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Characteristics and metabolism of different adipose tissues in fish

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Abstract

Lipids are the predominant source of energy for fish and are stored in fat depots in different parts of the body regions. This review focuses on visceral, subcutaneous and intramuscular adipose tissues that interfere with carcass and fillet yields and with flesh quality. The morphological, cellular and biochemical characteristics of these tissues are discussed as well as the different mechanisms involved in the regulation of their lipid metabolism. Particular emphasis is given to the modulation of these characteristics and mechanisms by different extrinsic (food composition, water parameters) and intrinsic (selective breeding, life cycle status) factors. This review focuses on recent studies that take into account the present challenges of fin-fish aquaculture, which are principally (i) the replacement of fish oil and meal by vegetable oil and meal due to the need for sustainability and the limited availability of fish to prepare food pellets, and (ii) selective breeding programs to improve fish growth and flesh quality. These studies apply various modern technologies to different fish species, including the development of cell culture systems and transcriptomic and proteomic techniques. This review highlights that fish adipose tissues differ in their localization and their morphological characteristics and that they show a large plasticity in their responses to variations of both extrinsic and intrinsic factors. These different responses reinforce the idea of their differential participation in fish lipid homeostasis.

Key words: Adipose tissue, regional localization, adiposity regulation, intrinsic and extrinsic factors, fish

Introduction

Adipose tissues present in different parts of fish play an important role in product quality. Subcutaneous and peri-visceral adipose tissues influence carcass and fillet yields, while muscle depots modulate flesh organoleptic quality. Compared to fisheries, one of the advantages of fin-fish aquaculture is the possibility to control product quality during the different phases of rearing. This control has been made possible by the development of artificial feeds and breeding programs, allowing for improvements to growth and phenotypic characteristics of interest for various aquacultured fish species.

The current need for sustainability and the limited availability of fish to prepare food pellets has given rise to attempts to replace fish meals in aquafeeds with plant products (Gatlin III et al., 2007). Selective breeding programs are now in progress in several aquaculture farms to obtain fish strains that grow well in particular environmental conditions when given standard traditional feed (fish meal) or new formulations (total or partial replacement of fish meals with vegetable meals).

The lipid dynamics in fish (absorption, transportation, deposition and mobilization) have been previously reviewed by Sheridan., 1988 and Sheridan, 1994. These reviews discuss the different sites of lipid accumulation (liver, brain, under the skin, in the abdominal cavity, and in red and white muscles). The major sites of deposition are perivisceral fat, muscle and liver and are species-dependent. Only one recent review (Leaver et al., 2008) focused on lipid metabolism in the liver and muscles in relation to the effect of the replacement of fish-based meals with vegetable-based meals.

None of these previous reviews focused on adipose tissues involved in fish quality. Here, we will describe the morphological and cellular characteristics as well as the lipid metabolism of these different tissues. Major emphasis will be given to the influence of intrinsic factors (genotype and sexual/endocrine/life cycle status) and extrinsic factors (environmental/rearing conditions, including traditional and novel dietary formulations) on tissue development, fat deposition and mobilization in different fish species. We will take into account the recent knowledge acquired on these particular topics. This knowledge has grown rapidly over the past 7-8 years thanks to the development of genomics and selective breeding for particular traits, combined with the increasing use of various methodologies such as cell culture systems and transcriptomic and proteomic techniques.

Morphological, cellular and biochemical characteristics of different adipose tissues involved in carcass quality

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Distribution of fat tissues involved in carcass quality

The fat depots that interfere with carcass quality can be roughly divided into discarded and consumed fat depots and are depicted in Figure 1 using a rainbow trout cutlet. Discarded fat depots include (1) the visceral fat (Vis), located in the abdominal cavity around the digestive tract and representing 2-25 % of the body weight (BW), depending on fish species and the status of the fish, and (2) the subcutaneous (SC) fat, which is located all around the body of the fish and is more prominent in particular dorsal or ventral zones in salmonid species. Dorsal subcutaneous fat is highly developed in a region situated between the head and the dorsal fin. Ventral subcutaneous fat is one of the components of the belly flaps localized in the abdomen of fish that represent the part of the flesh that hangs under the ribs. We have recently shown (Weil and Bugeon, unpublished results) that in a rainbow trout cutlet situated in front of the dorsal fin (Figure 1), the area of the subcutaneous dorsal tissue is 1.6 times lower than that of the fat tissue present in the belly flaps (4.4 % vs. 7% of the total area cutlet) in periovulated/postovulated females. Consumed fat depots are located in white and red muscles, with red muscles being richer in lipids than white muscles. As 90% of fish skeletal muscle is composed of white muscle (Johnston, 1981), we will focus mostly on white muscle in the present review.

Structural characteristics of the different adipose tissues

The structural characteristics of the different adipose tissues were studied using light and electron microscopy in various species (Ando et al., 1993; Shindo et al., 1986; Zhou et al., 1995, Nanton et al., 2007). Visceral fat depots consist almost entirely of adipocytes, which is not the case for the other sites. In muscle (both white and red), adipocytes are included in the myoseptum (Figure 1), a connective tissue that separates the muscle sheets or myomeres, allowing for a continuous muscle structure. Lipid storage in the myoseptum represents 40 % of white muscle lipid content in Atlantic salmon (Zhou et al., 1995, Nanton et al., 2007), with the remainder stored in muscle cells in intracellular lipid droplets, as demonstrated by electron microscopy in Atlantic salmon (Nanton et al., 2007). The belly flap tissue contains both muscle and adipocytes, with the latter being predominant in large salmonid species (Nanton et al., 2007). In the dorsal part of fish, there is a clear anatomical separation between subcutaneous adipose and muscle tissues.

Cellular characteristics of the different adipose tissues

The adipose tissue of fish is composed of adipocytes with a large variation of diameters (carp, Fauconneau et al., 1995; salmon, Zhou et al., 1996; trout, Fauconneau et al., 1997 and Albalat et al., 2005b). The presence of both small and large adipocytes indicates hyperplastic and hypertrophic development. The adipocyte size distribution may allow for a better understanding of the mechanisms involved in the development of fat tissues (hyperplasia/hypertrophy). Cell size measurements in various adipose tissues demonstrate different plasticities in response to rearing conditions such as nutrition and water temperature.

