rates of lactate and glycogen turnover and hence increased anaerobic potential. Why is it, then, that small fish with their high aerobic capacity do not have high muscle anaerobic potential as well? It may be, as discussed earlier, that the energetic demands during swimming can be provided largely through aerobic metabolism and hence a large anaerobic potential is not required.

The general relationships represented in Fig. 8 should be applicable to both ectotherms and endotherms, and to terrestrial as well as aquatic vertebrates. If species with high aerobic capacities are considered, e.g. the scombrids, then the aerobic power curve would be translated upward. This would result in a shift of the anaerobic

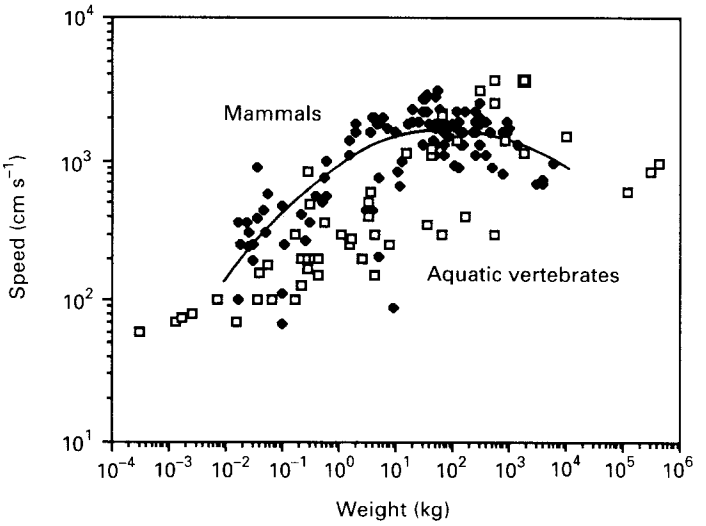

Fig. 9. Scaling relationships for the maximum (i.e. anaerobic) locomotor speed of terrestrial mammals (Garland, 1983; ●) and aquatic vertebrates (Aleyev, 1977; □). The data for terrestrial mammals are best described by a polynomial function.

threshold and 'optimum' to a larger size. Increases in the power requirements, due to e.g. higher speed or body morphology, would have the opposite effect.

The maximum locomotor speeds achieved by most animals occur as a result of anaerobic energy production (Seeherman *et al.*, 1981). The preceding analysis suggests, therefore, that the maximum speeds demonstrated by animals should not increase indefinitely but that they should decline at very large sizes. Data for the scaling of maximum locomotor speed is most complete for terrestrial mammals (Garland, 1983; Fig. 9). The form of the log-transformed relationship is not linear, but indicates that maximum speed declines beyond approximately 100 kg. It cannot be said at this time whether the decline in performance is the result of energetic (anaerobic) factors or because of structural limitations. In either case, however, the result would be the same, i.e. decreased reliance on anaerobic metabolism at very large sizes. Obtaining information on the maximum locomotor speeds of aquatic vertebrates is much more difficult, but the available data also suggests that the fastest species are not the largest (Aleyev, 1977; Fig. 9). Declines in swimming performance at large sizes may be due, in part, to the increase in white muscle contraction time which occurs with increased size (Wardle, 1975). Increases in muscle contraction time result in slower tail-beat frequencies and would therefore be expected to decrease anaerobic scope.

One final point is worth noting regarding the scaling relationships for maximum velocity in terrestrial mammals and aquatic vertebrates. It has previously been noted that, for animals of the same size, faster speeds can be obtained by running than by swimming (Bonner, 1965; Peters, 1983). From the data sets in Fig. 9 it appears that this is only true for animals up to several hundred kg, and that larger animals are able to obtain higher velocities swimming rather than running. The reasons for these interactions are likely to be complex but they will have implications for the scaling of anaerobic demand in both groups of animals.

IV. SUMMARY

1. The maximum metabolic rate of fish, measured during aerobic swimming, scales according to a mass exponent $\geqslant 1{\cdot}0$. This is not in accord with the negative allometry of aerobic metabolism predicted by the scaling of oxygen uptake and delivery.

2. An analysis of the tissue-specific distribution of aerobic capacity in fish indicates that only a small proportion, perhaps 10–20 %, of total capacity occurs in the red muscle tissue used during aerobic swimming. This is in sharp contrast to the situation in mammals where the majority of whole-body aerobic capacity is found in the skeletal muscles.

3. Because of its large mass, the characteristically anaerobic white muscle tissue of fish contains most of the whole-body aerobic capacity. This aerobic potential may be responsible for oxygen consumption rates following exercise (oxygen debt) which are higher than during aerobic swimming.

4. Total viscera aerobic capacity is also higher than red muscle capacity for small, i.e. fast-growing, individuals. This is aerobic capacity associated with food processing, and its negative allometry can account for the observation that postprandial elevations in oxygen consumption can exceed the active metabolic rate for small fish but not for large ones. The use of postprandial metabolic rate as the maximum metabolic rate for small fish should result in a scaling function for maximum metabolic rate which displays the expected negative allometry.

5. Because different physiological activities are responsible for maximum metabolic rate in different sized fish, no single 'use-based' theory (e.g. locomotor muscle power) should be able to account for the scaling of aerobic metabolism.

6. Enzymatic and metabolite evidence indicates positive allometry in the anaerobic potential of fish white muscle. This appears to be the situation for both intraspecific and interspecific scaling. The allometry of anaerobic demand is influenced by (1) higher weight-specific power requirements in larger fish during burst and sprint swimming and (2) decreasing weight-specific aerobic power production by the muscle of larger fish.

7. The swimming of very small (larval) fish appears to be powered primarily by aerobic metabolism even at burst and sprint speeds. This conclusion is based on (1) the scaling of performance at burst and aerobic swimming, (2) comparisons of power requirements and red muscle power output, and (3) the enzyme profiles of larval fish. Increased dependence on anaerobic energy production seems to occur at approximately 1–3 cm.

8. Upper limits to anaerobic metabolism in large fish are constrained by the scaling of glycogen reserves ($=L^3$), which do not increase as fast as the power requirements at burst speeds ($=L^{4{\cdot}4}$). More importantly, decreasing aerobic capacity at large sizes results in estimated glycogen restoration times which are prohibitively long ($>$ 10 days). Estimates of daily weight-specific anaerobic energy production, based on glycogen restoration times, decrease by approximately two orders of magnitude with increased size. This expression of anaerobic metabolism indicates, not positive, but rather negative allometry.

9. The scaling of anaerobic metabolism displays characteristics of both positive and negative allometry, which means that it may not be possible to accurately describe it

with any general mass exponent. These considerations also suggest that there is an optimal size for the practical exploitation of anaerobic metabolism during locomotion.

V. ACKNOWLEDGEMENTS

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