Modified Arrangement of the Lateral Segmental Vessels in the Japanese Horse Mackerel *Trachurus japonicus* (Carangidae)

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Abstract The arrangement of the segmental vessels of *Trachurus japonicus* is described using the corrosion casting method. A modified arrangement is found in the posterior half of the series of the lateral segmental vessles, where the consecutive vascular lanes are double-tracked with a set of an artery and a vein instead of being single-tracked with an artery and a vein by turns. The double-tracking mode is at such an intermediate stage that additional vascular components can be readily distinguished from basic ones showing full development. The area of additional segmental vessels is restricted to the bulky central portion of the superficial red muscle in the caudal region. Typically single-tracked vessels in the remaining segmental lanes are found to be accompanied by potential additional vessels of small size. The equipment of the additional vessels is interpreted as an invention to offset an excessive vascular resistance within a thick myomere, and ultimately as a compensation for myomere thickness consequent upon low vertebral counts.

The lateral musculature of fish is provided with arteries and veins in accordance with segmentation. In teleosts, there is less variation in the arrangement of these somatic vessels: viz. the dorsal segmental vessels along the neural spines, the intercostal vessels along the ribs, the ventral segmentals along the haemal spines, and the lateral segmentals on each side along the intersections of the horizontal septum and the myosepta. All of these segmental series are, in general, single-tracked with an artery and a vein alternately (Silvester, 1904; Allen, 1910; Górkiewicz, 1947; Pollak, 1960, 1961; Mosse, 1980; Iwamizu and Itazawa, 1986).

In the carangid *Seriola quinqueradiata*, we have found that every lane of the segmental vessels is double-tracked with an artery and a vein coupling up to the distal end (Iwamizu and Itazawa, 1989). This character is shared by tunas (Kishinouye, 1923), whose vascular specializations make them warm-bodied fish (Carey et al., 1971). The vascular anatomy of *Seriola* gives a clue to the origin of tuna vascular specializations, but segmental vascular double-tracking itself is still uncertain regarding functional significance.

According to Grodziński (1959), anamniote vertebrates share a common basic pattern in the early development of the segmental vessels. The dorsal segmentals appear first, followed by the formation lateral segmentals. From the beginning they develop as single-tracked vessels. The ventral segmentals develop much later, also as a single-tracked series, although the developmental manner may be complicated in some teleosts (Goniakowska, 1966). It is hence likely that the completely double-tracked arrangement in *Seriola* has evolved from the basic, single-tracked pattern through some intermediate stages.

The present study reveals that the carangid *Trachurus japonicus* exhibits incomplete double-tracking in the arrangement of the segmental vessels. This is considered to be an intermediate stage, which suggests how and why double-tracking has evolved.

Materials and methods

Live individuals of *Trachurus japonicus* (165-260 mm in fork length, 60-270 g in body weight) were provided by Kamiura Station of Japan Sea-Farming Association. They were subjected to vascular perfusion with acrylic resin at the station before transportation to our laboratory.

Each fish was anaesthetized with benzocaine until respiratory movements had ceased, then placed ventral side up in the anaesthetic water. The peri-