Biochemical characteristics of the different adipose tissues

Lipids present in fish flesh and non-consumed fat depots are neutral and polar lipids. The former are involved in energy storage while the latter (phospholipids) are considered structural lipids and are the main constituents of cell membranes. Neutral lipids consist of cholesterol, mainly triglycerides characterized by a high amount of n-3 long chain polyunsaturated fatty acids (omega 3). Polar lipids are characterized by a relative constant content and fatty acid composition. On the other hand, the lipid content and fatty acid composition of diets (fish or vegetable based diets) influence the global lipid content and the fatty acid composition of teleost fish (Henderson and Torcher, 1987; Torstensen et al., 2000, 2004, 2009; Nanton et al., 2007). An enrichment in dietary lipid content induces an increase in fish lipid content, preferentially occurring in the major site of deposition, which depends on the fish species: deposits mainly takes place in the muscle and visceral fat for seabream (Santinha et al., 1999), in the liver for turbot (Régost et al., 2001), and in the carcass, fillet and visceral fat in trout and Atlantic salmon (Sheridan, 1994; Jobling et al., 1998; Jobling and Johansen, 2003).

Only one study has examined the proteins that characterize non-consumed fat depots in relation to their location in rainbow trout (Weil et al., 2009). In mature adipocytes isolated from perivisceral and subcutaneous fat depots, no protein was evidenced to be specific to a particular adipose tissue. However, the higher expression of H-FABP in mature adipocytes originating from subcutaneous adipose tissue indicates a higher lipogenic activity of these adipocytes in females in the prepuberty period.

Regulation of the development of adipose tissues by extrinsic and intrinsic factors

For wild and farmed fish, the seasonal variation in lipid deposition in flesh and different fat depots provides global information on the metabolic (energetic) status of the fish. This status represents the effects of various extrinsic (temperature/salinity/quality of water, photoperiod and availability/quantity/composition/digestibility of nutriments) and intrinsic factors (genotype, hormonal factors involved in growth and reproduction strategies). Both environmental and intrinsic factors influence feeding behavior and food intake, which in turn affect the growth and adiposity of fish (Le Bail and Boeuf 1997; Volkoff and Peter 2006; Volkoff et al., 2010).

Modulation of adiposity by extrinsic factors

The quantitative and qualitative modifications of nutriments are known to modulate the global growth of different fish species as well as the global adiposity.

Starvation influences the mobilization of different fat tissues (Navarro and Gutiérrez, 1995) including those we are focusing on. Concerning those ones, the observed effects are probably due to the duration of application combined with the influence of rearing factors (water temperature, photoperiod) and intrinsic factors (life cycle status), that are specific to each studied species. For example, long term starvation (7-10 weeks) has been shown to decrease carcass and visceral lipids in white sturgeon (Hung et al, 1997), while in rainbow trout, lipids are preferentially mobilized from the viscera in comparison with muscle and liver (Jeziarska et al., 1982). On the other hand, a shorter period of starvation (2 weeks) induced a decrease in dress-out percentage with a visceral fat index remaining unchanged in the farmed Murray cod (Palmeri et al., 2008) while muscle and visceral fat deposits declined in juvenile sea-bass (Gutiérrez et al, 1991).

Dietary fat levels (high or low) have been shown to influence body growth as well as fat deposition in different fish species. In the context of aquaculture development, trials have been made to explore, in fresh water and marine fish, the influence of dietary fat levels on feed intake, growth and fat deposition. Concerning this last point, high lipid diets increase global fish adiposity linked to a decrease in water content without modifying protein content (Greene and Selivonchick, 1987). However all the compartments of the fish body are not influenced equally and the changes observed are depending on the major sites of lipid storage and on the life cycle status of the fish. Some data illustrating this assessment are reported, in the present review, for the fat depots we are focusing on. In rainbow trout, dietary fat levels have been shown to modulate fat deposition in viscera and carcasses, without a precise relationship due to the effects of muscle lipid content or subcutaneous fat (Jobling et al., 1998). However, a work conducted in Atlantic salmon fed high fat levels relates that, besides

higher total carcass lipid, larger belly flap and myoseptal deposits are observed (Bjerkeng et al., 1997). Concerning the effect of high lipid diet on visceral fat deposit development, it has been shown to be related to fish body size in rainbow trout: both hyperplasia and hypertrophy of adipocytes have been observed in small trout, while in larger trout, the response is due mostly to adipocyte hypertrophy (Gélineau et al 2001).

Concerning *fish meal replacement by plant meal*, it is difficult to give a shortcut of the trials made in the different species studied since the authors have tested various meal compositions. Globally, a genotype X plant based feed interaction was observed within strains of different fish species when fed with diets containing different amount of ingredients (protein included) derived from plants (rainbow trout: Smith et al., 1988, Palti et al., 2006, Pierce et al, 2008; European whitefish: Quinton et al., 2007). More precisely, at the muscle level, lipid content presented a genotype X plant-based diet interaction with a re-ranking of family performances with extremely contrasted diets in European sea bass (Le Boucher et al., 2011). In regards to the subcutaneous fat, partial replacement of fish oil (FO) by vegetable oil (VO) has been shown to have a differential effect on the hypertrophy of adipocytes originating from dorsal or ventral locations in a particular strain of rainbow trout (Fauconneau et al., 1997). Indeed, an increase in cell hypertrophy was observed only for subcutaneous adipocytes in the ventral position, with a positive interaction observed between lipid sources and thermal environment (8 or 18°C). These observations suggest a difference in metabolism depending on the location of subcutaneous adipose tissue. Visceral fat is also influenced by the replacement of FO by VO in different fish species, depending on the percentage of replacement (Atlantic salmon: Torstensen et al., 2011; juvenile gilthead sea bream: Cruz-Garcia et al., 2011; Bouraoui et al., 2011b). This replacement has been shown to promote, in gilthead sea bream, an increase in the adipocyte lipolytic activity (through an increase in hormone sensitive lipase -HSL- activity, see below) and in the proportion of large cells, which could be involved in their lower insulin sensitivity (Cruz-Garcia et al., 2011). These authors suggest that this higher lipolysis rate could produce an increase in lipid accumulation in the liver, as already proposed by Benedito-Palos et al 2008, in the same species.

Modulation of adiposity by intrinsic factors

Various intrinsic factors are known to modulate the adiposity of fish. However, because the observed effects result from *in vivo* studies, it is difficult to account for probable interactions with various other internal as well as external factors.

