

1 **Meta-analysis of factors associated with omega-3 fatty acid contents of wild**  
2 **fish**

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16

17 **Abstract**

18

Fish are recognized as the main source of physiologically important omega-3 long-chain

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polyunsaturated fatty acids, namely, eicosapentaenoic acid (EPA) and docosahexaenoic acid

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(DHA), for human nutrition. However, muscle tissue contents of these fatty acids in diverse fish

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species, i.e., their nutritive value for humans, varied within two orders of magnitude. We

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reviewed contents of EPA and DHA, measured by similar methods using an internal standard

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during chromatography as mg per g of wet mass in 172 fish species belonging to 16 orders, to

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evaluate probable variations in phylogenetic and ecological drivers. EPA+DHA content varied

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from 25.6 mg·g<sup>-1</sup> of wet mass (*Sardinops sagax*) to 0.12 mg·g<sup>-1</sup> (*Gymnura* spp.).

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Multidimensional redundancy analysis revealed that among phylogenetic, ecomorphological and

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abiotic environmental factors, the highest proportion of variation contribution belonged to the

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shared contribution of sets of phylogenetic and ecomorphological factors. Specifically, the

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highest values of EPA+DHA content were characteristic of fish belonging to the orders

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Clupeiformes or Salmoniformes, were pelagic fast swimmers, ate zooplankton and inhabited

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marine waters or migrated from fresh to marine waters (anadromous migrations). High EPA and

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DHA content in muscle tissues of the above species appeared to be a metabolic adaptation for

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fast continuous swimming. In contrast to common beliefs, our meta-analysis did not support the

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significant influence of higher trophic levels (piscivory) and cold environments (homeoviscous

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adaptation) on EPA and DHA content in fish. However, many causes of high and low levels of

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physiologically important fatty acids in certain fish species remained unexplained and require

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evaluation in future studies.

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**Keywords** Docosahexaenoic acid; Ecomorphological factors; Eicosapentaenoic acid; Nutritive

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value; Phylogenetic factors

41  
42 **Introduction**

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44 In the last few decades, omega-3 long-chain polyunsaturated fatty acids (LC-PUFAs), namely,  
45 eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3), were the focus  
46 of many biochemical, physiological (e.g., Lauritzen et al. 2001; Wall et al. 2010; De Caterina  
47 2011), ecological (Arts et al.2001; Parrish 2009; Gladyshev et al. 2013; Hixson et al. 2015;  
48 Twining et al. 2016), aquacultural (Sargent et al. 1999; Tocher 2015) and nutritional  
49 (Simopoulos 2000; Robert 2006; Woods and Fearon 2009; Rubio-Rodriguez et al. 2010; Kouba  
50 and Mourot 2011) reviews. These two LC-PUFAs are essential for various physiological and  
51 biochemical processes in all vertebrate organisms, including fish and humans. EPA is a precursor  
52 in the synthesis of the following bioactive lipid mediators (local hormones)/n-3 eicosanoids: 1)  
53 series-3 thromboxanes, which are vasodilators and inhibitors of platelet aggregation and thereby  
54 reduce blood pressure; 2) series-3 prostaglandins, which provide anti-inflammatory effects; and  
55 3) series-5 leukotrienes, which reduce allergy symptoms (Broughton et al. 1997; Lauritzen et al.  
56 2001; Kris-Etherton et al. 2002; SanGiovanni and Chew 2005; Wall et al. 2010). In general, n-3  
57 eicosanoids act as counterregulators of n-6 eicosanoids (synthesized from arachidonic acid  
58 (ARA, 20:4n-6)), which have opposite metabolic properties to those derived from the n-3 fatty  
59 acid, EPA. In turn, DHA is the major structural lipid of retinal, neural and brain cell membranes,  
60 comprising 10 – 30% of total fatty acids (SanGiovanni and Chew 2005; McNamara and Carlson  
61 2006). Moreover, DHA can decrease production of proinflammatory n-6 eicosanoids by  
62 inhibiting a key enzyme, cyclooxygenase (Adkins and Kelley 2010; Norris and Dennis 2012).

63         Studies of many fish species imply a key role of DHA in their neural development and  
64 functioning of brain and eye (Sargent et al. 1999; Tocher2003). EPA in fish, like in other  
65 vertebrates, has critical metabolic functions via eicosanoid production, maintaining  
66 cardiovascular health, immune and inflammatory responses, and gene expression (Tocher 2015).  
67 Reduction of these LC-PUFAs in fish diet affects behaviour, decreases growth rate,

68 development, survival and fecundity, delays response to visual stimuli, decreases burst and  
69 cruise swimming speed (Masuda et al, 1999; Francis et al., 2006; Benitez-Santana et al 2007;  
70 Rinchard et al. 2007; Kjørsvik et al 2009; Vizcaino-Ochoa et al. 2010; Zakeri et al. 2011;  
71 Fuiman and Perez 2015; Mozanzadeh et al 2015).

