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# Differentiation of Muscle Fiber Types in the Teleost *Brachydanio rerio*, the Zebrafish

## Posthatching Development

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**Summary.** The trunk musculature of adult zebrafishes contains three major fiber types: adult red, intermediate, and white; and two minor populations: red muscle rim and scattered intermediate fibers.

In this paper, the post hatching development of these muscle fiber types was studied by means of immunohistochemistry, using anti-myosin sera. Just hatched larvae contain two muscle fiber populations: embryonic red and white, which give rise to the red muscle rim and the intermediate fibers respectively. Adult red fibers arise post hatching as a new separate population with distinct myosin properties.

The differentiation of these fiber types occurs within the first four weeks after fertilization, when the adult pattern of peripheral axon bundles has become established.

Differences in the muscle fiber type composition between the midbody and the tail myotomes become apparent in two month old fries. The number of scattered intermediate fibers increases from rostral to caudal, the opposite holds for the red muscle rim fibers. The red and intermediate area is triangular in the midbody; in the tail part it is stretched out along the lateral surface of the myotomes. These changes are considered as adaptations to improve the efficiency of the swiming performance.

**Key words:** Teleost – Muscle fiber – Differentiation – Myosin

## Introduction

Adult myotomes of the teleost *Brachydanio rerio*, the zebrafish, contain three main fiber types: slow red fibers in a thin lateral strip, intermediate (or pink) fast fibers in a wedge-shaped area around the horizontal septum, and white fast fibers in a large medial portion of the myotome. In addition, there is

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a minor population of red muscle rim fibers (RMR) between the red and the intermediate area. Scattered throughout the dorsal and ventral part of the white area are some scattered dorsal and ventral (SD/SV) fibers with intermediate myofibrillar characteristics (van Raamsdonk et al. 1980). We are interested in the question as to which factors determine the differentiation of these fiber types (van Raamsdonk accompanying paper). Such a study requires information on the normal ontogenetical development of the fiber types. Unfortunately, the available data are incomplete and partly contradictory.

Thus far, the development of the RMR and SD/SV-fibers has not been described. Further, there is no agreement on how and when the main fiber types are formed. Waterman (1969) assumed that presumptive forms of red, intermediate and white muscle fiber types are present in embryonic myotomes of the zebrafish. Embryonic myotomes of the sturgeon, *Acipenser stellatus*, seem to contain a presumptive form of red fibers (Flood et al. pers. comm.). Nag and Nursall (1972) supposed that red fibers develop in post hatching stages of *Salmo gairdneri*. According to Proctor et al. (1980) the intermediate fiber type appears in the free living stage of *Salmo trutta*.

In these studies, electron microscopy and enzyme histochemical techniques were used to discriminate between the muscle fiber populations. However, these methods may be not the most sensitive to distinguish between myofibrillar types in developing muscles (Guth and Samaha 1972; van Raamsdonk et al. 1978). Recent studies showed that the use of specific anti-sera against myofibrillar proteins allows a reliable evaluation of muscle fiber type differentiation in vertebrate skeletal muscle (Gauthier 1980; Pool 1980; Perry and Dooth 1980; Rubinstein and Kelly 1981). Therefore we decided to study the myofibrillar differentiation of the muscle fiber types in the teleost *Brachydanio rerio* by means of immuno-histochemical techniques.

In an earlier study we described the differentiation of fiber types in embryonic myotomes (van Raamsdonk et al. 1978). The present study deals with the fiber type differentiation in post-hatching stages. [1]

## Materials and Methods

*Brachydanio rerio* was bred according to the prescription of Hisaoka and Battle (1958). Under these conditions the embryos hatch $3^1/_2$ days after fertilization.

The following post-hatching stages were collected: 0 days, $1^1/_2$ weeks (6 mm and 6.5 mm); $2^1/_2$ weeks (6.5 mm and 8 mm); $3^1/_2$ weeks (9 mm and 10 mm); $4^1/_2$ weeks (10 mm, 12 mm and 15.5 mm); $5^1/_2$ weeks (16.5 mm) and 11 weeks (22 mm and 24 mm).

