



Starvation in Fish: Sturgeon and Rainbow Trout as Examples

108

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Contents

Introduction	2104
Metabolic Modification During Starvation	2106
Liver Metabolism During Starvation	2106
Muscle Metabolism During Starvation	2109
Starvation and Antioxidant Defenses	2110
Oxidative Stress in Red Blood Cells and Liver During Starvation	2110
Oxidative Stress in Heart During Starvation	2111
Oxidative Stress in White Muscle During Starvation	2111
Starvation and Digestive Physiology	2112
Policies and Protocols	2113
Dictionary of Terms	2114
Summary Points	2114
References	2115

Abstract

All animals need the input of energy from the environment to stay alive. As a survival mechanism they have developed adaptive processes that allow them to continue living for a certain time when energy input does not occur. Periods of food deprivation are frequent in many species of fish in their natural environment. Climate changes, seasonal variations, competition for food, breeding migrations are common processes that involve starvation in fish. During starvation, adaptive physiological processes affect organs such as liver, brain, skeletal muscle, and digestive and produce changes in the intermediary metabolism of carbohydrates, lipids, and proteins to maintain the homeostasis. This book chapter focuses on

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metabolic changes, alterations in the oxidative state, and changes in digestive enzymatic activities in response to starvation in fish with the main focus on the trout *Oncorhynchus mykiss* and the sturgeon *Acipenser naccarii*.

Keywords

Fish · Sturgeon · Trout · Metabolism · Oxidative stress · Digestive · Starvation · Enzymes · Liver · Muscle

List of Abbreviations

ACoAT	Acetoacetyl CoA thiolase
CAT	Catalase
GDH	Glutamate dehydrogenase
GK	Glycerol kinase
GOT	Aspartate aminotransferase
GPT	Alanine aminotransferase
GPX	Glutathione peroxidase
GR	Glutathione reductase
HK	Hexokinase
HOAD	β -hydroxyacyl CoA dehydrogenase
LDH	Lactate dehydrogenase
PK	Piruvate kinase
ROS	Reactive oxygen species
SOD	Superoxide dismutase
β -OHBDH	β -hydroxybutyrate dehydrogenase

Introduction

All animals need the input of energy from the environment to stay alive. As a survival mechanism they have developed adaptive processes that allow them to continue living for a certain time when energy input does not occur. It is appropriate to name these periods of external limitation of food resources as starvation and not as fasting (McCue 2010).

Periods of food deprivation are frequent in many species of fish in their natural environment. Climate changes, seasonal variations, competition for food, breeding migrations are common processes that involve starvation in fish. To survive these periods with lack of food intake, fish have developed a series of adaptive physiological processes. These processes allow fish to endure starvation periods of several months and are closely related to biotic and abiotic factors. Thus, carnivorous species are better adapted to face periods of food restriction than herbivores and detritivores species which tend to eat continuously. Furthermore, the consequences of starvation are more pronounced in larvae and juvenile stages than in adult fish, probably due to a higher amount of energy reserves in the latter (Gadomski and Petersen 1988). Environmental variations such as temperature may also have an impact on these adaptive mechanisms.

During starvation, adaptive physiological processes affect organs such as liver, brain, skeletal muscle, and digestive and produce changes in the intermediary metabolism of carbohydrates, lipids, and proteins to maintain the homeostasis (McCue 2010; Rossi et al. 2015; Barreto-Curiel et al. 2017).

Short-term starvation promotes rapid mobilization of available reserves. In the first week of starvation, the glycogenolytic pathway increase in liver. Gluconeogenic processes, from the seventh day and onwards, tends to increase glycemia. At the same time, an increase in the ketogenic capacity of the liver occurs in order to produce alternative energetic substrates for its potential use in organs such as the brain. Glycogen depletion is followed by lipid and protein catabolism, as well as a loss of body weight. In addition, many anabolic pathways are diminished, such as the synthesis of glycogen, protein, lipids, and nucleic acid precursors (Rossi et al. 2015).

