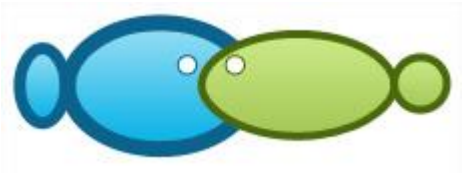

# Selective mobilization of fatty acids in common carp (*Cyprinus carpio*) during long-term starvation

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**Abstract**. Common carp *(Cyprinus carpio)* fingerlings (25 g; n=200) were introduced into a recirculation system in the Fish Laboratory of the Kaposvár University (Hungary). Fish were stocked into 60 L fish tanks (20x10 fish) in a recirculation system and feed was totally withdrawn for 12 weeks to test the selective depletion/conservation of hepatic and muscle originated fatty acids. Alterations in hepatic total fatty acid (FA) composition were: decrease of C16:1n7, C18:1n9 and increase C20:4n6, C20:5n3, C22:5n3 and C22:6n3 proportion, leading to an enormously increased unsaturation index, from 124.04 to 217.3). Changes of the fillet flesh phospholipid (PL) fraction were more expressed. The proportion of C16:1n7, C18:1n9 and C20:1n9 decreased, while C20:4n6, C22:6n3, polyunsaturated fatty acids (PUFA), total n3 and the unsaturation index increased. A moderate, but not statistically significant decrease of fillet malondyaldehide (MDA) concentration was detected. It was concluded that mostly the monoenoic fatty acids of the liver were utilized as a fuel source. Likewise, as an opposite reaction, fillet PUFAs were selectively conserved referring to the maintenance of membrane fluidity during prolonged starvation.
**Key Words**: Cyprinidae, feed restriction, malondyaldehide, membrane lipids, metabolism.

**Introduction**. Most of the fish species are exposed to short-term or long-term starvation periods during their lifespan in both natural and artificial conditions. Fish have a stronger capability to tolerate starvation than birds and mammals (Feng et al 2011). The ability to endure starvation depends on thermal conditions, nutritional status and species. European eel (*Anguilla anguilla*) has the highest tolerance to non-hibernating starvation (Boetius & Boetius 1985). In general, most of the fish are able to survive several months without any food (Moon 1983; Wilkins 1967; Woo & Cheung 1980).

During the starvation period, fish replace the lacking energy in a complex way, but mainly via the oxidation of stored fat (Einen et al 1998; Friedrich & Stepanowska 2001; Hung et al 1997). Lipid oxidation proceeds in a selective manner in fish, influenced by environmental factors. Significant changes of the fatty acid (FA) composition may befall within some weeks because of food deprivation.

Selective retention of essential fatty acids (EFA) is specific for most living organisms. It can be explained by the fact that the organism has to maintain the unsaturation level to preserve the fluidity of the biological membranes (Szabó et al 2005).

Common carp (*Cyprinus carpio*) is able to metabolize selected FA for its energy needs when they are in good condition, but if body fat content is low, it may metabolize all FA types equally to sustain metabolic functions during starvation in cold temperatures (Zajic et al 2013). Fillet FA composition of Atlantic salmon (*Salmo salar*) changes similarly in case of food deprivation; the proportion of saturated fatty acids (SFA) decreases, while proportion of mono (MUFA) and polyunsaturated fatty acids (PUFA) significantly increases (Einen et al 1998). Similarly, significant increase of PUFA in the

liver of hybrid tilapia (*Oreochromis mossambicus x O. niloticus*) was noted due to long-term starvation (De Silva et al 1997).

Proportional changes of the several FA groups in starving fish are different. FA composition of the phospholipid (PL) fraction changed significantly (MUFA increased) in sea bass (*Dicentrarchus labrax*) liver and fillet, while the triacylglycerol (TG) fraction remained unchanged (Delgado et al 1994).

Due to the significant metabolic shift (De Pedro et al 2003), the lipid peroxidation increases during starvation followed by a change of the antioxidant capacity (Morales et al 2004). The rate of oxidative damage is different among fish species. It is reversible in common dentex (*Dentex dentex*) after refeeding (Morales et al 2004), but the damage is irreversible in the liver of brown trout (*Salmo trutta*) (Bayir et al 2011).

