Dynamics of increase in muscle fibers in fishes in relation to size and growth

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Summary. Dynamics of increase of white myotomal muscle fibers of four species of freshwater teleosts *(Salmo gairdneri, Pimephales notatus, Esox masquinongy* and *E. americanus vermiculatus)* from three families (Salmonidae, Cyprinidae, Esocidae) representing a variety of maximum attainable sizes and growth rates, have been investigated. There are at least three major differences in these dynamics, and there appears to be an association between the ability of a fish species to attain large size (and grow fast) and its ability to recruit new fibers into this predominant tissue of the myotomal mass.

Key words. Teleost fish, freshwater; muscle, white myotomal; myotomal muscle; muscle fibers; fish size; growth.

The main axial (i.e. myotomal) muscles of fish comprise approximately 30–80% of the live weight. Such muscle must, therefore, despite being a postmitotic and highly differentiated tissue, also be capable of responding to whatever demands for increase the growing fish makes on it. The question of how this is managed is made the more interesting by the great intraspecific lability that characterizes fish growth rates[1,2] and by the fact that, in addition to its propulsive role, muscle serves fishes as their major protein storage from which they can satisfy energy needs not only during starvation, but during migration swims, and to elaborate reproductive products[3].

The origin of muscle fibers, which occurs during embryonic development, has been carefully described for rainbow trout[4]. It appears to follow a course typical of vertebrates and as in the higher vertebrates cells known as myosatellites function during development to 'add to the number of fibers in a muscle'[4,5]. Muscle growth in higher vertebrates, following myogenesis and early development, evidently results largely from increase in diameter of existing fibers and continued presence of myosatellites probably functions to maintain muscle integrity, replace damaged fibers or produce more fibers in growth[6,7]. These cells may also function similarly in fish muscle but evidence is lacking. The stimuli for our interest in fish muscle growth stem mainly from its spectacular intraspecific lability, and from the wide interspecific range of potential maxima of growth rates and final sizes[1,2]. Thus, among freshwater teleosts of eastern Canada alone, size ranges from that of the least darter *Etheostoma microperca* (2.5 cm maximum length), to that of the muskellunge *Esox masquinongy* which can grow to a length of 1 m in about a decade or less and even to a considerably greater eventual size[8]. Such size differences as these have led us to postulate the existence of a distinction between the dynamics of increase of the muscle mass of large[9], characteristically fast growing, fish species and small, slow growing, species. The postulate is that the larger species retain a capability for recruitment of new fibers (myogenesis) for a much greater time, or to a much greater size, than do smaller, slow growing, species.

We have investigated the dynamics of increase in the myotomal fiber mass in four species of three families of freshwater teleosts, representing a wide range of sizes and growth rates. Of the two species of Esocidae studied the muskellunge *E. masquinongy* is known to reach a maximum length of approximately 165 cm, and is the largest and fastest-growing member of the family[8]. The other esocid, the grass pickerel *E. americanus vermiculatus* is the smallest of the family with a greatest size that rarely exceeds 30 cm and relatively slow growth[8,10]. The rainbow trout *Salmo gairdneri*, of the family Salmonidae, can grow fast to a large size, but neither its growth nor its approximate maximum size of 103 cm[8,10], are as great as those of the muskellunge. The fourth species, the bluntnose minnow *Pimephales notatus*, a member of the Cyprinidae, is, by contrast, a very much smaller fish. By way of further comparison, approximate maximum sizes for the three larger species at age seven years would be as follows: *E. masquinongy*, 100 cm; *S. gairdneri*, 65 cm; *E. a. vermiculatus*, 27 cm. *P. notatus*, at the greatest age known (3+ yr) do not appear to exceed 11 cm[8,10].