In the fish brain, after 1 week of starvation, there is a depression of the glycolytic pathway and a greater use of ketone bodies as energetic substrates (Vigliano et al. 2002; Polakof et al. 2012). In addition, it is necessary to emphasize the gluconeogenic capacity of the brain in fish, since in other animals this occurs only in the liver and renal cortex (Lehninger et al. 1993; Polakof et al. 2012).

Muscle metabolism is characterized by a rapid consumption of glycogen, lipid, and protein reserves during starvation (Machado et al. 1988). Lack of food results in a decrease in the synthesis and secretion of enzymes in the digestive system (Gannam 2008; Shan et al. 2016). Recent studies have shown an alteration of the intestinal microbiota with an increase of bacteroidetes and a depletion of betaproteobacteria (Hong and Rhee 2014).

Finally, other notable change in response to fasting in fish is the alteration in oxidative state (Rossi et al. 2015).

All functional changes during fish starvation are controlled by the neuroendocrine system. Neuroactive and hormonal substances (cholecystokinin, neuropeptide Y, galanin and orexin, leptin insulin, glucagon, somatostatin, growth hormone, thyroid hormones, catecholamines, cortisol, corticosterone, and cortisone) have been shown to have important regulatory functions in physiological processes during starvation in fish (Bar 2014; Bond 1996).

This book chapter focuses on metabolic changes, alterations in the oxidative state, and changes in digestive enzymatic activities in response to starvation in fish with the main focus on the trout *Oncorhynchus mykiss* and the sturgeon *Acipenser naccarii*.

Trout is an actinoptergian fish belonging to the Salmonidae family. This family includes 3 subfamilies, 11 genera, and 176 species (Nelson et al. 2004). It is original of the rivers of the west of North America, although introduced in rivers almost all over the world. It lives in clear and relatively cold waters and has a longevity from 4 to 6 years. Sexual maturity is reached when they exceed 10 cm in length, in the second or third year of life. Predatory feeding is mainly composed of zooplankton, aquatic macroinvertebrates, and small fish. The size generally does not exceed 40–50 cm in length and 5 kg in weight.

Sturgeons are bony fishes, actinoptergios of the family Acipenseridos that includes two subfamilies. The genus *Acipenser* includes 21 species. Sturgeons have been revealed as fish with remarkable peculiarities in many aspects of their biology, in

particular in their physiology and metabolism, with respect to other fish groups. To a large extent, these peculiarities have been attributed to their remarkable phylogenetic antiquity (they are called authentic “living fossils”) estimated to having existed for 250 million years. Its habitat is associated with the great fluvial systems of the northern hemisphere, being abundant in the Black Sea, Caspian, and in seas and rivers of North America and Europe. *Acipenser naccarii* is a migrating species that reproduces in fresh water, using the sea for its growth. Sexual maturity reaches the age of 6–8 years. The adult specimens reach a weight greater than 100 kg and up to more than 2 m in length, being the larger females, although there is no evident sexual dimorphism (Domezain Fau 2003). It mainly feeds on benthic invertebrates, although they also consume remains of animals, plants, and seeds (Soriguer et al. 1999). This would explain that nutritional studies in this species have revealed a greater predisposition of the digestive and metabolic machinery for the use of carbohydrates than exists in a strictly carnivorous fish such as rainbow trout (*Onchorynchus mykiss*) (Furne et al. 2008). Likewise, Sanz et al. (1997) have found a better use of feed in this sturgeon species in which the protein/energy ratio is lower than that of a strict carnivore.

Metabolic Modification During Starvation

To maintain the vital processes and survival during periods of starvation, fish reduce their energy expenditures, which in a high percentage are derived from protein synthesis and mobilize their endogenous reserves to obtain the energy.

The utilization of energy reserves during starvation periods appears to differ according to the species of fish. Moreover, intraspecific adjustments to these conditions will depend on different factors, such as age or nutritional state (Navarro and Gutiérrez 1995). The metabolic responses of fish to starvation are also influenced by the feeding habits of the species.