Fish age modulates total fat content, which increases with fish size in rainbow trout (Kiessling et al., 1991). However, it seems that there is a variable influence of fish size and life cycle status of fish on different fat tissues. White muscle adiposity increases with fish size in rainbow trout (Kiessling et al., 1991) as well as in post-smolt and in older/larger Atlantic salmon (Jobling et al., 2002, Jobling and Johansen 2003), showing that muscle is an important fat depot in salmonid species that is characterized by a non-uniform distribution of lipids through the fillet (Katikou et al., 2001). Visceral fat content exhibits the same pattern of evolution as white muscle with fish age, whereas dorsal adipose tissue reaches a constant level once trout have reached a certain age (Kiessling et al., 1991).

Reproductive cycle modulates the global growth of salmonids. Growth is accelerated at the beginning of gametogenesis and then slowed down in maturing and spawning fish (Hunt et al., 1982, Le Bail 1988). A more precise study performed in rainbow trout over various gonadal stages (determined histologically) has shown that the condition factor and dorsal muscular lipid content increased significantly at the beginning of oogenesis and spermatogenesis, were stable during full spermatogenesis and vitellogenesis and then decreased during the ovulation/spermiation periods (Weil et al., 2000). The positive and then negative influence of female sexual development on global lipid fillet content was also observed by Aussanasuwannakul et al., 2011, by comparing 2n (fertile) and 3n (infertile) fish. Fat muscular deposits in cyprinids were also shown to vary seasonally, with higher lipid content observed in tench in spring and summer as compared to autumn and winter, with these effects attributed to water temperature, feeding behavior, and seasonal changes in reproductive status (Guijarro et al., 2003, Breton et al., 1980a, 1980b). Concerning extra-muscular fat depots, a recent preliminary work conducted by our team in female rainbow trout during the periovulation/post-ovulation period showed a variation in the amount of fat depots depending on their regional localization, while the condition factor decreased during this reproductive period (Weil and Bugeon, unpublished results, Table 1). Decreases in the visceral fat index and in the area occupied by subcutaneous fat in the dorsal position were observed during the pre- and post-ovulation period, whereas the subcutaneous fat tissue in the ventral position and the whole belly flap remained unchanged, indicating a differential utilization of fat stores during the last phases of sexual maturation. The mobilization of visceral fat in relation with ovary maturation is in agreement with the observation of Aussanasuwannakul et al. 2011 that the visceral index in 2n rainbow trout decreased compared to 3n fish.

Selective breeding has been performed in rainbow trout, either on traits directly linked to adiposity (low and high muscle lipid content) or on other traits (resistance to acute stress). These two types of genetic selection

have been shown to affect fat deposition in adipose tissues even if adiposity was not targeted. Indeed, adiposity was shown to be influenced by a divergent selection in response to an acute confinement stressor, evaluated by plasma cortisol levels (Pottinger and Carrick, 1999). When fish were reared separately (Pottinger, 2006), after four generations of selection, low-responders (LR) were characterized by higher body weight, length, muscular and visceral adiposity when compared to high responsive (HR) fish, (Table 2, unpublished results from Lefèvre, Bugeon and Pottinger) indicating a possible change in lipid metabolism linked to stress responsiveness and cortisol environment. We can hypothesize that a higher degree of lipolysis occurs in HR fish as cortisol treatments have been shown to activate lipolysis in coho salmon parr at the level of visceral adipose tissue (Sheridan, 1986). Furthermore, even when selection is directed to a particular site of adiposity, fat tissues in other locations can be affected. Indeed, a two-way selection for muscle lipid content (high lipid content and low lipid content) produced two lines of rainbow trout named the fat line (FL) and the lean line (LL), respectively (Quillet et al., 2005). After two generations of selection, the visceral fat deposits of pan-size fish (250 g body weight - BW) fed on a standard diet tended to increase in LL fish, which was confirmed in older fish (2-3 kg BW) of the third generation of selection (Weil et al., 2008). For FL fish of the 2nd generation of selection, a globally higher retention of lipid content was observed in larger fish (320-700 g BW) (Quillet et al., 2007). These observations indicate that selection for muscle lipid content modifies the ability of the fish to utilize nutriment and store more or less fat in the different fat tissues. This was particularly observed for subcutaneous fat deposits located in the middle of the dorsal part of the cutlet (Quillet et al. 2007a, see location on Figure 1) in FL fish issued from the third generation of selection. Compared with LL fish, the thickness of this fat tissue increased by 50% in FL fish (Quillet et al., 2007b; Table 3), whereas only an 18% increase was observed for the adipocyte diameter (Bugeon et al., unpublished results; Table 3), indicating that both hypertrophy and hyperplasia might cause this difference. In the same study, an interaction with ploidy was observed in both lines as the mean diameter of the adipocytes was higher in triploid fish than in diploid fish. In older fish (2-3 kg) of the same generation of selection that were also fed a standard diet, the reproductive cycle influenced muscular and visceral fat tissues (Weil et al., 2008). An increase in lipid muscular content was observed at the beginning of active gametogenesis between April and June. However, this increase seems only partially linked to a positive influence of sexual maturation through steroid circulating levels, as in LL fish, a 58 % increase in muscle lipid content was observed in maturing males and females while a smaller increase (35%) was observed in non-maturing fish. Aside from hormonal factors, external factors such as an increase in temperature may be involved by acting on nutriment utilization and digestibility (Kaushik, 1986). On the other hand, visceral fat values were

not different between maturing and non-maturing fish in the two lines, indicating that visceral fat reserves are not linked to the decision of maturation of the gonads in ad libitum feeding conditions. During full gametogenesis and gonadal growth (June to November), the muscle lipid content decreased faster in FL (28%) compared to LL fish (7%). In contrast, the visceral fat decreased similarly in both lines (29% in FL fish vs. 21% in LL fish). During the end of spermatogenesis/vitellogenesis and during the spermiation/ovulation period, the muscle and viscera lipid stores are mobilized in the same way in the FL and LL lines.

Lipid metabolism in the different fat tissues and its control by extrinsic and intrinsic factors

In the different previous reviews (Sheridan 1988, 1994, Fauconneau et al, 1990, Leaver et al., 2008) describing the regulation of lipid storage and the mobilization and depletion of lipids in fish, the reported data were gathered mostly from in vivo observations and did not use molecular and genomic techniques, except in Leaver et al., 2008. This review provides an overview of the current understanding of the mechanisms involved in fat deposition and mobilization in relation to different external (quantity and composition of food) and internal (selective breeding, hormones, cytokines) factors.