72 As mentioned, EPA and DHA are essential for human health. Indeed, for over 30 years,  
73 epidemiological studies and clinical trials, including several hundred thousand individuals,  
74 indicated that EPA and DHA supplementation considerably reduced the risk of morbidity and  
75 mortality of many cardiovascular diseases (Garg et al. 2006; Plourde and Cunnane 2007; Casula  
76 et al. 2013). Possible mechanisms by which EPA and DHA improved cardiovascular health  
77 included antithrombotic, anti-inflammatory and antiarrhythmic actions (Adkins and Kelley  
78 2010; Phang et al. 2011). The World Health Organization as well as numerous national health  
79 organizations recommended personal consumption of 0.5 – 1.0 g of EPA+DHA per day to  
80 reduce the risk of cardiovascular diseases (Harris et al. 2009; Kris-Etherton et al. 2009; Adkins  
81 and Kelley 2010; Nagasaka et al. 2014). Furthermore, a daily intake of ~1 g of DHA has been  
82 recommended to prevent neuropsychiatric disorders and to maintain optimal cognitive function  
83 throughout one's lifespan (Reis and Hibbeln 2006; Robert 2006; Plourde and Cunnane 2007;  
84 Dyall 2015; Weiser et al. 2016).

85 The main dietary source of EPA and DHA for humans is fish (Robert 2006; Adkins and  
86 Kelley 2010; Gladyshev et al. 2013, 2015a). Nevertheless, contents of EPA and DHA in edible  
87 biomass (muscle tissue) of diverse fish species vary by more than two orders of magnitude  
88 (Gladyshev et al. 2013). Therefore, it is difficult to consume the recommended daily intake by  
89 eating certain fish species (Kwetegyeka et al. 2008; Vasconi et al. 2015).

90 For applied science, continual database improvement for EPA and DHA contents in  
91 diverse fish species is necessary for an accurate assessment of the intake of these essential  
92 nutrients (Harris et al. 2009). Evidently, individuals as well as public health officials should be  
93 aware that not all fish are equally valuable sources of EPA and DHA (Chuang et al. 2012).

94 However, there is an acute problem, pointed out in recent reviews (e.g., Hixson et al. 2015): in  
95 most published works, EPA and DHA in fish were measured and presented as relative units,  
96 namely, percent of total fatty acids. Meanwhile, it was demonstrated that to estimate nutritive  
97 value for humans, measurements of LC-PUFAs should be reported per mass of consumed food,  
98  $\text{mg}\cdot\text{g}^{-1}$  wet mass, rather than their percent in total fatty acids provided (Gladyshev et al. 2007,  
99 2012b, 2017; Huynh and Kitts 2009; Woods and Fearon 2009). Therefore, only data regarding  
100 fatty acid content on a mass basis, as mg per g of biomass, are suitable for fish nutritive value  
101 databases (Litzow et al. 2006).

102 To understand how EPA and DHA are trophically conveyed, it is necessary to reveal  
103 mechanisms that account for the 200-fold difference in EPA and DHA contents in diverse wild  
104 fish species. Causes of fatty acid (FA) composition and content variations in wild fish, including  
105 those of EPA and DHA, are not completely understood yet (Gribble et al. 2016). There are two  
106 groups of factors, that may determine FA fish content: ecological and phylogenetic (e.g.,  
107 Vasconi et al. 2015). Relative contributions of ecological vs. taxonomic factors to FA profiles  
108 were quantified for phytoplankton (Galloway and Winder 2015) and diverse marine and  
109 terrestrial organisms (Colombo et al. 2017).

110 Among ecological factors, food has often been regarded as the main determinant of fish  
111 FA profiles, especially in aquaculture (Morton et al. 2014; Wijekoon et al. 2014; Betancor et al.  
112 2015). In natural water bodies, ecosystem trophic status (e.g., oligotrophic vs. eutrophic), which  
113 resulted in a different quality of phytoplankton as the base of the food web, feeding habits and  
114 fish trophic level were reported to determine FA composition via the quality of food resources  
115 (Ahlgren et al. 1996; Czesny et al. 2011; Vasconi et al. 2015). For example, the highest values of  
116 EPA and DHA were believed to be characteristic of either planktivorous fish or top predators  
117 (Tacon and Metian 2013; Hixson et al. 2015; Vasconi et al. 2015). However, other authors  
118 reported that PUFA and other FA fish profiles were of genetic character (i.e., species-specific)  
119 and could be decoupled from their diets (Sushchik et al. 2006; Kwetegyeka et al. 2008;

120 Gladyshev et al. 2012b; Lau et al. 2012). In addition, it was hypothesized (Ahlgren et al. 2009)  
121 that the quality of food resources was the main mechanism controlling PUFA content in  
122 herbivorous and omnivorous fish, while for carnivorous fish, the phylogenetic factor (species  
123 identity) was more important . Moreover, fish habitat may be important for PUFA contents. For  
124 example, marine fish were commonly regarded as having higher levels of EPA and DHA (Garg  
125 et al. 2006; Rubio-Rodriguez et al. 2010; Guler et al. 2011). However, there were no statistical  
126 comparisons between diverse marine and freshwater wild fish in the available literature (but see  
127 Moth et al. 2013 for the sum of omega-3 PUFA percentage). Fish size and swimming speed  
128 related to habitat (e.g., pelagic high-mobility fish vs. demersal low-mobility fish) have also been  
129 reported to affect EPA and DHA contents (Ahlgren et al. 1996; Tacon and Metian 2013; Vasconi  
130 et al. 2015).

131         Temperature has also been regarded as an important ecological factor determining EPA  
132 and DHA contents in fish (Arts et al. 2012). However, there was a discrepancy between results  
133 of several experimental studies as well as results of field studies, which should be further  
134 investigated (Gribble et al. 2016).

135         The aim of the present work was to conduct a meta-analysis of our data and published  
136 data regarding EPA and DHA contents in various wild fish species. Specifically, we aimed to  
137 determine a relative contribution of the following factors to the LC-PUFA content: 1) phylogeny  
138 (order identity); 2) type of feeding (trophic level); 3) habitat (marine - freshwater, cold - warm);  
139 and 4) size and movement.