Liver Metabolism During Starvation

Most studies report that glycemia never falls below the basal levels established for most fish species (65–70 mg 100 ml⁻¹) (Echevarría et al. 1997; Rios et al. 2006; Pérez-Jiménez et al. 2007). Plasma glucose levels in sturgeon notably decreased after 2 days of starvation, while in the trout plasmatic glucose showed a more gradual response over time (Furne et al. 2012) (Fig. 1). Plasma glucose levels decline in starved fish (Gillis and Ballantyne 1996; Soengas et al. 1996; Figueiredo-Garutti et al. 2002; Pérez-Jiménez et al. 2007, 2008; Rossi et al. 2015).

The maintenance of plasma glucose levels during food deprivation is attributed to three processes: glycogen mobilization, decreased glucose consumption, and gluconeogenesis.

In both sturgeon and trout, a mobilization of liver glycogen has been observed during the first few days of starvation. Although hepatic glycogen is consumed to cover energy demands in both species, this response has been reported to occur earlier in sturgeon. A

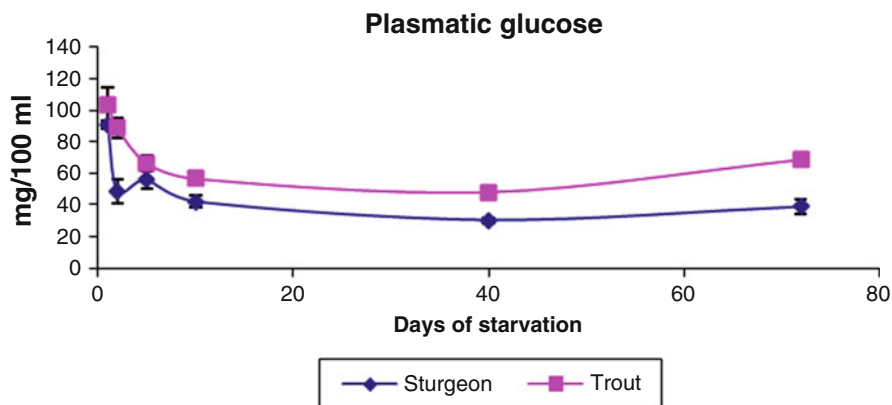


Fig. 1 Plasmatic glucose levels during starvation in sturgeon and trout. Values are mean \pm SEM ($n = 5$; number of fish sampled per sampled points) (Data are taken from Furne et al. 2012)

large reduction of liver glycogen has been reported in many starved fish species, at least during the initial stages of starvation (Navarro and Gutiérrez 1995; Metón et al. 2003; Rios et al. 2006; Pérez-Jiménez et al. 2007; Menezes et al. 2015), but in most fish species, glycogen deposits were not completely exhausted, suggesting that a strategy is operating to preserve liver reserves (Collins and Anderson 1997; Rios et al. 2006; Pérez-Jiménez et al. 2007; Pérez-Jiménez 2008).

The reduced activity of hepatic enzymes from the glycolytic and the pentose phosphate pathways, and enhanced or sustained hepatic gluconeogenesis from amino acids and glycerol, are other strategies operating in fish to maintain glycemia during starvation (Polakof et al. 2012).

The decrease of blood glucose in sturgeon in the first few days of food deprivation is accomplished by a peak in the activities of the glycolytic enzymes such as HK and PK (Figs. 2 and 3). Although glycogenolysis occurs in the sturgeon, glucose demands and a minor content of hepatic glycogen would explain the decrease of glycemia. On the other hand, in the trout, a higher gluconeogenic activity in the liver from noncarbohydrate substrates such as amino acids and lactate was found (increased of GPT and LDH activities). Induction of gluconeogenic processes and a decrease of glycolytic enzymes activity (HK and PK) in the trout liver during the starvation would explain the more gradual decline of glycemia in this specie (Furne et al. 2012).

