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1   **Planktivorous vendace (*Coregonus albula*) utilize algae-derived fatty acids**

2   **for biomass increase and lipid deposition**

3

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15

16   **Running head**: Fatty acid accumulation in vendace

17

18

Abstract

Spatial and seasonal variation in the abundance and composition of phytoplankton and other basal resources (bacteria, terrestrial detritus) influence the availability of essential polyunsaturated fatty acids (PUFA) for upper trophic levels in lake food webs. We studied accumulation, composition, and content of fatty acids in planktivorous vendace (*Coregonus albula*) muscle tissue during the summer feeding period (May to late September) in six boreal lakes. Vendace muscle fatty acid content increased from ~17.7 mg g^{-1} DW to ~28.1 mg g^{-1} DW from spring to summer, corresponding to a ~ 59 % increase in total fatty acids. PUFA accounted for 45-65 % of all fatty acids, and the most abundant fatty acid was docosahexaenoic acid (DHA, 22:6n-3). The DHA content remained relatively constant throughout the sampling period (~7-8 mg g^{-1} DW), but the proportion of DHA decreased from ~40 % in spring to ~30 % in summer and autumn. The decrease in DHA proportion was due to accumulation of other fatty acids, primarily C_{18} PUFA (predominantly synthetized by algae) and monounsaturated fatty acids. A similar fatty acid accumulation pattern was observed in lipid storing copepods, an important prey for planktivorous vendace. The abundance of bacterial and terrestrial biomarker fatty acids in vendace muscle and prey items was low (<5% and <0.1%, respectively). The increase in weight and the deposition of internal energy stores in vendace were achieved predominantly by algae-based food chain. This has ecological implications, as vendace requires sufficient lipid stores for reproduction in autumn and survival over winter.

Introduction

44

45 Planktivorous fish in boreal lakes experience high seasonal variability in prey availability.

46 The ability to store energy in the form of lipid deposits is crucial for winter survival when

47 zooplankton prey is less abundant (Ågren, Muje, Hänninen, Herranen & Penttilä, 1987; Lahti

48 & Muje, 1991; Linko, Rajasilta & Hiltunen, 1992). Reproductive success in late autumn is

49 also highly dependent on lipid gain during the previous summer (Ågren et al., 1987; Lahti &

50 Muje, 1991; Linko et al., 1992). For reproduction, the abundance of polyunsaturated fatty

51 acids (PUFA) from the n-6 and n-3 families have been shown to be particularly important

52 (Sargent, Bell, McEvoy, Tocher & Estevez, 1999). Animals need PUFA for various

53 physiological processes, e.g. maintaining membrane fluidity and as precursors of local tissue

54 hormones, but most organisms lack the ability to biosynthesize these molecules *de novo* and

55 therefore must obtain them from their diet (Glencross, 2009). In aquatic food webs, algae are

56 the major source of n-3 and n-6 PUFA (Ahlgren, Lundstedt, Brett & Forsberg, 1990; Brett,

57 Kainz, Taipale & Seshan, 2009; Taipale et al., 2013, 2016). Although some fish species are

58 able to synthesize the long chained PUFA, eicosapentaenoic acid (EPA 20:5n-3),

59 docosahexaenoic acid (DHA, 22:6n-3) and arachidonic acid (ARA 20:4n-6), from shorter C_{18}

60 PUFA, this process is generally regarded as inefficient (Tocher, 2003). Dietary EPA and

61 DHA are shown to be important for optimal health and somatic growth of zooplankton and

62 fish (Ahlgren et al., 1990; Mairesse, Thomas, Gardeur & Brun-Bellut, 2007). In aquatic

63 environments, algae (phytoplankton and attached algae) are the main producers of EPA and

64 DHA, but different algal classes have very distinct fatty acid compositions and they differ in

65 their EPA and DHA content (Ahlgren et al., 1990; Taipale et al. 2013; Galloway & Winder,

66 2015). For example, cryptophytes and dinoflagellates are able to biosynthesize EPA and

67 DHA, whereas green algae and cyanobacteria contain predominantly the shorter chained C_{18}

68 PUFA (α-linolenic acid, ALA, 18:3n-3). Thus, the phytoplankton community composition

69 strongly influences the food web processes and availability of PUFA to upper trophic level

70 consumers (Brett & Müller-Navarra, 1997; Müller-Navarra, Brett, Liston & Goldman, 2000;

71 Galloway & Winder, 2015; Strandberg et al., 2015b; Taipale et al., 2016).

72   The knowledge on fatty acids in different basal resources can be applied for tracing the

73 pathways of autochthonous and allochthonous organic carbon flow in lake ecosystems

74 (Desvilettes, Bourdier, Amblard & Barth, 1997; Galloway et al., 2014). Although consumer-

75 specific differences in lipid digestion and metabolism will modify the fatty acids at different

76 trophic levels, specific fatty acids may be traced through several trophic levels (Gladyshev et

77 al., 2011; Strandberg et al., 2015a). Odd-chained and/or branched fatty acids are typically

78 characterized as actinobacterial, whereas long-chain (≥ 24 carbon) saturated fatty acids are

79 considered to originate from detrital terrestrial particulate organic matter (t-POM)

80 (Desvilettes et al. 1997; Taipale, Kankaala, Hämäläinen & Jones, 2009; Galloway et al.,

81 2014). Similarly, low n-3/n-6 ratio (< 1) in zooplankton has been suggested to indicate an

82 allochthonous diet (Brett et al., 2009; Taipale, Kainz & Brett, 2015). In addition to dietary

83 differences in FA composition, zooplankton fatty acid composition is taxon-specific (Persson

84 & Vrede, 2006, Smyntek, Teece, Schulz & Storch, 2008; Hiltunen, Strandberg, Taipale &

85 Kankaala, 2015). Variation in the importance of autotrophic (algal) vs. heterotrophic

86 (bacterial) production at the base of the food web may also influence the fatty acid

87 composition and lipid accumulation of planktivorous fish.

88   Vendace (*Coregonus albula* (L.)) is a small (total length 10-25 cm) zooplanktivorous

89 coregonid inhabiting large to medium-sized boreal lakes, and is the most important

90 commercial fish in these lakes (Viljanen, 1986; Marjomäki, Keskinen & Karjalainen, 2016).