Fat deposition (lipogenesis) and modulation by extrinsic/intrinsic factors

Fat deposition depends on the incorporation of exogenous fatty acids (FA) as well as de novo lipogenesis (Figure 2).

In the plasma, exogenous FAs are either non-esterified (bound to albumin) or most often incorporated as triacylglycerols (TAG) into circulating lipoproteins (principally the chylomicrons from nutrition origin) and the very low density lipoproteins (VLDL) secreted by the liver. The hydrolysis of these circulating TAGs (in FA and 2-monoacylglycerol) and the incorporation of FA are controlled by lipoprotein lipase- LPL- (Mead et al., 2002). LPL is considered a key enzyme in lipid deposition and metabolism and is one of the precocious markers of preadipocyte differentiation into mature adipocytes. LPL has been biochemically characterized in rainbow trout (Skinner and Youssef, 1982) and cloned in different species (rainbow trout: Lindberg and Olivecrona, 2002; red sea bream: Oku et al 2002; gilthead seabream: Saera-Vila et al., 2005). Its gene expression or activity has been observed in the liver, in visceral adipose tissue (red sea bream: Liang et al 2002 a, 2002b; seabream: Saera

Vila et al 2005; rainbow trout: Albalat et al., 2006) and in total muscle (seabream: Saera Vila et al. 2005; rainbow trout: Albalat et al., 2006), whereas no data are available for subcutaneous adipose tissues.

Concerning the transport of FA through the membrane (see Figure 2), different membrane-associated fatty acid transporters have been identified in mammals (Glatz et al., 2010). Fatty acid binding protein (FABPm) was the first to be identified; it is peripherally bound at the outer leaflet of the plasma membrane of various tissues including adipose tissue and muscle. Others transporters are integral membrane proteins including fatty acid translocase (FAT/CD36), which is ubiquitous and present in both adipose tissue and muscle, and the fatty acid transport protein (FATP), which has been renamed FATP1. Subsequently, FATP isoforms (FATP 2-6) were shown to be present in different tissues. FATP1 is present in both adipose tissue and muscle, while FATP4 and FATP6 are present in muscle but not adipose tissue. Caveolins are small integral membrane proteins responsible for the invagination of plasma membranes, and currently, three members of the caveolin family have been identified. Data are scarce in fish and are available only for FAT/CD36 and FATP for perivisceral adipose tissue, whole muscle and cultured myotubes.

LPL and FA transporter expression/activities are modulated by extrinsic and intrinsic factors. A *seasonal variation* of LPL expression has been observed in juvenile seabream visceral adipose tissue and whole muscle; an increase during spring was observed for the former, whereas for the latter, it was delayed and observed in summer, indicating a differential tissue metabolic activity (Saera-Vila et al. 2005). *Feeding status* (fed vs starved conditions) modulates LPL expression/activity with higher levels in fed fish compared to fasted ones in visceral fat (red sea bream: Liang et al., 2002a, 2002b; rainbow trout: Albalat et al., 2006; gilthead sea bream: Albalat et al., 2007), in parallel with FAT/CD36 expression (Atlantic salmon: Sánchez-Gurmaches et al, 2011; rainbow trout: Sánchez-Gurmaches et al, 2012). A differential metabolic activity in relation with the localization of adipose tissues is suggested since at the whole white muscle level, feeding status induced no clear variation in LPL activity in relation with time post-feeding in red or white muscles in rainbow trout (Albalat et al., 2006) and no effect in Atlantic salmon (Sánchez-Gurmaches et al, 2011). We have to stress that in these studies, the different components of the muscle tissue were not studied separately and that adipocytes are less numerous than muscular cells. *Replacement of FO by VO* has either no significant effect on fat visceral LPL activity (European sea bass: Richard et al., 2006b; gilthead sea-bream: Cruz-Garcia et al., 2011; rainbow trout: Richard et al., 2006a) or a slight negative one (gilthead sea-bream Bouraoui et al. 2011b). At the muscle level, this replacement appears also to be variable between the studies and species-dependent since no effect on LPL activity was observed in rainbow trout (Richard et al., 2006a) while it was decreased in European sea bass

(Richard et al., 2006b) and in gilthead sea-bream (Bouraoui et al., 2011b). With regard to FA transporters, total replacement of FO by VO, in Atlantic salmon, modulates differently their gene expressions in visceral adipose tissue: FAT/CD36 was up regulated whereas FATP was down regulated indicating different roles of FAT/CD36 and FATP in the fatty acid uptake (Torstensen et al., 2009). Furthermore, at the muscle level, the nature of oil affected the FA uptake in dependence on the different components of the muscle tissue. Indeed, at slaughter size (~4 kg BW), when it is possible to separate the muscle and myoseptum, the lipid content is higher in the white muscle myoseptum than in the muscle cells in fish fed with VO (Nanton et al., 2007). This observation is in line with the lack of variation of FATP and FAT/CD36 gene expression at the myoseptum level and the decrease in the muscle cells observed by Torstensen et al., 2009, using fish originating from the same dietary experiment as Nanton et al., 2007. *Hormonal factors* also modulate endogenous lipogenesis. LPL expression/activity is positively regulated during induced in vitro differentiation of preadipocytes into mature adipocytes using a medium supplemented with different factors (red seabream: Oku et al. 2006; Atlantic salmon: Todorčević et al., 2008, Todorčević et al., 2010) and this in relation with the increase in FATP1 gene expression in Atlantic salmon (Todorčević et al., 2008). Insulin is one of these positive factors and exhibits effects by itself (red sea bream: Oku et al., 2006; gilthead sea bream: Albalat et al., 2007; rainbow trout: Albalat et al., 2006, Bouraoui et al., 2011a), while triiodothyronin (T3), retinoic acid, retinyl acetate and metabolites of D vitamins had no effect by themselves (Oku et al., 2006). However, T3 enhanced LPL gene expression in the presence of insulin. This last observation is in line with the positive action of acute in vivo insulin treatment on LPL, FATP1 or CD36 gene expression in the visceral adipose tissue of Atlantic salmon (Sánchez-Gurmaches et al., 2011). In the same work, this in vivo insulin treatment did not have a significant effect on the overall white muscle gene expression of LPL, FATP1 or CD36. However, as in cultured myotubes, the same authors report that insulin induced an increase in FATP1 expression and a decrease in CD36 and LPL, suggesting that FATP1 could be more involved in the insulin FA uptake at the muscle level. *Selective breeding* on muscle lipid content also modulates the whole muscle FA uptake, as in FL small rainbow trout (~ 80 g), the expression of fatty acid translocase FAT/CD36 was higher when compared to LL fish (Kolditz et al., 2010). This work does not indicate the various contributions of muscle and adipose tissues to this increase; however, as the myosepta in fish of this size contain only a few adipocytes, this increase is probably due to muscle cells.