The aim of this study was to analyze the FA compositional changes in the liver and fillet, and the lipid peroxidation of common carp (*C. carpio*) after a 12-week-long starvation period in warm temperatures. The changes of proximate body composition and somatic indices of the same population of carps during the 12-week-long starvation period were reported previously (Varga et al 2014).

## Material and method

***Experimental animals and design***. Common carp (*C. carpio*) fingerlings (4 g) were introduced into a recirculation system in the Fish Laboratory of the Kaposvár University (Hungary) in July 2013. Fish were reared in fish tanks until they reached 25 g live weight. Feeding during this period was *ad libitum* with a commercial fish feed (Aller Aqua, presented in Table 1). Fish were adapted to the artificial conditions and feed; thus, stress and disturbing environmental circumstances were excluded.

For the experiment, 200 individuals were used. They were stocked into 60 L fish tanks (20x10 fish) in a small recirculation system. Feeding was totally halted for 12 weeks from September to December. Water temperature was measured daily (n=84).

Table 1

Proximate composition of the feed fed prior to starvation

| *Chemical composition* | *Values* |
|---|---|
| Dry matter content (%) | 85.2 |
| Crude protein (%DM) | 45 |
| Crude fat (% DM) | 15 |
| Nitrogene-free extract (% DM) | 21.9 |
| Crude ash (%DM) | 6.9 |
| Crude fiber (%DM) | 3.3 |
| Gross energy (MJ $kg^{-1}$) | 20.8 |

Note: DM - dry matter.

***Sampling***. Sample collection for FA analysis was carried out initially and the end of the experiment. Sample collection for malondyaldehyde (MDA) was carried out every two weeks. 10 individuals at each sampling were over-anaesthetized with clove oil. The whole fillet and the whole liver were dissected freshly, washed in ice-cold physiological saline, wiped dry and stored frozen (-70$^{o}$C) until analysis.

***Lipid extraction, fractionation, FA analysis***. Tissue samples were extracted according to the method of Folch et al (1957). All solvents used were ultrapure-grade by Sigma–Aldrich (Schnelldorf, Germany). 100 mg $L^{-1}$ of butylated hydroxytoluene was added to the extraction mixture (chloroform/methanol 2/1 v/v) as antioxidant. Complex lipids of the fillet were fractionated on short silicagel columns (Leray et al 1997). Briefly, extracted lipids were transferred to glass chromatographic columns, containing 300 mg silicagel (230-400 mesh) for 10 mg of complex lipids. Neutral lipids were eluted with 10 mL of chloroform for the above fat amount, then 15 mL of acetone/methanol (9/1 v/v) was added, while 10 mL of pure methanol eluted the total phospholipids. Fatty acids of the PL

fraction were transmethylated by the base-catalyzed sodium-methoxide method and aliquots were solved in n-hexane (Christie 1982).

Gas liquid chromatography was performed on a Shimadzu 2010 apparatus, equipped with a Phenomenex Zebron ZB-WAX Capillary GC column (30 m x 0.25 mm ID, 0.25 micrometer film, Phenomenex, Inc. Torrance, CA, USA) and a flame ionization detector (FID $2\times10^{-11}$). The characteristic operating conditions were: injector temperature - 270°C; detector temperature - 300°C; helium flow - 28 cm $sec^{-1}$. The temperature program was the following: from 80 to 205°C - 2.5°C/min; 5 min at 205°C, from 205 to 250°C - 10°C/min, and 5 min at 250°C. To identify individual FA, an external FA standard (37 Component FAME Mix, Sigma-Aldrich, Cat. No.: CRM47885) was used. FA results were expressed as weight % of total fatty acids. Unsaturation index (UI) was defined as the number of double bonds in 100 fatty acyl chains.

***Determination of fillet MDA concentration***. The MDA concentration was determined from homogenized (Ultra Thurrax, Donau Lab AG, Linz), frozen stored samples, after the addition of 9 mL of physiological saline (0.9% w/vol NaCl) per 1 g of tissue. Estimation of thiobarbituric reactive substances (TBARS) levels was performed according to Placer et al (1966). The assay procedure was calibrated using tetra-ethoxypropane (Fluka, Buchs, Switzerland) as a MDA source, and levels of tissue sample MDA were calculated as µmol $g^{-1}$ of wet tissue.

