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**Tissue-specific response of fatty acid signatures to
diet in cultured carp (*Cyprinus carpio* L.).**

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Markus Böhm

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Einleitung

Fisch ist ein wichtiger Bestandteil einer gesunden Ernährung. Er ist eine gute Proteinquelle und reich an wertvollen Fetten, Mineralstoffen und Spurenelementen. Fettsäuren spielen in der Ernährung des Menschen eine wichtige Rolle (Crawford et al. 1999, Lands 2005). Besonders der Gehalt an langkettigen, mehrfach ungesättigten Fettsäuren bestimmt den Wert von Fisch als Nahrungsmittel für den Menschen (Stansby 1990, Calder 2001, Steffens 1997).

Meeresfisch ist besonders reich an wertvollen Omega-3-Fettsäuren wie Eicosapentaensäure (20:5n-3, EPA) und Docosahexaensäure (22:6n-3, DHA). Die Nachfrage an Fisch weltweit steigt, besonders durch aufstrebende Länder wie China. Die Fischerei muss allerdings immer höheren Aufwand betreiben, um die Nachfrage zu decken, eine Produktionssteigerung ist nur noch in wenigen Meeresregionen möglich. Durch die Überfischung der Weltmeere ist die Menge an gefangenem Fisch in vielen Meeresgebieten sogar zurückgegangen (FAO 2009). Der Fischfang kann den steigenden Bedarf nicht mehr alleine decken.

Die Aquakultur ist heute ein unverzichtbarer Lieferant von Fisch für den menschlichen Verzehr, 45,7% der Welt-Fischproduktion im Jahr 2008 stammte aus der Aquakultur (FAO 2009). Die durchschnittliche jährliche Wachstumsrate dieses Wirtschaftszweigs betrug weltweit zwischen 1970 und 2008 8,3% (FAO 2009). Die Aquakultur entlastet die natürlichen Fischbestände in den Meeren und versorgt die Menschen mit dem gewünschten Fisch.

Mit der neuen Aufgabe, Fische in großer Zahl und Dichte unter kontrollierten Bedingungen züchten zu wollen, ergibt sich eine Reihe von Fragen der Aquakultur an die Wissenschaft. Da die Fische gefüttert werden müssen, stellt sich die Frage nach dem richtigen Futter, um optimales Wachstum, Gesundheit und Fleischqualität der Fische zu erreichen. Welche Möglichkeiten gibt es, um die Qualität der Fische sogar noch zu verbessern und vielleicht sogar mit besonders erwünschten Attributen anzureichern?

Vielfach wird in der Fischzucht Fischmehl und Fischöl als Bestandteil des Futters für die Fische verwendet. Sie stellten lange Zeit eine billige und qualitativ hochwertige Energie- und Lipidquelle in der Nahrung dar. Aufgrund des starken Preisanstieges ist Fischöl aber langfristig nicht mehr ökonomisch nachhaltig (Tacon und Metian 2008). Außerdem ist der Einsatz von Fischöl auch wegen der Gewinnung aus ohnehin überfischem Meeresfisch nicht ökologisch nachhaltig (Deutsch et al. 2007).

Es stellt sich daher für die Aquakultur die Frage, wie das Fettsäureprofil der Fische durch die zugeführte Nahrung beeinflusst werden kann und wie der Fisch auf diese Nahrung reagiert. Daraus resultiert ein wissenschaftlicher Bedarf an physiologischem Wissen über die gezüchteten Fischarten, um das Futter an die jeweiligen physiologischen Besonderheiten der Fische anzupassen. Um die komplexen Auswirkungen der Nahrung auf den Fisch und dessen Physiologie zu erfassen, reicht es nicht, sich nur den Dorsalmuskel, der für den menschlichen Verzehr besonders interessant ist, anzusehen, sondern es müssen alle wichtigen Organe des Fisches in Betracht gezogen werden. Von besonderem Interesse ist die Reaktion des Fisches auf verschiedene Nahrungsqualitäten, wie zum Beispiel Fischöl oder verschiedene pflanzliche Lipidquellen. Es ist weiterhin wichtig zu wissen, in welchen Organen sich bestimmte Fettsäuren besonders anreichern, da für den menschlichen Verzehr nur die Fette relevant sind, die sich im Filet, also im Dorsalmuskel, anreichern.

In meiner Arbeit gehe ich daher der Frage nach, wie das Futter die Fettsäurezusammensetzung von Struktur- und Speicherfetten in verschiedenen Geweben und Organen des Karpfens beeinflusst und wie unterschiedlich verschiedene Gewebe und Lipidklassen auf unterschiedliche Nahrungsqualitäten reagieren können.

**Tissue-specific response of fatty acid signatures to diet in cultured carp
(*Cyprinus carpio* L.).**

**Markus Böhm^{1,2,3}, Sebastian Schultz^{1,2}, Apostolos-Manuel Koussoroplis¹,
Martin J. Kainz¹**

¹WasserCluster Lunz - Biologische Station; Dr. Carl Kupelwieser Promenade 5;
A-3293 Lunz am See, Austria

²Universität Wien; Department of Limnology; Althanstraße 14; A-1090 Wien, Austria

³Corresponding author:

a0648753@unet.univie.ac.at

Phone: +43 7486 20060 52

Fax: +43 7486 20060 20

Abstract

Fish depend on dietary supply of fatty acids (FA) to meet their physiological requirements. Our understanding of FA metabolism in common carp (*Cyprinus carpio*) is limited because most studies focused only on FA in muscle tissues and neglected other tissues. We investigated effects of diet on the FA composition of polar lipids (PL) and neutral lipids (NL) in eight different tissues (dorsal muscle, ventral muscle, heart, kidney, intestine, eyes, liver and adipose tissue) of common carp. We hypothesized that, a) carp organize their PLFA according to tissue-specific requirements ('quasi homeostasis') and thus modified from their dietary FA composition, whereas, b) NLFA of all investigated tissues reflect the dietary FA supply and are not tissue specific. Two-year old carp were introduced to aquaculture ponds with access to three different diet sources (i.e., only zooplankton, zooplankton plus additional vegetable oil feeds, or, zooplankton plus additional fish oil feeds). After 210 days, PLFA and NLFA of different tissues were analyzed using thin-layer and gas chromatography. The response of FA signatures to different diets was tissue and lipid class specific. Our major finding was that NLFA composition in carp was tissue specific at low TAG concentrations. PLFA did not reflect diet but reacted to n-3 rich diet sources (fish oil). Our findings offer new insights into tissue-specific FA patterns and expand our knowledge of fish lipid metabolism and requirements.

Keywords: carp, *Cyprinus carpio*, fatty acids, lipids, fish oil, vegetable oil

1 Introduction

Fatty acids (FA) play a major role in the nutrition of fish (Bell 1998, Sargent et al. 2002, Tocher 2003) and humans (Crawford et al. 1999, Simopoulos 2000, Lands 2005). Polyunsaturated FA (PUFA) of the omega-3 (n-3) and n-6 family, including eicosapentaenoic acid (20:5n-3, EPA), docosahexaenoic acid (22:6n-3, DHA), and arachidonic acid (20:4n-6, ARA) are particularly important for somatic growth, reproduction, and survival of freshwater fish (Sargent et al. 1999). As *animalia* cannot synthesize n-3 or n-6 PUFA *de novo* (Cook and McMaster 2004), fish entirely depend on dietary supply of these essential nutrients to meet their physiological requirements. Moreover, from a human consumption perspective, the composition of PUFA in fish strongly determines the nutritional fish quality (Stansby 1990, Steffens 1997, Calder 2001).

Total lipids and the FA composition vary among fish species and are influenced by their dietary supply (Henderson and Tocher 1987, Jobling 2001, Turchini et al. 2009, Guler et al. 2011). Several studies found that dietary FA affect the FA composition of carp, FA metabolism and somatic growth (Fauconneau 1995, Hadjinikolova 2004, Du et al. 2006, Steffens 2007). Most of these aquaculture-driven studies focused only on how different dietary lipids affect the FA composition of edible muscle tissues of fish and thus often neglect the response of other tissues. We therefore have a rather incomplete vision of the general FA metabolism in carp, and perhaps fish in general. As fish tissues have diverse physiological functions, biochemical requirements, and react differently to environmental or dietary conditions, it is important to study the composition and fluctuation of tissue-specific lipids to obtain more detailed understanding of fish lipid metabolism and requirements.

In freshwater fish tissues, FA occur as cell-membrane (polar lipid fatty acids, PLFA) and storage lipids (neutral lipid fatty acid, NLFA) (Dalsgaard et al., 2003). Fish typically contain high levels of PUFA in their cell membrane lipids that have important structural and

metabolic functions (Tocher 2003). Membrane bilayers rich in PUFA provide membranes higher membrane fluidity than SAFA or MUFA (Rawicz et al. 2000) and also increase water permeability in cell membranes (Olbrich et al. 2000). In contrast, NLFA can be stored as long-term energy sources in fish and mobilized during periods of high-energy demand, such as reproduction and migration or during starvation (Tocher 2003). Results of several studies demonstrate that the composition of NLFA usually reflects the FA composition of diet (Lie et al. 1986, Jobling 2002, Sargent 2002, Jobling 2004, Benedito-Palos 2010), whereas the PLFA composition in cell membranes is regulated to meet taxa-dependent requirements (Regost 2003, Tocher 2003, Benedito-Palos 2010). However, the current knowledge on PLFA and NLFA compositions and their degree of regulation is mostly limited to single-tissue studies.

Linoleic (18:2n-6, LIN) and α -linolenic acid (18:3n-3, ALA) are essential FA that cannot be synthesized by fish and must thus be supplied with diet (Sargent et al. 1999, Tocher 2003, Turchini et al. 2009). However, freshwater fish are, at various degrees, capable of converting these precursors to other physiologically important HUFA (Tocher 2003). In particular, DHA is the mostly retained PUFA in freshwater fish (Ahlgren et al. 1994) with particularly high concentrations in the brain and eyes of various fish species (Stoknes et al. 2004, Tocher and Harvie 1988, Mourente 2003, Skalli 2006) and tends to be conserved when DHA is short in dietary supply (Geurden 1999).

The aim of this study was to investigate how different diet composition influences the FA composition of polar and neutral lipids in eight tissues (dorsal muscle, ventral muscle, liver, heart, kidney, eyes, intestine and adipose tissue) of cultured carp (*Cyprinus carpio* L.), raised in commonly used semi-intensive aquaculture systems. Assuming that the response of common carp to dietary FA is organ- and lipid class-specific, it is hypothesized that, a) carp organize their PLFA according to tissue-specific requirements ('quasi homeostasis') and thus modified from their dietary FA composition, whereas, b) NLFA of all investigated tissues

reflect the dietary FA supply and are not tissue specific. Results of this study will provide detailed information about basic lipid physiology of common carp, one of the most important species in aquaculture worldwide (Tacon and Metian 2008, FAO 2009).

2 Material and Methods

2.1 Experimental design

To investigate the tissue- and lipid class-specific response of FA signatures to different diets, two-year old common carp (*Cyprinus carpio* L.) from the same stock were initially introduced to 3 different aquaculture ponds in temperate Lower Austria (N 48.815049, E 15.297321) (Table 3). Carp of all ponds had access to natural zooplankton. While carp of pond 1 fed exclusively on zooplankton (N), ponds 2 and 3 were supplied with a supplementary diet of different dietary lipid quality according to established aquaculture practice (Schultz et al. 2012). Carp of pond 2 obtained a commonly used cereal diet (triticale) enriched with 3% milk thistle (*Silybum marianum*) oil (vegetable oil; VO). Carp of pond 3 were additionally supplemented with a commercial compound feed based on marine fishmeal enriched with 18% marine fish oil (FO).