FAs that have been transported across the membrane are transferred through adipocyte cytosol by fatty acid binding proteins (FABPs), as indicated in Figure 2. In mammals, the genes of nine tissue-specific cytoplasmic transporters (FABP1-9) have been identified, including FABP4 and A-FABP in adipose tissue, and

FABP3 and H-FABP in heart and muscle (Chmurzynska 2006). Recently, in teleost fish, additional types have been characterized: FABP10 by Sharma et al., 2006, and FABP11 by Agulleiro et al., 2007. Using a proteomic approach, we have observed an influence of fat location on FABP3 expression in prepubescent rainbow trout, with higher levels in subcutaneous fat depots than in perivisceral depots (Weil et al., 2009). This indicates that at this stage of the sexual cycle, either subcutaneous fat tissues have a more active lipid metabolism or lipogenic activity is not synchronous between visceral and subcutaneous fat depots. Other data also suggest an influence of *intrinsic factors* on FABP gene expression. FABP3 (Todorčević et al., 2008) and FABP11 (Huang et al., 2010) expression increase during *in vitro* differentiation of visceral preadipocytes into mature adipocytes in Atlantic salmon using a differentiation medium supplemented with lipids and a cocktail of hormonal factors. Extrinsic factors such as *food composition* also modulate FABP gene expression. At the visceral adipose tissue level, FABP11 expression is down regulated in long-term 100 % VO-fed Atlantic salmon compared to 100% FO-fed fish (Torstensen et al., 2009). At the white muscle level (muscle +myoseptum), FABP3 and FABP10 gene expression are not influenced by the composition of food (75% VO or 100% FO) in Atlantic salmon, while the FABP3 protein reflects the dietary inclusion of VO levels because the protein expression is higher in fish fed 100% VO than in those fed 25% VO (Jordal et al., 2006). This seems to indicate the importance of studying the protein levels of such transporters to improve knowledge of the roles of different factors involved in lipogenesis.

In mammals, transported fatty acids activate genes involved in the regulation of adipogenesis through a complex network of transcription factors and cell-cycle regulators (Ntambi and Kim 2000, Farmer 2006, Lefterova and Lazar 2009, Christodoulides and Vidal-Puig, 2010, Cristancho and Lazar, 2011). Peroxisome proliferator-activated receptor gamma (PPAR γ) and CCAAT/enhancer binding proteins (C/EBPs α , β , and δ) have emerged as master regulators of adipogenesis. C/EBPs (α and β) and PPAR γ have recently been shown to cooperatively orchestrate adipocyte biology by adjacent binding, although the molecular details of this cooperation remain to be elucidated (Lefterova et al., 2011). Data on the regulation of these proteins and their roles during adipogenesis are scarce, although different isoforms have been cloned in different fish species, particularly for PPAR. Knowledge on PPARs in fish in comparison with mammals was reviewed by Leaver et al., 2008. The authors focused on the different isoforms of PPAR (α , β and γ) and their regulation by nutritional factors, principally considering the hepatic expression levels. The C/EBP gene family has received less study in fish, although different isoforms of C/EBP have been identified in different tissues, and those known to participate in adipogenesis (C/EBPs α , β and δ) have been cloned in Atlantic salmon (Huang et al., 2010). The major form expressed in visceral adipose tissue is PPAR γ (sea bass: Boukouvala et al., 2004; plaice and sea

bream: Leaver et al., 2005). Atlantic salmon and rainbow trout visceral preadipocytes that were differentiated in vitro into mature adipocytes by different factors expressed PPAR γ and C/EBP α proteins (Vegusdal et al., 2003, Bouraoui et al., 2008, respectively), while gene expression increased only for C/EBP α (Todorčević et al., 2010). In red sea bream, the 3 subtypes of PPAR genes were differentially expressed during induced in vitro differentiation of adipose precursors into mature adipocytes (Oku and Umino, 2008), but their exact role in this process is not yet well determined. Their gene expression is not influenced by *short fasting* or *post-feeding timing* in perivisceral adipose tissue of plaice and gilthead sea bream, whereas it is in the liver (Leaver et al., 2005). On the other hand, PPAR γ mRNA levels are higher in fat gilthead seabream than in lean gilthead seabream, and the mRNA LPL/HSL ratio is also higher (Cruz-Garcia et al., 2009), indicating PPAR γ involvement in visceral fat accumulation. In white muscle, the 3 forms of PPAR are equally present in plaice and seabream (Leaver et al., 2005), while in brown trout only PPAR α and β are detected (Batista-Pinto et al., 2005). In rainbow trout issued from the third *generation of selection for fat muscle content and fed with low-energy or high-energy diets* (10 and 23 %, respectively), the muscle PPAR α mRNA content was not different between FL and LL fish and was not affected by feed lipid content, whereas liver PPAR α expression was higher in FL fish, independently of the energy of the diets (Kolditz et al. 2008). This observation indicates a tissue-specific activation of PPAR genes by FA.