The larvae were fixed in cold ethanol (−60° C) and freeze-substituted for 1 or 2 weeks at −40° C. Next, they were transferred via chloroform to paraffin. The muscle fiber type composition of the myotomes in the anal region (somites no 18 to 20) was studied in cross-sections of 7 µm. The sections were deparaffinized as usual and incubated with anti-sera against different types of myosin. The anti-sera are described in Table 1. The unlabeled peroxidase method of Sternberger (1979) was used to visualize the first antibody.

The affinity spectra of the anti-sera were tested with the SDS-gel-immuno-peroxidase method (van Raamsdonk et al. 1977, 1980). The antigens were prepared as described earlier (van Raamsdonk et al. 1980).

Absorptions were carried out as follows: antiserum, diluted 1 to 10 in phosphate buffered saline (PBS) was incubated with acetone powder of muscle fibers from the trunk musculature of adult trouts (*Salmo gairdneri*) for 1 to 2 h at room temperature. The acetone powder was

1 Part of this study was presented at the X$^{th}$ European Meeting on Muscle and Cell Motility, Galway, 1981

**Table 1**

| Serum raised against | In rabbit no | Absorption | Reactivity in adult myotomes | Name |
|---|---|---|---|---|
| Actomyosin from red muscle of carp | JU(8) | white muscle | anti-adult red myosin | anti-A.R. |
| Myosin from chicken heart muscle | MAO(3) | red muscle | anti-red muscle rim myosin | anti-RMR |
| Myosin from chicken heart muscle | TSE(6) | red and white muscle | anti-intermediate myosin-1 | anti-Int-1 |
| Myosin from chicken pectoralis muscle | AD(8) | white muscle | anti-intermediate myosin-2 | anti-Int-2 |
| Actomyosin from white muscle of carp | KI(5) | red muscle | anti-intermediate and white myosin | anti-W.I. |

spun down at 10,000 *G* (15 min). The supernatant was used for incubations of the sections as described earlier (van Raamsdonk et al. 1978).

For the visualization of peripheral axon bundles we used an anti-serum, raised against glial fibrillary acidic protein (GFA). GFA was prepared as described by Liem et al. 1978. The specificity of this antiserum will be described by Heyting et al. (in preparation).

## Results

### *0 to $2^1/_2$ Weeks Post Hatching (4 mm to 8 mm)*

Just hatched larvae live on the food content of their yolk sac. Incidentally they make short quivering movements, but most of the time they are at rest. The anal somites of just hatched larvae contain two distinct muscle fiber populations: thin flat superficial fibers and large polygonal deep fibers (Fig. 1).

The superficial fibers run parallel to the body axis. In an epaxial myotomal part there are 14 to 16 of them. Their myofibrils react strongly with anti-A.R. and anti-RMR and weakly with anti-Int-1 serum. Thus, the immuno-histochemical properties are clearly different from those of the adult red fibers (Table 1). The superficial fibers are designated embryonic red.

The deep polygonal fibers are arranged in a helicoid pattern. These fibers react with anti-W.I. but not with anti-Int-1 or anti-Int-2 serum. Therefore the deep fibers are classified as the white type. Their myosin shares antigenic determinants with the myosin of adult intermediate fibers, because the reactivity of the anti.W.I. serum with the deep white fibers is lost when this serum is absorbed with acetone powder of intermediate muscle fibers.

We observed axon bundles in the myotomes of just hatched larvae. However, the bundles are very thin at that stage, so their branches could not unambiguously be determined. Figure 2 shows the distribution of the main peripheral axon bundles in a myotome of a 2 weeks old larva. At this stage the pattern is similar to that found in myotomes of adult zebrafishes.

### *$2^1/_2$ to $3^1/_2$ Weeks Post Hatching (8 mm to 10 mm)*

Two weeks old larvae have consumed most of their yolk. By that time they become more active. This change in behaviour is accompanied by alterations in the muscle fiber type composition of the myotomes.