91 Vendace is abundant in oligo-mesotrophic lakes with low to moderate humic content and

92 well-oxygenated cooler water layers (Dembiński, 1971; Rask, Viljanen, & Sarvala, 1999;

93 Winfield, Fletcher & James, 2004). It is generally not present in small shallow lakes with

94   high terrestrial dissolved organic carbon (DOC) concentration due to the absence of a well-

95   oxygenated hypolimnion. Weight gain and biomass increase of planktivorous fish is strongly

96   related to prey availability and abundance. In boreal lakes, the main feeding period for

97   planktivorous vendace is summer, when zooplankton (copepods and cladocerans) are

98   abundant (e.g. Hamrin, 1983; Viljanen, 1983; Helminen, Sarvala & Hirvonen, 1990). During

99   the feeding season, vendace accumulate lipids in their tissues to ensure spawning in autumn

100   and survival over winter (Ågren et al., 1987; Lahti & Muje, 1991; Linko et al., 1992). Almost

101   all vendace spawn for the first time during their second autumn (age 1+) and in intensively

102   harvested vendace populations, up to 80% of all spawners belong to this age group (Huusko

103   & Hyvärinen, 2005; Karjalainen et al., 2016).

104   We studied the composition and accumulation of fatty acids in pelagic food chains in large

105   (>100 km^2) boreal lakes in Eastern Finland with moderate (5 – 10 mg C L^{-1}) DOC

106   concentrations (Hiltunen et al., 2015; Strandberg et al., 2015a,b). Studies on fatty acids in

107   phyto- and zooplankton in these lakes have been previously published (see Hiltunen et al.,

108   2015; Strandberg et al., 2015a,b). Here we focus on seasonal changes in vendace fatty acid

109   composition and content during the feeding period before autumn spawning. We

110   hypothesized that 1) the seasonal changes in phytoplankton community composition, and

111   concurrent changes in zooplankton fatty acid composition, modify fatty acid composition of

112   planktivorous vendace, and 2) resources of allochthonous origin play a minor role in vendace

113   nutrition leading to low abundance of terrestrial and bacterial fatty acid biomarkers in

114   vendace.

115

Materials and methods

117   Pelagic food webs were studied in six large (area >100 km^2) lake basins in eastern Finland. In

118   2011 we sampled lakes Kallavesi, Suvasvesi, Orivesi, Paasivesi, and Pyhäselkä. Each lake

119   was sampled 3 times: late May-early June (spring samples), late July- early August (summer

120   samples), and at the end of September (autumn samples). Additional samples were collected

121   from Lake Karjalan Pyhäjärvi in August 2012. Due to the lack of samples, data from the

122   latter lake is presented separately and excluded from detailed analysis. All the lakes are

123   hydrologically connected within the Vuoksi water course (see Hiltunen et al., 2015, for a map

124   of the sampling area). The studied lake basins are oligotrophic or mesotrophic with total

125   phosphorus concentrations varying between ca. 5 - 12 µg L^{-1} and chlorophyll a concentration

126   ca. 2 – 6 µg L^{-1} (Table 1). The concentration of dissolved organic carbon (DOC) ranged from

127   ca. 5 to 10 mg C L^{-1}.

128   For phyto- and zooplankton sampling, laboratory methods and detailed results see

129   Hiltunen et al. (2015) and Strandberg et al. (2015b). The fish samples here are the same as in

130   Strandberg et al. (2015a). Vendace were caught by gill netting (mesh sizes 13-14, 16-17 and

131   15-18 mm) or by trawling (mesh sizes 12 or 13 mm, trawl bottom 5 mm). For each sampling

132   day and site, at least three random fish were taken for analyses and the weight and length of

133   the fish were measured (total n=52). Although not systematically determined, presumably all

134   caught individuals were mature based on their size (see Table 2, Lahti & Muje, 1991,

135   Karjalainen et al., 2016). Replicates of dorsal muscle tissue were dissected and stored in -70

136   °C until fatty acid analyses. We also opportunistically analyzed roe samples. Roe samples

137   were collected from lakes Paasivesi (n=2), Kallavesi (n=1), Orivesi (n=1), Pyhäselkä (n=2),

138   and Suvasvesi (n=1), and stored in -70 °C until further analysis.

139   **Laboratory analyses**

140   Vendace muscle and roe samples were freeze-dried prior to lipid analyses. Muscle tissue of

141   each fish was analyzed in duplicate and the mean value was used. Only one roe sample per

142   fish was analyzed. Total lipids were extracted twice with chloroform:methanol (2:1). Fatty

143   acids were transmethylated by adding methanolic sulfuric acid (1 % v/v) and heating for 16 h

144   at 50°C. The fatty acid methyl esters were extracted twice with *n*-hexane/diethyl ether (1:1 by

145   vol), evaporated to dryness and suspended into *n*-hexane. The fatty acid methyl esters of

146   vendace samples were analyzed with a gas chromatograph (Agilent 6890N) equipped with a

147   mass spectrometer (Agilent 5973N). The GC method was as follows: inlet temperature 250

148   °C, splitless injection, initial oven temperature 60 °C maintained for 1.5 min, after which

149   oven temperature ramped 10 °C/min to 100 °C, and then 2 °C/min to 140 °C, followed by 1

150   °C/min increase to 180 °C and finally 2 °C/min to 210 °C. The final oven temperature was

151   maintained for 6 minutes. Helium was used as the carrier gas with an average velocity of 36

152   cm/sec. The column was an Agilent DB-23 (30 m x 0.25 mm x 0.15 µm). Peak identification

153   was based on mass spectra and standard FAME mixes (37 FAME mix from Sigma-Aldrich

154   and GLC-68D from Nu-Chek Prep). The GLC-68D reference standard was used for the

155   calibration curve. For fatty acids not present in the reference standard, the calibration curve

156   was calculated based on the structurally most similar fatty acid.

157   **Statistical analyses**

158   Fulton condition index of fish (K) was calculated as follows: $K=W/L^3$, where W= weight (g)

159   and L= length (cm), a scaling factor of 100 was applied to bring the value close to 1.