Feeds were supplied using pendulum feeders that had to be activated by the fish. The quantity of feed supply and stocking rates of carp were designed according to established aquaculture methods (Mráz et al. 2012). Supply of supplementary fish feeds was 1.22 ± 0.24 kg fish⁻¹ pond⁻¹. In addition to fishmeal, the marine compound feed contained a mixture of soybean, wheat, and to a lesser degree rapeseed and corn meal (Table 1).

Zooplankton represent the main natural food source for farm-raised common carp (Schlott 2007). In all ponds, *Daphnia longispina* and *Bosmina longirostris* were the dominant zooplankton species, followed by cyclopoid (*Eucyclops* sp.) and, to a lesser extent, calanoid copepods (*Eudiaptomus* sp.). No benthic invertebrates were observed in sediments (analyses of sediments) or in carp guts (visual inspection of gut contents).

2.2 Sampling

Carp (n=5; per pond) and corresponding zooplankton of each pond were collected after the cultivation period (210 days; April to November). Fish were measured (± 0.1 cm),

weighed (± 0.1 g), and kept frozen (-80°C) to limit possible lipolytic degradation. Subsequently, samples of eight tissues were taken from each fish: dorsal muscle, ventral muscle, heart, kidney, intestine, eyes, liver and adipose tissue. Samples were stored at -80°C until further analyses.

2.3 Lipid analysis

Total lipids and FA were analyzed as described by Heissenberger et al. (2010). In brief, homogenized, freeze-dried samples (15-30 mg dry material, DM) were sonicated and vortexed (4X) in a chloroform-methanol mixture. Organic layers were removed after each turn and transferred into a clean vial. For gravimetric determination of total lipid concentrations per unit biomass (i.e., mg lipids g dry weight⁻¹), subsamples (100 μL) of the extracts (duplicates) were evaporated and weighed.

Extracts were then separated into lipid classes by thin-layer chromatography (TLC). Concentrations of lipid extracts were adjusted after gravimetry with chloroform to obtain similar lipid amounts (15-25 μg) in the volume (50 μL) applied to the TLC plates for all samples. Lipid classes (PL and TAG) were separated by one-dimensional TLC on 10 x 10 cm silica gel plates (Merck™ TLC silica gel 60) using hexane:diethyl ether:methanol:formic acid (90:20:3:2, v/v/v/v) as solvent system. After development, plates were sprayed with 0.05% (wt/vol) 8-anilino-4-naphthosulphonic acid in methanol and viewed under UV light to detect lipid fractions. An internal standard (5 μL ; nonadecanoic acid in chloroform; 4 mg mL⁻¹) was added to each lipid fraction before individual lipid fractions were scraped from the TLC plates and transferred into a clean vial.

Fatty acids were derivatized to obtain fatty acid methyl esters (FAME) using toluene and sulfuric acid-methanol-solution (1% v/v, 16 h at 50°C). In contrast to Heissenberger et al. (2010), hexane was used instead of BHT for the washing step after methylation. FAME were identified by comparison with known standards (Supelco FAME37) using a gas

chromatograph (Thermo Scientific TRACE GC Ultra™) equipped with a flame ionization detector (FID) and a Supelco™ SP™-2560 column (100 m, 25 mm i.d., 0.2 µm film thickness). Quantification of FA was performed by comparison with a known concentration of an internal standard (nonadecanoic acid, 19:0) using Excalibur 1.4™ (Thermo Electron Corporation).

2.4 Statistical analysis

One-way analysis of variance (ANOVA) was employed to analyze concentration differences of FA between samples. Fatty acid concentrations were converted to relative amounts and arcsine transformed before analysis to meet requirements for normal distribution and homogeneity of variances. The level of significance was set at $p < 0.05$.

Principal component analysis (PCA) were used to analyze the changes of tissue FA composition. The two principal components (PC1 and PC2), representing individual tissue FA were used for analyses. PCA was run separately for PLFA and NLFA. The sample scores on PC1 and PC2 for each tissue, were used as new variables (PCscores), representing the major trend in the FA composition (van Dooremalen et al. 2011).

Analysis of variance was used on the PC scores (separately for PLFA and NLFA) to test for differences of FA composition between tissues and diets. To test for a tissue-specific NLFA and PLFA response to diet the interaction between the independent variables “tissue” and “diet” was evaluated using analysis of covariance (ANCOVA). Differences in total lipid concentrations ($\text{mg g dry weight}^{-1}$) between tissue and diet were evaluated by ANOVA. All statistical tests were conducted by using Microsoft Office 2010 and the software package XLSTAT (version 7.5.2.; T. Fahmy).

3 Results

3.1 Total lipids

Muscle tissues (FO) and eyes (FO) had the highest concentrations of total lipids (482 ± 64.3 and 770.4 ± 47.2 mg g⁻¹, respectively). Lipid concentrations per unit tissue biomass (mg g dry weight⁻¹) increased by 50% between the natural diet (N) and FO, but increased >8X in ventral muscle and >4X in dorsal muscle tissues and eyes. Liver and intestine total lipid concentrations were less affected between diets N and FO (factor 1.6 and 1.5, respectively). Total lipid concentrations of FO-fed fish were significantly higher ($p < 0.0001$) than lipid concentrations of N and VO-fed fish, which did not differ significantly ($p = 0.27$).

3.2 Fatty acid composition

Experimental diets had relatively less PUFA (Table 2) than zooplankton (Table 3). Fatty acid concentrations among experimental diets and fish tissues differed significantly (Table 4). Palmitic acid (16:0), steric acid (18:0), oleic acid (18:1n-9), ARA, EPA, and DHA were the most abundant FA in PL of all tissues (Table A; supplemental material). The highest concentrations of PL were found in the kidneys of N-fed carp (66.2 ± 3.1 mg g⁻¹). Kidney had also the highest concentrations of SAFA, MUFA and PUFA. Fish eyes contained the lowest PUFA concentrations of all investigated tissues (4.4 ± 0.7 mg g⁻¹ (FO)). Dorsal muscle tissue (FO diet) showed the lowest SAFA concentrations of all tissues (9.5 ± 0.8 mg g⁻¹), whereas ventral muscle tissue (VO diet) had the lowest MUFA concentrations (4.4 ± 0.7 mg g⁻¹). Of all tissues the heart (VO) displayed the highest concentrations of LIN (3.3 ± 0.6 mg g⁻¹). Liver showed decreased concentrations of LIN and ALA compared to other tissues, but had the highest n-3/n-6 ratio (4.3 ± 0.4 ; FO diet). Adipose tissue and kidney had the highest DHA concentrations (7.9 ± 2.4 mg g⁻¹ and 7.8 ± 1.3 mg g⁻¹, respectively). For all tissues n-6 PUFA were lower in FO fish. The n-3/n-6 ratio was higher in all tissues of FO fish (>2) than in N

and VO-fed fish (<1.7). Fish fed on FO diet had a significantly higher EPA/ARA ratio than N and VO-fed fish.

Results of thin layer chromatography showed that NL mainly consisted of TAG. Palmitic acid (16:0), oleic acid (18:1n-9), LIN, and ALA were the most abundant FA in TAG (Table B; suppl. material). The eyes contained increased overall lipid concentrations for all diets. The highest concentration of TAG was found in the eyes of FO-fed carp ($661.9 \pm 74.1 \text{ mg g}^{-1}$), followed by ventral muscle tissue ($391.8 \pm 33.99 \text{ mg g}^{-1}$). Among tissues, all FA had the highest concentration in the eyes of FO-fed fish. Liver showed the lowest TAG concentrations of all tissues and for all diets and displayed the highest n-3/n-6 ratio (2.0 ± 0.2 ; FO). Fish of pond N and VO had low TAG concentrations (Table B), which increased in pond FO. In all tissues the n-3/n-6 ratio was higher for FO-fed fish than for the N or VO treatment.

3.3 Fatty acid patterns in polar and neutral lipids of common carp

Principal component analysis of PL (Figure 1) revealed that the first two components (PC1 and PC2) explained 52% of FA variation in carp. The first component (31%) separated n-6 PUFA (positive scores) from palmitic acid, MUFA and DHA (negative scores). The second component accounted for 21% of variation and discriminated between n-3 HUFA and the other FA. The factor score plot separated two groups, the n-6 PUFA in the upper right quarter, containing fish of the reference pond and pond VO, and n-3 PUFA in the lower left quarter, representing carp of the FO pond. The FA composition differed significantly between tissues and among diets ($p < 0.0001$, Table 4) and the interaction between these two factors (diet*tissue) was also significant ($p = 0.003$). On the tissue level, the FA composition of eyes was significantly different from all other tissues ($p < 0.0001$).

The two principal components for TAG explained 67% of the total FA variation (Figure 2). Component 1 accounted for 49% of the variation and separated n-3 PUFA from n-6 PUFA, SAFA and oleic acid. Component 2 (18%) separated n-6 PUFA, 20:3n-3, and ALA

from palmitic acid, 16:1-n7, and DHA. The factor score plot revealed three groups on basis of dietary treatment. Significant differences of tissue FA patterns were found between diets ($p < 0.0001$), tissues ($p < 0.0001$) with a significant interaction of these two factors (diet*tissue; $p = 0.01$). The first component did not separate FA of diets N and FO ($p = 0.545$), but the second principal component showed that FA of all diet sources were different from each other ($p < 0.0001$). Differences among tissues within the diet groups were significant for N ($p = 0.001$) and VO ($p = 0.009$), but not significant for fish fed on FO ($p = 0.097$; Fig. 2B). Liver FA patterns were significantly different from all the other tissues ($p = 0.006$) and liver FA concentrations were consistently lower compared with all other tissues.

4 Discussion

The present study demonstrates a tissue and lipid-class specific FA response to diet in common carp. Our results revealed that FA signatures of TAG are tissue specific at low TAG levels and represent the FA patterns of the diet at high TAG levels. However, the FA composition of PL was altered to a far lesser extent, as only when high amounts of n-3 rich fish oil were available, PL responded to diet by preferentially incorporating n-3 HUFA.

The composition of PL was highly influenced by the specific tissues, clearly indicating tissue-specific FA requirements of their cell membranes. Based on PCA, C18 FA (except 18:2n-6) differentiated the eyes and ventral muscle in carp exposed to FO from the other tissues, which were more influenced by DHA and EPA. Eyes and ventral muscle tissues showed lower PUFA concentrations in PL than other tissues, but had the highest total lipid content of all tissues. The high lipid content of these tissues may affect PLFA composition, as high lipid content generally affects FA composition in carp (Du et al. 2006).

Fatty acid signatures of PL did not change between carp feeding on natural and vegetable oil enriched diet. Omega-6 PUFA, mainly LIN and ARA, were present at high concentrations in PL of carp fed on N and VO diets that contained considerable concentrations of n-6 PUFA. In the presence of a n-3 PUFA-rich diet source (in particular FO), n-3 PUFA, mainly EPA and DHA, were preferentially incorporated into the polar lipid fraction at the expense of n-6 PUFA. In general, PUFA were more efficiently accumulated in PL than SAFA or MUFA, which lends support to previous observations (Linares and Henderson 1991, Sargent 2002, Skalli 2006, Glencross 2009). These findings show that both carp clearly respond to dietary n-3 and n-6 PUFA that are subsequently retained in PLFA.