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## 142 **Methods**

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144 Data

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146 Fatty acid data from diverse wild fish were primarily collected from peer-reviewed, scientific  
147 literature. No data on fish reared in aquaculture were included because many variables, used in  
148 multidimensional analysis (see below) of ecological features of wild fish, including feeding  
149 mode (piscivorous, benthivorous, etc.), habitats (pelagic, demersal, migratory, etc.) and  
150 swimming velocity are evidently senseless for fish reared in cages using artificial (formulated)  
151 food. We produced two data sets. The first set included data on EPA and DHA contents,  $\text{mg g}^{-1}$   
152 of wet mass (WM), from publications in Web of Science, Core Collection on 22 April 2016 for  
153 ‘fatty acid AND content AND fish’. From these publications, we selected only those that  
154 measured fatty acid content using an internal standard during gas chromatography, and we  
155 discarded data that were recalculated from lipid weighing. Data from studies, where wild and  
156 cultivated fishes were compared, were screened only for wild specimens (Amira et al. 2010;  
157 Heissenberger et al. 2010). We additionally screened studies to select FA data from the white  
158 muscle of fish, primarily because this tissue is most often used as the edible portion. Data from  
159 other tissues were discarded.

160 In some of the included literature sources, representative size of the analyzed fish was not  
161 reported, but in all cases, fish were obtained from the commercial catch and were adults.  
162 Evidently, fish fatty acid composition and content can change during growth and reproductive  
163 periods (Faleiro and Narciso 2010; Gladyshev et al. 2010; Fuiman and Perez 2015; Murzina et  
164 al. 2016). However, the aim of our present study was to evaluate the nutritive value of  
165 commercially caught fish for humans because humans mainly consume wild fish from  
166 commercial catches, i.e., fish of representative size. Therefore, we did not take variations of FA  
167 content in fish during growth into consideration but instead focused on FA content in fish of  
168 representative size.

169 In various of the articles examined, data on FAs were given relative to fish dry mass  
170 (Ahlgren et al. 1994; Heissenberger et al. 2010; Wagner et al. 2010). These data were re-  
171 calculated per WM, using data on either water content for individual species (Ahlgren et al.

172 1994;Chuang et al. 2012) or mean water content values for the relevant order (Gladyshev et al.  
173 2006, 2007; Sushchik et al. 2006, 2007). As mentioned above, the applied aim of the inventory  
174 of EPA and DHA contents in diverse fish species is the assessment of their nutritive value for  
175 humans, i.e., quantity of their healthy daily personal intake (portion), which is calculated per wet  
176 mass (e.g., Kwetegyeka et al. 2008; Chuang et al. 2012; Gladyshev et al., 2013). EPA and DHA  
177 content data from Zhang et al. (2012), Neff et al. (2014a, b) and Vasconi et al. (2015) were  
178 calculated using the data determined by percentages and total FA contents ( $\text{mg g}^{-1}\text{WM}$ ) specified  
179 in these papers. Three evidently artifact values from Cladis et al. (2014) and one from Chuang et  
180 al. (2012) were not included in the data set because they severely contradicted all known data.  
181 Our unpublished data, included in the set, were obtained using internal standards by methods  
182 described elsewhere (Sushchik et al. 2006; Gladyshev et al. 2014). To provide an equal statistical  
183 mass of each species reported by several authors on the same species, the mean value of each  
184 species was acquired for meta-analysis. There were 172 species in the first set.

185 The second dataset represented a subset of the first one and encompassed species for  
186 which percentage of total EPA and DHA contents and total FA contents ( $\text{mg g}^{-1}$  tissue) were  
187 additionally reported. There were 88 species in the second set.

188 Data on fish of representative size, habitat, feeding mode and cruise swimming velocity  
189 were acquired from relevant references (Nikolsky 1971; Aleyev 1976; Pavlov 1979; Atlas ...  
190 2003; Commercial fishes ... 2006; Kukhorenko and Kukuev 2010) or from Internet sources  
191 (<http://www.fishbase.org/>; <http://www.fao.org/>; <http://www.iucnredlist.org/>). Regarding cruise  
192 swimming velocity ( $V$ ,  $\text{m s}^{-1}$ ), fish were subdivided into three groups: slow ( $V < 1$ ), medium ( $1 \leq$   
193  $V \leq 2$ ) and fast ( $V > 2$ ). This parameter was determined on the basis of data regarding direct  
194 experimental estimations, analogies with phylogenetically and ecologically allied species,  
195 analysis of the shape of the body and structure of fins (obtained from above cited publications)  
196 and using the results of theoretical and experimental studies of swimming of fish and dolphins  
197 (Romanenko 2002).



198

199 Statistical analyses

200

201 To relate variance in fish EPA and DHA content to phylogenetic (species identity) and  
202 ecological effects, a redundancy analysis was used similar to Lau et al.'s study (2012). In brief, a  
203 gradient length was computed by a de-trended correspondence analysis using the fatty acid data  
204 matrix, and length values were 0.869 and 0.733 for the first and second axes, respectively,  
205 suggesting linear model responses to explanatory variables (Jongman et al. 1987; ter Braak and  
206 Prentice 1988). Therefore, partial redundancy analysis (pRDA) was used for the calculations  
207 (Borcard et al. 1992; Legendre and Legendre 1998).