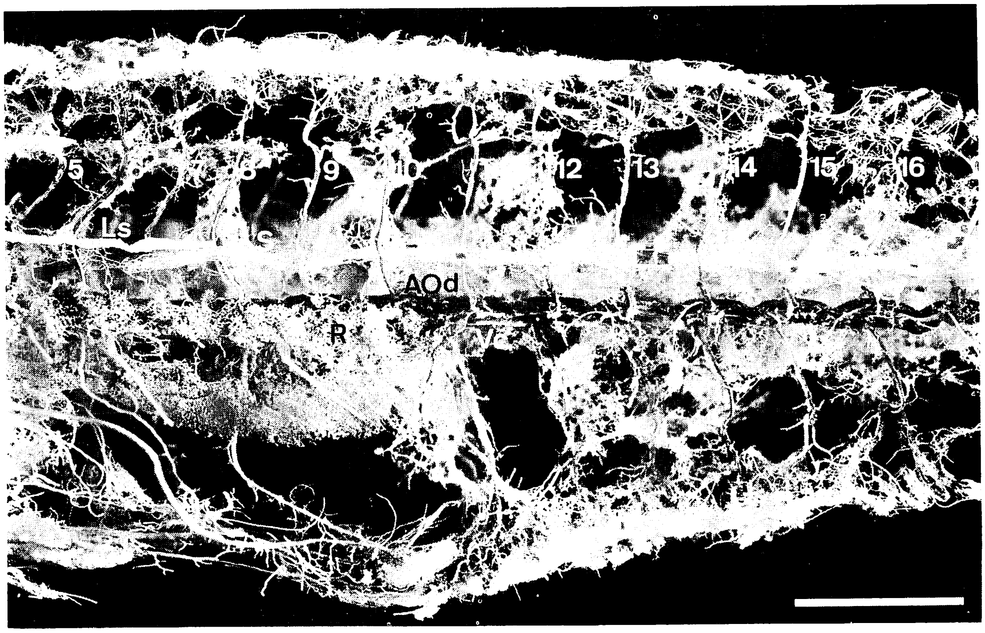

Fig. 1. Single-tracked arrangement of the dorsal and ventral segmental vessels, viewed from the left side after removal of the left lateral segmentals. The dorsal segmental vessels are numbered (5–16) according to vertebral number. Even-numbered segments convey arteries, odd-numbered segments convey veins, and the same pattern applies to the ventral series. AOd, dorsal aorta; Vc, caudal vein; Ls, spinal lymph vessel; R, renal vascular plexus; S, vascular plexus of the spinal cord. Bar = 10 mm.

cardium was opened, and heparin (1 unit/g body weight) was injected into the ventricle. The ventricle was then opened and the bulbus arteriosus cannulated.

The vascular system was perfused in turn with the following perfusates via the cannula with a static head of 60 cm: first with 50 ml heparinized saline (20 units/ml), second with unheparinized saline for about 10 min, third with 20–50 ml fixative (2.5% glutaraldehyde in 100 mM phosphate buffer, pH 7.4), finally with 20–50 g resin mixture of 3:2 Mercox CL (Dainippon Ink Inc.) and methyl methacrylate monomer (inhibitor free) with the addition of benzoyl peroxide as 1–2% of the mixture. Sometimes these perfusates were followed by the resin containing 0.5% Sudan IV for easy distinction between arteries and veins.

The perfused fish were kept in water for some days, and then corroded in concentrated HCl for one or two days. The resulting solution was cleared by overflowing with water, and the remaining vascular casts were observed under a stereomicroscope.

Results

We found that *T. japonicus* exhibited a kind of double-tracking in the arrangement of the segmental vessels. The extent of double-tracking was incomplete, being limited to the posterior half series of the lateral segmental vessels. The remaining series of segmental vessels showed a quite regular single-tracking pattern. Proximal portions of the single-tracked segmentals were, however, found to be accompanied by small vessels suggestive of potential double-tracking.

The arrangement of the dorsal and ventral segmental vessels is shown in Fig. 1. An artery follows the ordinary course at every second segment, alternating with a vein. The dorsal segmental artery or vein crossed the vertebra, randomly on either side. On the other side of the vertebra is a rudimentary vessel which hardly extends beyond the spinal cord.

Two patterns of the arrangement of lateral segmental vessels are shown in Fig. 2. The lateral segmentals in the trunk region are also single-tracked