De novo lipogenesis (Figure 2) is the metabolic pathway that synthesizes fatty acids from excess carbohydrates for incorporation in TAG for energy storage. In mammals, white adipose tissue is the main lipid storage tissue (Hillgartner et al., 1995, Strable et Nambi 2010) while the liver is considered the main tissue responsible for lipogenesis in fish (Lin et al., 1977). As a consequence, little information is available in the literature on this pathway in the depots related to fish carcass quality. In mammalian species, the movement, across the plasma membranes, of glucose as a lipogenic substrate, depends on glucose transporters (GLUTs). Several GLUT isoforms have been identified (Scheepers et al., 2004), and GLUT4 is the main glucose transporter expressed, predominantly in insulin-responsive tissues such as the heart, skeletal muscle and adipose tissue (Ishiki and Klip, 2005). Several members of the GLUT family have been cloned and characterized in different fish species: GLUT1 (rainbow trout: Teerijoki et al. 2000; common carp: Teerijoki et al. 2001; Atlantic cod: Hall et al., 2004); GLUT2 (rainbow trout: Krasnov et al., 2001; Atlantic cod: Hall et al., 2006); GLUT3 (Atlantic cod: Hall et al., 2005); and GLUT4 (brown trout: Planas et al., 2000; salmon: Capilla et al., 2004; Atlantic cod: Hall et al., 2006). Here, we focus on GLUT4 because it is the only form studied in recent in vivo and in vitro studies, aiming to investigate its role in glucose transport, its mechanisms of action and its regulation

by *hormonal and nutritional factors*, in muscle and visceral adipose tissue. In both tissues, the presence of GLUT4 protein or mRNA has been reported (rainbow trout visceral adipose tissue: Capilla et al., 2004; brown trout muscle: Díaz et al., 2007). The regulation of GLUT4 expression by insulin and insulin like growth factor I (IGF-I) or by low-protein high carbohydrate diet or fasting, which modify insulin plasma levels (muscle: Capilla et al., 2002, Díaz et al., 2007) as well as the signaling pathway by which insulin and IGF-I act on the transport of glucose (visceral adipose tissue: Bouraoui et al., 2010) have given rise to some recent studies. These studies showed the existence of glucose transport at the visceral adipocyte level and led the authors to suggest that, at the muscle level, the physiological regulation of GLUT4 takes place predominantly in red muscle.

Fatty acid synthase (FAS) is a key enzyme involved in *de novo* lipogenesis that catalyzes the synthesis of long chain fatty acids, mainly by catalyzing acetyl coenzyme A and malonyl coenzyme A (Smith et al, 2003). FAS gene cloning is limited in fish, with the result that data on its gene expression are scarce. FAS activity and modulation by *the substitution of FO for VO* in fish diets has principally been studied at the liver level (Leaver et al., 2008). A recent work reports a negative effect of increasing *dietary fat* on FAS activity and gene expression in the grass carp (Leng et al., 2012). FAS expression in visceral adipose tissue has been shown to increase during *in vitro* induced differentiation of precursors into adipocytes using a medium supplemented with a hormonal/lipid mixture in Atlantic salmon (Todorčević et al., 2010). This indicates the potential action of *internal factors* (hormones, cytokines) on FAS activity without directly demonstrating what factors are implicated. However, a recent *in vivo* work conducted in rainbow trout fed a high carbohydrate diet, indicates that insulin might be one of these factors: its infusion induces an increase in FAS mRNA expression (Polakof et al., 2011).

Fat degradation and modulation by extrinsic/intrinsic factors

Fat breakdown is an essential process for the regulation of energy homeostasis. The breakdown process includes fatty acid degradation and lipolysis (Figure 2).

β -oxidation, the principal pathway of FA degradation, takes place in the mitochondria and peroxisomes. Long chain FAs are transported through a transfer system composed of proteins and carnitine palmitoyltransferase 1 (CPT1) and carnitine palmitoyltransferase 2 (CPT2) are considered as key enzymes. The activity of this pathway has been reported in different tissues of Atlantic salmon, including liver, red muscle and white muscle. β -oxidation dominates in red muscle, but white muscle makes a significant contribution to the

overall fatty acid oxidation capacity in fish (Frøyland et al., 1998). Adipose tissue was not examined in this study, but recent data indicate that CPT2 gene expression is low in visceral fat depots compared to whole white muscle (Torstensen et al 2009). CPT2 gene expression is not affected by the *nutritional status* of fish (fed/fasted) in visceral adipose tissue or in the whole muscle (Atlantic salmon, Sánchez-Gumarches et al., 2011). On the other hand, *food composition* influences white muscle β -oxidation activity, which increases with the percentage of fish oil replaced with vegetable oil in Atlantic salmon (Stubhaug et al., 2005). When muscle fibers and myosepta are studied separately, *FO replacement by VO* induces a decrease in CPT2 expression in the fibers, while no significant difference was observed for myosepta (Torstensen et al 2009), indicating a difference of β -oxidation capacity among the different components of the whole muscle. Food composition is not the only extrinsic factor acting on white muscle β -oxidation activity; it is affected by *temperature* in different fish species (Guderley, 2004) and by *season* in Atlantic salmon (Nodgarden et al., 2003, Stubhaug et al., 2005). β -oxidation capacity is also influenced by intrinsic factors. *Selective breeding* of rainbow trout for muscle lipid content induces an increase in CPT1 gene expression of one isoform in the white muscle of FL fish compared to LL fish (Kolditz et al., 2008). Concerning *hormonal regulation* of genes involved in β -oxidation, long term in vivo insulin treatment has a suppressive effect on the expression of these genes in the visceral adipose tissue (Polakof et al., 2011) and muscle (Polakof et al., 2010) of rainbow trout. Thanks to the use of rainbow trout myocyte cultures, a direct negative effect of insulin and IGF-1 on oleic acid metabolism was shown (Sánchez-Gumarches et al. 2010). All these in vivo and in vitro observations are in accordance with the antilipolytic role of insulin in fish.

FAs stored in the form of triglycerides (TAGs) are the main source of energy in the absence of a dietary substrate. The hydrolysis of TAGs occurs through three consecutive steps and is principally catalyzed by HSL and monoglyceride lipase (MGL). HSL is involved in the first two steps (breakdown of triacylglycerol – TAG – into diacylglycerol – DAG – and then into monoacylglycerol – MAG) and is considered as the rate limiting enzyme; the participation of MGL occurs at the last step, and one molecule of TAG leads to the production of three FA molecules and one molecule of glycerol (Holm et al 2000, 2003, Lampidonis et al., 2011). HSL was characterized in rainbow trout (Harmon et al., 1991, Michelsen et al., 1994) and in dusky rockcod (Hazel and Sidell, 2004). Recently, two distinct cDNAs encoding HSL were cloned in rainbow trout and named HSL1 and HSL2 (Kittilson and al., 2011). HSL1 and HSL2 mRNAs were detected in various organs and tissues (brain, spleen, pancreas, kidney, gill, intestine, heart, white and red muscles, visceral adipose tissue and liver). Among tissues interfering with carcass quality, HSL1 is expressed at higher levels in visceral fat and white muscle than

