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Growth and meat quality relations in carp

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Abstract

Growth proceeds through an harmonious development of major tissues, namely bone, muscle and adipose tissues. Changes in chemical composition result from differential growth of these tissues. Little is known about the relative changes in morphometric traits during development of carp or about their genetic basis, but it seems that valuable criteria for selection on suitability for processing could be found in the mechanisms of bone and muscle development. The development of fatty tissues associated with growth of carp is stimulated by the use of lipid-enriched or high-energy artificial diets. Fat is accumulated in specific adipose tissues and the analysis of the relative development of these tissues could give valuable information on the over-accumulation of fat and its distribution in the whole body. Accumulation of fat has either positive or negative consequences for sensory evaluation depending on the source and the composition of fat. The main characteristics of muscle and connective tissues are presented in this paper. Different muscle tissues comprising different fibre types are found in cyprinids. These tissues together with adipose tissues compose the edible part of carp and explain most of protein retention. Protein content and composition are stable during development. Furthermore, a wide variability in the characteristics of muscle and connective tissues persists in commercial-size fish related to their mode of development. It is especially true for the main contractile protein: myosin. This is illustrated on expression of isoform of myosin but in early stages. The changes in the characteristics of the tissues and of the flesh after death and during postmortem storage and processing are reviewed. The structural components and the organization of tissues are very specific in fish and more sensitive to destruction. Thus, the degradative processes that affect the flesh during storage and processing have important consequences for sensory evaluation of the flesh which in freshwater species is generally rather soft and with neutral odour and taste. In this paper the possible role of biological characteristics of the flesh and of its constitutive tissues in quality is analyzed for the effect of body weight and for the effect of acclimation temperature. Temperature induces specific compensation for the maintenance of basic processes and the consequences for quality are analysed as well.

Keywords: *Cyprinus carpio*; Growth — fish; Tissues; Meat quality; Postmortem; Temperature

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1. Introduction

Growth of reared fish present a wide variability which results both from low intensity of genetic selection and from marked susceptibility to environmental conditions. Thus, fish of varying age/weight and fish produced under very different conditions are commercialized. How such variability in growth affects the quality of fish is a central question in aquaculture.

Growth can no longer be considered only as changes in whole-body size and composition. Growth proceeds through an harmonious development of important tissues such as bone, connective tissues, muscle and adipose tissues which comprise most fish products. The developmental changes in the structural characteristics of these tissues could be one of the first aspects related to quality. Changes in crude chemical composition – another important aspect of fish quality – result from stimulation or alteration of the turnover and the retention of the chemical components: proteins, lipids, carbohydrates and minerals with normal and altered development of the specific tissues. Furthermore, changes in the composition of these components – lipids classes, fatty acid composition, nature and functionality of proteins – also proceed with growth and differentiation of tissues.

Thus, variability in growth is associated with changes in relative development of tissues and in structural, chemical and biochemical characteristics which explain variability in what might be called the "biological characteristics" of commercialized fish. In themselves, the appearance and conformation of fish are important for the commercial value of the product. This will be true also for its chemical composition in the future (Borresen, 1992).

After slaughtering, wide changes affect the products due to the postmortem storage and processing of fish. Against a background of irreversible degradation of the product, the structure and the chemical and biochemical characteristics are relatively preserved or modified (improved) to obtain the required "technological characteristics" for processing.

In this paper, the main aspects related to growth and quality are tentatively reviewed for carp. Aquaculture of carp is practised worldwide and the commercialization of wild and reared carp has occurred since ancient times. Processing of carp products has also been widely developed (Berka, 1986). However, growth and quality of carp are often assessed only by global measurements as mentioned above. Thus, it is not easy to draw a clear picture of the characteristics of carp and carp products. Fortunately, due to its wide distribution and its easy rearing, carp is generally used as a model for research on physiology (especially on thermal adaptation), nutrition and processing, and basic information has been gained. From available data and personal results, this paper will try to give an overview of the characteristics of carp, of the role of specific factors influencing these characteristics and of how they are affected during processing.

2. Chemical composition

The chemical composition of carp and carp flesh has been given by various authors (see Berka, 1986). The changes in the chemical composition related to the size/age of fish and

to the effect of rearing conditions are very important for quality assessment. The fish industry and consumers will in the future need increasingly more information and guarantees on the chemical composition of fish.

Protein content and composition

During the ontogeny of carp, there is an early increase in the protein content of the whole body, carcass and muscle (Takeuchi et al., 1979; Hossain and Jauncey, 1989) and protein content reaches a plateau value (16–19% BW). Only minor changes are observed in that component even if carp are fasted (Shcherbina and Griyayev, 1990; Shimeno et al., 1990) or fed a deficient or imbalanced diet (Zeitler et al., 1984; Venugopal and Keshavanath, 1984; D'Mello et al., 1989; Viola et al., 1992). Furthermore, protein deposition and protein content increase if growth is stimulated by steroid administration (Lone and Matty, 1984; Sathynarayana Rao et al., 1988; Basavaraja et al., 1989), and wide effects of sexual maturation on protein content have been observed in carp (Dhawan and Toor, 1990).

The amino acid composition of protein synthesized at different ages is very similar (Zeitler et al., 1984). This is true also for fish of the same age fed on different protein sources (Schwarz and Kirchgessner, 1988). From protein content and composition data, one could conclude that the gross protein fraction is very stable with aging. However, 70–72% of the protein of flesh is composed of myofibrillar protein from muscle (Suzuki, 1981) and marked qualitative changes occur in myofibrillar proteins during development and under the influence of some factors reviewed in the following sections.

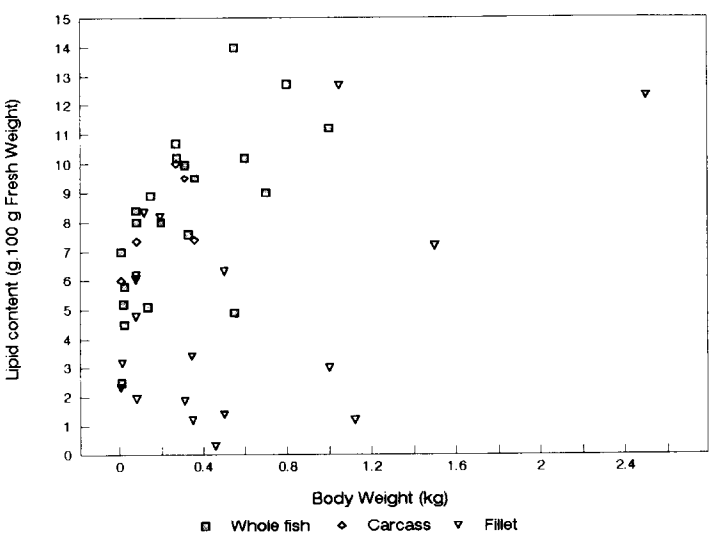

Fig. 1. Relationship between body size and lipid content in whole body and in the flesh of the carp. Data from Steffens (1974), Takeuchi et al. (1979), Viola et al. (1981), Lone and Matty (1984), Venugopal and Keshavanath (1984), Zeitler et al. (1984), Sathynarayana Rao et al. (1988), Schwarz et al. (1988), Viola et al. (1988b), Basavaraja et al. (1989), D'Mello et al. (1989), Schcherbina and Griyayev (1990), Papatsoglou et al. (1992), Viola et al. (1992).

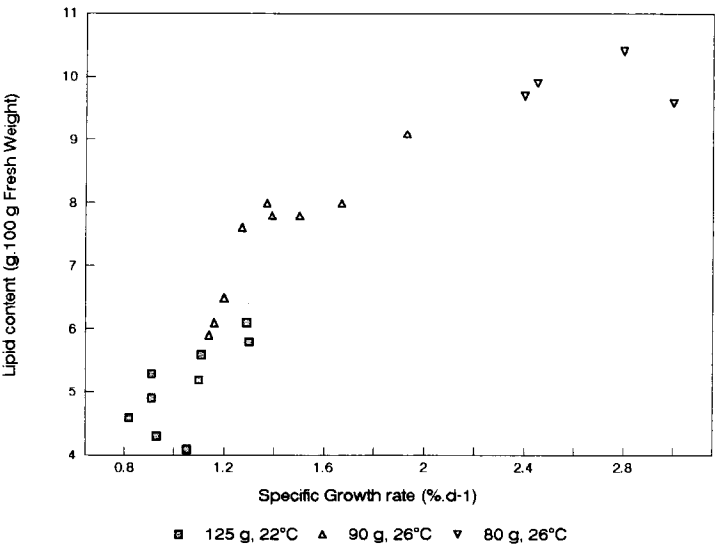

Fig. 2. Relationship between specific growth rate and lipid content in the carcass of carp fed on diet with similar lipid content. Data from D'Mello et al. (1989), Viola et al. (1988a).