Contrary to our hypothesis, FA in TAG showed a tissue specific response to diet. In the case of low TAG contents of fish feeding on N and VO, the FA composition of TAG was tissue specific. For example, when liver, heart, dorsal and ventral muscle tissues, as well as

intestine and adipose tissues had TAG concentrations $<30 \text{ mg g}^{-1}$ ($<250 \text{ mg g}^{-1}$ for eyes), their FA composition in TAG differed greatly among these tissues, demonstrating that the retention of FA in these tissues is not a simple function of dietary supply at such low lipid concentrations. In contrast, FO-diet supplied high dietary lipid concentrations and resulted in increased TAG concentrations in all sampled tissues. Moreover, FA compositions of tissues were similar among each other and, as hypothesized, represented those FA compositions of the diet, as was also shown in Atlantic salmon (*Salmo salar*; Nanton et al. 2007), Atlantic cod (*Gadus morhua*; Mørkøre et al. 2007), Murray cod (*Maccullochella peelii peelii*; Francis et al. 2006) and European sea bass (*Dicentrarchus labrax*; Mourente et al. 2005). Therefore, we conclude that the retention of dietary FA in tissues largely depends on the amount of TAG concentration.

Triacylglycerols consist of excess dietary lipids that were exported from the liver to be accumulated in specific lipid storage sites as mesenteric adipose tissue, red and white muscle and between skin and muscle (Tocher 2003). Mobilization and oxidation of TAG may differ among tissues. Fatty acid binding proteins that facilitate the intracellular transport of FA are known to be tissue specific (Veerkamp and Maatman 1995, Tocher 2003) and might therefore promote specific TAG FA patterns in carp with low levels of TAG. Fatty acid concentrations in NL are more variable than FA in PL, which may be due to the important structural and metabolic functions of PL, resulting in a more conservative FA composition, and the inhomogeneous total lipid content of carp, mainly reflected in NL, as also shown for carp of similar age (Fauconneau et al. 1995).

Fatty acid profiles of TAG in liver tissue were significantly different from all other tissues and showed high amounts of SAFA. The liver is the principal site of lipid metabolism and FA synthesis (Tocher 2003). The main products of the lipogenesis in fish are the SAFA palmitic acid (16:0) and stearic acid (18:0) (Sargent et al. 1989) and also their desaturation

products palmitoleic acid (16:1n-7) and oleic acid (18:1n-9) (Tocher 2003). However, dietary n-3 HUFA effectively reduce lipogenesis (Shikata and Shimeno 1994, Wang et al. 2005) and therefore liver FA patterns in those carp with dietary access to FO may have been less different from other tissues compared to carp exposed to N and VO, in which the products of lipogenesis caused a significant difference in the FA profile compared to all other tissues. We consequently reject or null hypothesis and state that NLFA of carp are tissue specific.

Polar lipids of muscle tissues reacted differently when fish oil was the dietary lipid source. Ventral muscle showed lower concentrations of EPA and DHA compared with dorsal muscle tissue. Ventral muscle contained higher total lipid concentrations than dorsal muscle. This affects the PL composition as PUFA increase more slowly with increasing total lipid content than other FA (Henderson & Tocher 1987, De Smet et al. 2004). Glencross et al. (2003) reported considerable variability in the retention efficiency among different FA in red seabream (*Pagrus auratus*). Biologically important FA, such as EPA and DHA, had only moderate retention efficiencies (Glencross 2009). Findings for muscle tissues support our hypothesis that PLFA are tissue specific.

Eyes had generally high lipid and highest DHA concentrations of all tissues. Eyes were particularly rich in TAG as was also reported for fatty fish species such as Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) (Stoknes et al. 2004). The distinct FA composition of eyes (see PCA; Fig. 1) was due to the amount of docosapentaenoic acid (22:5n-3, DPA) and palmitic acid. The low amount of PUFA in PL of the eyes compared to other tissues was unexpected because fish eyes are generally rich in PUFA, especially DHA (Bell et al. 1995). However, Stoknes et al. (2004) reported that the total amount of PUFA in eyes was higher for lean (<2% fat in muscle tissue) than for fatty fish species. Accordingly, Tocher and Harvie (1988) reported that cod (lean species) retinal lipids were more unsaturated than the trout retinal lipids. By having separated lipid classes of eyes we demonstrate that

most of the DHA in eyes of carp is associated with storage and less with structural lipids. Finally, it is evident that fish eyes clearly respond to dietary supply of high lipid concentrations and their FA as increasing TAG of eyes also retained dietary FA.

The present study revealed that the diet significantly affected intestine FA composition. Modification of lipid and FA composition of intestinal cells through diet has been shown in Gilthead seabream (*Sparus aurata*; Caballero et al. 2003), Atlantic salmon (*Salmo salar*; Ruyter et al. 2006) and rainbow trout (*Oncorhynchus mykiss*; Oxley et al. 2005). Resulting morphological and histological modifications of the intestine may cause altered digestion and absorption capabilities (Caballero et al. 2003, Martins et al. 2006). We found a decreased EPA/ARA ratio in PL of intestines in carp fed natural and vegetable oil diets. This may decrease membrane fluidity (Leray et al. 1984) and disturb the epithelial barrier function and function of membrane-bound enzymes, as reported for Atlantic salmon (Jutfelt et al. 2007). Therefore, it is evident that intestine PLFA do respond to dietary FA and our null hypothesis needs to be rejected.

Highly unsaturated fatty acid ratios showed various differences among tissues. The eyes had consistently increased DHA/EPA and DHA/ARA ratios compared to other tissues, emphasizing the important role of DHA in eyes (Bell et al. 1995, SanGiovanni and Chew 2005). High EPA/ARA ratios in muscle tissues were the result of low ARA concentrations in these tissues compared to other tissues. This ratio is especially important in PL as it affects the production and actions of eicosanoids (Tocher 2003, Wada et al., 2007). Arachidonic acid is the preferred substrate for eicosanoids in fish (Tocher 2003), but high levels of ARA derived eicosanoids are considered to be pathological (Okuyuma et al., 1996). Hence a high EPA/ARA ratio in fish muscle tissue should have positive effects on fish health and high tissue quality for consumers.

Carp exposed to FO diet contained high EPA/ARA ratios in all tissues compared to fish with dietary access to N and VO diets. The high EPA/ARA ratio was the result of higher concentrations of EPA supplied by dietary FO and decreasing ARA retention, resulting in low concentrations of ARA in all tissues. The effect of FO-induced higher EPA/ARA ratios in carp remains to be elucidated in an effort to understand how high diet quality affects somatic development of this important diet fish.

Adding high amounts of PUFA to the diet (FO) had severe effects on quality and quantity of FA in carp tissues. Feeding on FO resulted in increased total lipid concentrations of fish, increased n-3 FA in TAG, and a higher n-3/n-6 PUFA ratio in all tissues, suggesting that NLFA are strongly affected by dietary FA supply. Steffens and Wirth (2007) also found high amounts of n-3 PUFA in carp fed diets with high levels of fish oil. These findings may have direct implications on freshwater fish health, which is particularly sensitive to excess n-3 PUFA (Montero and Izquierdo 2011).

In conclusion, our controlled field study has shown that the response of FA signatures in carp to different diets is tissue and lipid class specific. Our major finding was that FA composition of TAG was tissue specific at low TAG concentrations, but reflected dietary FA composition at high TAG concentrations in carp. Despite the general robustness of PL FA signatures, PL changed their FA composition by preferentially incorporating n-3 HUFA when high amounts of fish oil were available.

Our findings provide new insights into tissue-specific FA patterns and expand our knowledge of basic carp physiology. In consideration of our results, rearing methods can be improved to increase the amount of beneficial n-3 PUFA in carp. Fish feeds should be formulated in consideration of the complex reactions and interactions of different organs and the effects on general fish health. Sustainable high quality fish feeds are desired as this study indicates that carp is strongly responsive to n-3 PUFA retention.

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Figures and Tables

Fig. 1:

Component plot (A) and factor score plot (B) of the principal component analysis for the fatty acid profile of polar lipids in 8 different tissues of carp fed 3 different diets. White symbols refer to the natural diet (N), grey symbols refer to the VO diet and black symbols refer to the FO diet. Tissues are labeled by shortcuts: adipose tissue (AT), dorsal muscle (DM), eyes (EYE), heart (H), intestine (INT), kidney (K), liver (L) and ventral muscle (VM). Data values are represented in the factor score plot as mean $\pm$ SEM (n=5).

Fig. 2:

Component plot (A) and factor score plot (B) of the principal component analysis for the fatty acid profile of neutral lipids in 8 different tissues of carp fed 3 different diets. White symbols refer to the natural diet (N), grey symbols refer to the VO diet and black symbols refer to the FO diet. Tissues are labeled by shortcuts: adipose tissue (AT), dorsal muscle (DM), eyes (EYE), heart (H), intestine (INT), kidney (K), liver (L) and ventral muscle (VM). Data values are represented in the factor score plot as mean $\pm$ SEM (n=5).

Fig. 1:

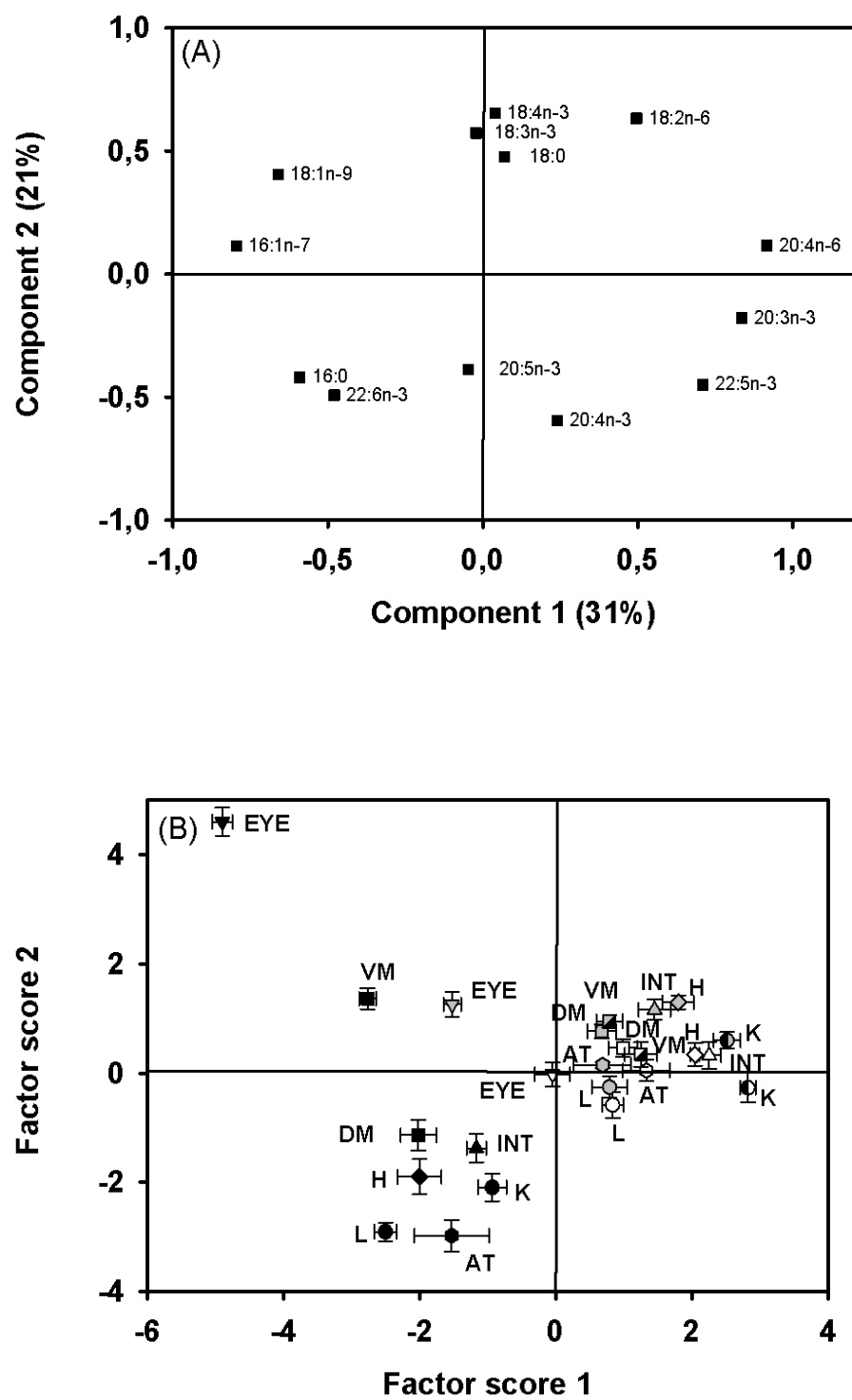


Fig. 2:

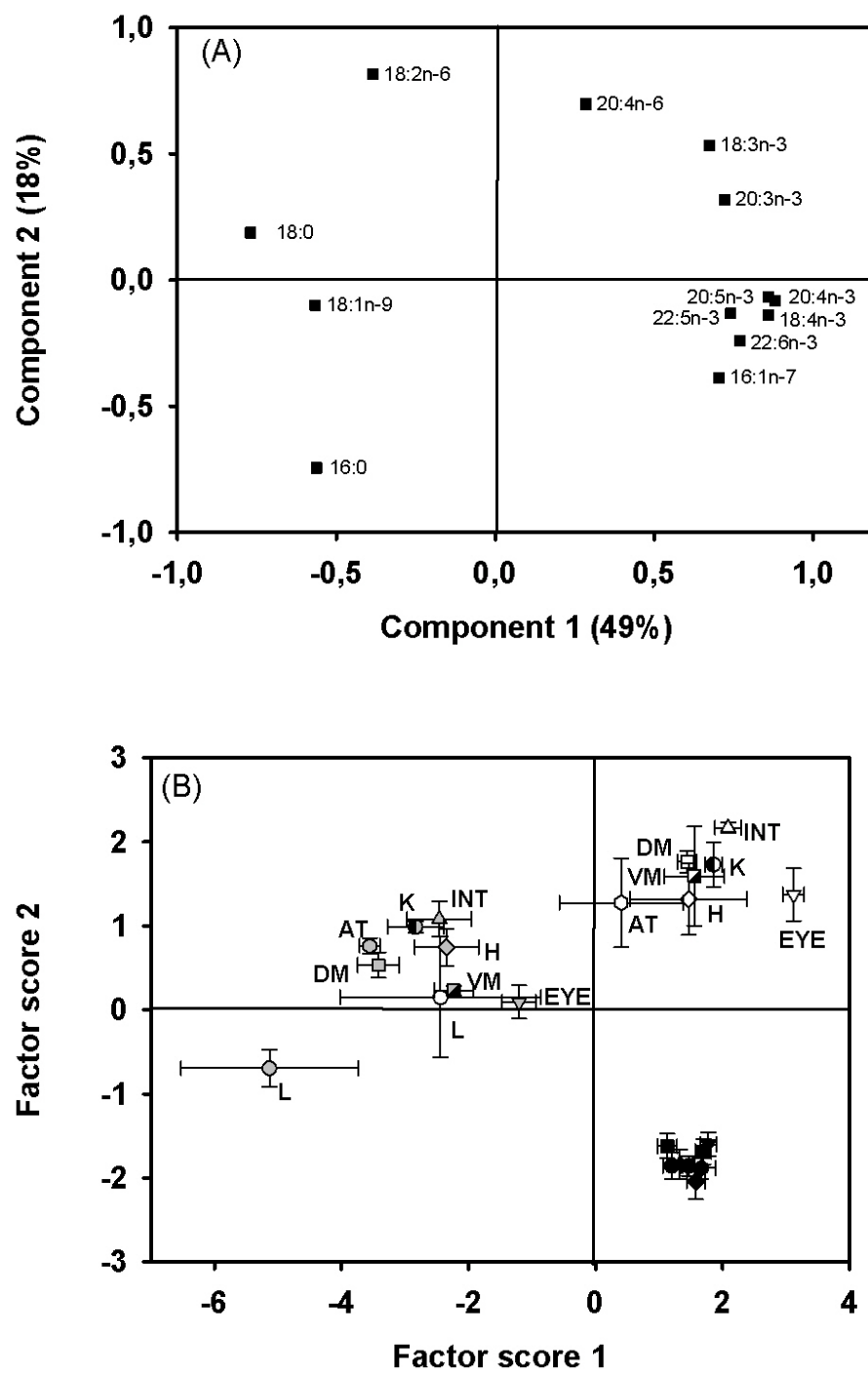


Table 1: Relative composition (>0.5%) and ingredients of commercial compound feeds
(Garant-Tiernahrung™, Austria)

Composition	FO
Crude protein	36.0
Total lipids	18.0
Fiber	2.5
Ash	9.0
Ingredients	FO
Soybean meal	25.3
Wheat	13.3
Rapeseed press cake	7.5
Corn	3.5
Peas	5.0
Fish meal (68%)	24.3
Soy beans	5.0
Fish oil	3.0
Fish oil (sprayed on)	10.5
Monocalciumphosphate	1.3
Calcium carbonate	0.5

Table 2: Fatty acid composition of experimental diets (% of total FAME, mean $\pm$ SD, n=3)

Asterisks indicate significant differences between diets: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$;

n.s. = no significant difference, $P \geq 0.05$ (Student's t-test, $P < 0.05$)

Fatty acid	VO	FO
14:0	1.1 $\pm$ 0.3	7.1 $\pm$ 0.3 *
15:0	0.1 $\pm$ 0.0	0.5 $\pm$ 0.0 ***
16:0	12.6 $\pm$ 1.4	19.5 $\pm$ 0.3 ***
16:1n-7	0.1 $\pm$ 0.0	6.8 $\pm$ 0.2 ***
17:0	0.1 $\pm$ 0.0	0.3 $\pm$ 0.0 ***
18:0	2.9 $\pm$ 0.4	3.0 $\pm$ 0.0 n.s.
18:1n-9	34.9 $\pm$ 3.2	17.6 $\pm$ 0.1 ***
18:2n-6	40.2 $\pm$ 3.3	7.2 $\pm$ 0.0 ***
18:3n-6	0.0 $\pm$ 0.0	0.2 $\pm$ 0.0
18:3n-3	3.8 $\pm$ 0.4	2.3 $\pm$ 0.0 **
18:4n-3	0.1 $\pm$ 0.0	3.9 $\pm$ 0.0 ***
20:0	0.8 $\pm$ 0.1	0.3 $\pm$ 0.0 ***
20:1n-9	0.8 $\pm$ 0.1	6.1 $\pm$ 0.1 ***
20:3n-6	0.0 $\pm$ 0.0	0.2 $\pm$ 0.0
20:3n-3	0.0 $\pm$ 0.0	0.1 $\pm$ 0.0
20:4n-6	0.0 $\pm$ 0.0	0.8 $\pm$ 0.0
20:4n-3	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0
20:5n-3	0.0 $\pm$ 0.0	10.3 $\pm$ 0.1
22:0	0.8 $\pm$ 0.1	0.1 $\pm$ 0.1 ***
22:1n-9	0.1 $\pm$ 0.0	0.5 $\pm$ 0.0 ***
22:6n-3	0.0 $\pm$ 0.0	11.0 $\pm$ 0.4
24:0	0.3 $\pm$ 0.0	0.1 $\pm$ 0.0 **
24:1n-9	0.1 $\pm$ 0.0	0.8 $\pm$ 0.0 ***
Σ SAFA	19.9 $\pm$ 1.5	31.2 $\pm$ 0.6 ***
Σ MUFA	35.9 $\pm$ 3.1	32.0 $\pm$ 0.0 n.s.
Σ PUFA	44.1 $\pm$ 3.7	36.8 $\pm$ 0.7 *
Σ n-3 PUFA	3.9 $\pm$ 0.4	28.5 $\pm$ 0.6 ***
Σ n-6 PUFA	40.2 $\pm$ 3.3	8.3 $\pm$ 0.1 ***

VO, diet enriched with 3% vegetable oil; FO, diet enriched with 18% marine fish oil; SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids

Table 3: Fatty acid composition of zooplankton (500µm) in the experimental ponds (% of total FAME, mean $\pm$ SD, n=3)

^{a,b,c}, Mean values within a row with unlike superscript letters were significantly different (P<0.05)

Fatty acid	N	VO	FO
14:0	4.4 $\pm$ 0.5 ^{ab}	4.6 $\pm$ 1.4 ^a	1.8 $\pm$ 0.3 ^b
15:0	1.6 $\pm$ 0.1 ^a	1.6 $\pm$ 0.2 ^a	0.4 $\pm$ 0.1 ^b
16:0	15.7 $\pm$ 0.7 ^{ab}	16.1 $\pm$ 0.2 ^a	14.4 $\pm$ 0.5 ^b
16:1n-7	6.4 $\pm$ 0.2 ^b	7.8 $\pm$ 0.6 ^a	4.7 $\pm$ 0.3 ^c
17:0	1.5 $\pm$ 0.1 ^a	1.5 $\pm$ 0.0 ^a	0.9 $\pm$ 0.0 ^b
18:0	5.0 $\pm$ 0.5	4.2 $\pm$ 0.6	3.8 $\pm$ 0.3
18:1n-9	6.7 $\pm$ 0.6 ^b	11.5 $\pm$ 0.2 ^a	4.0 $\pm$ 0.5 ^c
18:2n-6	5.7 $\pm$ 1.9 ^a	6.2 $\pm$ 0.1 ^a	2.9 $\pm$ 0.3 ^b
18:3n-6	0.5 $\pm$ 0.1 ^b	1.2 $\pm$ 0.0 ^a	0.3 $\pm$ 0.0 ^c
18:3n-3	11.1 $\pm$ 0.1 ^b	13.4 $\pm$ 0.2 ^a	13.1 $\pm$ 0.8 ^a
18:4n-3	10.6 $\pm$ 0.2 ^b	10.1 $\pm$ 0.3 ^b	22.9 $\pm$ 1.6 ^a
20:0	0.4 $\pm$ 0.2 ^a	0.1 $\pm$ 0.0 ^{ab}	0.1 $\pm$ 0.1 ^b
20:1n-9	0.2 $\pm$ 0.0 ^b	0.2 $\pm$ 0.0 ^b	0.5 $\pm$ 0.1 ^a
20:3n-6	0.2 $\pm$ 0.0 ^a	0.2 $\pm$ 0.0 ^a	0.1 $\pm$ 0.0 ^b
20:3n-3	0.3 $\pm$ 0.0 ^b	0.2 $\pm$ 0.0 ^b	0.6 $\pm$ 0.1 ^a
20:4n-6	3.0 $\pm$ 0.5 ^b	4.2 $\pm$ 0.2 ^a	1.0 $\pm$ 0.0 ^c
20:4n-3	1.6 $\pm$ 0.1 ^b	1.2 $\pm$ 0.2 ^b	3.2 $\pm$ 0.6 ^a
20:5n-3	14.7 $\pm$ 0.3 ^b	11.6 $\pm$ 0.6 ^c	17.3 $\pm$ 1.0 ^a
22:0	0.3 $\pm$ 0.1 ^a	0.1 $\pm$ 0.0 ^b	0.0 $\pm$ 0.0 ^c
22:1n-9	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
22:6n-3	8.8 $\pm$ 2.2 ^a	2.9 $\pm$ 0.4 ^b	7.3 $\pm$ 1.7 ^a
24:0	0.4 $\pm$ 0.0	0.2 $\pm$ 0.2	0.2 $\pm$ 0.0
24:1n-9	0.4 $\pm$ 0.1	0.3 $\pm$ 0.1	0.2 $\pm$ 0.0
Σ SAFA	29.7 $\pm$ 0.8 ^a	28.6 $\pm$ 1.3 ^a	21.7 $\pm$ 1.3 ^b
Σ MUFA	13.9 $\pm$ 0.3 ^b	20.0 $\pm$ 0.4 ^a	9.7 $\pm$ 0.1 ^c
Σ PUFA	56.4 $\pm$ 0.5 ^b	51.3 $\pm$ 1.7 ^c	68.7 $\pm$ 1.3 ^a
Σ n-3 PUFA	47.0 $\pm$ 2.1 ^b	39.5 $\pm$ 1.5 ^c	64.4 $\pm$ 1.1 ^a
Σ n-6 PUFA	9.4 $\pm$ 2.6 ^a	11.8 $\pm$ 0.2 ^a	4.2 $\pm$ 0.3 ^b