160   Multidimensional scaling (MDS) was used to visualize fatty acid profiles among vendace,

161   and permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was

162   used to test for differences in vendace fatty acid composition between different seasons (fixed

163   factor) and lake basins (random factor). Vendace sampled from Karjalan Pyhäjärvi only in

164   August 2012 were excluded from the analyses. Prior to the multivariate analyses, the fatty

165   acid data was arcsine square root transformed. Ordination was based on Euclidean distances,

166   where samples close to another are compositionally more similar than samples further apart.

167   Goodness of fit for the ordination is expressed as the stress value. The lower the stress, the

168   better objects are fitted in the multidimensional space. The significance of PERMANOVA

169   analyses was determined using unrestricted permutation of the raw data (9999 permutations)

170   with type III sums of squares, (Anderson, Gorley & Clarke, 2008). Multivariate analyses

171   (MDS, PERMANOVA) were done with PRIMER 6.0 with the PERMANOVA + add on.

172   Other statistical analyses were done with IBM SPSS Statistics 23 program package.

173   Correlations between the total fatty acid content and the proportions of PUFA,

174   monounsaturated fatty acids (MUFA), BAFA and the n-3/n-6 ratio were evaluated, and

175   bootstrapping (1000 bootstrap samples) was applied to estimate the confidence interval (95 %

176   biased corrected) for the correlation coefficient. Seasonal differences (spring, summer,

177   autumn) in the relative proportions of different fatty acid classes in seston, zooplankton and

178   vendace was investigated with ANOVA using Games-Howell post hoc test. Seasonal

179   differences in total fatty acid content of vendace were tested with Wilcoxon signed rank test

180   and proportional differences of specific fatty acids between vendace muscle and roe were

181   analyzed with Mann-Whitney U-test.

182

183   Results

184   The total amount of fatty acids in the vendace muscle tissue increased significantly from 17.7

185   mg g^{-1} DW in spring to 28.1 mg g^{-1} DW in summer in accordance with the simultaneous

186   increase in the condition index (Wilcoxon signed rank test, $p<0.05$, Table 2, Figure 1). The

187   fatty acid content of vendace in autumn did not differ from that of summer samples. The most

188   abundant fatty acids in the vendace dorsal muscle were 14:0, 16:0, 16:1n-7, 18:0, 18:1n-9,

189   18:1n-7, 18:2n-6, 18:3n-3, 18:4n-3, 20:4n-6 (ARA), 20:5n-3 (EPA), 22:5n-6, 22:5n-3 and

190   22:6n-3 (DHA), accounting for >89% of all fatty acids (Supplement 1). Polyunsaturated fatty

191   acids were the most abundant group of fatty acids, accounting for 45-65% of all fatty acids.

192   Of these, DHA and EPA were the most abundant ones accounting for ~ 34% and ~ 9% of all

193   fatty acids, respectively. Saturated fatty acids (SFA) accounted for ~33% of all fatty acids

194   during all seasons. The general fatty acid composition of vendace did not differ between the

195   lake basins (PERMANOVA, Pseudo-$F_{5,46}$ = 1.759, P = 0.1).

196   The seasonal differences in the fatty acid composition, especially between spring and

197   summer/autumn (Fig. 2), of vendace were significant (PERMANOVA, Pseudo-$F_{2,49}$=13.224,

198   P < 0.001). The proportion of C_{22} PUFA decreased in vendace muscle as the total fatty acid

199   content increased (r = -0.842, P<0.001, 95 % CI -0.896 – -0.782; Fig. 3). This was mainly

200   due to decreasing proportion of DHA, from ~40±4 % in spring, to 29±7 % in summer and

201   32±4 % in autumn, although the DHA content in vendace muscle remained at the same level

202   (spring 6.9±1.5, summer 7.3±1.6, autumn 8.0±1.2 mg g^{-1} DW). The seasonal increase in the

203   total fatty acid content in the muscle tissue was mainly due to accumulation of

204   monounsaturated fatty acids (sum of C_{14}, C_{16} and C_{18} MUFA), C_{18} and C_{20} PUFA, where

205   proportions correlated positively with increasing fatty acid content (Fig. 3). The n-3/n-6

206   PUFA ratio in vendace muscle varied between 3.2 and 10.0 (mean 6.0±1.3), decreasing as

207   total fatty acid content increased (r =-0.584, P<0.001).

208   Proportion of solely bacterial fatty acids (BAFA, branched or odd-chain) in vendace

209   muscle varied from less than 0.5 to 4 % and correlated positively with the total fatty acid

210   content of fish (r = 0.864, P < 0.001, Fig 3). Low proportions (≤ 0.5 %) of isoprenoid fatty

211   acids, 4,8,12- trimethyltridecanoic (4,8,12-TMTD) and 3,7,11,15-tetramethylhexadecenoic

212   (phytanic) acids were also detected. Trace values of very long chained PUFA (≥ 24 carbons)

213   were found in the summer samples (mean of all summer samples 0.1%). Traces (<0.1 %) of

214   lignoceric acid (24:0) was detected in the muscle of only 15% of the studied fish, while in

215   most fish 24:0 was not found at all.

216   The most abundant fatty acids in vendace roe, sampled in autumn, were generally the

217   same as in the muscle of adult fish (Supplement 2). PUFA accounted for about 48 % of all

218   fatty acids in the roe, but the proportion of DHA (~16 %) was significantly lower (Mann-

219   Whitney U test, P<0.001) than what was analyzed from the muscle tissue in autumn. The

220   total fatty acid content in roe was about 10 times higher than total fatty acid content of the

221   muscle tissue in the autumn. (279±35 mg g^{-1} DW). The mean DHA content of roe was ~

222   44±8 mg g^{-1} DW.