HSL2. Different factors have been shown to affect HSL activity (measured by glycerol content) and its gene expression. *Fasting* increases the lipolysis activity of visceral mature adipocytes collected from gilthead seabream starved for 11 days (Albalat et al., 2005a). In rainbow trout, the expression of both HSL1 and HSL2 is increased by a 4-week fasting period, with a larger effect observed for HSL1 mRNA. Both forms decline to the levels in fed fish during a prolonged fast (6 weeks), coincident with visceral fat depletion; on the other hand, liver HSL1 and HSL2 are still higher than in fed fish, indicating that different mechanisms and tissues are involved in regulating rainbow trout energy (Kittilson et al., 2011). HSL activity is also modified by the *diet composition* because basal lipolysis is increased in visceral mature adipocytes collected from gilthead seabream fed with plant diets enriched (Cruz-Garcia et al., 2011) or not (Albalat et al., 2005a) with VO. *Hormones and cytokines* modulate HSL activity, with data principally coming from studies conducted on visceral adipose tissue. One such factor is glucagon, which was shown to have a direct positive action in organotypic culture (rainbow trout: Harmon and Sheridan, 1992) or isolated mature adipocytes (gilthead sea bream: Albalat et al., 2005a; rainbow trout: Albalat et al., 2005b). GH was also shown to have a direct positive action on lipolysis at the adipocyte level in gilthead seabream (Albalat et al., 2005a). The cytokine tumor necrosis factor α (TNF α), recognized to be a modulator of glucose and lipid metabolism in mammals (Sethi and Hotamisligil, 1999), also increases lipolysis in rainbow trout isolated visceral adipocytes (Albalat et al., 2000c). On the other hand, insulin and norepinephrine down regulate lipolysis in isolated adipocytes in rainbow trout (Albalat et al., 2005b) and tilapia (Vianen et al., 2002), respectively. This last observation is in line with results obtained in visceral fat after *in vivo* administration of norepinephrine in different fish species (African cat fish: van Heeswijk et al., 2005; rainbow trout: Magnoni et al., 2008). So far, the regulation of lipolysis has not been studied in fish at the levels of subcutaneous fat and white muscle.

Conclusion

The use of novel techniques (adipose cell cultures, proteomic and transcriptomic studies), the availability of fish lines and the research of new formulations of food have led to an increase in knowledge of the mechanisms involved in lipid metabolism in fish tissues involved in carcass and flesh quality. The present review demonstrates the heterogeneity of fish fat depots in terms of morphology, biochemistry and metabolism. The review highlights the fact that the subcutaneous fat depot in fish has received less study than visceral depots. However, the studies conducted on both depots seem to indicate that in addition to their structural differences, they exhibit different plasticities in response to variations of extrinsic and intrinsic factors. Furthermore, the few

studies conducted on subcutaneous fat of different locations suggest that the subcutaneous fat depot is not a unique entity in terms of its structure and the regulation of its activity by internal and external factors. As a consequence, further work is necessary to understand the involvement of the different fat depots (muscle/myoseptum, visceral and subcutaneous fat in dorsal and ventral positions/belly flap) as well as their interactions in storing and restoring energy, in relation to life cycle and rearing conditions. This knowledge will help to control the carcass yield and flesh quality of farmed fish species.

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Table 1: Evolution of indicators of adipose tissue (AT) development in different body locations of rainbow trout during the pre-/post-ovulation period.

Visceral adipose tissue is estimated by the VSI % (viscera weight/carcass weight X 100). Subcutaneous adipose tissues in the dorsal and ventral positions and adipose tissue in the belly flaps are estimated by image analysis and expressed by their area/the total cutlet area. In each column, different superscripts indicate significant differences between sexual stages ($p < 0.001$). Values are reported as the mean \pm SD.

VSI: viscero-somatic index; SCD AT: subcutaneous adipose tissue in the dorsal position; SCVe AT: subcutaneous adipose tissue in the ventral position, BF AT: belly flap adipose tissue.

Sexual stages	VSI (%)	% SCD AT	% SCVe AT	% BF AT
Pre-ovulation (n=10)	4.62 \pm 1.27 ^a	4.88 \pm 0.81 ^a	4.31 \pm 0.93 ^a	7.58 \pm 1.60 ^a
Post-ovulation (n=9)	3.22 \pm 1.26 ^b	4.27 \pm 0.87 ^b	4.41 \pm 0.87 ^a	7.89 \pm 1.34 ^a

Table 2: Effects of four generations of divergent selection for acute stress response on rainbow trout adiposity.

The divergent selection was based on cortisol responsiveness to a confinement stressor. Two lines of fish were raised: High-Responders (HR) and Low-Responders (LR).

Adiposity was assessed (1) in muscle by fat meter measurement and dry matter content (2) in visceral fat tissue by the viscerosomatic index VSI% (viscera weight/body weight X 100).

Values are reported as the mean \pm SD, HR n=16, LR n=20. In each column, bold values indicate significant differences between the two lines ($p < 0.001$).

Line	Body weight (g)	Standard length (mm)	VSI %	Muscle fat meter value (%)	Muscle dry matter content %
HR	242 \pm 47	242 \pm 13	7.4 \pm 1.0	2.2 \pm 0.7	22.4 \pm 0.5
LR	271 \pm 45	256 \pm 16	9.1 \pm 1.4	3.3 \pm 0.8	23.7 \pm 1.1

Table 3: Effects of divergent selection for muscle lipid content on female and male rainbow trout subcutaneous adipose tissue characteristics in the 3rd generation of selection.

Two lines of fish were raised: fat line (FL) and lean line (LL). Subcutaneous (SC) adiposity was assessed on histological slides by fat tissue thickness (mm) as well as adipocyte diameter (μm) in triploid (sterile fish) and diploid (fertile fish).