***Statistical analysis***. The basic data were tested for normality (Shapiro-Wilk test). For the analysis of the effect of starvation on FA composition, independent T-tests were performed, and the effect of starvation on MDA concentration was determined by one way ANOVA at the significance level of 0.05. SPSS 20 for Windows was used for the statistical analyses.

***Ethical issues***. The experiment was approved by the Animal Experimentation Ethics Committee of the Kaposvár University, as allowed by the Somogy County Animal Health and Food Control Authority (allowance no.: XV-I-31/446-10).

**Results and Discussion**. The average water temperature was 18.3±1.5°C during the starvation period. No mortality was recorded. The changes in proximate body composition and somatic indices of the same carp population during the 12-week-long starvation period were reported previously (Varga et al 2014). Nevertheless, for the better understanding of the metabolic processes, the somatic indices of carps are presented in Table 2.

Table 2

Somatic indices of common carps (*Cyprinus carpio*) during 12-week-long starvation as mean±SD

| | *Weeks* | | | | | | |
|---|---|---|---|---|---|---|---|
| | *0* | *2* | *4* | *6* | *8* | *10* | *12* |
| A | 2.46±0.59$^{a}$ | 1.30±0.57$^{b}$ | 1.05±0.44$^{b}$ | 0.92±0.27$^{b}$ | 0.77±0.17$^{b}$ | 0.79±0.18$^{b}$ | 0.79±0.27$^{b}$ |
| B | 10.62±1.04$^{a}$ | 7.07±1.01$^{b}$ | 7.78±1.38$^{b}$ | 7.35±1.20b | 7.21±0.86$^{b}$ | 6.86±0.72$^{b}$ | 6.70±0.67$^{b}$ |
| C | 3.10±0.31$^{a}$ | 2.80±0.19$^{ab}$ | 2.70±0.23$^{bc}$ | 2.60±0.18$^{bc}$ | 2.46±0.71$^{bc}$ | 2.54±0.21$^{c}$ | 2.41±0.13$^{c}$ |

Note: A - hepato-somatic index; B - Viscero-somatic index; C - condition factor. Different superscripts in the same row show significant differences at P<0.01. Source: Varga et al (2014).

Almost all individual FA of the liver, the fillet PL fraction, and the derived FA data also showed significant differences after 12 weeks of starvation, compared to the initial state.

The most outstanding changes in liver FA composition are the decrease of C16:1, C18:1n9 and the increase of C20:4n6, C20:5n3, C22:5n3 and C22:6n3. The proportion of total MUFA significantly decreased, while the proportion of PUFA and total n3 content and the unsaturation index (UI) greatly increased (Table 3).

Table 3

Hepatic total fatty acid composition of the starved carps (*Cyprinus carpio*)