Fat content

The fat content of whole body and flesh increases regularly with size of carp (Fig. 1) and is associated with a decrease in water content as a general law for living organisms. It is a direct consequence of the increasing potentialities for fat deposition with aging. There is also a size/growth rate effect as a wide variability of fat content is observed in fish of the same age. Generally, if growth rate is stimulated at a given stage either in juvenile or in large commercial size carp, there is a concomitant increase in the fat content of whole fish and of flesh (Fig. 2). However, every (large) stimulation of growth rate in response to different factors is generally associated with an increase in food uptake. Thus, the main factor that controls fat content is the diet.

Feeding, supplementary feeding, feeding rate, and supplementation of a deficient diet (Venugopal and Keshavanath, 1984; D'Mello et al., 1989; Shcherbina and Griyayev, 1990; Shimeno et al., 1990; Shimeno and Shikata, 1993; Viola et al., 1992) increase (or restore) growth rate and it is generally associated with an increase in fat content. Other factors (temperature, exercise, steroid supplementation) indirectly stimulate feeding and thus increase fat content (Lone and Matty, 1984; Sathynarayana Rao et al., 1988; Basavaraja et al., 1989; Sanger, 1992a; Viola et al., 1992). This is very important because the supply of a high-quality diet to stimulate growth and thus reduce rearing time in aquaculture production implies an increase in fat content.

The most effective compounds in the diet that stimulate fat retention are lipid and to a less extent carbohydrates (Takeuchi et al., 1979; Viola et al., 1981, 1988a; Zeitler et al., 1984; Schwarz et al., 1988).

Another factor affecting fat content is of genetic origin (Fauconneau et al., 1991) and it could compensate for increasing fat content due to feeding, but there are no available data

on this aspect in carp. The induction of sterile fish by hormonal supplementation during the larval period (Manzoor Ali and Satyanarayana Rao, 1989) or by triploidy (Gervai et al., 1980; Wu, 1990; Recoubratsky et al., 1992) seems to induce stimulation of fat retention which is also associated with an increase in growth rate.

Fat content and quality

The involvement of lipid content in flesh quality is not clear and obviously depends on local customs. As far as "nutritive value" is concerned, the maximum lipid as well as protein should be reached in fish products. If wild fish or fish produced traditionally are used as a reference for lipid content, then low levels of lipids would be achieved (Sehgal and Thomas, 1987; Sehgal and Sharma, 1991; Sathynarayana Rao et al., 1988) and it is not yet clear whether it is natural food, low feeding, high age or low lipid content that would be desirable for good flavour and good taste. If one considers the problems related to sexual maturation, such as decrease in lipid and protein content of the carcass and thus a downgrading of the fish, the production of a monosex female population which comes to maturity later and of sterile fish would lead to better quality of fish due to higher lipid content (Wu et al., 1988).

If a panel of specialists trained for sensory evaluation is used as a reference, it should be known that the reference varies among countries. Interpretation of data from sensory evaluation is not so easy (Haard, 1992) and there are often no differences in organoleptic criteria even if large differences in composition and other characteristics of the flesh could be demonstrated (Jayaram et al., 1980; Nandeesha et al., 1988).

In some countries, lipids are less important, especially for taste, than other compounds (Yang and Lee, 1984). Different carp products have also been developed around the world. In these products based on raw or cooked meat, lipids are less important than proteins and their structural organization (Hatae et al., 1990b; Brillantes, 1992).

In other countries, a minimum lipid content, which has still to be defined for carp, would be required for both texture and taste of the flesh (Vallot and Demael-Suard, unpublished data). The effect of a high lipid content in the flesh is however not known. From data available on hormone-supplemented carp, if the lipid content is not affected by supplementation, there is no difference in sensory evaluation (Sathynarayana Rao et al., 1988), but if the lipid content increases due to hormone supplementation, a significant difference in sensory evaluation is observed for cooked flesh. Fish with a high lipid content seem to be preferred if no off-flavors are detectable (Basavaraja et al., 1989). If over-development of fat is obtained, as seems to be the case in grass carp, then the appearance and taste of flesh is negatively evaluated (Lin et al., 1989).

Lipid composition

Together with lipid content, lipid composition is also important for the nutritional quality of the flesh as demonstrated for cyprinid meat (Steffens et al., 1992). The fatty acid composition and especially the content of polyunsaturated fatty acids (PUFA) are essentially controlled by the fatty acid composition of the dietary lipids (Viola et al., 1981; 1988a,b, 1990b, 1992; Bakir et al., 1993; Demael and Vallot, unpublished data). The supply of high PUFA diets leads to a high PUFA in the lipids of the carcass and the supply of a given PUFA series (n-3 or n-6) leads to the enrichment of fatty acids of the corresponding

series in the lipids of the carcass. The fatty acid composition of the polar lipids which compose the cell membrane is less affected than that of neutral lipids stored in specific tissues (Choi et al., 1985).

Lipid composition and quality

The specific effect of fatty acid composition on sensory evaluation is not known although composition certainly plays a role in the texture of raw meat through the fluidity of fat and does not play a significant role in cooked flesh. A specific taste relative to a given fatty acid composition has not been reported in carp (Viola et al., 1990b).

The stability of lipid is an important point for producers, industry and consumers. At the level of the producer, if the diet contains a high level of PUFA, supplementation with α-tocopherol is needed to maintain growth (Runge et al., 1987; Schwarz et al., 1988), which is an indication of the high susceptibility of PUFA to oxidation. As far as nutritional quality is concerned, a minimum degradation of fatty acid during storage and processing is required both for the guarantee of PUFA content (Mai and Kinsella, 1979) and for the minimum development of lipid hydroperoxides (Viola et al., 1990b). It seems that compounds involved in vivo in protection against peroxidation such as glutathione peroxidase, which is a selenium-dependent enzyme, could play a role in protection against oxidative degradation of the flesh after death (Nakano et al., 1992). However, lipid oxidation affects both positively (detectable specific smell and taste) and negatively (rancidity) the organoleptic characteristics of fish (Josephson et al., 1984). The role of the relative degradation of neutral and polar lipids in different tissues such as adipose tissue and muscle (dark and white muscle) for the development of smell and taste is not known in carp. Dark muscle is richly vascularized, has a high lipid content (Henderson and Tocher, 1987), and contains large amounts of iron; thus it is more sensitive to oxidation than white muscle.

3. Relative growth and development of tissues

The changes in chemical composition during development and in response to different factors are the result of differential growth of tissues. The main tissues involved in whole-body growth are bone, muscle and adipose tissues. The relative development of these tissues is very important for the conformation of fish and thus its yield in processing (gutting, filleting). Flesh is composed mainly of skeletal muscle and adipose tissues but also of connective tissues.

Bone tissue development

The growth of bone (head and vertebral axis) is slower than that of the whole body starting from the end of embryonic development. It should mentioned that variability in the number of vertebrae can be observed (CV 3–4%) (Sumantadinata et al., 1990). It is generally the consequence of high rates of embryonic development which induce the non-recruitment of caudal somites. As there are very few studies on bone growth in fish, it is not known if all parts of bone tissues are equally affected by the decrease in relative growth rate. The increase in condition factor with body weight (Fig. 3) could be a simple index of a decrease in relative growth in length of fish and a thus a decrease in thickness growth of

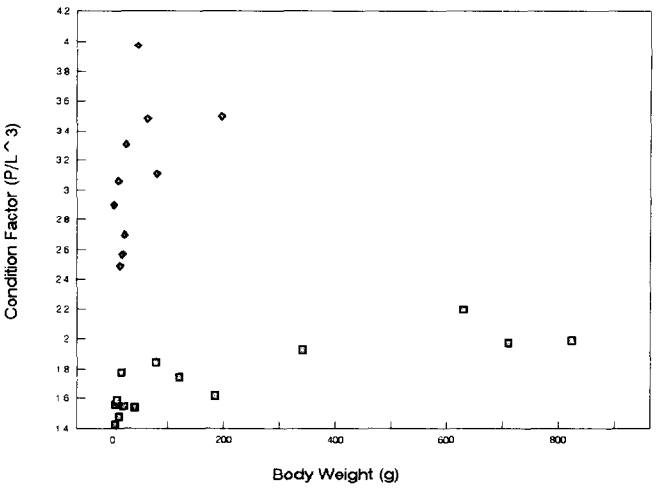

Fig. 3. Relationship between body weight and condition factor of carp (*Cyprinus carpio*). Data from Talasera and Urfi (1987), Taniguchi et al. (1986), Lone and Matty (1984), Venugopal and Keshavanath (1984), Ahmad and Matty (1989), Schcherbina and Griyayev (1990), Shimeno et al. (1990), Komen et al. (1993). Data indicated by a filled square are from carp of different origin from those indicated by a filled diamond.

vertebrae, but the relative increase in height and width of fish with size is certainly associated with a relative increase in diameter of vertebrae and in size and length of the epiphysis. The relative development of bone tissues, especially those of the head, is particularly important for carcass yield (Ivantcheva and Todorov, 1989; Geri et al., 1995) and fillet yield.