208 pRDA was conducted with the *Vegan* package (version 2.4-0) in R ([http://cran.r-](http://cran.r-project.org/)  
209 [project.org/](http://cran.r-project.org/)). We used the first data set for this analysis, and EPA and DHA contents (mg g<sup>-1</sup> of  
210 WM) and their sum (EPA+DHA) were used as the response variables. To reduce value  
211 distribution skewness, values were  $\ln+1$  transformed. Explanatory variables were grouped into  
212 three sets (matrices): phylogenetic, ecomorphological and abiotic environmental features. The  
213 phylogenetic set represented the identity of 16 orders (according to Nelson 2006). The  
214 ecomorphological set included type of feeding (piscivorous, omnivorous, planktivorous and  
215 benthivorous), habitats (pelagic, demersal, benthopelagic and migratory), swimming velocity and  
216 size. The abiotic environmental set encompassed two factors: temperature and salinity.  
217 Taxonomic orders, type of feeding and habitats were independent nominal data and were coded  
218 as a dummy variable (Jongman et al. 1987; ter Braak and Prentice 1988). Other explanatory  
219 factors except size ( $\ln+1$  transformed) were used in the RDA as rank-ordered data. First, we  
220 applied the redundancy analysis (RDA) for each explanatory matrix, and assessed the global  
221 significance using the *anova.cca* function with 1000 permutations. Then, we conducted a  
222 forward selection procedure based on an adjusted  $R^2$  value to reduce the number of explanatory  
223 variables (both 'forward.sel' and 'ordiR2step' functions were used and compared). Only

224 significant ( $P < 0.05$ ) variables were applied for the subsequent variation partitioning analysis  
225 (pRDA) based on the ‘varpart’ function. The significance of each testable fraction in variation  
226 partitioning analysis was tested using 1000 permutations. We additionally performed a total  
227 RDA for all significant variables selected from the explanatory sets. The forward selection  
228 procedure was repeated as well.

229 Standard errors (SE), Kolmogorov-Smirnov one-sample test for normality  $D_{K-S}$ ,  
230 Pearson’s correlation coefficient  $r$ , Kruskal–Wallis  $H$  test, and one-way ANOVA with Fisher’s  
231 LSD *post hoc* tests were calculated conventionally using STATISTICA software, version 9.0  
232 (Stat Soft Inc., Tulsa, OK, U.S.A.).

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234

## 235 **Results**

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237 Sum of EPA and DHA content in the studied fish species, belonging to 16 orders (data set 1, 172  
238 species), varied from 25.6 mg g<sup>-1</sup> WM (*Sardinops sagax*, order Clupeiformes) to 0.12 mg g<sup>-1</sup>  
239 (*Gymnura* spp., order Myliobatiformes) (Table 1). Statistical characteristics of EPA+DHA  
240 content for the orders, ranged by maximum values, are shown in Fig. 1. Although maximum  
241 values differed between many orders, minimum values were very close to each other, except for  
242 those of the order Osmeriformes (Fig. 1). However, there were only three species in the  
243 order Osmeriformes (Table 1), and therefore their minimum value should be specified in the  
244 future. All values for each order had a normal distribution according to the Kolmogorov-  
245 Smirnov one-sample test for normality  $D_{K-S}$ , except for the order Perciformes.

246 Analysis of the second dataset (88 species, Fig. 2) revealed an absence of correlation ( $r =$   
247  $-0.12$ ,  $P > 0.05$  for *log*-transformed data) between the sums of EPA+DHA content (mg g<sup>-1</sup>) and  
248 the levels (% of total FAs). *Gadus merlangus* had the highest percentage of EPA+DHA at  
249 55.8%, while the EPA+DHA content in this species, 0.56 mg g<sup>-1</sup>, was close to the lowest value

250 (Fig. 2). Using the second data set, correlations between the percentage of EPA and DHA and  
251 the content of total FAs ( $\text{mg g}^{-1}\text{WM}$ ) were calculated. There was no correlation between the  
252 percentage of EPA and the content of total FAs:  $r = 0.16$ ,  $P > 0.05$ . In contrast, there was a strong  
253 significant negative correlation between the percentage of DHA and the content of total FAs:  $r =$   
254  $-0.61$ ,  $P < 0.05$  (Fig. 3).

255 Using RDA based on the forward selection procedure, the significant variables in three  
256 sets of explanatory matrices were identified: identity in orders *Clupeiformes*, *Salmoniformes*,  
257 *Scorpaeniformes* and *Osmeriformes* in the taxonomic set, planktivory, swimming velocity and  
258 migratory in the ecomorphological set, and temperature and salinity in the set of abiotic  
259 environments (Table 2). However, order *Osmeriformes*, migratory and temperature were  
260 excluded from total RDA ( $p < 0.001$ ) after the forward selection. In addition, variance inflation  
261 factors (VIF) were inspected for all remaining explanatory variables, which were low ( $\text{VIF} < 10$ )  
262 and therefore assumed no evidence of collinearity. The highest proportion of explained variation  
263 contribution, 16.5%, belonged to the shared contribution of sets of phylogenetic and  
264 ecomorphological factors (Fig. 4). The highest proportion of unique contribution, 7.0%,  
265 belonged to the set of phylogenetic factors (Fig. 4). In general, all explanatory variables  
266 significantly explained 35.6% of the total variance in EPA and DHA contents (Fig. 4).