In all four of these species, the myotomal muscles are organized along similar histological and histochemical lines, with white (glycolytic) fibers comprising by far the largest percentage of the bulk and concentrated, for the most part, into a uniform and dominant mass in each myotome[9,11]. It has therefore seemed reasonable to make interspecific comparisons of the histological changes in this muscle during growth. Details of the techniques are given elsewhere[9], as are accounts of the relative growth of various tissues and effects of differences in growth rate on body composition (i.e. protein, lipid, dry weight, caloric content)[12–14].

Figure 1 illustrates the consequences of different dynamics of increase of myotomal muscle in the four species. In the smal-

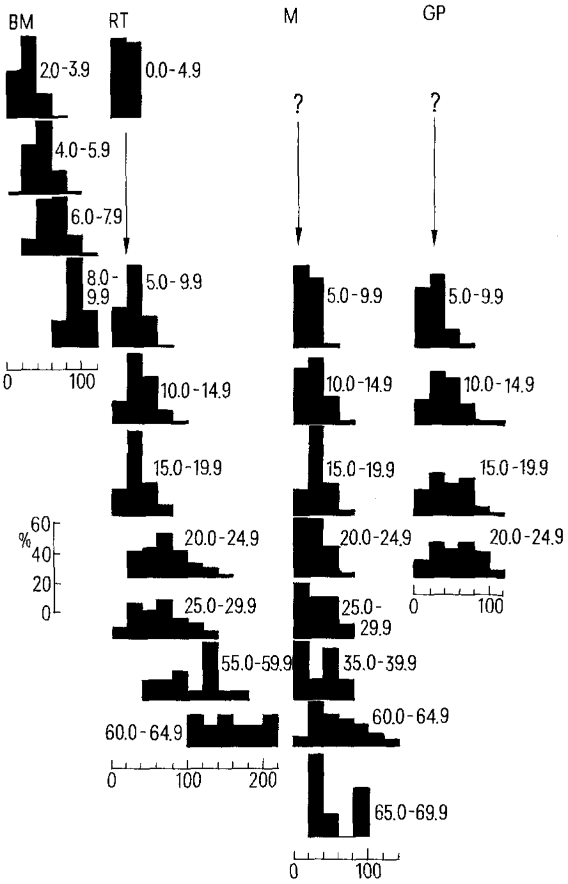

Figure 1. White muscle fiber diameter (horizontal scale: each division represents a diameter class with a 20 μm range) frequency (%) classes in bluntnose minnow (BM), rainbow trout (RT), muskellunge (M), and grass pickerel (GP), for fish of various length ranges (cm, shown beside each histogram). See text for further explanation. Fiber diameter frequencies for rainbow trout show negligible change over the 30–55 cm length range and have thus been omitted.

lest species, bluntnose minnow *P. notatus*, the predominant (52%) fiber diameter class, even in fish of < 4 cm length, is 20–39.9 µm, though 30% of the fibers are of smaller diameter. At fish lengths of > 6 cm, fibers of < 20 µm no longer occur, while beyond 8 cm there are no fibers of < 60 µm. Among the largest minnows, a general increase in diameter of the white fiber population leads to a dominant mode of 80–99.9 µm. In rainbow trout, small fibers (< 40 µm) disappear only as fish approach 50 cm, and beyond 60 cm no fibers are smaller than 100 µm, while some exceed 200 µm. In the largest species, the muskellunge, small diameter fibers (< 40 µm) persist and even predominate beyond 65 cm length though, after 60 cm, fibers < 20 µm appear to be scarce or absent.

Thus, in the smallest species, the fiber mass increases mainly as a result of fiber diameter increase. However, among the two largest species it is mostly the result of recruitment of new fibers (probably from the myosatellite system). In the rainbow trout these dynamics break down at about 50 cm; subsequent muscle increase results from fiber diameter increase. In the muskellunge, fiber recruitment is maintained to a much larger size. In figure 2, the results are viewed from an alternative standpoint, by use of regressions of fiber diameter v. length for the three species. As evidence of the significance of the great separation between these three regression slopes, we note that at a single mean fiber diameter (60 µm) the respective fish lengths for minnow, trout and muskellunge would be 6.5, 25 and 69 cm. The fiber growth dynamics of these three fish species would, therefore, appear to vindicate our general hypothesis. Moreover, data from other species appear to harmonize fairly well with the above[9].