| *Fatty acid* | *Day 0* | *Day 84* | *Significance* |
|---|---|---|---|
| | *Mean±SD* | *Mean±SD* | *P* |
| C12:0 | 0.026±0.005 | 0.034±0.01 | NS |
| C14:0 | 1.55±0.21 | 1.40±0.32 | NS |
| C14:1n5 | 0.057±0.01 | nd | |
| C15:0 | 0.19±0.03 | 0.25±0.03 | <0.01 |
| C16:0 | 19.47±0.6 | 19.54±1.82 | NS |
| C16:1n7 | 7.7±0.73 | 3.21±1.08 | <0.01 |
| C17:0 | 0.15±0.03 | 0.18±0.02 | NS |
| C18:0 | 5.79±0.61 | 5.52±0.74 | NS |
| C18:1n9t | 0.128±0.02 | 0.11±0.03 | NS |
| C18:1n9 | 38.56±1.82 | 22.22±7.07 | <0.01 |
| C18:1n11 | 4.42±0.37 | 3.69±0.22 | <0.01 |
| C18:2n6 | 6.65±1.06 | 6.92±2.10 | NS |
| C18:3n3 | 1.17±0.35 | 1.11±0.46 | NS |
| C18:3n6 | 0.064±0.01 | 0.08±0.02 | NS |
| C20:0 | 0.26±0.04 | 0.24±0.03 | NS |
| C20:1n9 | 3.95±0.58 | 3.08±0.31 | <0.01 |
| C20:2n6 | 0.43±0.07 | 0.53±0.08 | <0.01 |
| C20:3n6 | 0.32±0.08 | 0.27±0.06 | NS |
| C20:3n3 | 0.1±0.03 | 0.17±0.02 | <0.01 |
| C20:4n6 | 0.73±0.26 | 2.29±0.75 | <0.01 |
| C20:5n3 | 1.59±0.49 | 2.71±0.51 | <0.01 |
| C22:1n9 | 0.08±0.03 | 0.13±0.02 | <0.01 |
| C22:5n3 | 0.39±0.12 | 1.49±0.23 | <0.01 |
| C22:6n3 | 6.18±1.9 | 24.73±8.19 | <0.01 |
| C24:1 | 0.06±0.02 | 0.11±0.02 | <0.01 |
| | | | |
| SFA | 27.42±1.1 | 29.87±2.06 | <0.05 |
| MUFA | 54.95±2.6 | 32.55±8.4 | <0.01 |
| PUFA | 17.63±2.9 | 37.59±6.6 | <0.01 |
| ∑n3 | 9.44±2.3 | 27.5±7.9 | <0.01 |
| ∑n6 | 1.11±0.3 | 2.635 | <0.01 |
| n6/n3 | 0.12±0.04 | 0.1±0.01 | NS |
| UI | 124.04±12.04 | 217.3±38.9 | <0.01 |
| ACL | 17.8±0.09 | 18.83±0.32 | <0.01 |

Note: nd - not determined; NS - not significant; SFA - saturated fatty acids; MUFA - monounsaturated fatty acids; PUFA - polyunsaturated fatty acids; UI - unsaturation index; ACL – average chain length.

Alterations in fillet PL fraction are more expressed, as compared to the liver, with a preferred retention of SFA and MUFA. The proportion of C16:1, C18:1n9 and C20:1n9 decreased, while C20:4n6, C22:6n3, PUFA, total n3 contents and the UI value increased (Table 4).

A moderate, but not statistically significant decrease of fillet MDA concentration was detected (Figure 1).

Starvation had significant effects on the PL FA composition of carp fillet and on the total FA composition of the liver, as previously described in Atlantic salmon also (Einen et al 1998; Wathne 1995).

During starvation, intramuscular triacylglycerol (TAG) fraction (pool) provides the main fuel source for fish (e. g. during swimming), releasing free fatty acids (FFA), mostly for β-oxidation (Reshef et al 2003). This may explain the greater changes of the FA profile in the liver, as compared to the fillet, because TAG content of the liver exceeds that of the fillet in cyprinids (Varga et al 2014). In addition, the hepatic recruitment of dietary fatty acids is non-selective (Kiessling & Kiessling 1993), while dietary lipids are primarily built of TAGs.

Table 4

Fillet phospholipids fatty acid composition of the starved carp (*Cyprinus carpio*)