Muscle

Skeletal muscle demonstrated a higher growth rate than that of the whole body. This is observed from larval development (Alami-Durante, 1990) up to large carp (Oikawa and Itazawa, 1984; Goolish and Adelman, 1988; Geri et al., 1995) (Table 1). Indirectly the increase in condition factor (Fig. 5) with aging is also a consequence of the increasing proportion of muscle. It is obvious also if one observes the shape of fish that the different

Table 1
Allometry coefficient for growth of different tissues of common carp (*Cyprinus carpio*)

Stage	Larvae[a] (5–500 mg)	Adult[b] (2–2000 g)
Muscle	1.09	1.05[c]
Liver	1.19	0.85
Pancreas	1.19	
Intestine	1.00	0.89
Nervous system (brain)	0.073	0.46

[a]Alami-Durante (1990).
[b]Goolish and Adelman (1988).
[c]Muscle mass was assessed as carcass without head.

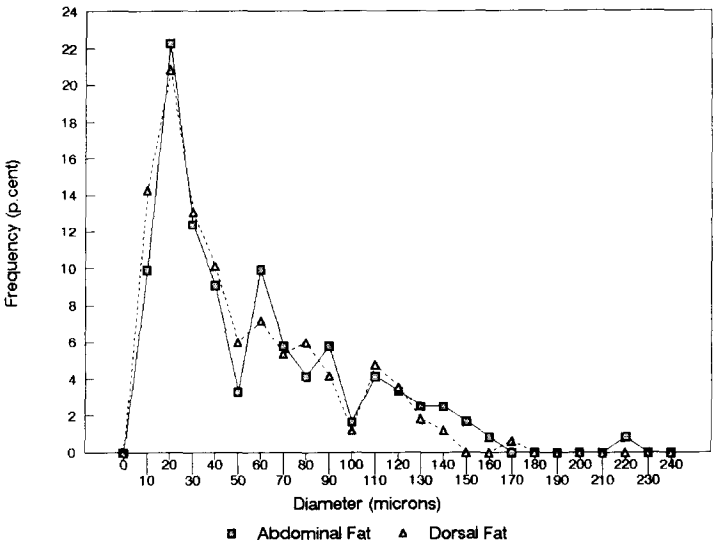

Fig. 4. Distribution of diameter of adipose cells in subcutaneous dorsal and ventral fat of carp flesh (1.5 kg body weight) (Fauconneau, unpublished data).

parts of skeletal muscle have not the same allometry for growth. It is partly the result of an anteroposterior gradient of growth and development of tissues of the vertebral axis which is observed in the early development of fish (Nag and Nursall, 1972) and is certainly present in larger fish even at commercial size. In some species of mirror carp (high back carp), the development of back muscle (dorsal muscle) is higher than in normal carp (Ivantcheva and Todorov, 1989). It could be a consequence of acceleration in the sequence of development of muscle tissues.

It has also been shown that the relative percentage of red muscle to total skeletal muscle is relatively stable during aging (Talasera and Urfi, 1987); however, it could be largely affected by exercise (Sanger, 1992b). There is no further information available concerning possible differential growth of different parts of skeletal muscle (between muscle tissues and within muscle tissues).

Further data on the allometries for growth of different parts of skeletal muscle together with their genetic basis (Kohlmann, 1987) are required if one wants to manipulate the shape or conformation of carp. Large variations in body height and body width relative to standard length (CV 7–8%) are observed in carp domesticated and selected over a long period (Sumantadinata et al., 1990). Large differences were also observed between different strains of carp (Pokorny, 1990) and within strains (Geri et al., 1995) especially for body conformation and percentage of fillet flesh.

Due to the specific role of muscle and muscle components in fish flesh quality, the development of muscle and its main characteristics will be discussed separately.

Adipose tissues

The development of adipose tissues has never been analyzed in fish even if some of them are anatomically distinct and could thus be dissected. Some fish preferentially store their lipid in liver and others in red muscle (Henderson and Tocher, 1987). However, almost all

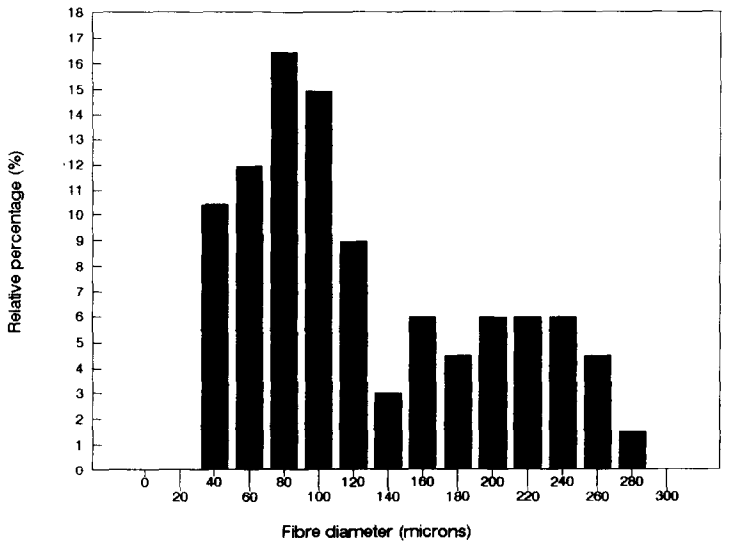

Fig. 5. Distribution of diameter of muscle fibres in white muscle of (25–30 cm) carp (calculated from Rowlerson et al., 1985).

fish store lipids in adipose tissue located around the digestive tract, in cavities of the head, under the skin, in the flesh between myomeres and in the myomeres (Fauconneau et al., 1991). It should be emphasized that in cyprinids, as in salmonids, adipose tissue has a positive allometry of growth with the whole body because the fat content of carcass and flesh increases with body weight (Fig. 1).

Adipose tissue of carp is composed of different populations of adipose cells (Fig. 4). The presence of small adipocytes is an indication of an active hyperplastic development of adipose tissues. Thus the development of adipose tissues in fish is, as in mammals, the consequence of both recruitment of new adipocytes and increase in size of existing adipocytes due to fat deposition. Further data have to be obtained and analysed for the different phases of development of adipose tissues and the effect of different factors using cellularity of adipose tissues.

The dynamics of development of the different adipose tissues mentioned above is not known although visceral fat and subcutaneous abdominal fat could be observed earlier in development than subcutaneous dorsal and subcutaneous lateral fat (Fauconneau et al., 1991). The relative contribution of visceral fat to total fat is very important for processing yield (gutting, filleting). It seems from the data obtained in small carp (Ahmad and Matty, 1989) and in large carp (Choi et al., 1985; Viola et al., 1988a,b) that a high content of lipid could be achieved in carcasses with low viscerosomatic indices and that visceral fat contributes only to 20–25% of total fat.

The development of adipose tissues between the myomeres and in the myomeres seems to occur later in development even if adipose cells could be observed early in muscle of small commercial-size fish (1 kg) (Fauconneau, unpublished results). The development of fat in the flesh could play an important role not only in the visual appearance of the flesh

and the processing yield but also its taste. This has been reported, for instance, in grass carp fed on green manure (Lin et al., 1989).

Connective tissues

Another important tissue of fish flesh and fillet is the connective tissue as it ensures the cohesiveness of the flesh (Bremner, 1992). The distribution of connective tissues between the myomeres and around fibres is very specific to each species (Ando et al., 1992). Although there are few data on the tissue itself, its main component, collagen, has been analysed (Sato et al., 1986a,b, 1989). Its content in the flesh varies in different species depending on their swimming performance (Sato et al., 1986b), but it is generally very low ($<3\%$) compared with the collagen content in mammals (Sato et al., 1989). Due to a lower amount of hydroxyproline and thus to less possible reticulation, fish collagen is less thermostabile than mammalian collagen. In carp, the amount of collagen is relatively low, 0.6% of the fresh weight, which accounts for 3.2% of flesh protein and half of it is soluble in acid solution without any thermal treatment. It is composed mainly of collagen I and V, the main components of intramuscular connective tissue; collagen III has not been found in carp (Sato et al., 1989).

The changes observed in the hydroxyproline content of collagen (Sato et al., 1986a) suggest that there is a quantitative development of that tissue during ontogenesis and also qualitative changes. It is possible that intramuscular connective tissues and collagen content increase with aging and that reticulation of collagen also increases with aging.

The effects of collagen on flesh quality are rather controversial (Dunajski, 1979) and it seems that collagen could play a role in the texture of raw flesh as it maintains cohesiveness (Sato et al., 1986b) but also in cooked flesh for juiciness and softness due to its low temperature of denaturation ($<60°C$) and its high water-holding capacity (Hatae et al., 1986). However, such a relationship is obtained by comparison between very different species (Hatae et al., 1986; Sato et al., 1986b) and it is less clear how to analyse the role of collagen within a species. In cyprinids, the temperature of denaturation of collagen is amongst the highest observed in fish (Sikorski et al., 1984); thus the texture of carp flesh could be partly affected by collagen through its stability in raw flesh and its gelification characteristics in cooked flesh.