223

Discussion

225   The content and composition of fatty acids in vendace muscle tissue changed significantly

226   from spring to autumn. The low fatty acid content in spring can be explained by depletion of

227   internal energy stores during spawning in autumn and by limited food availability and in

228   winter (Ågren et al., 1987). Summer is the main feeding period for vendace, and the 1.6-fold

229   increase in total fatty acid content from spring to summer reflects the accumulation of lipids

230   and building of internal energy stores in preparation for reproduction and overwintering

231   (Ågren et al., 1987; Lahti & Muje, 1991). Fatty acids that most contributed to the increase in

232   total fatty acid content were MUFA (particularly 16:1n-7, 18:1n-9) and C$_{18}$ PUFA (18:2n-6,

233   18:3n-3, 18:4n-3), whereas long chain polyunsaturated DHA declined from ca. 40 % in

234   spring to 30 % in summer. Similar trends of declining proportion of C$_{22}$ PUFA and increasing

235   proportion of C$_{18}$ PUFA was also seen in calanoid copepods (*Limnocalanus macrurus*,

236   *Eudiaptomus* spp.) in the study lakes (Hiltunen et al., 2015, Table 3).

237   The seasonal trends in fatty acid composition of vendace and zooplankton corresponded

238   with changes in the phytoplankton community composition (Strandberg et al., 2015b). In

239   seston (fraction 0.22 – 50 µm), the most abundant group of fatty acids were the C$_{18}$ PUFA, ~

240   30 % of all fatty acids during all the seasons (Strandberg et al., 2015b, Table 3). C$_{18}$ PUFA is

241   common in a wide variety of algal groups, including cryptophytes and chrysophytes, as well

242   as green algae and cyanobacteria (Taipale et al., 2013), thus explaining the abundance and

243   availability of C$_{18}$ PUFA in the pelagic food chain throughout the sampling season.

244   Cryptophytes and diatoms were the most abundant phytoplankton groups in all the lakes and

245   seasons, but the proportion of dinoflagellates decreased and the proportion of cyanobacteria

246   and green algae increased from spring to fall (Strandberg et al., 2015b). Dinoflagellates are

247   abundant source of DHA and the decrease in the abundance of dinoflagellates from spring to

248   summer coincided with the decrease of DHA in seston (Strandberg et al., 2015b) as well as in

249   zooplankton and vendace (Table 3), thus, supporting our first hypothesis.

250   Zooplankton are an important link for the transfer of energy and nutrients from producers

251   to upper trophic level consumers. In pelagic food webs, EPA and DHA originating from

252   seston accumulate in zooplankton and fish (Kainz, Arts & Mazumder, 2004; Strandberg et

253   al., 2015a). The general fatty acid composition of vendace muscle tissue was characterized by

254   a high proportion of PUFA (45-65 % of all fatty acids), which was similar in magnitude to

255   copepod zooplankton, but greater than in cladocerans and seston (Hiltunen et al., 2015;

256   Strandberg et al. 2015a, Table 3). Taxonomic differences in fatty acid composition between

257   cladocerans and copepods might be an important factor determining the transfer of fatty acids

258   to vendace. Cladocerans are known to efficiently retain C_{20} PUFA (EPA and ARA), but

259   almost completely lack C_{22} PUFA, whereas copepods are abundant in DHA (Persson &

260   Vrede, 2006; Smyntek et al., 2008; Hiltunen et al., 2015).

261   Stomach content analyses have indicated that vendace predominately prey on cladocerans

262   in summer (Hamrin, 1983; Viljanen, 1983), corresponding with the decline of DHA

263   proportion in vendace from spring to summer. The dominance of cladocerans in vendace diet

264   in summer was also observed in our study lakes, Pyhäselkä and Kallavesi, where ~ 90% of

265   prey remains in vendace guts (n=13) consisted of cladocerans (Viljanen & Lehtovaara,

266   unpublished). In autumn, vendace diet has been suggested to shift more to copepods

267   (Northcote & Hammar, 2006). This shift could be expected to increase the proportion and

268   content of DHA in the muscle; however, we did not observe any such pattern. Allocation of

269   DHA to reproduction may also partly explain why copepod diet was not clearly reflected in

270   the muscle fatty acid composition (Dabrowski, 1982; Pickova, Kiessling, Pettersson & Dutta,

271   1999; Tocher, 2003). Nevertheless, the high proportion of DHA (on average 34 % of all fatty

272   acids) in vendace muscle suggests that copepods are an important prey item. Alternatively,

273   vendace may have elongated and desaturated shorter chain n-3 PUFA (e.g. 18:3n-3 and/or

274   20:5n-3) to produce DHA. Coregonid *Coregonus lavaretus maraena* has been shown to

275   biosynthesize DHA from shorter chained analogues (Watanabe et al., 1989), suggesting that

276   vendace may also elongate shorter chained fatty acids to DHA. However, it remains

277   questionable if this metabolic pathway would be efficient enough to result in high proportions

278   of DHA, analyzed in vendace muscle (Kaitaranta, 1980; Muje, Ågren, Lindqvist & Hänninen,

279   1989). Additionally, the very long chained polyunsaturated fatty acids (C_{24}-C_{26} PUFA),

280   which are specific biomarkers for the large copepod *Limnocalanus macrurus* (Hiltunen,

281   Strandberg, Keinänen, Taipale & Kankaala, 2014), were found in vendace muscle,

282   demonstrating a clear dietary link between the copepod and vendace.

283   Reproductive success is highly dependent on lipid reserves in many fish because the

284   formation of gonads is very energy intensive and the produced eggs need to be provisioned

285   with lipids (Marshall, Yaragina, Lambert & Kjesbu, 1999; Pickova et al., 1999, Tocher,

286   2003). The fatty acid content of vendace roe was high (279 ± 35 mg g^{-1}) demonstrating that

287   reproduction requires substantial allocation of lipids, particularly in females (Lahti & Muje,

288   1991). About 50% of fatty acids in roe were PUFA, and although the proportion of DHA in

289   roe was lower than in the muscle tissue, due to the high total fatty acid content, the amount of

290   DHA in roe was about 6 times higher than in the muscle tissue.

291   We could not find any between-lake differences in the fatty acid composition and content

292   of vendace. This may be partly due to low number of analyzed individuals per lake, but

293   presumably also due to the similarity of the sampled lakes, which are interconnected in the

294   Vuoksi water course (Table 1). Although some differences in phytoplankton community

295   structure in relation to DOC concentration was observed in the study lakes, taxonomic

296   identity was the most important determinant (62%) of zooplankton fatty acid composition and

297   the role of environmental factors was minor (Hiltunen et al., 2015). The proportion of DHA

298   was much lower (~ 13%, Linko et al., 1992) in vendace of mesotrophic Säkylän Pyhäjärvi

299   (SW Finland) compared to vendace in our study lakes suggesting lower availability of DHA

300   from phytoplankton via zooplankton to vendace. Lake trophic state and increased nutrient

301   concentrations with concurrent changes in phytoplankton community composition is

302   connected to decreasing EPA and DHA in a predatory fish, the Eurasian Perch (*Perca*

303   *fluviatilis*, Taipale et al., 2016). In contrast to our study lakes, Lake Säkylän Pyhäjärvi has

304   suffered from eutrophication and experiences occasionally cyanobacteria blooms (Ventelä et

305   al., 2011), which may influence the availability of DHA to vendace.