Triglycerides are the main form of energy storage in fish. During starvation, fatty acids derived from triglyceride hydrolysis are preferentially used through β -oxidation as fuels for most fish tissues. Triglycerides may be deposited as perivisceral fat, in liver or in muscle. Liver is the main site for lipid storage in sturgeon, while salmonids like the trout accumulate perivisceral fat. Despite the storage site, a marked reduction in fat storage occurs in starved fish (Grigorakis and Alexis 2005; Rios et al. 2006; Furne et al. 2008; Pérez-Jiménez 2008; Barreto-Curiel et al. 2017) (Fig. 4). Regarding the enzymes involved in fatty acid catabolism, it has been

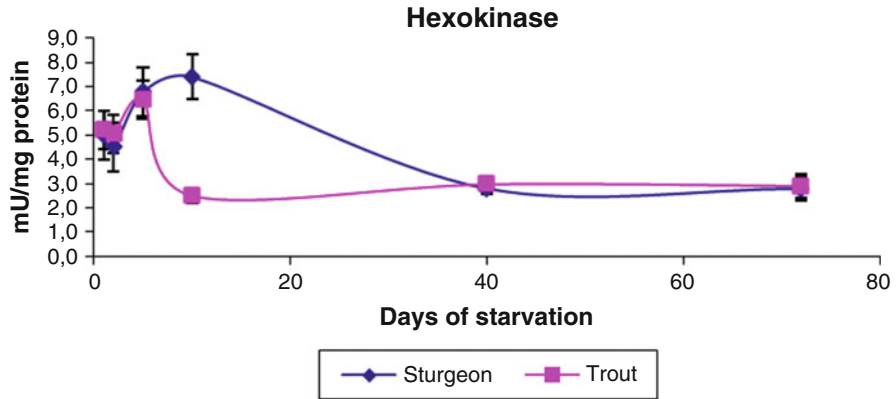


Fig. 2 Hepatic hexokinase activity during starvation in sturgeon and trout. Values are mean \pm SEM ($n = 5$; number of fish sampled per sampled points) (Data are taken from Furne et al. 2012)

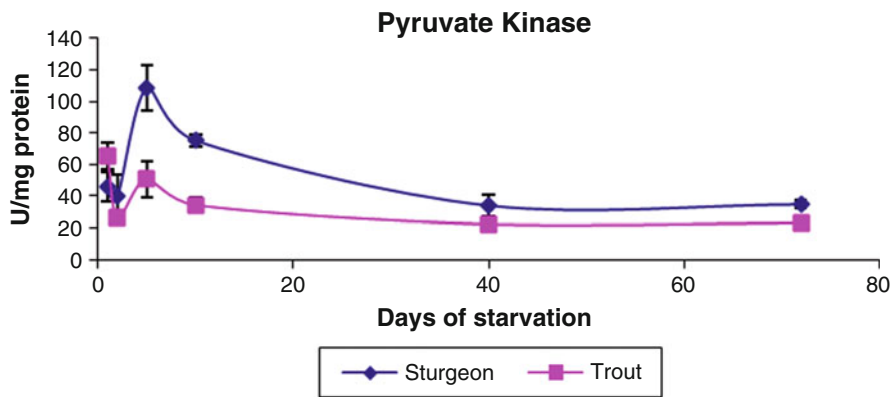


Fig. 3 Hepatic pyruvate kinase activity in the liver during starvation in sturgeon and trout. Values are mean \pm SEM ($n = 5$; number of fish sampled per sampled points) (Data are taken from Furne et al. 2012)

reported an increase in hepatic HOAD activity in starved sturgeon but not in trout, which agrees with a higher lipid content storage in the liver in the sturgeon (Fig. 5).

It has been suggested by some authors that ketone bodies do not play an important role as an energy source during starvation in fish (Zammit and Newsholme 1979; Black and Love 1986). However, many studies have already demonstrated β -OHBDHB activity in several teleost species. Furthermore, an increase in plasma levels of ketone bodies and in the activity of enzymes involved in ketone body synthesis has been reported in fish deprived of food (Soengas et al. 1996; Furne et al. 2008). In the sturgeon, the maintenance of triglyceride catabolism, which produces acetyl-coA, encourages the use of this metabolite for the synthesis of ketone bodies in the liver. This fact was supported by high β -OHBDH and ACoAT activities in