4. Skeletal muscle development

Characteristics of muscle fibres

Skeletal muscle is composed of different muscles: a red superficial muscle (also called dark or brown muscle in marine fishes), a pink muscle and a deep white muscle. These tissues contain very different fibre types. The main characteristics of these fibre types relative to growth and quality are summarized in Table 2. Roughly, there are three main fibre types. The "red fibres" are characterized by relatively small size (cross-sectional area), oxidative metabolism (SDH activities and high content of active mitochondria), and low speed and intensity of contraction in response to a stimulus. They contain specific myofibrillar proteins as demonstrated histochemically (ATPase) and immunologically (Rowlerson et al., 1985). The "white fibres" have a larger size and a glycolytic metabolism for energy supply, and

Table 2
Characteristics of different fibre types in skeletal-muscle of common carp (*Cyprinus carpio*)

Fibre type	Red	Pink	White Small	White Large
	Slow-twitch	IIb	?	Fast-twitch
	I		?	IIa
	βR	αR	?	αW
Size of fibres (μm)[a]				
At hatching	3			5
In adults	36	60		100
Metabolic activity[b]				
mATPase				
Alkali	−(+)	+(+)	++(−)	++(−)
Acid	−	−	++	++
SDH	+	−	−	−
PAS	+	++	+	++
Parvalbumin[d]	−	++	++	++
Contractile components[c]				
Myosin (total and heavy chain)				
anti Slow	+	−	+	−
anti Fast	−	+	+	+

[a]Talasera and Urfi (1987).
[b,c]Rowlerson et al. (1985).
[b]Data within brackets are from Talasera and Urfi (1987).
[d]Zawadowska and Supikova (1992) in tench (*Tinca tinca*).

respond with high speed and high intensity of contraction to a stimulus. Such high speed of contraction could be achieved by a high rate of delivery of Ca^{2+} that is achieved by Ca^{2+}-binding proteins such as parvalbumin. The fact that white fibres use glycogen as an energy source is associated in some cyprinids (carp) with a higher content of glycogen (Rowlerson et al., 1985), but in other cyprinids, as is generally the case in fish, slow red fibres contain more glycogen than white fibres due to their more active metabolism. White muscle contains also specific myofibrillar proteins. The "pink fibres" are intermediate between "red" and "white" fibres for energy metabolism, contractile characteristics and speed of contraction. In fact, two subclasses of fibres could be distinguished for red, intermediate and white fibres of cyprinids (Akster, 1983; Rowlerson et al., 1985; Scapolo and Rowlerson, 1987). One type of red fibre found only in skeletal muscle is a remnant from embryonic red muscle and it participates in cutaneous respiration of fish (El-Fiky and Wieser, 1988). Two white fibres are found which differ mainly in size and glycogen content but also for cyprinids in their contractile protein characteristics (Rowlerson et al., 1985).

Characteristics of skeletal muscles

The different fibres described above are localized separately in the three main skeletal muscles. Other muscles such as fin muscle or muscle of the head are composed generally of the three different types of fibres. In white muscle the presence of fibres of different size gives it a classical mosaic appearance and a specific distribution pattern (Fig. 5). The small

Table 3
Characteristics of different muscles in vertebral axis of cyprinid fish

Muscle	Red	Pink	White
Type of fibre[a]			
In adults	Red a,b	Pink a,b	White L,s
Metabolic activity[b]			
Mg^{2+}-mATPase	100	248	436
Creatine PK	100	142	215
SDH	100	33	15
Cytochrome oxidase	100	36	13
Biochemical components[c]			
(mg/100 g DM)			
Myoglobin	12.7	5.4	2.8
Glycogen	5.6	3.8	0.7
Lipid	20.2	8.3	5.8
Contractile components[d]			
Myosin heavy chain[f]	HC_s		HC_f
Myosin light chain	$LC1_s$,$LC2_s$		$LC1_f$,$LC2_f$,$LC3_f$
Myosin/actin ratio	2.9	3.1	4.0
Parvalbumins	PA I		PAI,II,II,IV,V
Swimming speed of recruitment[e]	0.5 L/s	1.3–1.5 L/s	2 L/s

[a]Akster (1983, 1985).
[b,c]Johnston et al. (1977).
[d]Focand et al. (1976), Johnston et al. (1977), Huriaud and Focand (1985), Rowlerson et al. (1985), Akster et al. (1989), Johnston et al. (1989).
[e]Johnston and Altringham (1990).
[f]From histoimmunological determination and peptide mapping.

white fibres are considered as new fibres which are built up or recruited within muscle for growth (Weatherley et al., 1988).

The characteristics of the three skeletal muscle types in cyprinids (Table 3) are mainly the consequence of specificities in fibre type. Red muscle is richly vascularized and thus contains high amounts of myoglobin. It also contains a very large amount of lipid (Johnston et al., 1977; Sanger, 1992a). Enzymes of oxidative metabolism have higher activities in red muscle than in white muscle. White muscle is characterized by a higher ATPase activity than red muscle. The activities of these different muscles during swimming are very different. Red muscle is always active. At moderate swimming speed, contractions are observed in pink muscle. It is only at high sustained swimming speeds that white muscle is recruited. White muscle also permits a burst of swimming activities.

The contractile characteristics of different fibres correspond to different protein composition and especially to different isoforms of myosin (Karasinski and Kilarski, 1989), the main protein of muscle which constitutes the thick filament of muscle. Slow and fast isoforms of myosin are observed respectively in red and white muscle. Myosin is composed of high-

molecular-weight subunits (myosin heavy chain: MHC) and low-molecular-weight subunits (myosin light chain: MLC). White and red muscle have different isoforms for both MHC and MLC. Some other regulatory proteins of the thick filament are also different in red and white muscle (tropomyosin, troponin). Actin, which constitutes the thin filament of muscle, does not demonstrate such polymorphism in skeletal muscle. Myofibrils also contain a structure called the "third filament" which together with the Z-line (where the thin filament is attached) ensures maintenance of structure during contraction. It is composed of nebulin/connectin and titin. Different isoforms of these proteins are also found in red and white muscle of fish (Akster et al., 1989). Finally, white muscle has very high content of parvalbumins of different isoforms from those found in red muscle (Focand et al., 1981).

Ontogeny of variability in characteristics

Different contraction properties are associated with different contractile protein sets of isoforms in white and red muscle. We have analysed during early development when carp larvae build their red muscle and subsequently their pink muscle (El-Fiky and Wieser, 1988), the effect of some factors on muscle characteristics (Alami-Durante et al., unpublished data) and protein isoforms. There is an increase in red muscle isoforms with development of red muscle in larvae. It is known that supplementation with GH or T4 during these early stages affect quantitatively and qualitatively the growth and development of cyprinid larvae (Reddy and Lam, 1992). It also seems to affect the composition of the isoforms (Table 4). After the larval stage, the relative proportion of the different muscle types seems to be relatively unchanged during development (Talasera and Urfi, 1987) although large fish have never been analysed in carp. Swimming activity is important for fibre-type expression, especially for oxidative fibres (Nai, 1987). Furthermore, the proportion of red and pink muscle seems to increase with exercise (Sanger, 1992b), so that muscle becomes more oxidative in trained fish. Immobilization also modifies the fibres

Within the same muscle different subpopulations of fibres are present which represent a potential variability in the characteristics of muscle and thus of the flesh. There are however very few data on such variability in carp. During post-larval development, growth of muscle is the result of both an increase in the number of fibres and an increase in their size (Weatherley et al., 1988). The consequence of the possible recruitment of new fibres within muscle is certainly one of the main causes of variability in the contractile and metabolic characteristics of muscle. There are no specific data about developmental changes in white muscle of carp, but from data on fibre size in white muscle (Rowlerson et al., 1985; Talasera and Urfi, 1987; Koumans et al., 1993) and ultimate body size it seems that recruitment of new fibres decreases during development and is insignificant in carp of 60 cm.

At the origin of recruitment of new fibres, there are muscle cells which are attached to fibres and could be induced both for building new fibres (hyperplasia) and for increasing the number of nuclei in the multinucleated fibres by fusion with the growing fibres. The only complete work on satellite cells has been performed in carp partly by using cell culture which had made it possible to reproduce myogenesis in vitro (Koumans et al., 1990) and to demonstrate the expression of a specific early isoform myosin (Fauconneau et al., unpublished data). These authors demonstrated that during ontogeny, from 3 to 60 cm, the total number of myosatellite cells seems to be constant but the percentage and the concen-

Table 4
Effect of GH supplementation by immersion of eggs in concentrated hormone solution and GH and T4 supplementation by regular immersion in concentrated hormone solution on relative expression of myosin isoforms (in %) in carp larvae (*Cyprinus carpio* L.)