306   Phytoplankton are the ultimate source of PUFA in pelagic food web, but other basal

307   resources may be important in providing energy and specific fatty acids. For instance,

308   branched and odd-chained fatty acids are thought to originate from bacterial production

309   (Taipale et al., 2009), which utilize both phytoplankton-derived and terrestrial-origin DOC as

310   a carbon source (e.g. Simon, Cho & Azam, 1992; Pérez & Sommaruga, 2006). The

311   proportion of BAFA in the seston was ~ 2% (Strandberg et al., 2015b) and in zooplankton

312   ~1-5% (Hiltunen et al., 2015), indicating that bacterial fatty acids are incorporated into the

313   pelagic food web but have a low contribution. This suggests that BAFA are not markedly

314   utilized for biomass increase and lipid deposition in vendace. However, the proportion of

315   BAFA increased with increasing lipid content in vendace, indicating direct dietary input.

316   Since fatty acid content in actinobacteria is relatively low (Taipale et al., 2014), it is not

317   surprising that the proportion of BAFA in vendace was minimal (0.5-4%) in comparison to

318   algae-derived PUFA. In an oligotrophic clear-water alpine lake, Lake Annecy (area 28 km^2),

319   whitefish (*Coregonus lavaretus*) larvae contained similar proportions (2-4 %) of BAFA

320   (Perga, Bec & Anneville, 2009). Various fatty acid biomarkers have been applied to estimate

321   autochthonous and allochthonous sources of fatty acids in aquatic biota. Increased

322   proportions of n-6 PUFA (e.g. 18:2n-6) and lower n-3/n-6 ratio may indicate the abundance

323   of terrestrially derived fatty acids, as n-6 PUFA are generally more abundant in terrestrial

324   than aquatic environments (Hixson, Sharma, Kainz, Wacker & Arts, 2015). A low n-3/n-6

325   ratio (< 1) in fish and zooplankton may indicate a significant contribution of terrestrial fatty

326   acids (Ahlgren, Sonesten, Boberg & Gustafsson, 1996; Taipale et al., 2015). In the current

327   study, the mean n-3/n-6 ratio in vendace was high; varying from 3 to 10, suggesting that

328   allochthonous resources would not directly contribute to vendace diet. Another suggested

329   indicator for terrestrial fatty acids is lignoceric acid (C24:0; Perga et al., 2009). In the current

330   study only 15% of the studied fish contained trace levels of 24:0 (<0.1% of total fatty acids).

331   Thus, our second hypothesis was supported. In Lake Annecy, zooplankton and whitefish

332   larvae contained higher, but still small, proportions of 24:0 (0.5-2.9% of total fatty acids;

333   Perga et al., 2009). However, laboratory feeding experiments indicate that 24:0 is not

334   efficiently assimilated by cladocerans or copepods, suggesting that this fatty acid is a poor

335   indicator of terrestrial contribution in consumer diets (Taipale et al., 2015; Taipale et al.,

336   unpublished).

337   Our results indicate that the commercially important planktivorous fish, vendace, is

338   dependent on the algae-based food chain for deposition of internal energy stores in summer.

339   Compared to algal fatty acids, the proportion of terrestrial and microbial fatty acid

340   biomarkers were low suggesting that the utilization of terrestrial resources in pelagic food

341   webs of large boreal lakes is limited. The importance of algae-derived fatty acids in biomass

342   increase and fatty acid accumulation in vendace is ecologically significant because the

343   survival of coregonids in winter depends on body condition and presence of sufficient lipid

344   stores (Pangle, Sutton, Kinnunen & Hoff, 2004). Additionally, reproductive success is linked

345   with the accumulation of these lipids, particularly DHA (Sargent et al., 1999).

346   **Acknowledgements**

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562 *Fennici*, 41:155-164.

563 Table 1. Location, mean depth and total lake area of the studied lakes as well as mean (±SD) water color, Secchi depth, and concentrations of

564 DOC, total nitrogen, total phosphorus, and chlorophyll *a* at the sampling sites in six lake basins in the eastern Finland. The values for color are

565 from 1 m depth and the others pooled for 0-4 m depth sampled in May-June, early August and late September 2011, with the exception of Lake

566 Karjalan Pyhäjärvi, which was sampled in August 2012.

567

Lake basin	Coordinates	Mean depth (m)	Surface area (km²)	Colour (mg Pt L⁻¹)	Secchi depth (m)	DOC (mg L⁻¹)	totN (µg L⁻¹)	totP (µg L⁻¹)	Chl *a* (µg L⁻¹)
Karjalan Pyhäjärvi	61°48'N; 29°52'E	8.8	247	15	5.1±0.3	5.3±0.5	228±20	4.9±0.9	2.2±0.3
Orivesi	62°10'N; 29°43'E	9	601	28±10	2.1±0.3	7.0±0.3	304±32	11.8±1.0	6.3±2.6
Paasivesi	62° 8'N; 29°26'E	21	124	43±6	2.5±0.5	8.4±0.4	349±27	5.7±3.2	2.0±1.1
Suvasvesi	62°40'N; 28°12'E	10.4	233	32±3	3.1±0.5	8.8±0.4	490±42	10.0±7.3	2.8±1.0
Pyhäselkä	62°28'N; 29°48'E	8.8	361	57±6	1.9±0.0	9.5±0.5	399±48	9.3±0.6	1.5±0.8
Kallavesi	62°49'N; 27°52'E	8.6	478	45±5	2.3±0.6	10.2±0.2	639±107	12.1±7.1	3.4±1.3

568

569   Table 2. Length, weight and fatty acid content of vendace sampled from five large boreal

570   lakes in spring (n=15), summer (n=18) and autumn (n=15). Values are mean (±SD).