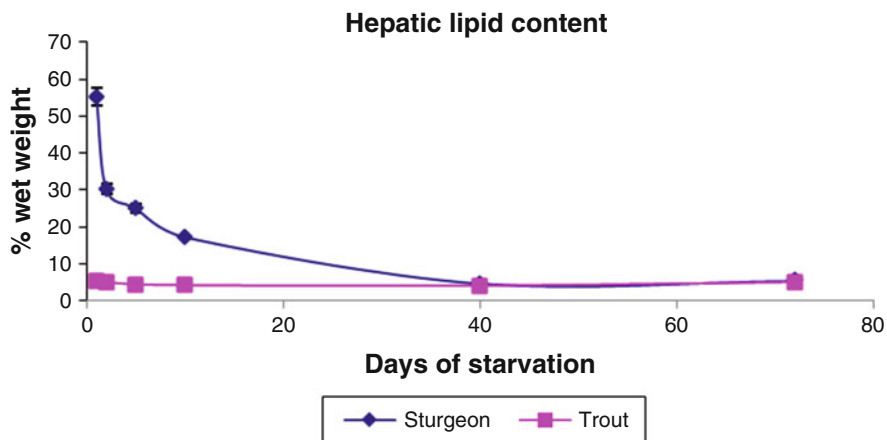


Fig. 4 Lipid content levels in liver during starvation in sturgeon and trout. Values are mean \pm SEM ($n = 5$; number of fish sampled per sampled points) (Data are taken from Furne et al. 2012)

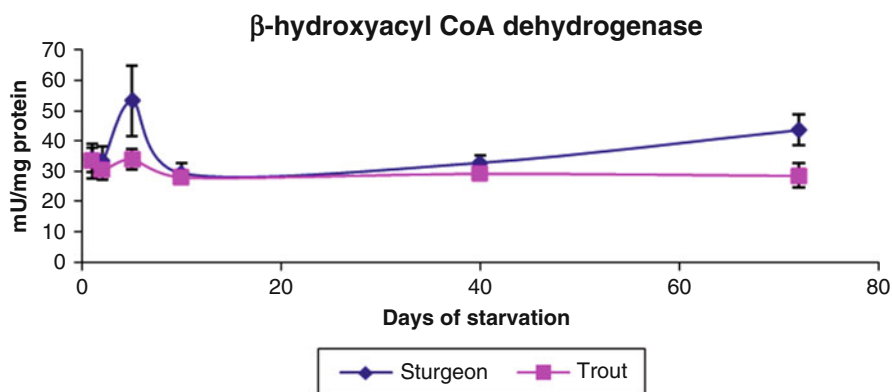


Fig. 5 Hepatic β -hydroxyacyl CoA dehydrogenase activity during starvation in sturgeon and trout. Values are mean \pm SEM ($n = 5$; number of fish sampled per sampled points) (Data are taken from Furne et al. 2012)

sturgeon. However, the trout synthesizes ketone bodies in the liver (increased of ACoAT) as a response to the excess of acetyl CoA produced by Krebs cycle from catabolic activity during starvation (Furne et al. 2012).

Muscle Metabolism During Starvation

Muscle is one of the tissues that is considerably affected by starvation in fish (Johansen and Overturf 2006). As muscle glycogen is a short-term reserve, during periods of starvation, lipid stores and muscle protein breakdown provide the bulk of energy.

In a few days of starvation, a mobilization of carbohydrate stores in white muscle was detected as an energy resource in both sturgeon and trout (Furne et al. 2012). Mobilization of carbohydrates during starvation has been reported in Atlantic cod by Black and Love (1986), whereas other species showed no variations in muscle glycogen reserves (Gutierrez et al. 1991; Blasco et al. 1992; Barcellos et al. 2010).

Sturgeon and trout mobilize lipids and proteins from the muscle during starvation. In both species, an increase in lipid catabolism enzymes (HOAD and GK) has been reported and the fish keep protein catabolism enzymes active (GPT, GOT and GDH). In contrast to the sturgeon which showed a decrease in enzymes involved in gluconeogenesis during starvation periods, the trout keeps the gluconeogenic pathways active using lactate as a substrate. Because protein is the main muscle component, they are the main energy source in muscle under prolonged starvation.

Starvation and Antioxidant Defenses

Oxidative stress arises from an imbalance between antioxidant defenses and oxidative processes. The high quantity of ROS present in situations of oxidative stress can provoke tissue damage, affecting biomolecules, which in the case of lipids could be quantified by peroxide formation (Halliwell and Gutteridge 2015).