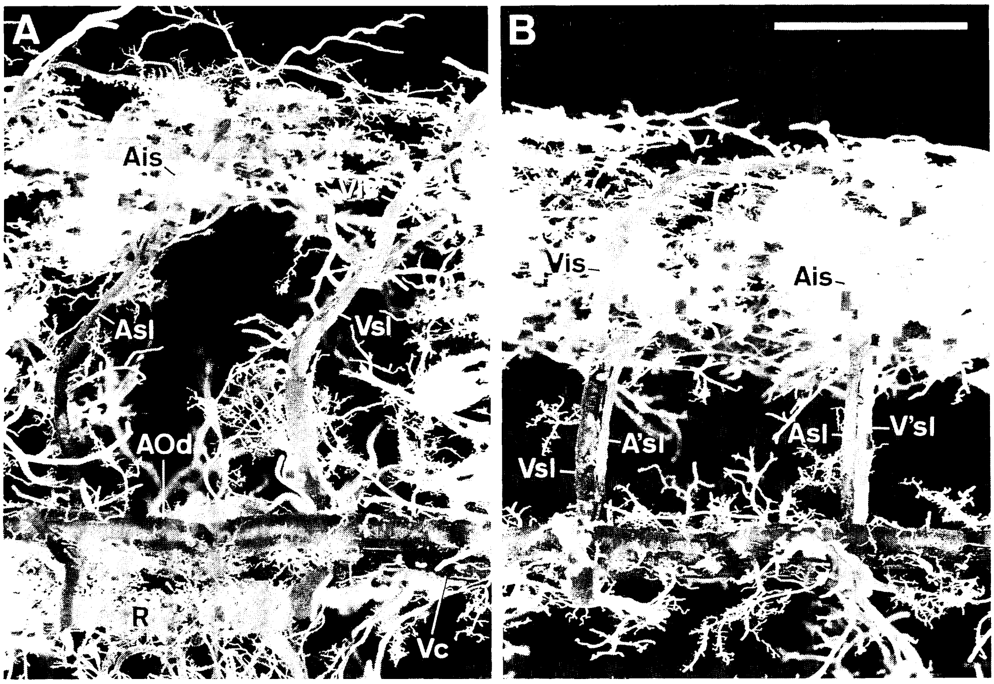

Fig. 2. Arrangement of the lateral segmental vessels, single-tracked in the trunk region (A) and double-tracked in the caudal region (B), viewed from the left dorsal side after removal of the dorsal and the left lateral segmentals. AOd, dorsal aorta; Ais, intersegmental artery; Asl, lateral segmental artery; A′sl, additional lateral segmental artery; Vc, caudal vein; Vis, intersegmental vein; Vsl, lateral segmental vein; V′sl, additional lateral segmental vein; R, renal vascular plexus. Bar = 5 mm.

(Fig. 2A). In the caudal region, on the other hand, every vascular lane carries two vessels, an artery and a vein pairing in parallel (Fig. 2B). The two components of a pair so differ in branching pattern that they are unambiguously classified into a basic and an additional vessel.

The basic vessels are identified as ordinary lateral segmental vessels. They give off intersegmental branches in the same manner as the single-tracked lateral segmentals in the trunk region. The alternating order of artery and vein is also continued from the trunk region. Each basic vessel stem lies anterior to that of the additional vessels in most cases.

The additional artery or vein is a little smaller in diameter than the basic artery or vein, and its branches are less extended. The main branch penetrates the red muscle mass along the horizontal septum, deviating from the myoseptum somewhat backward toward the mid-portion of the myomere. In addition, small branches given off from the additional artery follow the intersegmental veins but only for a short distance, and the additional vein rarely has such branches. Thus the area within which the additional vessels extend their tributaries is essentially limited to the bulky central portion of the red muscle, and the intersegmental vessels are virtually single-tracked throughout the body.

Two kinds of small vessels accompanying proximal portions of the segmental vessels are shown in Fig. 3. The segmental vessels, whether they are dorsal, ventral or lateral ones, are paralleled by one or two small vessels. Of these small vessels, those accompanying the segmental arteries are connected by axial trunks paralleling the dorsal aorta. This type of vessel, which corresponds to Vegel's (1985) secondary artery, is found even in the double-tracked series. The others accompanying the segmental veins with less regular appearance are arteries arising from the dorsal aorta. They occur only where the segmental vessels are single-tracked.

Figure 4 shows one more type of small accompanying vessel. The dorsal segmental artery is paral-

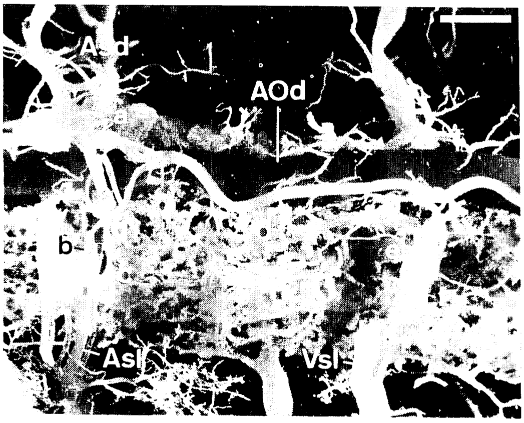

Fig. 3. Proximal portion of the segmental vessels in the trunk, viewed from the left dorsal side. The dorsal segmental artery (Asd) and the lateral segmental artery (Asl) are accompanied by small vessels (a, b, c), which connect with an axial trunk (d) of the secondary arterial system. The small vessels (e, f) accompanying the lateral segmental vein (Vsl) are arteries given off from the dorsal aorta (AOd). Bar = 1 mm.

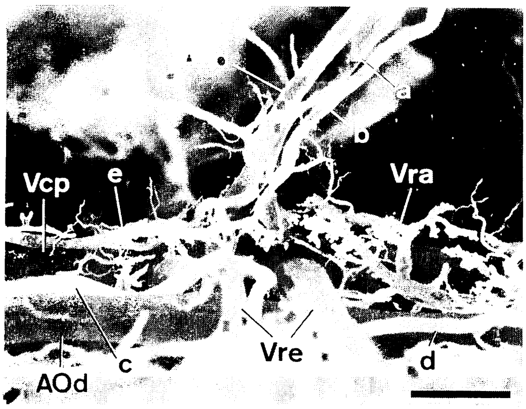

Fig. 4. The dorsal segmental artery accompanied by two kinds of small vessels, viewed from the left dorsal side. One of the accompanying vessels (a) is, as in Fig. 3, a branch of the secondary arterial trunk (c–d). The other (b) is a vein which breaks into some afferent renal veins within the kidney. One of these proximal endings anastomoses with an afferent renal branch (e) extending posteriorly from the dorsal segmental vein in front. AOd, dorsal aorta; Asd, dorsal segmental artery; Vcp, posterior cardinal vein; Vra, afferent renal vein derived from the dorsal segmental vein of the next segment; Vre, efferent renal vein draining the left fork of the kidney. Bar = 1 mm.

leled by one small vein as well as one secondary artery. The occurrence of an accompanying vein is less frequent than that of an accompanying artery, and is also confined to the single-tracked segmental lanes.