571   Approximate lipid content (Lipid %) in the muscle tissue was calculated assuming that fatty

572   acids comprise 70 % of all lipids in fish muscle (Ahlgren et al. 1996). The fatty acid content

573   of the muscle tissue and the weight of vendace as well as condition index (Fulton's K) were

574   significantly lower in spring than in summer or autumn (marked with +; Wilcoxon signed

575   rank test, P<0.05). The length of vendace did not differ between seasons.

	Length (mm)	Weight (g)	FA content (mg g^{-1} DW)	Lipid %	Condition index (K)
Spring	139±25	17.2±9.6[+]	17.7±4.3[+]	2.5	0.58±0.07[+]
Summer	148±13	23.0±6.1	28.1±13.1	4.0	0.69±0.07
Autumn	146±19	23.6±11.0	25.7±6.1	3.7	0.70±0.07

576

577 Table 3. Average (±SD) proportion (%) of saturated fatty acids (SFA), monounsaturated

578 fatty acids (MUFA) and polyunsaturated fatty acids (separately for C_{18}, C_{20} and C_{22} PUFA) in

579 seston (0.22 – 50 µm) PLFA (from Strandberg et al., 2015b), and total fatty acids of major

580 zooplankton taxa (from Hiltunen et al., 2015) and in vendace during spring, summer and

581 autumn in five lakes (names in Table 1) in Eastern Finland (n = 21 – 48 in each). Different

582 letters (a-c) denote significant between-season difference in the relative proportion of the

583 specific FA class within each group/taxa (ANOVA, Games-Howell post hoc test).

FA class	Group/taxa	Spring	Summer	Autumn
SFA	Seston	26.6 ± 4.0 [a]	36.9 ± 6.8 [b]	29.7 ± 9.1 [ab]
	Cladocera	36.8 ± 3.9 [a]	36.5 ± 4.9 [a]	30.3 ± 2.0 [b]
	Limnocalanus	30.2 ± 4.9 [a]	12.1 ± 3.2 [b]	14.0 ± 3.3 [b]
	Eudiaptomus	31.3 ± 4.7 [a]	40.4 ± 6.1 [b]	28.1 ± 1.6 [a]
	Cyclopoida	35.6 ± 5.4 [a]	45.3 ± 7.1 [b]	29.8 ± 8.2 [a]
	Vendace	33.6 ± 3.8	33.0 ± 2.6	32.6 ± 2.3
MUFA	Seston	16.4 ± 6.3	19.0 ± 2.2	20.8 ± 3.9
	Cladocera	24.2 ± 6.3	24.0 ± 4.2	27.6 ± 4.8
	Limnocalanus	12.9 ± 3.7	15.0 ± 3.0	15.9 ± 2.0
	Eudiaptomus	13.9 ± 3.0 [a]	7.6 ± 0.6 [b]	9.5 ± 1.4 [c]
	Cyclopoida	13.8 ± 3.2	10.6 ± 4.2	14.0 ± 6.6
	Vendace	7.2 ± 2.2 [a]	12.2 ± 4.0 [b]	10.8 ± 2.8 [b]
C_{18} PUFA	Seston	29.5 ± 7.0	30.5 ± 5.1	31.4 ± 5.4
	Cladocera	18.8 ± 3.6	19.0 ± 3.6	17.7 ± 5.1
	Limnocalanus	7.5 ± 1.6 [a]	14.2 ± 2.9 [b]	17.1 ± 2.1 [c]
	Eudiaptomus	16.6 ± 4.3 [a]	16.2 ± 4.2 [a]	27.9 ± 3.8 [b]
	Cyclopoida	16.5 ± 6.0 [a]	15.7 ± 3.1 [a]	23.0 ± 9.5 [b]
	Vendace	2.9 ± 2.4 [a]	7.2 ± 3.5 [b]	5.8 ± 2.0 [b]
C_{20} PUFA	Seston	16.1 ± 2.5 [a]	7.1 ± 3.9 [b]	10.6 ± 2.4 [b]
	Cladocera	15.7 ± 5.6	16.9 ± 6.1	19.6 ± 2.1
	Limnocalanus	19.1 ± 4.6 [a]	25.3 ± 2.1 [b]	23.6 ± 1.4 [b]
	Eudiaptomus	13.2 ± 2.2	13.0 ± 2.3	13.6 ± 1.0
	Cyclopoida	13.1 ± 2.9 [a]	9.5 ± 2.7 [b]	13.2 ± 2.7 [a]
	Vendace	13.4 ± 1.7 [a]	15.1 ± 1.6 [b]	15.5 ± 1.7 [b]
C_{22} PUFA	Seston	9.5 ± 3.6 [a]	2.4 ± 2.7 [b]	2.8 ± 1.7 [b]
	Cladocera	0.7 ± 0.4	0.5 ± 0.6	0.4 ± 0.7
	Limnocalanus	28.5 ± 3.3 [a]	23.2 ± 3.4 [b]	23.2 ± 2.8 [b]
	Eudiaptomus	19.5 ± 4.6 [a]	19.5 ± 2.2 [a]	13.7 ± 2.1 [b]

	Cyclopoida	16.9 ± 3.6	15.7 ± 2.6	14.8 ± 3.0
	Vendace	42.4 ± 4.1 [a]	31.3 ± 6.8 [b]	34.5 ± 4.2 [b]
BAFA	Seston	1.5 ± 0.9	2.2 ± 1.1	2.3 ± 0.8
	Cladocera	4.2 ± 1.8	4.6 ± 1.1	5.0 ± 0.3
	Limnocalanus	3.4 ± 1.8 [a]	1.2 ± 0.7 [b]	1.2 ± 0.3 [b]
	Eudiaptomus	5.0 ± 1.6 [a]	3.4 ± 0.7 [b]	4.3 ± 0.5 [a]
	Cyclopoida	5.4 ± 2.6	5.4 ± 1.3	4.8 ± 1.8
	Vendace	0.9 ± 0.4	1.5 ± 0.9	1.0 ± 0.3