N, natural diet (zooplankton); VO, diet enriched with 3% vegetable oil; FO, diet enriched with 18% marine fish oil; SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids

Table 4: Differences between diet groups, tissues and the interaction of diet and tissue tested by analysis of covariance (ANCOVA) for two lipid classes, phospholipids (PL) and triacylglycerols (TAG). Asterisks indicate significant differences: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = no significant difference

Factors	<i>d.f.</i>	<i>F</i>	<i>P</i>
PL			
Diet	7	61.5	***
Tissue	2	544.5	***
Interaction	14	2.6	**
TAG			
Diet	7	8.2	***
Tissue	2	132.0	***
Interaction	14	2.3	*

Table A: Fatty acid composition of polar lipid fraction of tissues of common carp (*Cyprinus carpio*) fed different diets (mg FAME g⁻¹ dry weight, mean ± SD, n=5)

^{a,b,c}, Mean values within a row with unlike superscript letters were significantly different (p<0.05)

Table B: Fatty acid composition of neutral lipid fraction of tissues of common carp (*Cyprinus carpio*) fed different diets (mg FAME g⁻¹ dry weight, mean ± SD, n=5)

^{a,b,c}, Mean values within a row with unlike superscript letters were significantly different (p<0.05)

1 Table A (suppl. material)

	Intestine			Eye			Kidney			Liver		
	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18
16:0	10,6 ^{ab} +/- 2,0	9,7 ^b +/- 1,7	14,8 ^a +/- 3,9	7,4 ^{ab} +/- 1,1	8,0 ^a +/- 1,0	6,1 ^b +/- 0,6	18,0 ^{ab} +/- 1,5	16,1 ^b +/- 3,7	21,9 ^a +/- 2,3	13,7 +/- 2,3	10,9 +/- 1,9	12,8 +/- 1,4
16:1n-7	1,3 ^{ab} +/- 0,4	0,8 ^b +/- 0,2	1,5 ^a +/- 0,3	1,3 +/- 0,2	1,1 +/- 0,2	1,2 +/- 0,3	1,9 ^b +/- 0,2	1,3 ^c +/- 0,3	2,7 ^a +/- 0,2	2,0 ^a +/- 0,4	1,1 ^b +/- 0,3	1,7 ^a +/- 0,3
18:0	6,0 +/- 1,2	5,4 +/- 1,0	5,5 +/- 1,2	3,7 ^a +/- 0,4	3,8 ^a +/- 0,4	2,8 ^b +/- 0,3	7,2 +/- 0,5	7,0 +/- 1,3	7,8 +/- 0,9	3,6 ^a +/- 0,5	3,4 ^a +/- 0,4	2,6 ^b +/- 0,1
18:1n-9	3,9 +/- 0,9	3,3 +/- 0,8	4,6 +/- 0,8	4,0 ^{ab} +/- 0,8	4,3 ^a +/- 0,5	3,1 ^b +/- 0,5	5,5 ^b +/- 0,6	5,1 ^b +/- 1,3	7,2 ^a +/- 0,4	4,5 +/- 0,9	3,6 +/- 0,7	3,9 +/- 0,4
18:2n-6	2,0 ^a +/- 0,7	1,7 ^{ab} +/- 0,3	1,0 ^b +/- 0,3	1,2 ^b +/- 0,3	1,6 ^a +/- 0,2	0,8 ^c +/- 0,1	2,9 ^a +/- 0,7	3,1 ^a +/- 1,1	1,4 ^b +/- 0,1	1,9 ^a +/- 0,7	1,3 ^a +/- 0,2	0,6 ^b +/- 0,1
18:3n-3	0,6 ^a +/- 0,2	0,3 ^b +/- 0,1	0,3 ^b +/- 0,1	0,3 +/- 0,1	0,3 +/- 0,1	0,4 +/- 0,1	0,6 ^a +/- 0,1	0,4 ^b +/- 0,1	0,4 ^b +/- 0,1	0,4 ^a +/- 0,2	0,2 ^b +/- 0,1	0,1 ^b +/- 0,0
18:4n-3	0,5 ^a +/- 0,2	0,3 ^b +/- 0,1	0,4 ^b +/- 0,1	0,3 +/- 0,0	0,2 +/- 0,0	0,3 +/- 0,1	0,8 ^a +/- 0,2	0,5 ^b +/- 0,2	0,5 ^b +/- 0,1	0,5 ^a +/- 0,2	0,3 ^{ab} +/- 0,0	0,2 ^b +/- 0,0
20:4n-6	6,5 ^a +/- 1,7	4,8 ^a +/- 1,1	2,0 ^b +/- 0,4	3,0 ^a +/- 0,4	2,4 ^a +/- 0,5	0,3 ^b +/- 0,1	11,6 ^a +/- 1,5	9,8 ^a +/- 2,1	3,8 ^b +/- 0,7	5,5 ^a +/- 1,3	4,1 ^a +/- 0,7	1,1 ^b +/- 0,1
20:5n-3	3,4 ^{ab} +/- 1,2	1,7 ^b +/- 0,4	3,7 ^a +/- 1,4	1,5 ^a +/- 0,1	1,1 ^b +/- 0,2	1,0 ^b +/- 0,2	4,6 ^a +/- 0,6	2,9 ^b +/- 0,5	5,8 ^a +/- 1,3	2,7 ^a +/- 0,6	1,4 ^b +/- 0,3	2,2 ^a +/- 0,2
22:5n-3	0,8 ^a +/- 0,2	0,4 ^b +/- 0,1	0,6 ^{ab} +/- 0,2	0,6 ^a +/- 0,1	0,5 ^b +/- 0,1	0,0 ^c +/- 0,0	2,0 ^a +/- 0,2	1,3 ^b +/- 0,2	1,5 ^b +/- 0,3	1,0 ^a +/- 0,2	0,9 ^{ab} +/- 0,0	0,7 ^b +/- 0,1
22:6n-3	4,1 ^{ab} +/- 1,1	2,5 ^b +/- 0,6	5,7 ^a +/- 1,7	4,8 ^a +/- 0,4	3,7 ^b +/- 0,5	1,6 ^c +/- 0,3	4,7 ^b +/- 0,6	2,9 ^c +/- 0,8	7,8 ^a +/- 1,3	3,6 ^a +/- 0,7	2,3 ^b +/- 0,6	4,5 ^a +/- 0,4
ΣSAFA	19,6 +/- 3,6	16,7 +/- 2,7	22,3 +/- 5,6	12,4 ^a +/- 1,6	12,7 ^a +/- 1,5	9,6 ^b +/- 1,0	29,2 ^{ab} +/- 1,4	25,3 ^b +/- 5,1	31,8 ^a +/- 3,2	20,3 ^a +/- 3,3	15,8 ^b +/- 2,2	16,8 ^{ab} +/- 1,7
ΣMUFA	6,0 ^{ab} +/- 1,4	4,6 ^b +/- 1,0	7,8 ^a +/- 1,7	5,7 +/- 1,1	5,7 +/- 0,7	4,8 +/- 0,9	8,3 ^b +/- 0,9	7,1 ^b +/- 1,7	12,0 ^a +/- 0,6	7,0 ^a +/- 1,4	5,0 ^b +/- 0,9	6,8 ^{ab} +/- 0,9
ΣPUFA	18,8 ^a +/- 4,5	12,2 ^b +/- 2,3	14,3 ^b +/- 3,8	12,2 ^a +/- 0,3	10,1 ^b +/- 1,5	4,4 ^c +/- 0,7	28,6 ^a +/- 1,0	22,1 ^b +/- 5,0	21,9 ^b +/- 3,5	16,3 ^a +/- 3,3	10,9 ^b +/- 1,6	9,6 ^b +/- 0,5
Σn-3	9,8 ^a +/- 2,9	5,2 ^b +/- 1,1	10,9 ^a +/- 3,0	7,7 ^a +/- 0,3	5,7 ^b +/- 0,9	3,1 ^c +/- 0,6	13,2 ^a +/- 1,2	8,2 ^b +/- 1,6	16,2 ^a +/- 2,9	8,4 ^a +/- 1,8	5,2 ^b +/- 0,8	7,8 ^a +/- 0,4
Σn-6	9,0 ^a +/- 2,2	7,0 ^a +/- 1,4	3,4 ^b +/- 0,7	4,5 ^a +/- 0,2	4,4 ^a +/- 0,6	1,3 ^b +/- 0,2	15,4 ^a +/- 1,4	13,9 ^a +/- 3,5	5,8 ^b +/- 0,7	7,9 ^a +/- 1,8	5,7 ^b +/- 0,8	1,8 ^c +/- 0,2
n-3/n-6	1,1 ^b +/- 0,3	0,7 ^c +/- 0,1	3,2 ^a +/- 0,2	1,7 ^b +/- 0,1	1,3 ^c +/- 0,1	2,3 ^a +/- 0,4	0,9 ^b +/- 0,1	0,6 ^b +/- 0,1	2,8 ^a +/- 0,3	1,1 ^b +/- 0,2	0,9 ^b +/- 0,1	4,3 ^a +/- 0,4
EPA/ARA	0,5 ^b +/- 0,2	0,3 ^b +/- 0,0	1,8 ^a +/- 0,4	0,5 ^b +/- 0,1	0,4 ^b +/- 0,0	2,9 ^a +/- 0,6	0,4 ^b +/- 0,1	0,3 ^b +/- 0,0	1,5 ^a +/- 0,2	0,5 ^b +/- 0,1	0,3 ^b +/- 0,0	2,0 ^a +/- 0,2
DHA/EPA	1,2 +/- 0,2	1,5 +/- 0,2	1,5 +/- 0,3	3,1 ^a +/- 0,4	3,5 ^a +/- 0,4	1,6 ^b +/- 0,2	1,0 ^b +/- 0,1	1,0 ^b +/- 0,1	1,3 ^a +/- 0,2	1,4 ^b +/- 0,2	1,6 ^b +/- 0,2	2,1 ^a +/- 0,2
DHA/ARA	0,6 ^b +/- 0,2	0,5 ^b +/- 0,1	2,8 ^a +/- 0,2	1,6 ^b +/- 0,2	1,5 ^b +/- 0,2	4,7 ^a +/- 0,7	0,4 ^b +/- 0,1	0,3 ^b +/- 0,0	2,1 ^a +/- 0,3	0,7 ^b +/- 0,2	0,6 ^b +/- 0,1	4,2 ^a +/- 0,5