| *Fatty acid* | *Day 0* | *Day 84* | *Significance* |
|---|---|---|---|
| | *Mean±SD* | *Mean±SD* | *P* |
| C14:0 | 0.38±0.04 | 0.21±0.04 | <0.01 |
| C15:0 | 0.19±0.02 | 0.15±0.02 | <0.01 |
| C16:0 | 20.85±0.1 | 20.41±0.68 | NS |
| C16:1n7 | 2.12±0.38 | 1.31±0.18 | <0.01 |
| C17:0 | 0.2±0.03 | 0.17±0.02 | <0.05 |
| C17:1 | 0.1±0.02 | 0.07±0.03 | <0.05 |
| C18:0 | 6.84±0.58 | 7.88±0.39 | <0.01 |
| C18:1n9t | 0.12±0.01 | 0.08±0.01 | <0.01 |
| C18:1n9 | 15.28±0.95 | 13.65±1.31 | <0.01 |
| C18:1n11 | 2.88±0.27 | 3.45±0.22 | <0.01 |
| C18:2n6 | 3.97±0.38 | 3.17±0.34 | <0.01 |
| C18:3n3 | 0.52±0.04 | 0.21±0.04 | <0.01 |
| C18:3n6 | 0.073±0.02 | 0.03±0.01 | <0.01 |
| C20:0 | 0.43±0.06 | 0.30±0.03 | <0.01 |
| C20:1n9 | 3.53±0.77 | 2.11±0.56 | <0.01 |
| C20:2n6 | 0.33±0.02 | 0.32±0.04 | NS |
| C20:3n3 | 0.11±0.01 | 0.08±0.01 | <0.01 |
| C20:3n6 | 0.71±0.16 | 0.57±0.09 | <0.05 |
| C20:4n6 | 3.02±0.34 | 4.20±0.34 | <0.01 |
| C22:0 | 0.12±0.05 | 0.06±0.05 | <0.01 |
| C22:1n9 | 0.09±0.01 | 0.07±0.08 | NS |
| C22:5n3 | 2.49±0.11 | 2.23±0.15 | <0.01 |
| C22:6n3 | 27.24±1.39 | 30.11±2.52 | <0.01 |
| C24:0 | 8.35±0.78 | 9.13±0.7 | <0.01 |
| C24:1n9 | 0.08±0.02 | 0.05±0.01 | <0.01 |
| | | | |
| SFA | 56.25±1.14 | 59.28±1.92 | <0.01 |
| MUFA | 24.17±1.4 | 20.79±1.47 | <0.01 |
| PUFA | 38.47±1.11 | 40.92±2.01 | <0.01 |
| ∑n3 | 30.37±1.41 | 32.63±2.62 | <0.01 |
| ∑n6 | 3.80±0.46 | 4.80±0.41 | <0.01 |
| n6/n3 | 0.13±0.02 | 0.15±0.03 | <0.01 |
| UI | 225.0±7.44 | 239.05±12. 59 | <0.01 |
| ACL | 19.38±0.08 | 19.55±0.13 | <0.01 |

Note: nd - not determined; NS - not significant; SFA - saturated fatty acids; MUFA - monounsaturated fatty acids; PUFA - polyunsaturated fatty acids; UI - unsaturation index; ACL – average chain length.

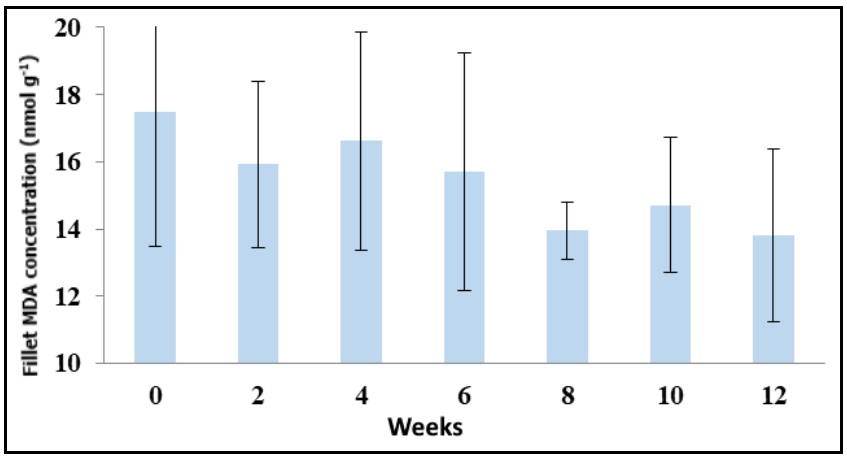


Figure 1. Changes of fillet malondyaldehide (MDA) concentration during starvation.