267 To specify the above RDA results, the Kruskal–Wallis  $H$  test was used because numerous  
268 compared variables did not have normal distribution according to the Kolmogorov-Smirnov  $D_{K-S}$   
269 test. Concerning the swimming velocity, fast swimming species on average had significantly  
270 higher EPA+DHA content than the medium and slow swimming fish (Fig. 5A). For salinity, the  
271 most important abiotic environmental factor, migratory (anadromous) and marine species had  
272 significantly higher EPA+DHA contents than freshwater-brackish water fish, while freshwater  
273 and marine-brackish water species had intermediate values of EPA+DHA contents (Fig. 5B).  
274 Regarding type of feeding, planktivorous fish had significantly higher EPA+DHA contents than  
275 all other feeding groups, except for omnivores-planktivores (Fig. 5C).

276 In addition, the remaining explanatory variables, which did not give significant effects in  
277 RDA, were analyzed. For habitat temperature, species from temperate-cold waters had  
278 significantly higher EPA+DHA contents than species from temperate warm and warm waters,  
279 while fish from cold and temperate waters had intermediate values of EPA+DHA content (Fig.  
280 5D). However, pelagic fish appeared to have a significantly higher average EPA+DHA content  
281 than that of demersal species (Fig. 5E). It is also worth noting that there were no significant  
282 correlations between the representative size of a species and EPA (*In data*:  $r = -0.185$ ,  $P > 0.05$ ),  
283 DHA ( $r = 0.03$ ,  $P > 0.05$ ) and their sum ( $r = -0.06$ ,  $P > 0.05$ ).

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285

## 286 Discussion

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288 The highest contents of EPA+DHA were found in fishes which belonged to the order  
289 Clupeiformes or Salmoniformes, swam fast, ate zooplankton and inhabited marine waters or  
290 migrated from fresh to marine waters (anadromous migrations). Moreover, fish with highest  
291 contents of EPA+DHA were pelagic species (naturally, as they were planktivores) and inhabited  
292 temperate-cold waters.

293 Specific traits were associated with high EPA and DHA contents in fish muscle tissues.

294 First, the phylogenetic factor gave comparatively high contribution to the content variations (Fig.  
295 4). The principal role of phylogenetic factors compared to that of ecological factors for FA  
296 composition and content was recently demonstrated for aquatic invertebrates (Makhutova et al.  
297 2011; Lau et al. 2012), phytoplankton (Galloway and Winder 2015), birds (Gladyshev et al.  
298 2016) and many marine and terrestrial organisms (Colombo et al 2017). For fish, phylogenetics  
299 also played an important role, as demonstrated in our present study and in the literature (Weber  
300 et al. 2016; Colombo et al 2017). However, according to our data, the interaction of phylogenetic  
301 and ecological factors appeared to be of the highest importance for EPA+DHA contents (Fig. 4).

302 Similar conclusion resulted from an in-depth examination of ecological (biome, trophic level)  
303 and taxonomic factors (Colombo et al 2017). Indeed, in the course of biological evolution, a  
304 species' genotype was created by an adaptation to different lifestyles in certain environments.  
305 Therefore, high EPA and DHA contents may be regarded as an adaptive feature of fish species.  
306 For example, Clupeiformes species mainly inhabit surface waters of open seas and oceans, and  
307 therefore they are adapted to fast continuous swimming during long-distance migrations  
308 searching plankton productive zones. Fast continuous swimming may be supported by high  
309 contents of LC-PUFAs in muscle tissue as follows.

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311

312 Type of swimming

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314 PUFAs, in particular DHA, were recently proposed to be “pacemakers” for the metabolism of  
315 animal cells (Hulbert et al. 2002; Turner et al. 2003; Hulbert 2007). In many vertebrate tissues,  
316 including skeletal muscle, a strong positive correlation was found between DHA content of cell  
317 membrane phospholipids and rate of metabolism (Hulbert et al. 2002). Polyunsaturated FAs have  
318 comparatively low potential barriers for rotation around the carbon-carbon single bonds on either  
319 side of the double bonds, and thereby their chains move rapidly, exerting very high lateral  
320 pressure on neighboring molecules in a cell membrane (Hulbert 2007). The greater the lateral  
321 pressure in the membrane, the greater the activity of membrane-associated enzymes (Hulbert  
322 2007). For example, high DHA content in membrane phospholipids was found to provide higher  
323 activity of the ubiquitous enzyme, the sodium pump ( $\text{Na}^+$ ,  $\text{K}^+$ -ATPase), which is especially  
324 important for providing action potential in excitable cells, including muscle cells or fibers  
325 (Turner et al. 2003, 2005; Hulbert 2007). Furthermore, DHA is additionally believed to enhance  
326 activity of membrane-bound enzymes of the mitochondrial electron transport chain (ETC);  
327 therefore, the most active (high-frequency contraction) muscles that provide high respiration

328 rates have higher concentrations of DHA compared with less active muscles (Infante et al. 2001).  
329 Moreover, long-distance migratory birds use high storages of dietary EPA and DHA as  
330 performance-enhancing agents to activate membrane-related enzymes of the lipid fuel pathway  
331 from adipose tissue to  $\beta$ -oxidation and ETC in muscle mitochondria (Weber 2011). Similarly, the  
332 high EPA and DHA contents in muscle tissue of Clupeiformes species appeared to be due to the  
333 adaptation for fast continuous swimming. The same may be true for migrating representatives of  
334 Salmoniformes.