584

585

586 **FIGURE LEGENDS**

587

588 Figure 1. Mean content of saturated fatty acids (SFA), monounsaturated fatty acids (MUFA),

589 C_{18}, C_{20} and C_{22} polyunsaturated fatty acids (PUFA) and bacterial fatty acids (BAFA) during

590 different seasons in the muscle of vendace from different lake basins (n=3-5 in each lake and

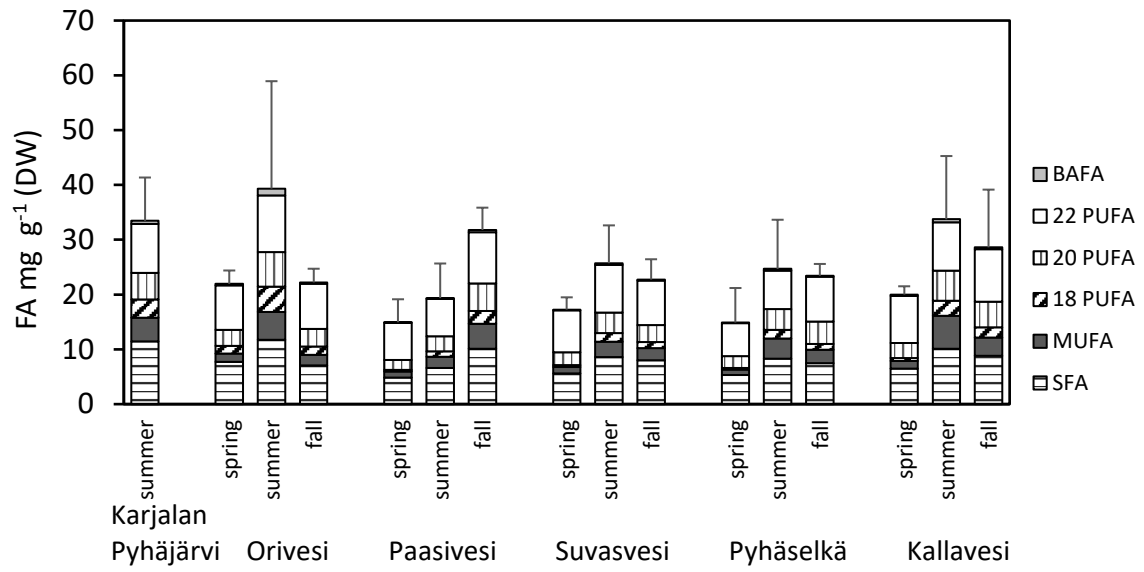591 season). Error bars represent SD of the total FA content.

592

593 Figure 2. Multidimensional scaling ordination of fatty acid proportions (42 fatty acids) in the

594 dorsal muscle of vendace in different lake basins and seasons. Euclidean distance was used

595 for the scaling (2D stress: 0.05). Seasonal differences of the fatty acid composition of

596 vendace is statistically significant (see text), specifically the spring samples differ from

597 summer and autumn samples (results of the PERMANOVA post hoc test in the figure).

598

599 Figure 3. Correlation (with 95 % confidence intervals) of the total fatty acid content of

600 vendace muscle and the proportion of A) MUFA (mainly C_{16} and C_{18}), B) C_{18} PUFA, C)

601 C_{22}PUFA, and D) BAFA. Note the different scales on the y-axis.

602

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605

606   Figure 1.

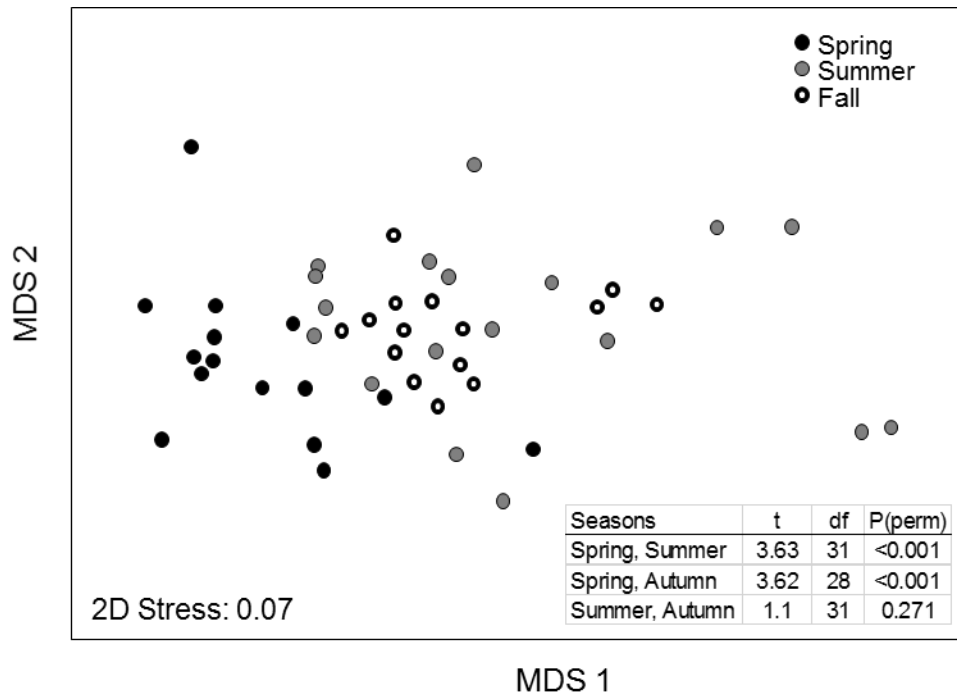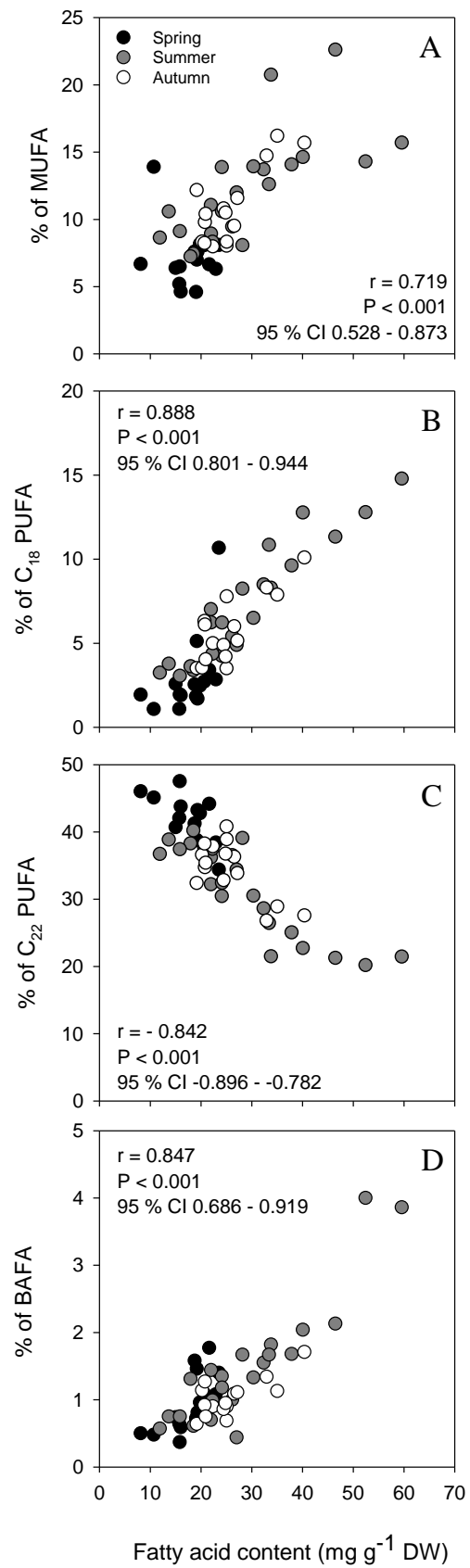| Seasons	t	df	P(perm)
Spring, Summer	3.63	31	<0.001
Spring, Autumn	3.62	28	<0.001
Summer, Autumn	1.1	31	0.271