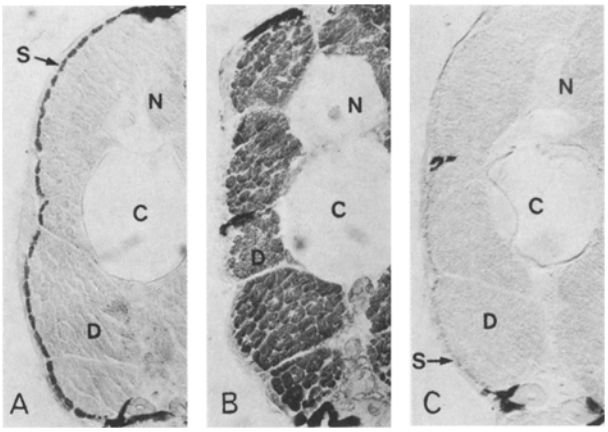


**Fig. 1 A–C.** Cross-sections from the anal region of a just hatched zebrafish (4 days after fertilization), incubated with **A** anti-A.R.; **B** anti-W.I; **C** anti-Int-1. *S* superficial embryonic fibers; *D* deep white fibers; *N* neural tube; *C* notochord

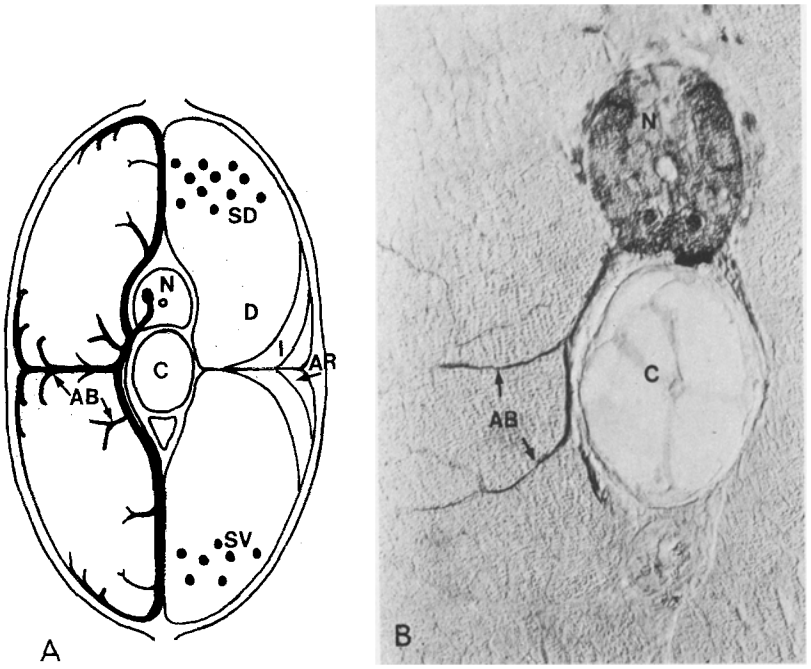


**Fig. 2. A** Reconstruction of the peripheral axon bundles in a myotome of an adult zebrafish. The reconstruction is based on serial sections incubated with anti-GFA; **B** cross-section from an anal somite of a two weeks old larva, incubated with anti-GFA. *N* spinal cord; *C* vertebral column; *AR*=adult red fibers; *I*=intermediate fibers; *D* deep white fibers; *SD*=scattered dorsal –; *SV* scattered ventral intermediate fibers

All deep myotomal fibers react with anti-W.I. serum, as in previous post-hatching stages. A few deep fibers, adjacent to the layer of superficial flat cells, also show a reaction with anti-Int-1 serum (Fig. 3). A subpopulation of the Int-1 positive fibers reacts with anti-Int-2 serum. These fibers are oriented parallel to the body axis, so they have the anatomical and the immuno-histochemical characteristics of intermediate muscle fibers (van Raamsdonk et al. 1980).

In $2^1/_2$ weeks old larvae a population of small tubulous muscle fibers appears between the skin and the superficial cells. Their myofibrils react strongly with anti-A.R. serum and only very weakly with anti-RMR serum. These fibers run parallel to the body axis. They have the anatomical and immuno-histochemi cal characteristics of adult red muscle fibers (van Raamsdonk et al. 1980).

In $3^1/_2$ to 4 weeks old larvae, we observed a fragmentation of the superficial fibers. At the same time small tubulous fibers appear, lying in the row of superficial cells; their myofibrils react with anti-RMR serum (Fig. 4). These small fibers are called red muscle rim (RMR) fibers.

The reaction of the anti-RMR and the anti-Int-1 serum with myofibrils in the embryonic red fibers is reduced in this and following stages.