335         In addition to providing the metabolic adaptation for fast continuous swimming during  
336 migrations, high EPA and DHA contents in a subset of anadromous salmonids, may have one  
337 additional ecological cause. Salmonids reproduce in oligotrophic streams and die after spawning.  
338 Their carcasses in oligotrophic streams are the main food supply for their juveniles via benthic  
339 food chains, which provide valuable food with a high content of n-3 PUFA (Heintz et al. 2004).  
340 Therefore, high EPA and DHA contents in the anadromous Salmoniformes may be due to an  
341 adaptation for their peculiar way of reproducing in their specific ecological niche while they feed  
342 their juveniles with food of high nutritive value that is essential for their growth and  
343 development.

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345

346 Type of feeding

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348 The second characteristic of the fish with high EPA+DHA contents was planktivory, namely,  
349 zooplanktivory. Why did planktivorous fish have higher EPA+DHA content compared to that of  
350 benthivorous fish (Fig. 5C)? The cause may be due to a higher content of EPA and DHA in  
351 primary producers, planktonic microalgae, diatoms and dinophytes, compared to that of benthic  
352 algae and terrestrial inputs (e.g., Ahlgren et al., 1996, Parrish, 2013). Thus, the primary  
353 consumers, zooplankton, may have a higher nutritive value for fish concerning EPA+DHA

354 content compared to that of zoobenthos. Moreover, zooplankton mainly consist of comparatively  
355 small Crustacea, such as Copepoda and Cladocera, that have thin chitin exoskeletons compared  
356 to the hard thick exoskeletons of most benthic invertebrates. Barely digestive chitin exoskeletons  
357 evidently compose a different portion of biomass of zooplankton and zoobenthos; therefore, the  
358 nutritive value of zooplankton, i.e., content of EPA+DHA per mass unit of organic carbon,  
359 appears to be higher than that of zoobenthos. However, this oversimplified presumption cannot  
360 be reliably checked at present because most data on LC-PUFAs in aquatic invertebrates were  
361 presented in relative units, as percentages of total FAs, while quantitative data, mg of EPA and  
362 DHA per g of organic carbon (C), were very sparse. According to these sparse data, species of  
363 the dominant taxa of marine zooplankton, calanoid copepod, had an average EPA+DHA content  
364 of 17-19 mg g<sup>-1</sup> C (Chen et al. 2011, calculated from Table 2 of the reference; Koussoroplis et al.  
365 2011, calculated from Table 2 of the reference). Freshwater zooplankton, composed of Cladocera  
366 and Copepoda, had an average content of approximately 19-77 mg g<sup>-1</sup> C (Gladyshev et al. 2015b,  
367 calculated from Table 3 of the reference). Meanwhile, freshwater zoobenthos (gammarids, insect  
368 larvae, oligochaets and gastropods) had an average EPA+DHA content of approximately 22 mg  
369 g<sup>-1</sup> C (Kalacheva et al. 2013, calculated from Table 1 of the reference). These data generally  
370 supported the above presumption regarding the higher nutritive value of zooplankton compared  
371 to that of zoobenthos. However, more research should be conducted, especially in marine  
372 ecosystems, to compare the nutritive values of zooplankton and zoobenthos regarding LC-  
373 PUFAs for elucidating causes of higher EPA and DHA contents in planktivorous fish compared  
374 to that of benthivorous fish.

375           For piscivorous species, their average EPA+DHA content was significantly lower than  
376 that of planktivorous species (Fig. 5C). For example, the piscivorous species in the order  
377 Clupeiformes, the dorab wolf-herring *Chirocentrus dorab*, had lower contents of the sum of LC-  
378 PUFAs than all other species in this order, which were planktivorous (Table 1). For benthivorous  
379 and omnivorous fish, they had an average EPA+DHA content similar to that of piscivorous fish

380 (Fig. 5C). This finding concerning the comparatively low EPA and DHA contents in piscivorous  
381 fish contradicted the general belief regarding the increase of these LC-PUFAs with trophic level  
382 (Hixson et al. 2015; Strandberg et al. 2015; Colombo et al. 2017). However, to our knowledge,  
383 there were no direct quantitative comparisons of EPA and DHA contents as  $\text{mg g}^{-1}$  of wet mass  
384 or per organic carbon of piscivorous fish and their real prey in specific ecosystems. Therefore,  
385 the increased EPA and DHA contents of piscivorous fish require additional research.

386 It is worth noting that there was no increase in EPA+DHA content in muscles of the  
387 arctic grayling, *Thymallus arcticus*, compared to its food (Sushchik et al. 2006). Therefore, the  
388 general impression regarding the increase of LC-PUFA content across trophic levels at present  
389 was supported only by data on the trophic pair ‘phytoplankton-zooplankton’ (Gladyshev et al.  
390 2011) rather than by data on fish and their food.

391

392

393 Marine and freshwater environments

394

395 According to RDA, the designated abiotic environment ‘salinity’ appeared to be of the lowest  
396 importance compared to those of factors from the phylogenetic and ecomorphological sets;  
397 however, ‘salinity’ was only moderately important in combination with these two sets (Fig. 4).  
398 Indeed, differences between average EPA+DHA contents in marine, anadromous and freshwater  
399 species, were not statistically significant (Fig. 5B). What ecomorphological and feeding factors  
400 potentially might provide high EPA+DHA contents in marine and anadromous species compared  
401 to that of freshwater fish? First, high EPA+DHA contents may be due to fast continuous  
402 swimming during long-distance migrations of marine and anadromous species. In freshwater  
403 ecosystems, which have small sizes compared to seas and oceans, there is less need and  
404 opportunity for long-distance migration. The second factor may be a difference between the  
405 nutritive value of marine and freshwater zooplankton. As mentioned above, marine zooplankton



406 consist of copepods, while in many freshwater ecosystems cladocerans are the dominant taxa.  
407 Cladocera are known to have significantly lower EPA+DHA contents,  $\text{mg g}^{-1} \text{C}$ , than Copepoda  
408 (Gladyshev et al. 2015b). However, data on EPA and DHA contents in marine zooplankton are  
409 too sparse for any relevant quantitative comparison with freshwater zooplankton. This desirable  
410 comparison is believed to be possible in the future when relevant measurements are conducted.