Food deprivation leads to depletion of antioxidant stores and increased levels of ROS in organs of living organisms. Starvation has been reported to have pro-oxidant effects in mammals as ROS generation is not adequately neutralized by antioxidant systems (Robinson et al. 1997; Domenicali et al. 2001). It is known that a lack of available food can affect the antioxidant defenses in fish but, as opposed to studies on mammals, few publications are available on the consequences of starvation with regard to antioxidant mechanisms in fish. Most available studies on the impact of starvation on antioxidant defenses of fish are focused on liver, since it is the main organ for metabolic control and has a key role in ROS generation.

Oxidative Stress in Red Blood Cells and Liver During Starvation

Sturgeon and trout under prolonged starvation showed an increase in the lipid peroxidation levels in liver and in red blood cells. Studies in fish unanimously show that starvation augments lipid peroxidation. However, with respect to the activity of antioxidant enzymes, studies disagree, particularly depending on the tissue examined. In liver and red blood cells in sturgeon and trout, there was an early decline at 10 days starvation in both species. This decline, triggered by the restriction of enzyme synthesis substrates, was probably responsible of the rise of the lipid peroxidation levels seen (Furne et al. 2009). The enzymes SOD, CAT, GPX, and GR constitute the main enzymatic mechanism of antioxidant defense. The rise in the lipid peroxidation levels, together with a fall in the activity of the main antioxidant enzymes, appears to indicate the incapacity of the liver to meet the stress

situation provoked by prolonged starvation, leading ultimately to the oxidation of biomolecules.

Hepatic GR activity decreased in rainbow trout subjected to 3 weeks of starvation (Blom et al. 2000). Atlantic cod (*Gadus morhua*) showed an increased activity of antioxidant enzymes in liver, while in muscle those enzymes did not vary after 12 weeks of starvation (Guderley et al. 2003). Lipid peroxidation increased due to food deprivation in gilthead seabream (*Sparus aurata*). A decrease of CAT activity was found while SOD, GR, and GPX activities increased. Moreover, it has been detected new isoforms of the SOD enzyme (Pascual et al. 2003). An increase in activity in SOD, CAT, and GPX, and a decreased in GR activity in the liver of Common dentex (*Dentex dentex*) submitted to 5 weeks of starvation was reported by Morales et al. (2004). Zhang et al. (2008), in lang yellow croaker (*Pseudosciaena croceae*), showed an increase in hepatic SOD and GPX activities during starvation. Several studies have also evaluated the transcriptional responses to starvation of major antioxidant enzyme genes in the liver of some fish species. In rockbreem (*Oplegnatus fasciatus*) significant alterations were apparent, whereas mRNA levels of SOD, CAT, GPX, and GST in the liver increased in fish subjected to short-term starvation (Nam et al. 2005). In rainbow trout (*Oncorhynchus mykiss*) starved for 3 weeks, expression levels of GST and GPX were reduced (Salem et al. 2007). Also in the zebrafish (*Danio rerio*), genes involved in neutralizing ROS, such as SOD, GPX, and several other selenium-binding proteins, were downregulated in livers of fish starved for 21 days (Drew et al. 2008). These results indicate that prolonged starvation decreases the capacity of fish liver to ameliorate oxidative stress.

Oxidative Stress in Heart During Starvation

Studies analyzing the antioxidant defenses of the heart in starved fish are scarce and the results contradictory. In Adriatic sturgeon and rainbow trout, a starvation period of 10 weeks did not induce lipid oxidative damage in the heart. The activity of antioxidant enzymes in the heart of starved sturgeon remained unchanged, whereas cardiac CAT and SOD activities were enhanced by starvation in rainbow trout (Furne et al. 2009). These observations might indicate that the heart, being a crucial organ for life, would be in some way protected from stressful circumstances such as starvation. However, in common dentex, 5 weeks of starvation depressed cardiac activities of SOD, GPX, and GR. Although CAT activity increased during these circumstances, it was not sufficient to avoid an increase in lipid peroxidation (Pérez-Jiménez 2008).