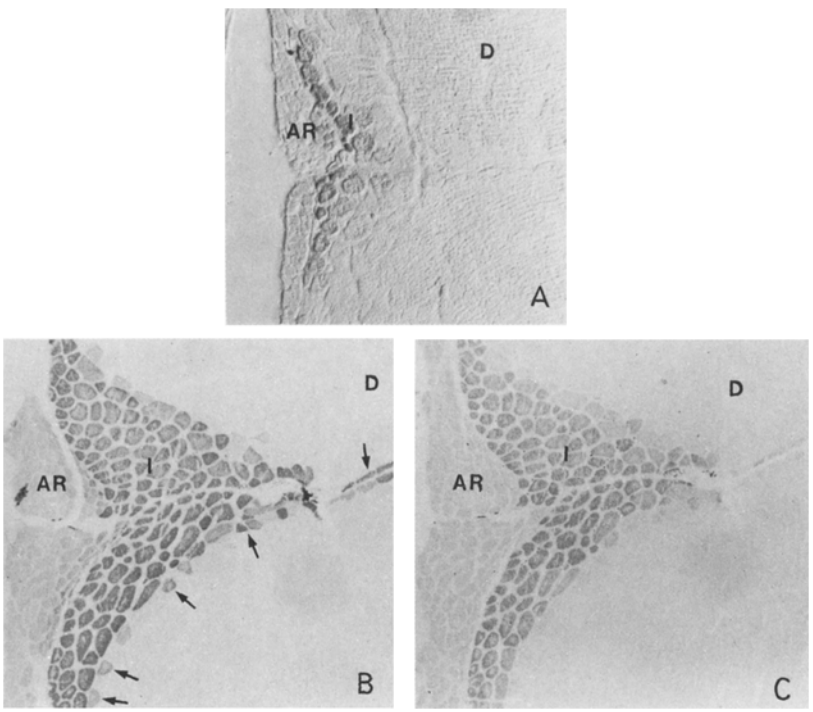


**Fig. 3A–C.** Differentiation of intermediate fibres. **A** Cross section from an anal somite of a $2^1/_2$ week old larva, incubated with anti-Int-1. **B** and **C** serial cross-sections from a 11 weeks old fry, incubated with anti-Int-1 **B** and anti-Int-2 **C**, *arrow* point to fibers which react with anti-Int-1 but not with anti-Int-2. *AR* adult red fibers; *I* intermediate fibers; *D* deep white fibers

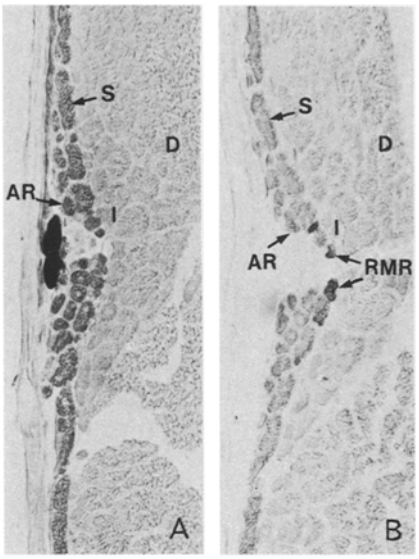


**Fig. 4A, B.** Differentiation of adult red and red muscle rim fibers in a $3^1/_2$ week old larva.
**A** incubation with anti-A.R.;
**B** incubation with anti-RMR. *AR* adult red fibers; *I* intermediate fibers; *RMR* red muscle rim fibers; *S* superficial embryonic red fibers

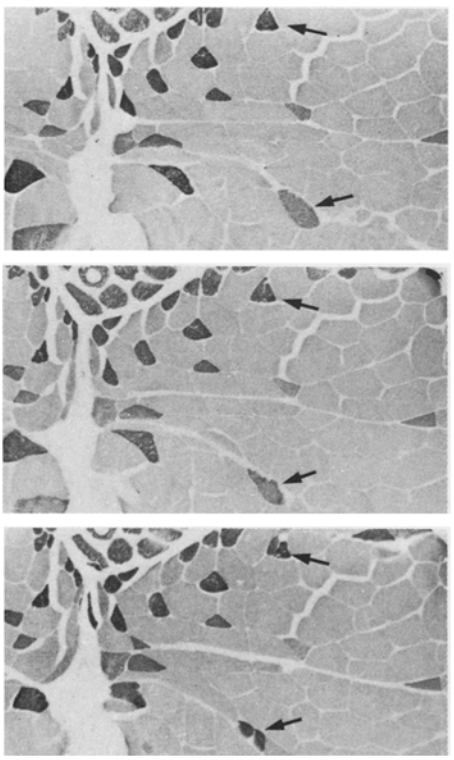

**Fig. 5.** Serial cross-sections from an anal myotome of an adult zebrafish (dorsal part), incubated with anti-Int-1. *Arrows* point to branching SD fibers