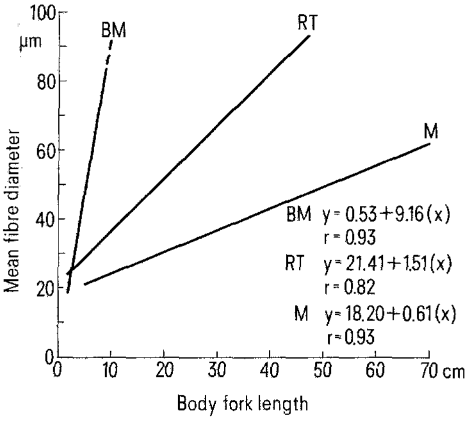

Figure 2. Regressions of muscle fiber diameter (µm, mean diameter for each specimen; data points omitted for simplicity) versus body fork length (cm) for bluntnose minnow (BM, n = 55), rainbow trout (RT, n = 85), and muskellunge (M, n = 45). See text for further explanation.

In earlier studies in rainbow trout and bluntnose minnows[9,15–18] we found that even marked intraspecific differences in growth rate, induced by differences in temperature or ration size, have only slight or negligible influence in altering the muscle fiber diameter frequencies typical of each species at any specific size during growth. From this we infer that the dynamics of fiber increase can be regarded as species-specific (note again difference between minnow and trout, fig. 1) and therefore genetically programmed. In cautiously suggesting a causal connection between these differences in dynamics and fish size, it can be noted that muscle growth as a result of increasing diameters in a fixed fiber complement would eventually produce diameters beyond which the metabolic exchanges of fibers could not be effectively maintained; the muscle of smaller species appears to grow mainly by increase in fiber diameter. Continued input of new fibers up to some very much greater fish size – e.g. as in trout, muskellunge – would certainly forestall the achievement of limiting diameters. Slight extrapolation of the regression for minnow data (fig. 2) indicates a mean fiber diameter of approximately 90 µm for the largest minnows reported[8,10]. However, in minnows > 8 cm, 24% of the fibers already exceed 100 µm (fig. 1). Further, in large rainbow trout 20% of the fibers exceed 200 µm and we can postulate that, in trout exceeding 100 cm in length, a mean fiber diameter of about 250 µm would occur, unless there was a further burst of fiber recruitment. It is, of course, not unreasonable to expect some interspecific differences in the limiting diameter.

The exception to the above results and discussion is the grass pickerel (fig. 1). Although few pickerel exceed 30 cm, the fiber dynamics of this species resemble those of its much larger congener (muskellunge) or, more particularly, those of rainbow trout. In the pickerel, however, whose growth and size fall between those of minnow and trout, it seems that, as the limiting size is approached, the fiber dynamics retain the postulated condition for achievement of larger size – recruitment of new fibers, indicated by the continued presence of small diameter fibers. We shall be experimenting to obtain growth to a larger size than reported for this species, on the assumption that factors other than an unsuitable growth dynamics are responsible for its size limitations. We assume, for example, that a genetic failure to maintain growth hormone levels in some members of a muskellunge, or pike, population, could lead to the formation of a species with pickerel-like growth and size characteristics, but without an accompanying major change in the muscle fiber dynamics. Simple hormonal stimulation might, then, be presumed a priori capable of stimulating pickerel to grow to a larger than normal size, since the fiber dynamics for this would still be available.

Acknowledgment. This work is supported by grants from the Natural Sciences and Engineering Research Council of Canada. We thank D. Shephard for work done in connection with the Esocidae, and J.F. Gorrie for supplying muskellunge.

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0014-4754/85/030353-02$1.50 + 0.20/0