Oxidative Stress in White Muscle During Starvation

In white muscle, specific activity of the antioxidant enzymes did not differ between fed and starved cod (Guderley et al. 2003). Also in common dentex, the specific activity of antioxidant enzymes, as well as the levels of lipid peroxidation, remained

unchanged by starvation (Pérez-Jiménez 2008). An increased activity of antioxidant enzymes and no variation in lipid peroxidation in white muscle was found in Adriatic sturgeon and rainbow trout starved for 10 weeks (Furne et al. 2009). Probably, cellular disruption during macromolecular mobilization may increase the sensitivity to damage by ROS, explaining why maintenance of antioxidant defenses would be useful during starvation.

Starvation and Digestive Physiology

The lack of food is a situation undergone and tolerated by many fish species in the natural environment. The metabolic strategy used to supply energy to the organism depends on several factors such as species, physiological state of the fish, and environmental conditions. Thus, some fish use protein as the main energy source, maintaining the hepatic glycogen reserve by means of glyconeogenesis, while other fish use lipids ahead the glycogen reserve. In addition, not all body tissues contribute to such reserves in the same way; some fish have a large energy reserve in the mesenteries of the digestive tract, while other fish have storage in the liver and still others in muscle.

Because the gastrointestinal tract and its associated organs can account for up to 40% of an animal's metabolic rate (Cant et al. 1996), one would have the a priori expectation for the digestive tract to atrophy during periods of food deprivation and flourish during food abundance (Theilacker 1978; Bogé et al. 1981; McLeese and Moon 1989; Diamond and Hammond 1992; Wang et al. 2006). Indeed, fish enduring food deprivation have been observed to decrease their gut length (Rios et al. 2004), intestinal fold and microvilli length (Gas and Noailliac-Depeyre 1976; German et al. 2010), and digestive enzyme activities (Krogdahl and Bakke-McKellep 2005; Chan et al. 2008; Furne et al. 2008; Abolfathi et al. 2012).

In the trout, the digestive somatic index declined during starvation, which could indicate a quicker mobilization of energy reserves from the digestive tract with respect to the overall body mass. Similar findings have been reported by other authors in rainbow trout (Storebakken et al. 1998). Metabolic and digestive results suggest that the trout mobilizes preferentially energy from the perivisceral tissues, while sturgeon mobilizes energy from muscle and liver tissues.

Regarding digestive enzymes, sturgeon and trout showed a decrease in protease, amylase, and lipase activities after 10 weeks of starvation. Sturgeon and trout have shown different eating habits. Trout has higher protease activity than sturgeon and sturgeon has higher amylase activity. Furthermore, sturgeon has greater digestive capacity for carbohydrates than trout (Furne et al. 2005). With respect to starvation, amylase activity in both species decreased more than 50% at 10 days of food deprivation. However, the protease activity did not change until 3 weeks of starvation. The literature shows that alkaline phosphatase, an enzyme located in the microvilli of the intestinal epithelium, gradually diminishes in starved carp, and after 13 month of starvation this activity cannot be detected (Gas and Noailliac-Depeyre 1976). A decline in trypsin activity during prolonged starvation in Atlantic

salmon was reported by Bélanger et al. (2002). On the other hand, a very different effect was noted after a brief starvation, with an increase in digestive enzymatic activities in Nile tilapia (Mommsen et al. 2003). Krogdahl and Bakke-McKellep (2005) detected a decrease in the total activity of enzymes in the intestinal microvillousities in Atlantic salmon after 40 days of starvation and a rapid recuperation after 7 days of re-feeding. A proteolysis of the intestinal mucosa, a progressive degeneration of exocrine pancreatic cells, and a decrease of zymogen activity during 48 h of starvation were observed in tench by Ostaszewska et al. (2006). Studies realized with catfish submitted to 150 days of starvation showed that the fish reduced the surface area of their intestines by 70% and reduced the microvilli surface area by 52% (German et al. 2010).