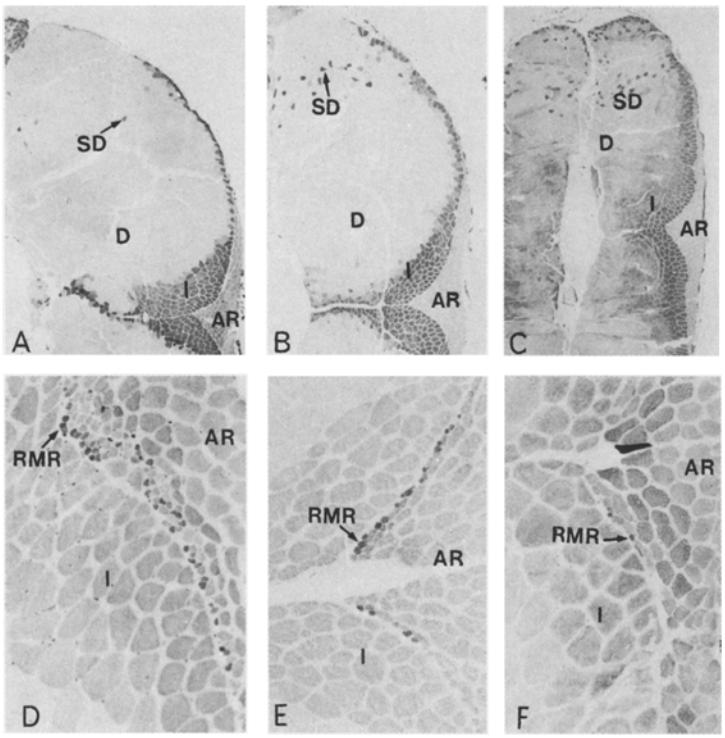


**Fig. 6 A–F.** Cross-sections of a midbody myotome (**A** and **D**) an anal myotome (**B** and **E**) and a tail myotome (**C** and **F**), to show the increase of SD fibers and the decrease of RMR fibers toward the caudal region; the red and intermediate muscle part is triangular in the midbody and dorso-ventrally stretched along the lateral side of the myotome in the tail part. **A, B, C,** incubated with anti-Int-1; **D, E, F,** incubated with anti-RMR. *AR* adult red, *I* intermediate, *D* deep white portion of the myotome. *SD* scattered dorsal fibers; *RMR* red muscle rim fibers

### *$4^1/_2$ to 11 Weeks Post Hatching (15 to 24 mm)*

The development in these stages is characterized by a rapid increase in the number of muscle fibers. In the deep myotomal part appears a mosaic pattern of small and large white muscle fibers with similar immuno-histochemical properties. Scattered dorsal and ventral fibers (SD/SV) are developed in the deep myotomal part of 10 weeks old zebrafishes. These fibers have the same myofibrillar characteristics as the intermediate muscle fibers; they are positive after incubation with anti-Int-1 serum. A part of this fiber population reacts also with the anti-Int-2 serum. Some of the fibers have small diameters; others have the same diameters as the surrounding large white fibers. Among the small ones we observed branched fibers that may be in a process of fiber-splitting (Fig. 5).

From the 8 weeks stage we observed characteristic differences in the distribution of the muscle fiber types between the midbody and the caudal part of the trunk musculature. The RMR fibers become abundant in the midbody

myotomes, in the caudal myotomes we find only a few of them. The opposite holds for the SD/SV fibers (Fig. 6).

The intermediate fibers in the midbody myotomes are concentrated around the horizontal septum, in the caudal part they cover the whole lateral area of the deep myotomal part. The adult red area in the midbody myotomes is triangular, in the caudal part it forms a thin strip along the lateral surface of the myotomes (Fig. 6).

## Discussion

The post-hatching development of the trunk musculature in the zebrafish is characterized first by an increase in the number of muscle fiber types, and in later stages by the appearance of differences in the distribution of the main fiber types between the midbody and the caudal region of the trunk musculature.