	Fast myosin			Slow myosin
	LM 1	LM 2	LM 3	LM 4
Egg immersion				
At hatching				
Control immersed	6	52	34	8
	(1)	(3)	(5)	(4)
GH (50 mg/l)	7	46[a]	32	16[a]
	(1)	(4)	(4)	(3)
3 weeks post-hatching				
Control immersed	11	45	38	6
	(5)	(5)	(4)	(2)
GH (50 mg/l)	10	55[a]	27[a]	9
	(1)	(5)	(5)	(2)
Larvae immersion				
4 weeks post-hatching				
True control	13	58	26	3
	(2)	(8)	(5)	(4)
Control immersed	11	64	22	3
	(1)	(8)	(3)	(4)
GH (1 mg/l)	12	58	30	n.d.[a]
	(1)	(6)	(8)	–
T4 (1 mg/l)	11	61	24	8[a]
	(1)	(4)	(2)	(1)

[a]Data significantly different from the control ($P < 0.05$).
LM = larval myosin.

tration of satellite cells decrease from 3 to 60 cm carp (Koumans et al., 1991; Koumans et al., 1993). There is therefore always a capacity for recruitment of new fibres in large fish but with greatly decreasing probability.

Thus, variability of muscle and flesh characteristics of fish at higher commercial size of 25–30 cm would be lower than at early stages, although in adult fish different populations of fibres, especially in white muscle, still persist (Fig. 5 and Table 2). It is well known in mammals that the quality of meat depends on its fibre type composition. In fish, it seems that the proportion of the different muscles varies, their oxidative capacities varies and that, within the main muscle, different populations of fibres are present accounting for the growth history of this tissue. Such changes in muscle characteristics could explain the variability in carp flesh quality, but the relationship has not been studied further. We will give an example after analysing the main components of flesh quality of carp.

5. Postmortem changes in fish flesh

Sequence of events

After the death of fish, all the structures and all the components which compose tissues are subject to physical and chemical degradation depending on their stability. However, another important event occurs during postmortem storage. There is a contraction of muscle

Table 5
Postmortem changes in carp flesh during storage on ice and potential effects of antemortem stress (stressed vs. unstressed fish)

	Effect of stress
Metabolic changes[a]	
ATP consumption	−
Depletion of creatine P	−
Depletion of glycogen, and glucose 6P	−
Lactate accumulation	−
IMP increase	?
pH fall (> 6.0)	−
Ca^{2+} release	+ or ?
No increase in activities of proteases:	+ or ?
Cathepsin D and B	
Ca^{2+}-dependent calpain	
Ca^{2+}-non-dependent neutral protease	
Alkaline protease	
Structural changes[b]	
Rigor mortis: contraction of actomyosin	−
Breakdown of structure (high MW components)	
Extracellular matrix: collagen	+ +
Z-line: α-actinin	+
3rd filament: titin/connectin and nebulin	
Partial destruction of cellular compartmentalization	
Destruction sarcoplasmic reticulum	+
Increase in Ca^{2+} concentration	+
Physical changes[c]	
Increase in brightness of muscle	+
Decrease in intensity of colour	+
Water-holding capacity increase	
Tenderization of muscle	+
(lower firmness, breaking strength)	
Increase in solubility of protein	

[a,b]Tokiwa and Matsumiya (1969), Yamanaka et al. (1978), Manikodan et al. (1984), Ando et al. (1991a,b), Hwang et al. (1991), Ushio et al. (1991), Tsuchiya et al. (1992), Seki and Tsuchiya (1991), Nakayama et al. (1992).
[c]Laroche and Marcel (unpublished data).

which corresponds to strong binding of myosin to F-actin, probably due to the release of Ca^{2+} in the intracellular space. This central event called "rigor mortis" has various consequences (summarized in Table 5):

(1) The contraction of muscle actomyosin is ATP-dependent and thus all the energy stores of muscle are consumed to produce ATP and maintain contraction of muscle. It involves degradation of phosphorylated compounds such as creatine-P, glucose-6-P and fructose-1,6-di-P, the two latter being mainly produced by degradation of glycogen. Creatine-P and glycogen are depleted consecutively (Misima et al., 1990; Hwang et al., 1991). The consumption of nucleotides implies accumulation of the end-product of their catabolism, IMP. Thus, IMP content is one of the indices of freshness of fish.

(2) The end-product of glycolysis is lactate which accumulates in muscle in vitro and thus induces a decrease in pH. The fall in pH is however less important in fish than in mammals as the final pH is seldom lower than 6.0.

(3) The tetanic contraction of fibres induces sustained tension on the third filament built up with α-connectin and nebulin, on the Z-line built up with α-actinin, and on the extracellular matrix around the fibres and in the surrounding connective tissues. The proteins of the third filament and of the Z-line are degraded (Tsuchiya et al., 1992; Kumano and Seki, 1993). If the speed and the intensity of contraction are high, partial disruption of these different components could be induced. A disruption of cell membrane and sarcoplasmic reticulum also occurs, facilitating Ca^{2+} release and enzymatic degradation.

All these events take place within a few hours as the onset of rigor is observed 6–24 h post mortem in unstressed fish and the maximum rigor tension is observed 1–3 days post mortem. When all energy stores are consumed, then muscle tension progessively disappears and complete resolution is achieved within a few days (5–7 days) (Ando et al., 1991b; Hwang et al., 1991; Nakayama et al., 1992; Kumano and Seki, 1993). During recovery from rigor there are two phases (Hwang et al., 1991) and the lower rate constant phases could be associated with progressive disruption of the different structure mentioned above.

The degradative process is based mainly on different proteinases: acidic (cathepsins), neutral (Ca^{2+}-dependent, such as calpain, and Ca^{2+} non-dependent) and basic (Manikodan et al., 1979, 1984, 1985; Tsuchiya and Seki, 1991). The activities of these proteinases do not seem to change during postmortem storage (Manikodan et al., 1984), although there is increased access to substrates due to structure degradation. At the same time protein tends to be more soluble and less stable (Tokiwa and Matsumiya, 1969; Seki and Tsuchiya, 1991).

Variability in the postmortem process

The time course of the process is largely dependent on the temperature of storage. If temperature decreases, then all the processes are slowed down (Hwang et al., 1991; Watabe et al., 1991).

The duration and intensity of postmortem rigor depend on energy stores and Ca^{2+} content of muscle on the one hand and on the characteristics of muscle on the other. Changes in muscle characteristics with temperature acclimation will be analysed latter to illustrate such relationships. Energy stores and Ca^{2+} content could be affected mainly by stress, both metabolic and physical, although metabolic stress (without muscle activity) affects only glycogen consumption.

If fish are stressed before slaughtering so that their glycogen stores are partially depleted, theoretically rigor starts earlier: 30 min to 6 h post mortem (Berka, 1986; Nakayama et al., 1992) and the maximum is reached earlier: 12–24 h (Nakayama et al., 1992). The intensity of contraction is less affected by stress although it seems to depend on experimental conditions. Due to low stores of glycogen, lactate accumulation is lower and minimum pH is higher in stressed fish than in unstressed fish.

The acceleration of rigor mortis with stress could induce more rapid disruption of the structure and thus both acceleration of the degradative processes and muscle softening. The stability component of stressed fish could be however also lowered when compared to that of unstressed fish if the duration of the stress is long enough. Pavlov et al. (1990) reported

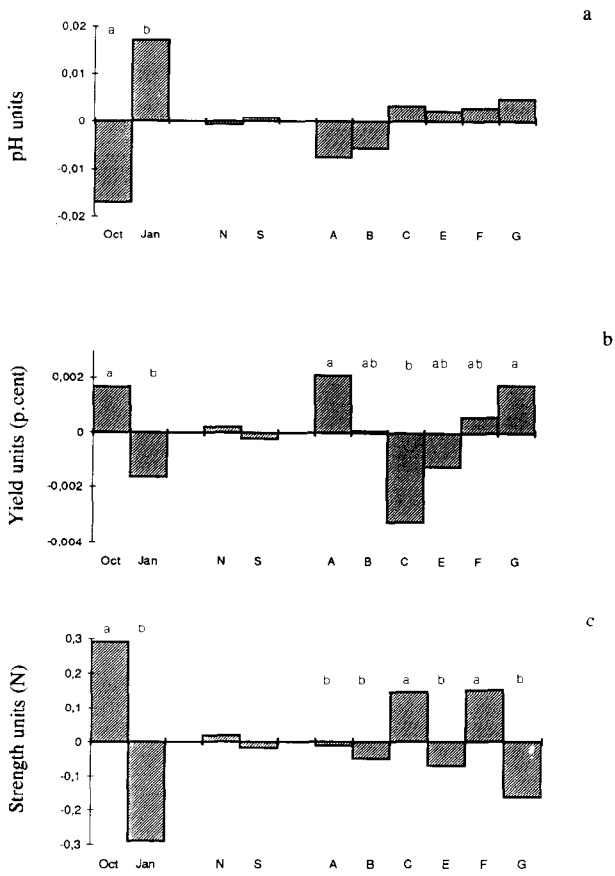

Fig. 6a,b,c. Comparison of the effect of fasting due to wintering (Oct and Jan) and different slaughtering method on variability of pH, water-holding capacity and texture (maximum compression strength) of raw flesh of carp (1000–2000 g) (*Cyprinus carpio*). *Methods*: (A) natural anoxia, (B) natural anoxia and filleting alive, (C) warm shock, (E) electrocution, (F) cold shock, (G) carbon dioxide anoxia. Fish were either bled (S) or not bled (N). Data are expressed as the difference from general mean. Bars with different letters are significantly different (from Laroche and Marcel, unpublished data).

that the enzymes of proline hydroxylation on collagen chains which ensure the collagen bonds and thus the strength of the extracellular matrix are dependent on environmental factors and stress of fish.