	Dorsal muscle			Heart			Adipose tissue			Ventral muscle		
	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18
16:0	8,0 +/- 1,1	7,3 +/- 0,8	6,8 +/- 0,7	10,2 +/- 1,8	13,5 +/- 1,9	14,2 +/- 3,3	14,4 ^b +/- 1,0	13,3 ^b +/- 2,1	19,6 ^a +/- 3,6	6,3 +/- 0,8	6,7 +/- 1,0	7,1 +/- 0,8
16:1n-7	1,1 ^a +/- 0,1	0,7 ^b +/- 0,1	1,1 ^a +/- 0,2	1,3 +/- 0,4	1,3 +/- 0,2	1,7 +/- 0,4	1,3 +/- 0,4	1,2 +/- 0,1	1,7 +/- 0,5	0,8 ^b +/- 0,1	0,6 ^b +/- 0,1	1,3 ^a +/- 0,1
18:0	3,2 ^a +/- 0,4	2,7 ^b +/- 0,3	2,1 ^c +/- 0,2	4,9 ^b +/- 1,1	7,3 ^a +/- 0,9	4,6 ^b +/- 1,0	5,4 +/- 1,2	4,8 +/- 0,3	6,6 +/- 2,0	2,7 +/- 0,5	2,7 +/- 0,3	2,8 +/- 0,5
18:1n-9	4,0 ^a +/- 0,5	3,8 ^{ab} +/- 0,5	3,2 ^b +/- 0,4	3,6 ^b +/- 0,7	5,2 ^a +/- 0,7	4,7 ^{ab} +/- 0,7	5,1 +/- 0,3	4,5 +/- 0,7	5,4 +/- 0,9	3,3 +/- 0,5	3,6 +/- 0,6	3,2 +/- 0,2
18:2n-6	2,3 ^a +/- 0,6	2,3 ^a +/- 0,5	0,7 ^b +/- 0,1	1,9 ^b +/- 0,8	3,3 ^a +/- 0,6	0,8 ^c +/- 0,1	2,3 ^a +/- 0,8	1,6 ^{ab} +/- 0,3	0,9 ^b +/- 0,2	1,8 ^a +/- 0,4	2,0 ^a +/- 0,3	0,8 ^b +/- 0,1
18:3n-3	0,9 ^a +/- 0,3	0,5 ^b +/- 0,1	0,4 ^b +/- 0,1	0,6 ^a +/- 0,3	0,6 ^a +/- 0,1	0,3 ^b +/- 0,1	0,4 +/- 0,1	0,2 +/- 0,0	0,2 +/- 0,2	0,7 ^a +/- 0,2	0,4 ^b +/- 0,1	0,6 ^a +/- 0,1
18:4n-3	0,4 ^a +/- 0,1	0,2 ^b +/- 0,0	0,2 ^{ab} +/- 0,0	0,5 ^a +/- 0,1	0,5 ^a +/- 0,1	0,3 ^b +/- 0,0	0,4 ^a +/- 0,1	0,3 ^{ab} +/- 0,0	0,2 ^b +/- 0,0	0,3 +/- 0,0	0,2 +/- 0,0	0,4 +/- 0,1
20:4n-6	2,9 ^a +/- 0,4	2,5 ^a +/- 0,3	0,8 ^b +/- 0,1	5,9 ^a +/- 1,3	7,5 ^a +/- 0,7	1,8 ^b +/- 0,6	7,3 ^a +/- 0,9	6,3 ^a +/- 0,1	3,0 ^b +/- 0,6	2,5 ^a +/- 0,2	2,3 ^a +/- 0,2	0,6 ^b +/- 0,1
20:5n-3	3,1 ^a +/- 0,3	1,9 ^c +/- 0,2	2,4 ^b +/- 0,2	2,5 +/- 0,6	2,8 +/- 0,2	2,9 +/- 0,7	2,5 +/- 0,7	1,3 +/- 0,1	5,4 +/- 3,5	2,5 ^a +/- 0,3	1,7 ^b +/- 0,2	1,9 ^b +/- 0,3
22:5n-3	0,8 ^a +/- 0,1	0,6 ^b +/- 0,1	0,5 ^c +/- 0,1	1,0 +/- 0,3	1,0 +/- 0,2	0,7 +/- 0,2	1,0 +/- 0,2	0,8 +/- 0,1	0,8 +/- 0,2	0,8 ^a +/- 0,1	0,6 ^b +/- 0,1	0,3 ^c +/- 0,0
22:6n-3	3,6 ^a +/- 0,4	2,8 ^b +/- 0,4	3,4 ^{ab} +/- 0,6	4,2 +/- 1,2	4,2 +/- 0,9	5,8 +/- 1,3	4,1 ^b +/- 0,3	3,0 ^b +/- 0,8	7,9 ^a +/- 2,4	3,1 ^a +/- 0,3	2,2 ^b +/- 0,3	2,2 ^b +/- 0,5
ΣSAFA	12,6 ^a +/- 1,3	10,8 ^b +/- 1,1	9,5 ^b +/- 0,8	17,7 +/- 3,8	22,8 +/- 2,8	20,2 +/- 4,5	22,0 +/- 1,3	19,6 +/- 2,5	27,5 +/- 5,3	10,1 +/- 1,4	10,1 +/- 1,4	10,5 +/- 1,3
ΣMUFA	5,5 +/- 0,6	4,8 +/- 0,6	5,2 +/- 0,6	5,4 ^b +/- 1,2	7,1 ^b +/- 0,9	7,8 ^a +/- 1,1	7,1 +/- 0,6	6,1 +/- 0,8	8,4 +/- 1,4	4,5 +/- 0,7	4,4 +/- 0,7	5,3 +/- 0,4
ΣPUFA	14,5 ^a +/- 1,9	11,3 ^b +/- 1,2	8,7 ^c +/- 1,0	17,4 ^{ab} +/- 4,4	20,7 ^a +/- 2,2	13,0 ^b +/- 2,8	18,8 +/- 2,8	14,0 +/- 0,8	18,9 +/- 6,8	11,9 ^a +/- 0,7	9,9 ^b +/- 0,9	7,0 ^c +/- 1,1
Σn-3	8,9 ^a +/- 1,0	6,1 ^b +/- 0,5	7,0 ^b +/- 0,8	9,1 +/- 2,5	9,1 +/- 1,2	10,0 +/- 2,1	8,6 +/- 1,2	5,6 +/- 0,6	14,6 +/- 6,2	7,4 ^a +/- 0,6	5,2 ^b +/- 0,5	5,2 ^b +/- 0,9
Σn-6	5,6 ^a +/- 1,0	5,2 ^a +/- 0,7	1,7 ^b +/- 0,2	8,3 ^b +/- 1,9	11,7 ^a +/- 1,3	3,1 ^c +/- 0,7	10,2 ^a +/- 1,7	8,4 ^a +/- 0,2	4,3 ^b +/- 0,8	4,6 ^a +/- 0,3	4,7 ^a +/- 0,4	1,8 ^b +/- 0,3
n-3/n-6	1,5 ^b +/- 0,1	1,2 ^c +/- 0,1	4,1 ^a +/- 0,3	1,1 ^b +/- 0,1	0,8 ^b +/- 0,1	3,3 ^a +/- 0,3	0,8 ^b +/- 0,1	0,7 ^b +/- 0,1	3,3 ^a +/- 1,1	1,6 ^b +/- 0,2	1,1 ^c +/- 0,1	2,9 ^a +/- 0,2
EPA/ARA	1,1 ^b +/- 0,1	0,8 ^b +/- 0,0	3,2 ^a +/- 0,3	0,4 ^b +/- 0,1	0,4 ^b +/- 0,0	1,6 ^a +/- 0,3	0,3 ^b +/- 0,1	0,2 ^b +/- 0,0	1,8 ^a +/- 1,1	1,0 ^b +/- 0,1	0,7 ^c +/- 0,0	3,5 ^a +/- 0,2
DHA/EPA	1,2 +/- 0,1	1,4 +/- 0,2	1,4 +/- 0,2	1,7 ^{ab} +/- 0,1	1,5 ^b +/- 0,3	2,0 ^a +/- 0,3	1,6 +/- 0,3	2,4 +/- 0,7	1,5 +/- 0,7	1,2 +/- 0,1	1,3 +/- 0,2	1,2 +/- 0,1
DHA/ARA	1,2 ^b +/- 0,1	1,1 ^b +/- 0,2	4,5 ^a +/- 0,6	0,7 ^b +/- 0,1	0,6 ^b +/- 0,1	3,1 ^a +/- 0,5	0,6 ^b +/- 0,1	0,5 ^b +/- 0,1	2,6 ^a +/- 0,8	1,2 ^b +/- 0,1	0,9 ^c +/- 0,1	4,0 ^a +/- 0,2

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3 Table B (suppl. material)