### *Superficial and Deep Fibers*

Just hatched larvae of the zebrafish contain embryonic red superficial fibers and polygonal deep white fibers. These two populations arise from an embryonic cell population in which all myofibrils have immuno-histochemical properties in common with myofibrils of adult red fibers (van Raamsdonk et al. 1978). Myofibrils of the superficial embryonic red fibers react with anti-A.R., anti-RMR and also, though weakly, with anti-Int-1 serum. This can be explained by assuming either a mixture of different myosins in these fibers or an embryonic type of myosin which has antigenic determinants in common with the myosin of adult red, RMR and intermediate fibers.

The deep fibers of just hatched larvae react only with the anti-W.I. serum. Thus, intermediate fibers do not occur in embryonic and in early larval stages (cf. Waterman 1969).

The functional importance of the embryonic red fibers in the larval stages is not clear. They may function during embryonic development when slow, swinging tail movements are performed (van Raamsdonk et al. 1974). However, this activity is not shown by the larvae. Probably only the deep white fibers have a function for the motility of the early larvae (Nag and Nursall 1972). E.M.G. recordings have revealed that white fibers in adult fishes are infrequently recruited; they are active only during short vigourous bursts of swimming activity (Johnston et al. 1977). This may hold also for early larvae which show only infrequent rapid bursts of activity, or a startle response after tactile or vibratory stimulation (Kimmel et al. 1974).

### *Intermediate Fibers*

By the time the zebrafish larvae have consumed their yolk, they become active in the search for food. This change in activity pattern of the musculature is accompanied by the formation of intermediate and adult red fibers. This is in agreement with observations on the behaviour and myogenesis of *Salmo gairdneri* and *Salmo trutta*. Also in these species, the transition from burst swimming to a sustainable swimming behaviour correlates with a gradual in-

crease in the "red-like" character of the superficial cell population (Nag and Nursall 1972; Proctor et al. 1980).

The formation of the intermediate fibers commences after the adult pattern of the main axon bundles in the trunk musculature has been established. We could discern three steps in the differentiation of these fibers. First they become orientated parallel to the body axis, next they acquire an affinity for the anti-Int-1 serum and in the last step they develop a reactivity with anti-Int-2 serum. The changes in the immuno-histochemical properties of the myofibrils may indicate that myosin polymorphism occurs, but the results can also be explained by assuming a rebuilding of "white" myosin into "intermediate".

The stepwise transformation suggest that the intermediate fibers originate from white fibers, probably in the same way as the fast oxidative glycolitic (F.O.G.) fibers in mammals are formed from fast glycolitic (F.G.) fibers (Müller 1974; Pool 1980; Salmons and Henriksson 1981).

*Adult Red Fibers*

Adult red fibers are formed in the "empty space" between the skin and the superficial cells. Form an ultrastructural analysis on myogenesis in *Acipenser stellatus*, Flood et al. (pers. comm.) assumed that the adult red fibers develop from the flat superficial embryonic red cells. This is probably not the case in the zebrafish, because the rim of superficial cells remains complete while the adult red fibers are being formed. We suggest that the adult red fiber population is newly formed. Rubinstein and Kelly (1981) showed that the slow red fibers in mammals develop from embryonic white fibers as a consequence of a change in innervation pattern. In this aspect the slow red fibers in fish seem to differ fundamentally from those in mammals. This hypothesis remains subject to further study.

*Red Muscle Rim Fibers*

We observed fragmentation of the superficial fibers in the same developmental stage at which RMR-fibers appear. Therefore we suggest that the latter population arises from the former by longitudinal splitting. It is not known whether embryonic red and RMR-fibers have their counterparts in mammalian skeletal muscle.

*SD/SV-Fibers*

Myotomes in advanced developmental stages of the zebrafish show a mosaic pattern of small and large white and of SD/SV-fibers (Fig. 6). The SD/SV-fibers show the same spectrum of affinities for anti-Int-1 and Int-2 serum as the fibers of the intermediate area. We therefore assume that they arise from the white fibers as the fibers of the intermediate muscle part. They may also increase in number by fiber-splitting (Fig. 5).