411 In this paper, we focused on the probable advantage of marine pelagic planktivorous  
412 species over freshwater species because ranges of EPA+DHA contents of marine and freshwater  
413 benthivorous and piscivorous species evidently overlap (Table 1). Meanwhile, fast-swimming  
414 marine planktivores, the Clupeiformes, namely, the South American pilchard *Sardinops sagax*,  
415 the longtail shad *Hilsa macrura* and the European pilchard *Sardina pilchardus*, had more than a  
416 four-fold higher EPA+DHA content than fast swimming freshwater planktivores, the rainbow  
417 smelt *Osmerus mordax* (order Osmeriformes) (Table 1).

418 In this paper, we regarded marine and freshwater environments as a whole rather than  
419 salinity as a separate abiotic variable. Meanwhile, data on the effect of salinity on LC-PUFA  
420 percentages in fish were contradictory: both an increase (Xu et al. 2010; Hunt et al. 2011) and a  
421 decrease (Cordier et al. 2002; Kheriji et al. 2003) of percentages with an increase of salinity were  
422 reported. However, to our knowledge, there were no data on the effect of salinity on EPA and  
423 DHA contents ( $\text{mg g}^{-1} \text{WM}$ ) in fish.

424

425

426 Water temperature

427

428 In the present work, we did not find any significant differences between average EPA and DHA  
429 contents in cold and warm environments, although in temperate-cold habitats, EPA and DHA  
430 contents were significantly higher than those in temperate-warm and warm waters. Nevertheless,  
431 there is a common impression based on the theory of homeoviscous adaptation that an inverse

432 relationship between temperature and LC-PUFA levels exists. According to this theory,  
433 exothermic animals, invertebrates and fish, have a decreased unsaturated fatty acid content with  
434 a low melting point in cell membranes and have an increased content of more saturated fatty  
435 acids with comparatively high melting points to provide optimal cell membrane fluidity (Farkas  
436 et al. 1984; Arts and Kohler 2009). However, many authors questioned a peculiar role of EPA  
437 and DHA in the homeoviscous adaptation compared to that of mono-unsaturated and short-chain  
438 saturated fatty acids (Stillwell and Wassall 2003; Arts and Kohler 2009; Dymond 2015).  
439 Moreover, membrane fluidity or membrane viscosity, in addition to the degree of unsaturation,  
440 strongly depends on the type of lipid head-groups as well as the presence of another lipid  
441 species, cholesterol (Arts and Kohler 2009; Dymond 2016). Therefore, the notion that the  
442 differences in DHA contents between species are dictated by temperature-dependent membrane  
443 fluidity needs is simplistic (Infante et al. 2001).

444         Indeed, literature data regarding the effect of temperature on EPA and DHA contents in  
445 fish are ambiguous. In laboratory experiments, some fish species showed an increase of DHA  
446 but not EPA under decreased temperature (Arts et al. 2012), while in other species, levels of  
447 EPA and DHA remained unchanged when temperature varied (Laurel et al. 2012; Wijekoon et  
448 al. 2014). In natural conditions, various researchers found an increase of EPA and DHA in fish  
449 from cold waters compared to those from warm waters (Wall et al. 2010; Pethybridge et al.  
450 2015). In contrast, other researchers did not find an increase of these PUFAs in relatively cold  
451 habitats and seasons (Gokce et al. 2004; Murzina et al. 2013; Gribble et al. 2016). Evidently,  
452 beliefs concerning the simple relationship between water temperature and LC-PUFA contents in  
453 fish, which implies higher EPA and DHA production in cold habitats, underestimate the  
454 complexity of interactions between the abiotic environment and fish biochemistry (Litzow et al.  
455 2006). Therefore, more work should be completed to determine ecological and phylogenetic  
456 mechanisms that control FA composition and content in fish.

457 It should be emphasized that most data regarding the temperature effect were based on  
458 relative measurements, i.e., EPA and DHA percentages in total fatty acids. Meanwhile, the target  
459 data for estimation of environmental effects on the nutritive value of fish in humans are based on  
460 LC-PUFA contents in the catching biomass. Therefore, in the future, the effect of water  
461 temperature should be re-evaluated for EPA and DHA contents.

462

463

464 Percent vs. content

465

466 There were no significant correlations between EPA+DHA content ( $\text{mg g}^{-1}$ ) and level (% of total  
467 FAs). Indeed, there were many fish species with high EPA+DHA contents,  $\sim 10 \text{ mg g}^{-1}$ , and low  
468 percentage,  $< 20\%$ , e.g., chum salmon(*Oncorhynchus keta*), coho salmon(*Oncorhynchus kisutch*),  
469 lake trout(*Salvelinus namaycush*), rainbow trout(*Oncorhynchus mykiss*) and landlocked  
470 shad(*Alosa fallax lacustris*) (Fig. 2). On the other hand, there were many species with a high  
471 percentage,  $> 40\%$ , and low content,  $< 4 \text{ mg g}^{-1}$ , e.g., whiting(*Gadus merlangus*), Atlantic  
472 cod(*Gadus morhua*), sardine cisco(*Coregonus sardinella*), Arctic char(*Salvelinus alpinus*) and  
473 humpback whitefish(*Coregonus pidschian*) (Fig. 2). Meanwhile, there were species with very  
474 high contents and percentages of EPA+ DHA, e.g., sardine(*Sardinops sagax*), as well as species  
475 with very low contents and percentages, e.g., marbled lungfish (*Protopterus aethiopicus*) and  
476 bonito(*Sarda sarda*) (Fig. 2).