Discussion

The additional vessels are locally and simply added to the basic vascular plan without any reductions in scale. Such a type of vascular modification appears to cope with an increased demand for blood flow in local circulation.

The area of the additional vessels is limited within the superficial red muscle. Furthermore, the distribution of the additional vessels is restricted to the caudal region where the red muscle is bulked up, wedging deeply towards the midline. In general, the red muscle of fish is used for prolonged cruising, sustained by aerobic metabolism, and its great demand for blood flow is represented by high capillary density being more than tenfold that of white muscles (Bone, 1978). It is likely that the increase of red muscle mass has induced the development of the additional vessels.

The additional vessels do not coexist with the small accompanying vessels except the secondary arteries. The non-overlapping distribution of these large and small accompanying vessels suggests that the former correspond to an enlarged form of the latter.

The small accompanying vessels represent a shortcut plumbing: arising from the axial vascular trunks to service an area just around the proximal portion of the segmental artery or vein, whereas the drainage or supply should otherwise necessitate a detour from the neighbouring segments. These small vessels may occur rather commonly in fish. In fact, similar small vessels, although mixed up with secondary vessels, have been reported in two species of flathead (Mosse, 1980).

It is probable that the additional vessels are derived from the small accompanying vessels, because enlargement of vessels already present seems to be the most easy and practical solution to increased demands for blood flow, from both an evolutionary and ontogenetic point of view. If it is also true that small accompanying vessels are commonly present in fish, development of additional vessels must be an easy modification for any fish, and *T. japonicus* may have simply realized what is a potential property in all fishes.

Even though it may be an easy modification, the equipping of additional vessels is unique in *T. japonicus.* Such a modification does not occur in the rainbow trout which has equally well-developed red muscles (Górkiewicz, 1947), nor even in the non-tuna scombrids which have more abundant red muscles than *T. japonicus* (Kishinouye, 1923). There should be certain matters specifically applicable to *T. japonicus.*

The vertebral number of *T. japonicus* is 24, the smallest number among fishes except the Tetraodontiformes and some minor groups. Because the number of myomeres corresponds to the number of vertebrae, and the segmental vessels are arranged between myomeres, *T. japonicus* has a small number of segmental vessels serving relatively thick myomeres. Accordingly, each segmental vessel must convey blood at a high rate.

In the basic plan, all the vascular circuits within a myomere must form in a one-way traffic bridging segmental vessels of neighbouring segments. The length of the circuits increases with myomere thickness, but corresponding elongation of fine vessels with high resistance should be avoided. This might be achieved if large vessels could freely penetrate the muscle substance up to the vicinity of each capillary. However, the segmental vessels run within the vertical and horizontal septum, and their large tributaries hardly deviate from their spread along connective tissue sheets continuous with the septa. These septa and sheets of connective tissue, including both the dermis and that between red and white muscle, divide the myomere and surround the subdivisions into which the large tributaries on the surface give off many fine vessels. In such architecture, myomere thickness affects the length of microvascular circuits, thus bringing resistance to blood flow.

Each of the additional vessels is an additional and concurrent partner for the original segmental vessel, making recurrent microvascular circuits. Such circuits can provide shortcuts by making U-turns at any place. This involves rearrangement so as to reduce flow resistance. Our conclusion is that the additional vessels have a compensatory function in offsetting resistance caused by thick myomeres.

The preceding explanation can be extended to *Seriola quinqueradiata* which has completely double-tracked segmental vessels. This species attains about three times the length of *T. japonicus*, but has the same vertebral number and consequently myomeres of inordinate thickness.

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マアジにおける側方体節血管の特異な配列

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マアジの体節血管の配列を腐食鋳型法によって観察した．水平隔壁中を走る側方体節血管のうちの尾部の列に限り，各節で動・静脈が並走する複線化配列が認められた．複線化は末梢部までには至らない不完全なもので，本来の体節血管と，分枝の分布域が血合筋の肥厚部に限られる付加的な血管とに区別された．単線配列を示す他の体節血管にも，付加的血管へと発達し得るような小血管が付随していた．付加的血管の出現は，発達した尾部血合筋の血流要求が単線配列ではまかないきれなくなったことを示唆する．マアジは体節数が少なく個々の筋節が厚いので，個々の体節血管への負荷がもともと大きく，複線化によって過負荷を解消しながら血合筋を発達させてきたものと解釈した．

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