There are two general concepts as to the significance of the mosaic pattern in the deep myotomal part of teleost fishes: one concerns the function and the other the growth of myotomes.

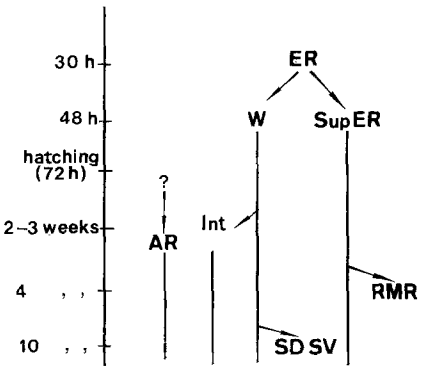


**Fig. 7.** Hypothetical scheme of the ontogenetical relationship between the muscle fiber types in the zebrafish. The age indicated on the vertical axis, is in hours or weeks after fertilization. *AR* adult Red; *Int* intermediate; *W* white; *ER* embryonic red; *RMR* red muscle rim; *SD SV* scattered dorsal and ventral fibers. *SupER* superficial embryonic red fibers

In many teleost species the deep fibers differ in histochemical properties related to oxidative capacity (Boddeke et al. 1959), glycogen content (Proctor et al. 1980) and myofibrillar ATP-ase activity (Johnston et al. 1975).

Therefore it was thought that the mosaic structure reflects a functional diversity among the fibers of the deep myotomal part (Boddeke et al. 1959), which may explain the E.M.G. activity recorded from the deep fibers in the carp at low swimming speeds (Bone et al. 1979).

The presence of small and large fibers in *Anguilla,* in *Salmo* and in *Mugilidae* was explained by hypertrophy and hyperplasia in the deep myotomal part (Willemse and van de Berg 1978; Weatherley et al. 1980; Carpène and Vegetti 1980). In *Mugilidae* the differences in diameter coincide with differences in myofibrillar ATP-ase properties; these myofibrillar differences fade as the muscle fibers increase in girth (Carpène and Vegetti 1980).

For several reasons it is unlikely that the SD/SV-fibers represent growing white fibers: they develop relatively late during ontogeny, their diameters vary over a wide range and there is no unequivocal correlation between the intensity of their reaction with anti-intermediate sera and their diameters. We assume that the development of the SD/SV-fibers is somehow related to the activity pattern of the trunk musculature, because, their numbers correlate with the degree of lateral bending of the body and their formation can be induced when the fish is forced to make anomalous undulating movements (van Raamsdonk et al. accompanyving paper).

### *Differences in the Red and Intermediate Area Between Midbody and Tail Myotomes*

Mosse and Hudson (1979) observed in marine teleosts an increase of the relative amount of red muscle towards the caudal fin. This holds not only for the red but also for the intermediate and SD/SV fibers in the zebrafish (Fig. 6). This distribution of muscle fibers provides an increase in "staying power" towards the tail.

Another difference between the midbody and the tail myotomes concerns the shape of the red and the intermediate area. This area is triangular in the midbody and dorso-ventrally stretched in the tail myotomes. Thus, in the caudal

part the most active muscle portion is in delete the most advantageous position for bending the body. It remains to be ascertained whether these differences between the midbody and the tail part arise as a consequence of differences in the bending of the body during normal swimming.

In summary: we have shown that during post-hatching development the number of muscle fiber types increases after the adult pattern of peripheral axon bundles has become established. A hypothetical ontogenetical relationship between the muscle fiber types is presented in Fig. 7. We consider the increase in number of fiber types, the increase of the relative amount of red and intermediate fibers towards the tail, and the arrangement of red and intermediate muscle along the lateral side of the tail myotomes to be adaptations for delete improving the efficiency of the swimming performance.