Fluctuations in food availability are natural in most aquatic systems, and fish show an impressive capacity to withstand prolonged periods of food limitation, particularly in comparison with mammals. Despite the many ways in which food limitation affects the metabolic capacities of fish, perhaps even more striking is their capacity to rebound from these difficulties. In fact, after starvation, fish enter a period of compensatory growth during which they rapidly accumulate reserves and reinstate their metabolic capacities. This compensatory growth occurs despite the previous atrophy of the digestive system. The malleability of the piscine digestive system and its capacity to rise to renew feeding opportunities is impressive. There are several areas in which information about oxidative defense mechanisms is scant, so new investigations concerning the control of oxidative defense mechanisms during renewed tissue growth after starvation should help elucidate how and why fish are so adapted to survive prolonged periods of food limitation.

This book chapter describes the mechanisms that allow fish to enhance prolonged starvation periods. The ability to face prolonged starvation is higher in fish than for example in humans, and the following two facts might contribute to the explanation of this phenomenon. First, fish are ectotherms (animals that do not regulate the body temperature) and maintaining vital processes requires lower energy levels in comparison to endotherms like humans (endotherms require high expenditures of metabolic energy in order to keep a constant body temperature). Second, fish do not need to keep balance since they live in aquatic environment, whereas humans require the performance of the antigravity muscles. Consequently, during food deprivation events, the energy balance in fish is less negative than in humans. The mechanisms of mobilization of energetic reserves occur at a lower rate in fish such that energy reserves last longer and allow prolonged starvation periods.

Policies and Protocols

The animals to which this study refers were sturgeons (*Acipenser naccarii*) and trout (*Oncorhynchus mykiss*) of 1+ year of age. The maintenance and feeding conditions were those of the fish farm. The fish were starved during a total period of 72 days. Five fish for each species were sampled on days 1, 2, 5, 10, 40, and 72 of food deprivation. All the procedures were conducted according to the guidelines of the

Council Directive 609/86/EEC (European Communities 1986) on the use of animals for experimental and scientific purposes. Animals were anesthetized with clove oil. Blood samples were taken from the caudal vessels using heparinized syringes and transferred to heparinized tubes, to be kept on ice until centrifugation. Following blood collection, the heart, liver, and a white-muscle portion, from anterior dorsal region, were quickly removed. Tissue samples were frozen in liquid nitrogen and stored in the laboratory at -80°C until analyze.

Dictionary of Terms

- **Glycogenolysis** – Process by which glycogen, the primary carbohydrate stored in the liver and muscle cells of animals, is broken down into glucose to provide immediate energy and to maintain blood glucose levels during fasting.
- **Gluconeogenesis** – Metabolic pathway that results in the generation of glucose from non-carbohydrate substrates such as lactate, glycerol, and amino acids
- **Glycemia** – Level of glucose in blood.
- **Ketone bodies** – Three related compounds (acetoacetic acid, acetone, and beta-hydroxybutyric acid) produced during the metabolism of fats, they are used as a source of energy instead of glucose during a period of fasting.
- **Reactive oxygen species (ROS)** – A type of unstable molecule that contains oxygen and that easily reacts with other molecules in a cell.

Summary Points

- The decrease in blood glucose in trout during the first days of starvation is more gradual than in sturgeon. One of the reasons could be a greater gluconeogenic capacity of the liver of the trout in comparison to the sturgeon liver and increased glycogen storage capacity in trout liver.
- Although it seems to be that ketone bodies do not play an important role as an energy source during starvation in fish, the synthesis of ketone bodies in the liver of the sturgeon comes from the catabolism of hepatic triglycerides, whereas trout liver comes from the Krebs cycle.
- In a few days of starvation, a mobilization of carbohydrate, lipid, and protein in the muscle was detected as an energy resource in both sturgeon and trout.
- Sturgeon and trout under prolonged starvation show an increase in the lipid peroxidation and a decrease in antioxidant enzymes in liver and in red blood cells. Conversely, the oxidative state of the sturgeon and trout heart and muscle is less disturbed by the starvation than the liver.
- The trout mobilizes preferentially energy from the perivisceral tissues, while sturgeon mobilizes energy from muscle and liver tissues.
- The starvation motivates a decrease of the amylase activity earlier than that of the protease in both species.

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