	Intestine			Eye			Kidney			Liver		
	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18
16:0	3,3 ^b +/- 1,4	2,7 ^b +/- 2,4	14,5 ^a +/- 6,9	12,7 ^c +/- 3,7	51,6 ^b +/- 16,8	164,3 ^a +/- 23,6	2,1 ^b +/- 1,3	2,9 ^b +/- 3,0	48,5 ^a +/- 27,0	0,4 ^b +/- 0,3	0,5 ^b +/- 0,7	11,3 ^a +/- 10,1
16:1n-7	1,5 ^b +/- 0,7	0,7 ^b +/- 0,6	5,8 ^a +/- 2,9	6,6 ^b +/- 2,6	15,6 ^b +/- 6,3	68,7 ^a +/- 10,7	0,9 ^b +/- 0,7	0,9 ^b +/- 1,1	21,4 ^a +/- 12,6	0,1 ^b +/- 0,1	0,2 ^b +/- 0,3	5,0 ^a +/- 4,4
18:0	1,1 +/- 0,5	0,9 +/- 0,8	1,9 +/- 1,0	3,1 ^c +/- 1,0	10,5 ^b +/- 3,1	19,0 ^a +/- 1,7	0,7 ^b +/- 0,4	0,8 ^b +/- 0,6	6,3 ^a +/- 3,0	0,1 ^b +/- 0,1	0,1 ^b +/- 0,2	1,5 ^a +/- 1,3
18:1n-9	3,6 ^b +/- 1,6	3,6 ^b +/- 4,1	11,5 ^a +/- 6,1	14,6 ^c +/- 3,9	65,0 ^b +/- 21,8	135,4 ^a +/- 12,0	2,1 ^b +/- 1,3	3,9 ^b +/- 3,7	41,7 ^a +/- 23,2	0,3 ^b +/- 0,3	0,4 ^b +/- 0,7	9,7 ^a +/- 8,5
18:2n-6	3,5 +/- 0,9	2,8 +/- 2,7	4,1 +/- 2,5	14,1 ^b +/- 8,2	40,3 ^a +/- 6,8	46,5 ^a +/- 8,2	2,2 ^b +/- 1,6	3,0 ^b +/- 3,0	11,8 ^a +/- 5,5	0,3 ^b +/- 0,4	0,2 ^b +/- 0,3	2,8 ^a +/- 2,3
18:3n-3	2,1 ^a +/- 0,7	0,4 ^b +/- 0,3	2,3 ^a +/- 1,3	7,9 ^b +/- 4,0	7,3 ^b +/- 2,7	32,4 ^a +/- 6,1	1,2 ^b +/- 1,0	0,5 ^b +/- 0,8	6,5 ^a +/- 3,1	0,2 ^b +/- 0,2	0,1 ^b +/- 0,1	1,7 ^a +/- 1,5
18:4n-3	0,5 ^b +/- 0,2	0,1 ^b +/- 0,1	2,0 ^a +/- 1,2	2,5 ^b +/- 1,0	2,8 ^b +/- 0,9	22,2 ^a +/- 4,0	0,3 ^b +/- 0,3	0,2 ^b +/- 0,2	4,8 ^a +/- 2,4	0,0 ^b +/- 0,0	0,0 ^b +/- 0,0	1,3 ^a +/- 1,1
20:4n-6	0,6 +/- 0,4	0,2 +/- 0,1	0,3 +/- 0,1	1,9 ^b +/- 0,6	2,1 ^{ab} +/- 0,7	3,0 ^a +/- 0,4	0,3 ^b +/- 0,2	0,2 ^b +/- 0,1	0,7 ^a +/- 0,4	0,0 ^{ab} +/- 0,0	0,0 ^b +/- 0,0	0,2 ^a +/- 0,2
20:5n-3	1,1 ^b +/- 0,7	0,2 ^b +/- 0,1	2,9 ^a +/- 1,5	4,3 ^b +/- 1,7	2,7 ^b +/- 0,9	36,1 ^a +/- 5,2	0,6 ^b +/- 0,3	0,1 ^b +/- 0,2	8,4 ^a +/- 4,4	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	2,1 ^a +/- 1,8
22:5n-3	0,1 ^b +/- 0,0	0,0 ^b +/- 0,0	0,3 ^a +/- 0,1	0,9 ^b +/- 0,2	0,6 ^b +/- 0,2	4,8 ^a +/- 0,6	0,1 ^b +/- 0,0	0,0 ^b +/- 0,0	1,2 ^a +/- 0,5	0,0 ^b +/- 0,0	0,0 ^b +/- 0,0	0,4 ^a +/- 0,3
22:6n-3	0,3 ^b +/- 0,2	0,0 ^b +/- 0,0	1,9 ^a +/- 0,8	6,9 ^b +/- 1,2	3,5 ^b +/- 1,0	24,2 ^a +/- 3,2	0,2 ^b +/- 0,1	0,0 ^b +/- 0,0	5,9 ^a +/- 3,1	0,0 ^b +/- 0,0	0,0 ^b +/- 0,0	1,4 ^a +/- 1,2
ΣSAFA	5,9 ^b +/- 2,6	4,2 ^b +/- 3,7	21,7 ^a +/- 10,7	21,9 ^c +/- 7,7	71,6 ^b +/- 21,7	240,5 ^a +/- 33,5	3,5 ^b +/- 2,1	4,3 ^b +/- 4,3	70,0 ^a +/- 38,2	0,6 ^b +/- 0,5	0,7 ^b +/- 0,9	16,6 ^a +/- 14,6
ΣMUFA	5,7 ^b +/- 2,4	4,5 ^b +/- 4,8	21,7 ^a +/- 11,0	23,3 ^c +/- 7,0	84,9 ^b +/- 28,4	242,0 ^a +/- 26,9	3,4 ^b +/- 2,1	5,8 ^b +/- 6,3	76,4 ^a +/- 42,0	0,5 ^b +/- 0,5	0,6 ^b +/- 1,0	17,7 ^a +/- 15,3
ΣPUFA	8,6 ^{ab} +/- 2,8	3,8 ^b +/- 3,1	14,5 ^a +/- 8,0	40,7 ^b +/- 15,1	61,8 ^b +/- 12,9	179,5 ^a +/- 20,0	5,1 ^b +/- 3,5	4,2 ^b +/- 4,5	42,0 ^a +/- 20,5	0,7 ^b +/- 0,8	0,4 ^b +/- 0,5	10,5 ^a +/- 8,9
Σn-3	4,2 ^b +/- 1,6	0,7 ^b +/- 0,4	9,0 ^a +/- 4,6	22,7 ^b +/- 5,8	16,9 ^b +/- 5,0	115,2 ^a +/- 17,1	2,4 ^b +/- 1,6	0,8 ^b +/- 1,2	26,0 ^a +/- 12,9	0,3 ^b +/- 0,4	0,1 ^b +/- 0,3	7,0 ^a +/- 6,0
Σn-6	4,4 +/- 1,3	3,1 +/- 2,8	5,6 +/- 3,5	17,9 ^c +/- 9,4	44,8 ^b +/- 8,2	64,3 ^a +/- 9,4	2,7 ^b +/- 1,9	3,3 ^b +/- 3,3	16,0 ^a +/- 7,6	0,4 ^b +/- 0,4	0,2 ^b +/- 0,3	3,5 ^a +/- 2,9
n-3/n-6	0,9 ^b +/- 0,2	0,3 ^c +/- 0,1	1,7 ^a +/- 0,2	1,4 ^b +/- 0,4	0,4 ^b +/- 0,1	1,8 ^a +/- 0,3	1,0 ^b +/- 0,2	0,2 ^b +/- 0,1	1,6 ^a +/- 0,1	0,5 ^b +/- 0,3	0,2 ^b +/- 0,3	2,0 ^a +/- 0,2
EPA/ARA	1,9 ^b +/- 0,7	0,9 ^b +/- 0,1	11,4 ^a +/- 1,3	2,3 ^b +/- 0,6	1,3 ^c +/- 0,1	12,0 ^a +/- 0,2	2,1 ^b +/- 0,7	0,9 ^c +/- 0,2	11,3 ^a +/- 0,5	3,0 ^b +/- 0,4	1,6 ^b +/- 0,0	11,8 ^a +/- 0,6
DHA/EPA	0,3 ^b +/- 0,2	0,2 ^b +/- 0,2	0,6 ^a +/- 0,2	1,6 +/- 1,2	1,3 +/- 0,4	0,7 +/- 0,0	0,3 ^b +/- 0,1	0,2 ^c +/- 0,3	0,7 ^a +/- 0,1	0,3 ^b +/- 0,2	0,4 ^{ab} +/- 0,0	0,7 ^a +/- 0,1
DHA/ARA	0,5 ^b +/- 0,5	0,2 ^b +/- 0,2	7,4 ^a +/- 1,2	3,7 ^b +/- 1,6	1,7 ^c +/- 0,5	8,1 ^a +/- 0,4	0,9 ^b +/- 0,5	0,2 ^b +/- 0,2	7,9 ^a +/- 0,6	0,8 ^b +/- 0,5	0,6 ^b +/- 0,0	8,0 ^a +/- 1,1