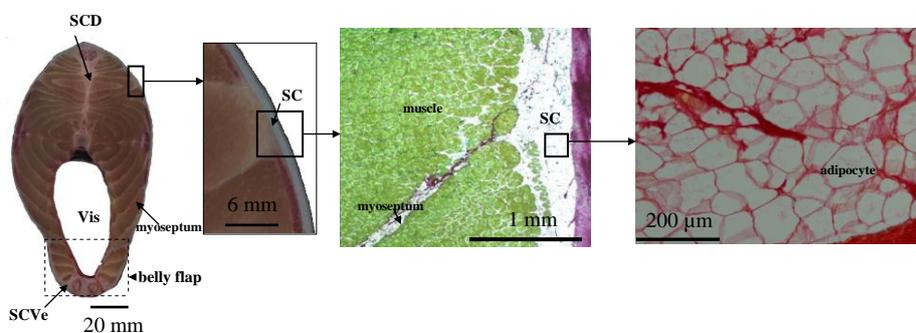
Values are reported as the mean \pm SD. For FL and LL, n=15. In each column, bold values indicate significant differences between lines ($p < 0.001$); different superscripts indicate significant differences according to ploidy ($p < 0.001$).

Line	Ploidy	Body Weight (g)	SC fat tissue thickness (mm)	SC adipocyte diameter (μm)
FL	2n	295 \pm 44	0.53 \pm 0.16	33.3 \pm 3.4^a
	3n	256 \pm 54	0.58 \pm 0.15	38.4 \pm 3.2^b
LL	2n	294 \pm 33	0.29 \pm 0.1	29.8 \pm 3.1 ^c
	3n	291 \pm 52	0.27 \pm 0.09	31.3 \pm 3.3 ^d

Figure 1: Representation of a rainbow trout cutlet (situated in front of the dorsal fin) and adipose tissues involved in carcass quality.

Paraffin sections (10 μm) of tissue containing muscle, subcutaneous adipose tissue and skin were stained with Rojkind's dye (Sirius Red and Fast Green 0.1% in saturated picric acid). The muscle fibers are stained in green and the connective tissue in red.

Vis: location of the visceral adipose tissue; SCD, SCVe: subcutaneous adipose tissues in the dorsal and ventral positions, respectively. SC: subcutaneous adipose tissue



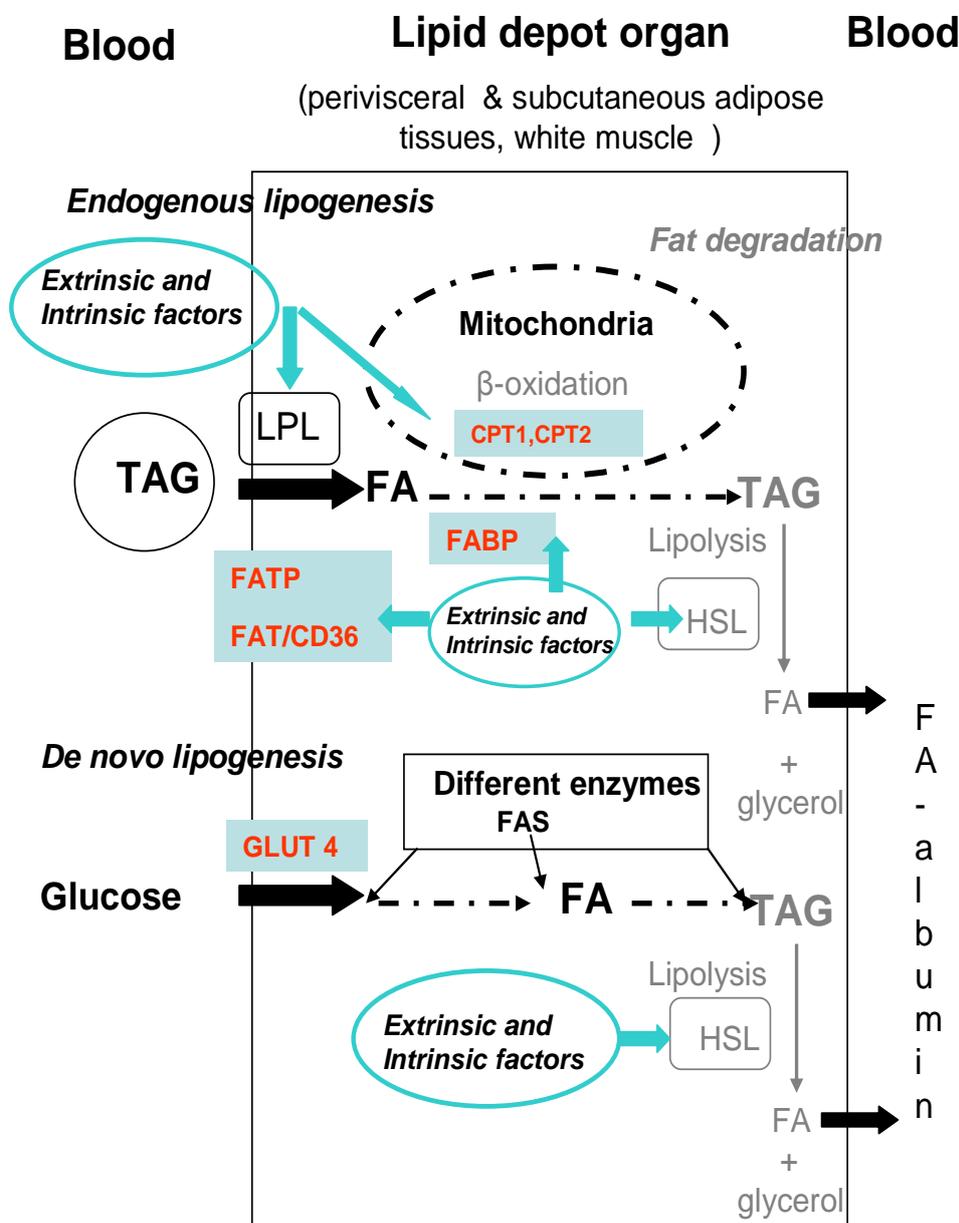
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Figure 2: Schematic representation of lipid metabolism in adipose tissues from different regions and its regulation by extrinsic and intrinsic factors.

See the text for more details on the mechanisms involved and the adipose tissues targeted.

Endogenous and *de novo* lipogenesis pathways are depicted in black; lipid degradation (β -oxidation and lipolysis) pathways in grey. TAG: triacylglycerol; FA: fatty acid; LPL: lipoprotein lipase; HSL: Hormone-sensitive lipase; FAS: fatty acid synthase; FATP, FAT/CD36: fatty acid transporters; FABP: fatty acid binding protein. GLUT4: glucose transporter, CPT1, CPT2: transport system involved in β -oxidation.



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