607

608   Figure 2.

Figure 3.

Supplement 1. Fatty acid profile of vendace muscle (% of all fatty acids). Samples from 5 lake basins were combined for each season: spring (n=15), summer (n=18), fall (n=15), because no significant differences were found in the fatty acid profile between lakes (PERMANOVA. P=0.178). See the text for details. Samples from Lake Karjalan Pyhäjärvi are presented separately due to lack of samples from spring and fall (n=4).

	Spring		Summer		Fall		Karjalan Pyhäjärvi	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
14:0	1.0	0.5	2.0	1.3	1.7	0.8	3.6	1.0
4.8.12-TMTD	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1
i15:0	0.0	0.0	0.2	0.2	0.1	0.1	0.3	0.1
ai15:0	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1
15:0	0.3	0.2	0.3	0.2	0.3	0.1	0.3	0.1
i16:0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0
16:0	24.8	3.3	23.6	3.3	24.6	2.2	25.6	2.0
16:1n-9	0.1	0.0	0.2	0.1	0.1	0.1	0.4	0.1
16:1n-7	0.7	0.4	2.4	1.4	1.9	0.7	2.4	1.0
16:1n-5	0.2	0.1	0.3	0.1	0.2	0.1	0.4	0.1
i17:0	0.1	0.1	0.2	0.1	0.1	0.0	0.2	0.1
ai17:0	0.1	0.1	0.2	0.2	0.1	0.0	0.3	0.1
16:2n-4	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
17:0	0.4	0.2	0.4	0.1	0.4	0.1	0.4	0.1
Phytanate	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
17:1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
18:0	7.0	0.9	6.2	1.2	5.7	0.4	4.6	0.5
18:1n-9	4.7	1.6	6.9	2.5	6.4	1.9	6.7	1.4
18:1n-7	1.6	0.4	2.3	0.6	2.1	0.4	2.6	0.4
18:2n-6	1.1	0.7	2.0	1.0	1.7	0.6	2.2	0.7
18:3n-6	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1
18:3n-3	1.3	0.8	2.8	1.1	2.5	0.9	3.0	1.1
18:4n-3	0.5	0.9	2.0	1.5	1.5	0.7	4.0	1.7
20:0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
20:1n-9	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.0
20:2n-6	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.0
20:4n-6	5.0	1.0	4.5	0.7	4.9	1.1	4.5	0.3
20:3n-3	0.0	0.0	0.1	0.1	0.0	0.1	0.2	0.0
20:4n-3	0.3	0.3	0.7	0.5	0.6	0.3	1.0	0.1
20:5n-3	8.1	1.3	9.9	1.3	10.0	1.3	8.7	0.7
22:4n-6	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
22:5n-6	1.8	0.65	1.8	0.6	1.5	0.5	1.5	0.3
22:5n-3	0.9	0.4	1.3	0.4	1.0	0.3	1.3	0.1
22:6n-3	39.7	4.3	28.9	7.1	32.0	4.1	25.2	6.3
24:1n-9	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.0

Supplement 2. Fatty acid composition of vendace roe (n=7). Only the quantitatively most important fatty acids are presented (mean proportion > 1%). These 14 fatty acids account for 92.0-95.6% of all fatty acids in the roe. Values are mean (±SD).

Fatty acid	w%	Fatty acid	w%	Fatty acid	w%
14:0	2.81 (*0.49*)	18:2n-6	3.81 (*1.10*)	22:5n-3	1.94 (*0.13*)
16:0	17.85 (*1.63*)	18:3n-3	5.53 (*1.05*)	22:6n-3	16.31 (*3.17*)
18:0	2.01 (*0.27*)	18:4n-3	4.34 (*1.01*)	n3/n6	4.04 (*0.69*)
16:1n-7	5.27 (*1.12*)	20:4n-6	4.85 (*0.70*)	sumSFA	22.66 (*1.49*)
18:1n-9	13.22 (*3.18*)	20:4n-3	1.97 (*0.45*)	sumMUFA	22.36 (*4.35*)
18:1n-7	3.87 (*0.47*)	20:5n-3	9.89 (*0.71*)	sumPUFA	48.65 (*4.07*)