	Dorsal muscle			Heart			Adipose tissue			Ventral muscle		
	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18	N	VO3	FO18
16:0	0,7 ^b +/- 0,3	1,0 ^b +/- 0,6	46,3 ^a +/- 22,6	1,2 ^b +/- 1,0	6,2 ^b +/- 4,7	53,0 ^a +/- 36,7	0,5 ^b +/- 0,4	1,3 ^b +/- 1,4	27,4 ^a +/- 2,9	1,2 ^b +/- 0,6	1,7 ^b +/- 1,1	93,3 ^a +/- 7,1
16:1n-7	0,3 ^b +/- 0,1	0,2 ^b +/- 0,2	19,5 ^a +/- 9,3	0,5 ^b +/- 0,4	1,7 ^b +/- 1,4	23,5 ^a +/- 16,7	0,2 ^b +/- 0,2	0,3 ^b +/- 0,3	12,1 ^a +/- 1,6	0,5 ^b +/- 0,3	0,4 ^b +/- 0,2	41,1 ^a +/- 2,1
18:0	0,2 ^b +/- 0,1	0,3 ^b +/- 0,1	6,0 ^a +/- 2,8	0,4 ^b +/- 0,4	1,6 ^b +/- 1,1	6,4 ^a +/- 3,9	0,2 ^b +/- 0,1	0,5 ^{ab} +/- 0,5	3,5 ^a +/- 0,3	0,4 ^b +/- 0,2	0,5 ^b +/- 0,4	12,2 ^a +/- 1,1
18:1n-9	0,8 ^b +/- 0,3	1,3 ^b +/- 0,7	38,4 ^a +/- 17,1	1,1 ^b +/- 0,9	8,2 ^b +/- 6,7	44,0 ^a +/- 29,3	0,5 ^b +/- 0,4	1,9 ^{ab} +/- 2,4	23,5 ^a +/- 3,1	1,4 ^b +/- 0,7	2,5 ^b +/- 1,9	84,2 ^a +/- 6,6
18:2n-6	0,7 ^b +/- 0,2	0,9 ^b +/- 0,5	12,0 ^a +/- 5,5	1,0 +/- 0,6	6,4 +/- 4,9	12,6 +/- 9,7	0,5 ^b +/- 0,4	1,3 ^{ab} +/- 1,6	6,4 ^a +/- 0,6	1,4 ^b +/- 1,0	1,6 ^b +/- 1,1	26,2 ^a +/- 6,3
18:3n-3	0,4 ^b +/- 0,1	0,1 ^b +/- 0,1	8,0 ^a +/- 4,6	0,6 ^b +/- 0,4	1,1 ^b +/- 1,0	8,7 ^a +/- 5,9	0,2 ^b +/- 0,2	0,2 ^b +/- 0,2	4,1 ^a +/- 0,2	0,8 ^b +/- 0,5	0,2 ^b +/- 0,1	16,7 ^a +/- 4,0
18:4n-3	0,1 ^b +/- 0,0	0,0 ^b +/- 0,0	5,7 ^a +/- 3,2	0,2 ^b +/- 0,1	0,3 ^b +/- 0,3	6,5 ^a +/- 4,7	0,1 ^b +/- 0,1	0,1 ^b +/- 0,1	3,0 ^a +/- 0,2	0,2 ^b +/- 0,1	0,1 ^b +/- 0,1	12,6 ^a +/- 3,0
20:4n-6	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	0,8 ^a +/- 0,4	0,2 +/- 0,2	0,3 +/- 0,2	0,9 +/- 0,6	0,1 +/- 0,1	0,0 +/- 0,0	0,4 +/- 0,0	0,2 ^b +/- 0,1	0,1 ^b +/- 0,0	1,6 ^a +/- 0,2
20:5n-3	0,2 ^b +/- 0,0	0,0 ^b +/- 0,0	9,1 ^a +/- 4,5	0,4 ^b +/- 0,5	0,3 ^b +/- 0,2	10,3 ^a +/- 7,1	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	5,2 ^a +/- 0,4	0,3 ^b +/- 0,2	0,1 ^b +/- 0,0	21,1 ^a +/- 2,5
22:5n-3	0,0 ^b +/- 0,0	0,0 ^b +/- 0,0	1,3 ^a +/- 0,6	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	1,3 ^a +/- 0,8	0,0 ^b +/- 0,0	0,0 ^b +/- 0,0	0,7 ^a +/- 0,1	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	3,1 ^a +/- 0,5
22:6n-3	0,0 ^b +/- 0,0	0,0 ^b +/- 0,0	1,4 ^a +/- 0,6	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	6,8 ^a +/- 4,6	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	3,9 ^a +/- 0,5	0,1 ^b +/- 0,1	0,0 ^b +/- 0,0	14,4 ^a +/- 1,7
ΣSAFA	1,3 ^b +/- 0,4	1,4 ^b +/- 0,8	68,2 ^a +/- 32,7	2,1 ^b +/- 1,9	9,0 ^b +/- 6,8	76,7 ^a +/- 53,3	0,8 ^b +/- 0,6	2,0 ^b +/- 2,2	39,4 ^a +/- 4,1	2,0 ^b +/- 1,0	2,6 ^b +/- 1,7	135,6 ^a +/- 11,0
ΣMUFA	1,3 ^b +/- 0,5	1,6 ^b +/- 0,9	70,9 ^a +/- 31,5	1,8 ^b +/- 1,6	10,6 ^b +/- 8,5	80,8 ^a +/- 55,0	0,6 ^b +/- 0,5	2,4 ^b +/- 2,9	42,6 ^a +/- 5,4	2,1 ^b +/- 1,1	3,1 ^b +/- 2,3	154,3 ^a +/- 9,5
ΣPUFA	1,6 ^b +/- 0,4	1,2 ^b +/- 0,7	41,1 ^a +/- 20,8	2,7 ^b +/- 2,2	8,8 ^b +/- 6,8	50,1 ^a +/- 35,1	1,1 ^b +/- 0,9	1,6 ^b +/- 1,9	25,5 ^a +/- 2,0	3,2 ^b +/- 2,1	2,1 ^b +/- 1,3	101,8 ^a +/- 17,1
Σn-3	0,7 ^b +/- 0,2	0,2 ^b +/- 0,2	24,7 ^a +/- 13,1	1,3 ^b +/- 1,3	1,7 ^b +/- 1,5	31,8 ^a +/- 21,4	0,5 ^b +/- 0,5	0,2 ^b +/- 0,2	16,3 ^a +/- 1,2	1,5 ^b +/- 0,9	0,4 ^b +/- 0,2	65,5 ^a +/- 9,6
Σn-6	0,9 ^b +/- 0,2	1,0 ^b +/- 0,5	16,4 ^a +/- 7,7	1,3 ^b +/- 1,0	7,1 ^{ab} +/- 5,4	18,2 ^a +/- 13,8	0,6 ^b +/- 0,5	1,4 ^{ab} +/- 1,7	9,2 ^a +/- 0,8	1,7 ^b +/- 1,2	1,7 ^b +/- 1,2	36,3 ^a +/- 7,9
n-3/n-6	0,8 ^b +/- 0,1	0,2 ^c +/- 0,1	1,5 ^a +/- 0,1	0,9 ^{ab} +/- 0,2	0,2 ^b +/- 0,1	2,6 ^a +/- 2,0	0,9 ^b +/- 0,2	0,3 ^c +/- 0,2	1,8 ^a +/- 0,2	1,5 ^{ab} +/- 1,3	0,3 ^b +/- 0,1	1,8 ^a +/- 0,2
EPA/ARA	1,7 ^b +/- 0,6	1,0 ^c +/- 0,5	11,7 ^a +/- 0,3	2,0 ^b +/- 0,5	1,1 ^c +/- 0,1	11,4 ^a +/- 0,5	2,0 ^b +/- 1,0	1,0 ^b +/- 0,2	11,9 ^a +/- 1,2	2,0 ^b +/- 0,6	1,1 ^c +/- 0,2	13,0 ^a +/- 0,4
DHA/EPA	0,3 ^a +/- 0,1	0,0 ^c +/- 0,0	0,2 ^b +/- 0,0	0,3 ^b +/- 0,2	0,1 ^c +/- 0,1	0,7 ^a +/- 0,1	0,4 +/- 0,7	0,0 +/- 0,0	0,7 +/- 0,3	0,3 ^b +/- 0,1	0,3 ^b +/- 0,2	0,7 ^a +/- 0,1
DHA/ARA	0,5 ^b +/- 0,3	0,0 ^c +/- 0,0	1,8 ^a +/- 0,2	0,6 ^b +/- 0,1	0,2 ^b +/- 0,1	7,5 ^a +/- 0,8	0,8 ^b +/- 0,5	0,0 ^b +/- 0,0	8,9 ^a +/- 2,4	0,6 ^b +/- 0,4	0,3 ^b +/- 0,2	8,9 ^a +/- 0,8

Zusammenfassung

Unser Wissen über den Fettsäuremetabolismus im Karpfen ist beschränkt, da sich die meisten wissenschaftlichen Studien vor allem mit den Fettsäuren im Dorsalmuskel beschäftigen und anderen Geweben wenig Beachtung geschenkt wird. Wir untersuchten daher den Effekt des Futters auf die Fettsäurezusammensetzung von Struktur- und Speicherfetten in verschiedenen Geweben und Organen des Karpfens (Dorsalmuskel, Ventralmuskel, Herz, Niere, Darm, Augen, Leber und Fettgewebe) und beobachteten wie unterschiedlich verschiedene Gewebe und Lipidklassen auf unterschiedliche Nahrungsqualitäten reagieren können.

Unsere Hypothesen waren, dass Karpfen die Fettsäurezusammensetzung ihrer Phospholipide gewebespezifisch regulieren und sich diese daher von der Fettsäurezusammensetzung der Nahrung unterscheidet. Die Zusammensetzung der Speicherlipide hingegen sollte die Fettsäuremuster der Nahrung widerspiegeln und sich nicht gewebespezifisch verhalten.

Zur Überprüfung dieser Hypothesen wurden drei Aquakulturtische mit zwei Jahre alten Karpfen besetzt. Jeder Teich bot den Karpfen ein unterschiedliches Nahrungsangebot (Zooplankton, Zooplankton plus Pflanzenöl-Pellets, Zooplankton plus Fischöl-Pellets). Nach 210 Tagen wurden die Fische entnommen und die Fettsäurezusammensetzung der Struktur- und Speicherfette mit Hilfe von Dünnschichtchromatographie und Gaschromatographie analysiert.

Die Fettsäuremuster reagierten lipidklassen- und gewebespezifisch auf die unterschiedlichen Nahrungsqualitäten. Unsere größte Entdeckung war, dass die Fettsäurezusammensetzung der Speicherlipide bei niedrigen Lipidkonzentrationen gewebespezifisch war. Die Fettsäurezusammensetzung der Nahrung wurde durch die

Strukturlipide nicht abgebildet. Phospholipide reagierten allerdings auf Nahrung, die reich an Omega-3-Fettsäuren war (Fischöl). Die Resultate meiner Arbeit geben neue Einblicke in gewebespezifische Fettsäuremuster im Karpfen und erweitern das Wissen über die Physiologie dieses wichtigen Zuchtfisches.

Perspektive

Mit Hilfe dieser Studie lassen sich Zuchtmethoden verbessern, um den Gehalt an wertvollen Omega-3 Fettsäuren im Karpfen zu steigern. Bei der Auswahl und Zusammensetzung des Fischfutters müssen die komplexen Reaktionen und Interaktionen der verschiedenen Organe auf das Futter, sowie die Auswirkungen auf die Gesundheit des Fisches berücksichtigt werden. Besonders wünschenswert ist der Verzicht auf marine Ressourcen (Fischöl), da diese durch den steigenden Bedarf und die daraus resultierende Überfischung vieler Meeresgebiete nicht mehr nachhaltig zu gewinnen sind. Ein qualitativ gleichwertiger und billiger Ersatz für Fischöl mit seinem hohen Gehalt an Omega-3-Fettsäuren ist aber noch nicht gefunden. Nachhaltige und qualitativ hochwertige Futtermittel sind in hohem Maße erstrebenswert, da in dieser Studie eine hohe Retention von gesundheitsfördernden Omega-3-Fettsäuren im Karpfen beobachtet werden konnte. Weitere Studien an wichtigen Zuchtfischen wie dem Karpfen sind notwendig, um das nötige Wissen zu schaffen, damit die Aquakultur auch in Zukunft die steigenden Forderungen an Qualität und Quantität durch den Konsumenten befriedigen wird können.

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Curriculum Vitae

Markus Böhm

DATE AND PLACE OF BIRTH

7th Mai 1987, Zwettl (Austria)

CONTACT INFORMATION

Propstei 34
3910 Zwettl
0664/5119066
boehm.markus@gmx.at

EDUCATION

06/2011 – 06/2012

Master thesis within FWF project L516-B17 at WasserCluster Lunz (LIPTOX):
Tissue-specific response of fatty acid signatures to diet in cultured carp
(*Cyprinus carpio* L.)
Supervisor: Priv.-Doz. Dr. Martin Kainz

03/2007 – 06/2012

Master of Ecology at the University of Vienna (Austria) with special emphasis
on Limnology

09/2006 – 03/2007

Mandatory military service (TÜPL Allentsteig)

09/2001 – 05/2006

Bundeshandelsakademie Zwettl (High School)

09/1997 – 06/2001

Bundes- und Bundesrealgymnasium Zwettl (Middle School)

WORK EXPERIENCE

Laboratory assistant within a collaborative research project between
WasserCluster Lunz (AUT) and the Government of Queensland (AUS):

Kainz M.J., Marshall J., Jardine T., Woods R., Valdez D., Lobegeiger J.
Dietary biomarkers in food webs of semi-arid, turbid waterholes: combined
assessment of stable isotopes and fatty acids

Advisor: Priv.-Doz. Dr. Martin Kainz, **Aquatic lipid and ecotoxicology research group (LIPTOX)**, WasserCluster Lunz

SELECTED LIMNOLOGY COURSES

06/2012

Aquatic and semiaquatic Heteroptera –guide to identification for advanced learners

Advisors: Ao. Univ. Prof. Dr. Johann Waringer and Mag. Dr. Wolfgang Rabitsch, University of Vienna

06/2011

Malacostraca –guide to identification for advanced learners

Advisors: Ao. Univ. Prof. Dr. Johann Waringer and Dr. Manfred Pöckl, University of Vienna

10/2010 – 01/2011

Trichoptera – identification course for advanced learners

Advisors: Ao. Univ. Prof. Dr. Johann Waringer and Dr. Wolfram Graf, University of Vienna

06/2010

Ephemeroptera –guide to identification for advanced learners

Advisors: Ao. Univ. Prof. Dr. Johann Waringer (University of Vienna), Dr. Ernst Bauernfeind (Museum of Natural History of Vienna), Doz. Ao. Univ.-Prof. Uwe Humpesch (Austrian Academy of Science)

03/2010 – 06/2010

European Water Framework Directive (WFD) – European standards and field mapping of the aquatic vegetation

Advisor: Ao. Univ.-Prof. Dr. Georg Janauer, University of Vienna

SKILLS AND QUALIFICATIONS

Languages

German (first language)

English (fluent in speech and writing)

French (basics)

Computer literacy

MS Office, Sigma Plot, MS Access, graphics software (Photoshop etc.)

Additional qualifications

Electron microscopy (TEM and SEM)