Fasting also decreases glycogen content and depletes other components (protein, lipids) in muscle (Shcherbina and Griyayev, 1990; Shimeno et al., 1990). Thus it could theoretically induce more rapid postmortem changes and probably a softening of muscle.

Consequences of postmortem changes for quality

Physical disruption of the different structures due to rigor mortis could be amplified by mechanical stress due to handling of the flesh in a state of rigor. Dunajski (1979) has mentioned also that the consequences of rigor mortis on the fillet were more important than

on the whole fish as the skeleton lowered the intensity of contraction and thus helped to maintain structure. In the fillet, it could even observed that contraction is not homogenous and affects differentially the different muscle types. Due to differences in height and depth along the fish, full rigor is observed later in the anterior part of fish or fillet than in the posterior part (Fauconneau, personal observation).

Other changes result in physical and chemical (oxidation, catabolism) degradative processes. The colour of the flesh fades, the flesh tends to soften, and the water-holding capacity of the flesh increases (Laroche and Marcel, unpublished data). It has been demonstrated that the tension of muscle during rigor mortis, which is associated with a loss of extensibility, does not explain the softening of the flesh which proceeds independently (Ando et al., 1991a,b; Tsuchiya et al., 1992; Kumano and Seki, 1993). However, some characteristics of texture such as breaking strength could be related to the time of postmortem storage of carp (Iso et al., 1987).

In a preliminary experiment on these criteria in fish fed or fasted (wintering) and submitted to different slaughtering methods, Laroche and Marcel (unpublished data) have found that the effect of fasting is more important than the slaughtering method for postmortem changes as it could be seen for minimum pH and for softening of raw and cooked flesh (Fig. 6a,b,c). It suggests that not only glycogen stores, but also other components (protein, lipids) are affected by fasting and contribute to postmortem changes.

6. The effects of some processes on flesh quality

Freezing/Thawing

During freezing there is a disruption of membranes, Z-line and third filament (Table 6) due to the increased concentration of salt in the unfrozen solution that surrounds these structures (Takahashi et al., 1993). The different physical degradative processes mentioned for postmortem changes could be accelerated by freezing although the rate of chemical degradative processes is lowered. During thawing, the higher Ca^{2+} concentration around the myofibrils allowed further contraction of actomyosin and consumption of ATP and glycogen and a "thaw rigor mortis" is observed (Yamanaka et al., 1978; Ma and Yamanaka, 1991; Ma et al., 1992; Kumano and Seki, 1993). Consequently, on thawing a temporary increase in breaking strength could be observed. The release of enzymes from intracellular structures could induce a higher susceptibility to degradation and especially oxidative degradation of the flesh (Hamm, 1979).

Washing

If the flesh or fillet is washed early after slaughtering of fish, it induces an acceleration of the rigor mortis process. This has been observed for the specific Japanese preparation called "Arai". There is more rapid consumption of ATP, which is associated with an increase in muscle contraction and thus of flesh toughness (Hatae et al., 1990b; Watabe et al., 1990). More rapid release of C^{a2+} could also play a role.

Table 6
Summary of the effects of some processes on carp flesh characteristics

Effect of freezing/thawing[a]
Dehydration due to freezing
Increase concentration of salt in unfrozen solution
Destruction of cellular compartmentalization (release of intracellular enzymes (mitochondrial enzymes, lysosomal enzymes)
Destruction of blood vessels (blood spots)
Further destruction of myofibrils
Decrease in connectin
Decrease in activity and stability of myofibrillar ATPase
Decrease in breaking strength
Thaw rigor[b]
Glycogen and ATP decrease and lactate increase
Increase in Ca^{2+} concentration in myofribrils
Activation of myofibrillar ATPase
Temporary higher firmness and shearing strength
Effect of washing (either in chilled or in heated water)[c]
Acceleration of rigor process
Rapid degradation of ATP
Increase in intracellular Ca^{2+}
Increase in muscle toughness and fibre length
Effect of moderate cooking after washing[d]
Gel formation at moderate temperature in fish paste
Thermal gelation of actomyosin or myosin B
Increase in elasticity of gel
Cross-linking and interaction between:
Tails of myosin heavy chain
Tail and head of myosin
Myosin and actin
Effect of transglutaminase on cross-linking
Effect of peroxidized oil
Effect of cooking[e]
Denaturation of myosin and actin
Thermal gelation of protein
Decrease in viscosity
Increase in firmness of flesh
Decrease in water-holding capacity
Decrease in intensity of colour
Increase in pH

[a]Nakayama et al. (1979), Hamm (1979), Bito (1984), Kitamikado et al. (1990), Kumano and Seki (1993), Takahashi et al. (1993).
[b]Yamanaka et al. (1978), Ma et al. (1991, 1992).
[c]Hatae et al. (1990b), Watabe et al. (1990, 1991).
[d]Sano et al. (1990a,b), Kishi et al. (1991), Pavlova (1992), Araki and Seki (1993).
[e]Akahane et al. (1985), Sano et al. (1988), Sano et al. (1990a,b), Iso et al. (1991), Hatae et al. (1990b), Laroche and Marcel (unpublished data).

Cooking

When analyzing the effect of different rearing factors on flesh quality, the flesh was evaluated in both the raw and the cooked state. However, the process of cooking itself is very important to detect differences in the flesh characteristics and probably in many cases no differences are observed because cooking is not properly designed.

At low cooking temperatures (40–50°C), there is both thermal denaturation of the extracellular matrix (Sikorski et al., 1984) and thermal gelation of actomyosin. The gelation of myosin corresponds to development of bonds (cross-linking) between the tails of free myosin heavy-chain molecules. If these molecules are not free as in intact flesh, then few bonds are developed, except for weak bonds between the tail and head of the myosin heavy chain and the tail of the myosin heavy chain and actin, and a poor gel is obtained (Nakayama et al., 1979; Sano et al., 1989, 1990a,b; Pavlova, 1992). The development of the thermal gelation properties of myosin is thus limited although possible in flesh. On the contrary, in fish paste (surimi) where myosin in solution is unfolded and many hydrophobic sites are apparent, the setting of gels occurs, which makes it possible to obtain different fish products. It seems that an enzyme of muscle—transglutaminase—facilitates cross-linking of myosin and explains most of the differences between fish species in thermal gelation ability (Kishi et al., 1991; Araki and Seki, 1993). It should also be mentioned that peroxidised oil stimulated cross-linking of myosin (Kawasaki et al., 1992).

At higher cooking temperatures, myofibrillar proteins are degraded (Akahane et al., 1985; Iso et al., 1991). The temperatures for denaturation of myosin and actin in carp (respectively 50 and 75°C) are at least 10°C lower than those of mammals (rabbit). Further degradation of protein unmasks many hydrophobic sites for interaction between molecules, mainly between heavy chains of myosin. If molecules are in solution, as is almost the case in fish paste, the gel is strengthened with increasing temperature and a more resistant product is obtained.

In whole flesh or minced flesh the changes are more complex. There is also in situ coagulation or gelification of proteins. Myofibrillar components certainly bonds together and an increase in mechanical strength of the contractile structure is observed. It has been observed that muscle fibre structures are preserved (Hatae et al., 1990a). It is suspected also that sarcoplasmic proteins are released and coagulate in the interstitial and extracellular spaces, forming a gel. The components of the extracellular matrix and connective tissues between myomeres also enter into the gelification process. Thus the texture of cooked flesh depends (a) on the size of fibres after cooking, (b) on the gel formed in interstitial spaces which allow sliding of the fibres (Hatae et al., 1990a), and (c) on the gel formed by collagen and lipids (Mai and Kinsella, 1987) which allows sliding of the myomeres.

The role of initial structure is important as demonstrated by the effect of moderate cooking on minced flesh and on intact flesh. At the temperature of denaturation of myosin (40–50°C) the maximum compression strength of the flesh decreases while that of minced flesh increases (Laroche and Marcel, unpublished data). However, maximum sliding strength of whole flesh increases regularly with temperature of cooking.

Other changes are associated with alteration in structure on cooking: an increase in brightness and decreases in pH and water-holding capacity of the flesh (Laroche et Marcel, unpublished results).

7. The effects of some factors on flesh quality

The structure of muscle, especially the size of the fibres, and the protein components of the flesh, especially contractile components such as myosin and to a lesser extent collagen, play an important role both in the texture of intact flesh and in the processing of carp flesh. This role is illustrated by the effects of body weight and temperature acclimation.