## References

Boddeke R, Slijper EJ, Stelt A van der (1959) Histological characteristics of the body musculature of fishes in connection with their mode of life. Proc K Ned Akad Wet Ser C 62:576–588

Bone Q, Kiceniuk J, Jones DR (1979) On the role of the different fibre types in fish myotomes at intermediate swimming speeds. Fish Bull 76:691–699

Carpene E, Vegetti A (1981) Increase of muscle fibres in the lateralis muscle (white portion) of *mugulidae* (Pisces, Teleostei). Experientia 37:191–193

Flood PR, Kryvi H, Gulyaev D (1981) The origin and early differentiation of red and white muscle fibres in the sturgeon (*Acipenser stellatus*) (In preparation)

Gauthier GF (1980) Distribution of myosin isoenzymes in adult and developing muscle fibers. In: Pette D (ed) Plasticity of muscle. De Gruyter, Berlin, pp 83–96

Guth L, Samaha FJ (1972) Erroneous interpretations which may result from application of the "myofibrillar ATP-ase histochemical procedure" to developing muscle. Exp Neurol 34:465–475

Hisaoka KK, Battle HI (1958) The normal developmental stages of the zebrafish *Brachydanio rerio* (Hamilton Buchanan). J Morphol 102:311–327

Johnston IA, Ward PS, Goldspink G (1975) Studies on the swimming musculature of the rainbow-trout. I. Fibre types. J Fish Biol 7:451–458

Johnston IA, Davison W, Goldspink G (1977) Energy metabolism of carp swimming muscle. J Comp Physiol 114:203–216

Kimmel CB, Patterson J, Kimmel RO (1974) The development and behavioural characteristics of the startle response in the zebrafish. Dev Psychobiol 7:47–60

Liem RKH, Yen SH, Salomon GD, Shelanski ML (1978) Intermediate filaments in nervous tissue. J Cell Biol 79:637–645

Mosse PRL, Hudson RCL (1977) The functional roles of different muscle fibre types identified in the myotomes of marine teleosts: a behavioural, anatomical and histochemical study. J Fish Biol 11:417–430

Müller W (1974) Temporal progress of muscle adaptation to endurance training in hindlimb muscles of young rats. Cell Tissue Res 156:61–87

Nag AC, Nursall JR (1972) Histogenesis of white and red muscle fibres of trunk muscles of a fish *Salmo gairdneri*. Cytobios 6:227–246

Perry SV, Dooth GK (1980) Biochemical aspects of muscle development and differentiation. In: Goldspink DF (ed). Development and specialization of skeletal muscle. Cambridge Un Press, Cambridge

Pool CW (1980) An immune- and enzyme-histochemical determination of striated muscle fibre characteristics. Thesis Univ Amsterdam, Rodopi, Amsterdam pp 142–167

Proctor C, Mosse PRL, Hudson RCL (1980) A histochemical and ultrastructural study of the development of the propulsive musculature of the brown trout, *Salmo trutta* L., in relation to its swimming behaviour. J Fish Biol 16:309–329

Raamsdonk W van, Stelt A van der, Diegenbach PC, Berg W van de, Bruyn H de, Dijk J van, Mijzen P (1974) Differentiation of the musculature of the teleost *Brachydanio rerio*. I. Myotome shape and movements in the embryo. Z Anat Entwickl Ges 145:321–342

Raamsdonk W van, Pool CW, Heyting C (1977) Detection of antigens and antibodies by an immuno-peroxidase method applied on thin longitudinal sections of SDS-polyacrylamide gels. J Immunol Meth 17:337–348

Raamsdonk W van, Pool CW, Kronnie G te (1978) Differentiation of muscle fiber types in the teleost *Brachydanio rerio*. Anat Embryol 153:137–155

Raamsdonk W van, Kronnie G te, Pool CW, Laarse W van der (1980) An immune histochemical and enzymic characterization of the muscle fibers in myotomal muscle of the teleost *Brachydanio rerio*, Hamilton Buchanan. Acta Histochem 67:200–216

Rubinstein NA, Kelly AM (1981) Development of muscle fiber specialization in the rat hindlimb. J Cell Biol 90:128–144

Salmons S, Henriksson J (1981) The adaptive response of skeletal muscle to increased use. Muscle and Nerve 4:94–105

Sternberger LA (1979) Immunocytochemistry. John Wiley and Sons, New York,

Waterman RE (1969) Development of the lateral musculature in the teleost *Brachydanio rerio*: a fine-structural study. Am J Anat 125:457–494

Weatherley AH, Gill HS, Rogers SC (1980) The relationship between mosaic muscle fibres and size in rainbow trout (*Salmo gairdneri*). J Fish Biol 17:603–611

Willemse JJ, Berg PG van de (1978) Growth of striated muscle fibre in the m-lateralis of the european eel *Anguilla anguilla* (L.) (Pisces, Teleostei). J Anat 125:447–460

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