The significant decrease of palmitoleic (C16:1n7) and oleic acids (C18:1n9) in the liver due to starvation was described previously in Nile tilapia (De Silva et al 1997), similarly

to our results. In addition, the preferred utilization of monoenoic FAs is evincible by the significant decrease of total MUFA percentage in the liver (Table 3). The reason of this FA selective mobilization for energy production has two main reasons. Firstly, essential (C18:3n3 and C18:2n6) FAs are likewise paradoxically conserved, mostly to maintain membrane structure (Kiessling & Kiessling 1993). Secondly, the order of FA mobilization: FAs are more readily mobilized when they are short-chain and unsaturated (Raclot & Oudart 1999). This is especially the case when a high n-3 PUFA diet is fed, resulting in a preferential partitioning of ingested energy towards oxidation at the expense of storage. Moreover, FAs are key mediators of gene expression in the liver. Hepatic FAs that were primarily conserved during starvation in carp had the following order: docosahexaenoic acid (C22:6 n3 n3) > arachidonic acid (C20:4 n6) > eicosapentaenoic acid (C20:5 n3) > docosapentaenoic acid (C22:5 n3), all being characteristic membrane lipid components. The increase of long chain PUFA with the simultaneous decrease of the ratio of SFA and MUFA in starving organisms is a well-known process, resulting from the FA selective mobilization and from the percentage data representation. We here suggest selective retention of essential FA to maintain membrane homeostasis, as reported earlier in other vertebrates (Szabó et al 2005). Though hepatic lipids were not analyzed in a fractionated manner, TAG depletion is proposed (Szabó et al 2005), besides membrane structure maintenance in the background of the results.

When analyzing the fillet, it has to be mentioned that with the exception of the dominant saturated FA, palmitate, nearly all highly unsaturated FA contents were affected by starving. EFA showed a clear proportional decrease, unequivocally induced by their absence from the diet and their essentiality. In contrast, the UI value and even the average FA chain length increased significantly. The major individual FAs leading to this condition were arachidonic acid (C20:4n6) and docosahexaenoic acid (C22:6n3). The former is known as the precursor root component of the inflammatory mediator eicosanoids. It is, however, interesting that the FAs with the highest unsaturation were protected during a drastic starvation. This has not been described in an earlier avian forced moult study (Szabó et al 2005), but the maintenance of the primary membrane components suggests a sarcolemma protective process. In vertebrates, it is regular that TAGs are preferentially oxidized, but this process shows deposit specificity. Accordingly, spatially isolated fat deposits might be handled as different organs, because there are significant differences between their structural and metabolic properties (Arner 1997).

Moreover, intramuscular TAGs are the spatially better available targets for mitochondrial, carnitine-mediated β-oxidation. Thus, intramuscular TAG depletion consequently augments a skeletal muscle PUFA proportional increase (i.e. the maintenance of the sarcolemma polyunsaturation), as clearly demonstrated in this study.

For the PL FA profile, the marked PUFA conservation may as well be related to the Lands mechanism (Lands 1960), playing a primary role in the membrane integrity maintenance via FA trans-acylation steps, even in case of full nutrient deprivation. Thus, for the findings in the fillet, namely the maintenance of unsaturation, chain length and expressed PUFA retention, we suggest intramuscular TAG depletion, FA and deposit selective mobilization, along with the hypothesis of the onset of the Lands mechanism, as multiple means for membrane lipid compositional protection.

Non-enzymatic lipid peroxidation is often characterized with the determination of MDA, a cytotoxic and mutagenic end-product formed from FAs with over three double bonds (Mead et al 1986). The increase of MDA concentration in fish liver (Pascual et al 2003) and fillet (Zhang et al 2008) started approximately at the third week of starvation. Surprisingly, in our study, a moderate decrease of fillet MDA concentration was detected. The reason may be that the primary substrates for MDA development were present in a rather preserved form, mostly in the sarcolemma in esterified form, and not as free acids. Moreover, it is also known that slower metabolism is matched with a slowed down lipid peroxidation (Wu et al 2004).

***Conclusions***. Summarizing the results, it seems that mostly the MUFA of the liver were utilized in the β-oxidation. In contrast, with an opposite reaction, fillet PUFAs were highly conserved. Fillet PL FA composition has undergone slighter changes during the starvation

period, which refers to the importance of membrane fluidity. From a practical viewpoint, this is rather advantageous, since live fish are kept under non-feeding conditions in the markets, thus providing a biologically more valuable fat source for possible consumers.

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