Effect of body weight

The first example deals with the effect of body weight of fish in the commercial size range. Early data demonstrated that there are no differences in quality between 2- and 3-year-old carp (Adamova et al., 1971). However, as previously mentioned, the lipid content

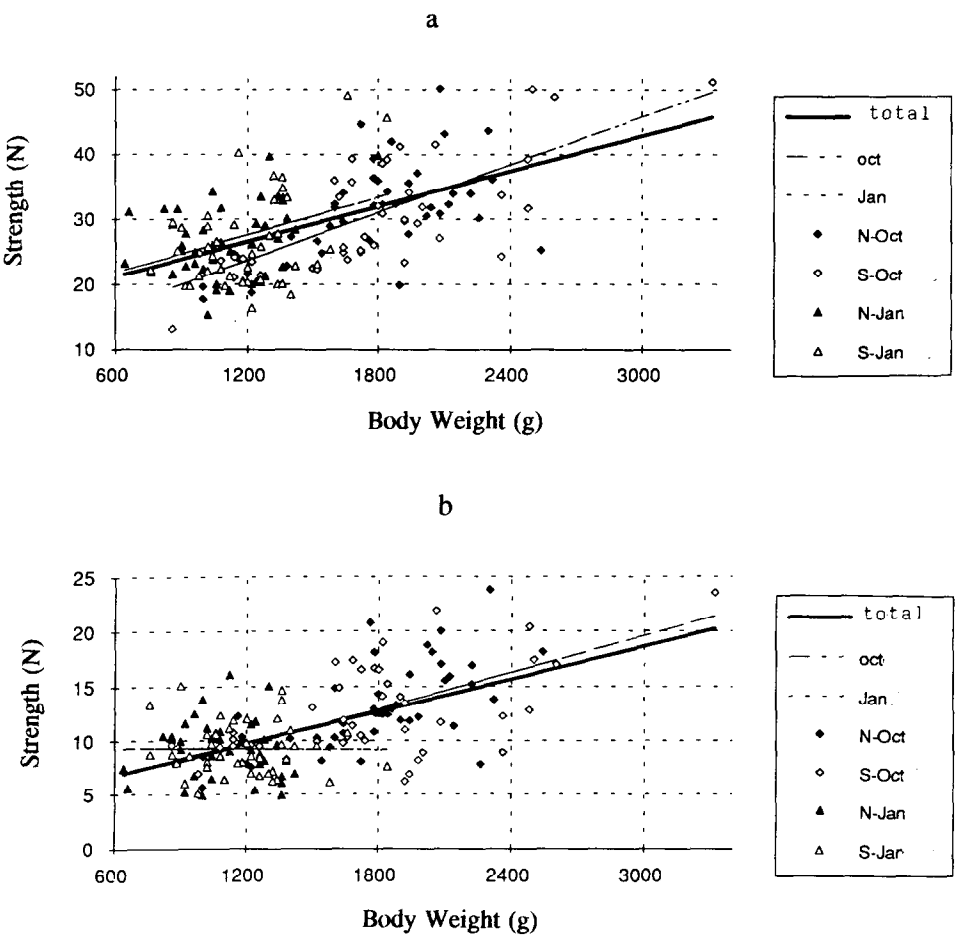

Fig. 7 a,b. Relationship between body weight and maximum modulus for compression in raw (a) and cooked (b) carp (*Cyprinus carpio*) of the same age (2-year class) (from Laroche and Marcel, unpublished data). Lines represent regression between the two parameters for whole data (solid line), for autumn data (Oct and diamond symbol) and winter data (Jan and triangle symbol). Fish were either bled (S) or not bled (N) during slaughtering.

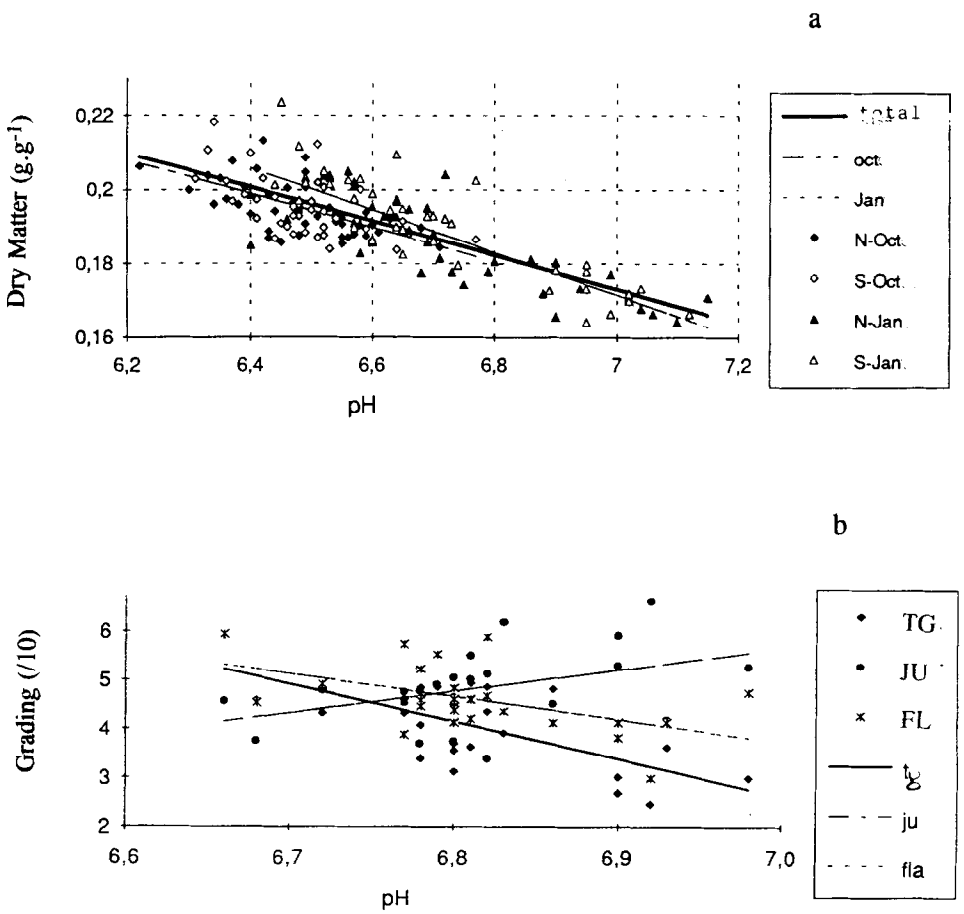

Fig. 8. Relationship between minimum pH of raw flesh after postmortem changes and (a) dry matter of fillet in carp (*Cyprinus carpio*) and (b) sensory evaluation of the flesh (TG = firmness, JU = juiciness, FL = flavour). Fish have the same age (2 years: October and January) but with a large range of body weight: 650–3500 g (from Laroche and Marcel unpublished data). For further explanation, see Fig. 7.

of flesh and the size of muscle fibres increase with aging of fish. Hatae et al. (1990a) suggested by comparison between species that the size of fibres and the characteristics of collagen partly explain the texture of cooked flesh: fish with rather small fibres are more firm or tough than fish with large fibres. If such a concept is applied to the age/body weight effect, it could be proposed that the texture of large fish would be softer than that of small fish. The increasing amount of lipid and collagen more susceptible to gelification also participates in softening of the flesh of large fish. The activities of proteinases, especially acid proteinase, follow the decrease in overall metabolic activity of muscle with aging (Manikodan et al., 1984). The effect of proteinase on maturation processes would thus decrease with aging and this would counterbalance the effect of the other factors mentioned above on the texture of larger fish.

Table 7
Effect of temperature acclimation on metabolic activity in fast skeletal muscle of cyprinids

	Temperature of acclimation	
	Low (2–10°C)	High (20–30°C)
Oxidative capacity[a]		
Mitochondria (nb/mm^2)	0.54	0.29
Cytochrome oxidase (nmol/min/mg)	3.68	1.81
Glycolytic capacity[b]		
Glycogen content (mg/100 g)	4.4	1.1
Glycolytic enzymes[d] (measured in pair-fed fish)		
G6PDH, PGDH, PGI	2	1
GOT, G6Pase, FDPase		
Lipid metabolism[c]		
Fatty acid synthesis enzyme activities[d] (in slow muscle)	2–3	1
Fat retention (g/130 g fish) (in pair-fed fish)	16.2	2.5

[a]Johnston and Maitland (1980), Johnston (1982), Johnston et al. (1985).
[b,c]Johnston et al. (1977), Johnston et al. (1985), Shimeno and Shikata (1993).
[d]Enzyme activities are reported relative to high temperature data: basis 100.

If the effect of body weight on fish of the same age is analysed, then the role of other factors such as feeding rate, stress and exercise due to competition could be observed. Analyses of the development of tissues related to different growth rate for fish of the same age have shown both a development of adipose tissues and thus an increase in lipid content and an increase in muscle mass due mainly to hyperplasia. Thus, skeletal muscle of larger fish probably contains more small immature fibres of intermediate type such as those observed by Rowlerson et al. (1985) than smaller fish. Red muscle, which contains small oxidative fibres, is more firm than white muscle in tuna (Hatae et al., 1990a); thus the texture of the flesh, which is composed of more immature fibres in white muscle, would be firmer. We have also observed in rainbow trout that fish whose growth has been restrained show marked development of connective tissues (Fauconneau et al., 1992a) which would participate in the softening of cooked flesh for small fish supposed to be restrained (Fauconneau et al., 1992b).

In fact, in carp of the same age but of different body weight, the texture of raw and cooked flesh of large fish is more firm (maximum strength for compression, extrusion and sliding) than that of small fish of the same age (Fig. 7a,b). It should be also mentioned that an increase in intensity of colour and in water-holding capacity occurs. The hypothesis of differential feeding in fish of the same age is strengthened by the fact that there is a clear relationship between dry matter of flesh (inversely related to lipid content) and minimum pH of the flesh which is an indication of initial content of energy stores such as glycogen (Fig. 8).

Table 8
Effect of temperature acclimation on contractile properties in fast skeletal muscle of common carp (*Cyprinus carpio*)

	Temperature of acclimation	
	Low (8–10°C)	High (20–30°C)
Contractile enzyme activity[b]		
Mg^{2+}-ATPase (at 20°C)		
Myosin B ATPase activity	190	100
Myosine B K_D	190–210	100
Myosin ATPase activity	180	100
Myosin ATPase K_D	130–140	100
S1 ATPase activity	183	100
S1 fragment K_D	200	100
Mg^{2+}-ATPase Q_{10}	2.4	3.2
Force-velocity characteristics[c] (measured at 7–8°C)		
Isometric force ($kN \cdot m^{-2}$)	230	100
Maximum power output ($W \cdot kg^{-1}$)	280	100
Isometric contraction time ($t_{1/2}$ in ms at 8°C)		
Twitch activation	18	28
Twitch relaxation	23	42
Critical swimming speed Q_{10}	1.1	2.9

[a]Some parameters are reported relative to high temperature data: basis 100.
[b]Watabe et al. (1992), Guo and Watabe (1993), Shimeno and Shikata (1993).
[c]Johnston et al. (1985), Heap and Goldspink (1986), Crockford and Johnston (1990), Johnston et al. (1989), Rome et al. (1990).
Myosin B = actomyosin; K_D = inactivation rate constant after thermal treatment (30–40°C). Enzyme activities in μmol Pi/min/mg.

Effect of acclimation temperature

The fact that wild and reared cyprinids undergo marked changes in their thermal environment has stimulated basic research on the different mechanisms of adaptation implemented by fish. Some of these adaptations are related to the maintenance of contractile activity of muscle for swimming activity and thus could directly affect the quality of the flesh.

The consequences of thermal acclimation on different metabolic and contractile activities of muscle are summarized in Tables 7 and 8. The oxidative and metabolic capacity of muscle is greatly enhanced (more than twice higher) in cold-acclimated cyprinids. Thus, oxidative and metabolic activities – carbohydrate and lipid metabolism – measured at the temperature of acclimation are roughly maintained (Johnston and Maitland, 1980; Johnston et al., 1985). The stimulation of feeding with temperature of acclimation could compensate for differences in metabolic capacities (Shimeno and Shikata, 1993).

The activities of the enzymes responsible for muscle contraction are also enhanced (when measured at the same temperature for different acclimation temperatures) in cold-acclimated

Table 9
Effect of temperature acclimation on expression of myofibrillar protein isoforms in fast skeletal muscle of common carp (*Cyprinus carpio*)

	Temperature of acclimation	
	Low (8–10°C)	High (20–30°C)
Contractile protein		
Myosin heavy chain[a]	*Cold* isoform	*Warm* isoform
Myosin rod and S1[b]	*Cold* isoform	*Warm* isoform
mRNA MHC[c]		Specific *Warm* cDNA
Myosin light chain[d]	*2LC3$_f$* isoforms	*1 LC3$_f$* isoform
LC3$_f$/LC1$_f$[d]	2.3	2.9
Regulatory protein		
Troponin I[d]	*1 Tn I* isoform	*2 Tn I* isoforms

[a]Johnston et al. (1989), Watabe et al. (1992).
[b]Watabe et al. (1992).
[c]Gerlach et al. (1990).
[d]Crockford and Johnston (1990), Johnston et al. (1989).

carp (Guo and Watabe, 1993). It has been demonstrated that such compensation affects more specifically myosin Mg^{2+}-ATPase located in the head of myosin (Watabe et al., 1992). However, such compensation decreases the temperature dependency in the range of living temperature and decreases the thermal stability of this enzyme in the range of processing (Johnston et al., 1989; Watabe et al., 1992). As a consequence of both metabolic and contractile enzyme compensation, the force and speed of contraction are enhanced if measured at the same temperature or at least maintained if measured at the temperature of acclimation (Johnston et al., 1985, 1989; Crockford and Johnston., 1990; Langfeld et al., 1991). The thermal dependency of contraction, however, also decreases (Heap and Goldspink, 1986). The fibre type distribution is also modified by temperature acclimation (Sidell, 1980).

It has been demonstrated for many metabolic pathways that thermal compensation is the consequence of molecular compensations due to conformational changes in enzymes as well as to differential expression of isoenzymes (Hazel and Prosser, 1974). In the past few years, it has been demonstrated that the compensations for contractile activity are the consequences of the expression of different isoforms of the main structural protein (myosin and its subunits) (Crockford and Johnston, 1990; Gerlach et al., 1990; Watabe et al., 1992) (Table 9). This could be partly the case for other multigenic regulatory proteins of the thick filament such as troponins (Crockford and Johnston, 1990) and other sarcoplasmic proteins (Watabe et al., 1993).

It has been shown that contractile proteins are at the center of many changes during postmortem storage and during processing of flesh. The consequences of such metabolic compensation have just started to be analysed (Table 10). Cold thermal acclimation due to the lower thermal dependency of contractile enzymes demonstrated higher activities of these enzymes when stored at low temperature (Misima et al., 1990, 1991). As a result of thermal

Table 10
Effect of temperature acclimation on flesh quality in common carp (*Cyprinus carpio*) (for enzyme activities, see legend of Table 8)

	Temperature of acclimation		
	Low (10°C)		High (30°C)
Myofibrillar ATPase[a]			
Ca^{2+}/Mg^{2+}-ATPase K_m		<	
Ca^{2+}/Mg^{2+}-ATPase V_{max}		>	
Mg^{2+}-ATPase Q_{10}	1.8		2.2
Ca^{2+}-ATPase Q_{10}	1.8		1.4
Postmortem changes (at 32°C)[b]			
ATP/ADP/AMP decrease	$17\% \cdot h^{-1}$	>	$7\% \cdot h^{-1}$
IMP increase	$10\% \cdot h^{-1}$	>	$3\% \cdot h^{-1}$
Glycogen fall (mg/100 g)	400		200
Lactic acid increase (mg/100 g)	350		200
pH initial	7.2		6.8
Time to reach pH 6.0	6 h		12 h
Post-mortem changes[c] *at 20°C*			
Rigor mortis onset (h)	16		24
Maximum rigor tension (h)	32		32
ATP depletion (h)	32		32
at 0°C			
Rigor mortis onset (h)	8		2
Maximum rigor tension (h)	60		32
ATP depletion (h)	60		32

[a]Watabe et al. (1989), Misima et al. (1990).
[b]Tsuchimoto et al. (1988).
[c]Hwang et al. (1991).

compensation, an acceleration of all postmortem changes due to cold acclimation has been observed: consumption of phosphorylated compounds and glycogen, increase in lactate and IMP and speed to reach minimum pH (Tsuchimoto et al., 1988). However, such changes were only observed at high storage temperatures. If flesh is stored at low temperatures, then all processes are decreased. It seems that the intensity of the processes is not very much altered (Hwang et al., 1991). The consequences for the final quality of the flesh are not known, but the same effect of rapid postmortem changes due to stress on softening of flesh could be suspected in warm- as compared to low-temperature-acclimated carp when stored on ice at 0°C.

8. Conclusions

The growth of carp is associated with changes in morphometric traits and in chemical and biochemical composition. These changes are the result of differential development of

the main tissues which compose the fish: bone, muscle and adipose tissues. Analysis of the mechanism of development of these tissues will provide future tools for the control of body conformation parameters that are important for the suitability for processing of carp (gutting, filleting) and for the control of development of undesirable fat (visceral, abdominal) and favorable fat (flesh).

The flesh is also composed of different tissues: muscle tissues, adipose tissues and connective tissues, which exhibit different modifications during postmortem storage and processing. Analysis of these changes will permit optimal processing of carp flesh. Furthermore, the characteristics of these tissues are controlled by rearing conditions up to slaughtering of the fish. Analyses of the effects of all rearing factors on the characteristics of tissues and their postmortem evolution are not possible. But it seems that more attention will have to be paid to some factors important for controlling flesh quality, especially those controlling the size and type of muscle fibres, collagen content, glycogen content and postmortem pH.

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