477 In contrast, we found a significant negative correlation between DHA content and content  
478 of the sum of the total FAs in fish. It is worth noting that the sum of FAs used in our study could  
479 be regarded as a proxy for total lipid content because the sum content of total fatty acids in fish  
480 was correlated with total lipid content (Ahlgren et al. 1996). A similar phenomenon, namely, a  
481 negative relationship of LC-PUFAs to the total lipid content in fish, was reported by other  
482 authors (Mairesse et al. 2006, see Litzow et al. 2006). This phenomenon may be explained as

483 follows. EPA and DHA are mostly contained in phospholipids (PL), i.e., in the structural lipids  
484 of cell membranes, which should remain constant in proportion to muscle tissues (Mairesse et al.  
485 2006).

486 In contrast, reserve neutral lipids, triacylglycerols (TAG), which are poor in LC-PUFAs,  
487 are of high variance in muscles of diverse fish species (Kiessling et al. 2001; Litzow et al. 2006;  
488 Benedito-Palos et al. 2013). Some species, so-called “fatty” fish (Moth et al. 2013), accumulate  
489 relatively more neutral lipids that contain predominantly saturated and monounsaturated fatty  
490 acids. As a result, the total lipid proportions of EPA and DHA could have become diluted by the  
491 accumulation of neutral lipids in muscles, while the LC-PUFA content (as mg g<sup>-1</sup> tissue)  
492 remained equal compared to that in “lean” fish.

493 Nevertheless, a relation between contents of total lipids and contents of EPA and DHA  
494 there may be more complex. For instance, Kainz et al. (2017) found, total lipid status of fish was  
495 better predictor of their PUFA contents, than trophic positions or feeding sources.

496

497

498 Unstudied factors and other uncertainties

499

500 In general, all explanatory variables significantly explained 35.6% of the total variance in EPA  
501 and DHA contents (Fig. 4). This is a typical variance portion explained in RDA for biological  
502 systems (Roy et al. 2014). In similar meta-analysis of FA in phytoplankton, RDA explained  
503 48.4% - 56.8% of the total variation in phytoplankton fatty acids (Galloway and Winder 2015).  
504 However, 64.4% of factors affecting EPA and DHA contents in fish remained unknown. For  
505 example, in the freshwater order Cypriniformes the species with the highest content of  
506 EPA+DHA was the slow swimming benthivorous Siberian stone loach (*Barbatula* (= *Orthrias*)  
507 *toni*) rather than the planktivorous bleak (*Alburnus alburnus*) (Table 1). In the order  
508 Salmoniformes, the planktivorous-omnivorous European whitefish (*Coregonus*

509 *macrophthalmus*) with medium swimming speed had approximately a 10-fold higher EPA+DHA  
510 content than the planktivorous fast swimming sardine cisco (*Coregonus sardinella*) (Table 1).  
511 Demersal Scorpaeniformes, the sablefish (*Anoplopoma fimbria*) and the Canary rock fish  
512 (*Sebastes pinniger*), had very high EPA and DHA contents, nearly similar to those of fast  
513 swimming pelagic migrants from the orders Clupeiformes and Salmoniformes (Table 1). The  
514 marine planktivorous fast swimming Indian mackerel (*Rastrelliger kanagurta*, order  
515 Perciformes) had extremely low EPA and DHA contents (Table 1), which absolutely  
516 contradicted the general tendency, found by RDA, except for phylogenetic identity. Therefore,  
517 causes of high or low EPA and DHA contents in many fish species still remain unknown and  
518 should be explained in future studies.

519       Unknown factors omitted in our present meta-analysis were eutrophication and pollution.  
520 Trophic status of aquatic ecosystems is known to significantly affect EPA and DHA contents in  
521 fish. In oligotrophic ecosystems, dominant primary producers, including microalgae, diatoms  
522 (Bacillariophyceae), chrysophytes (Chrysophyceae), cryptophytes (Cryptophyceae) and  
523 dinoflagellates (Dinophyceae), can synthesize EPA and DHA, whereas in eutrophic waterbodies  
524 the dominant taxa are green algae (Chlorophyceae) and cyanobacteria, which cannot produce  
525 LC-PUFAs (Ahlgren et al. 1992; Taipale et al. 2016). Therefore, in oligotrophic ecosystems, fish  
526 that obtain EPA and DHA from primary producers through trophic chains had a higher EPA and  
527 DHA content than those in eutrophic ecosystems (Ahlgren et al. 1996; Taipale et al. 2016). As  
528 seen with eutrophication, anthropogenic pollution by organic substances and heavy metals also  
529 decreased EPA and DHA contents in fish (Gladyshev et al. 2012a). However, more studies are  
530 necessary for quantitative estimations regarding the effects of eutrophication and pollution on  
531 LC-PUFA contents in diverse fish species.

532

533

534 **Conclusions**

535           The highest contribution of total explained variance for EPA and DHA contents in fish  
536 was by the combination of phylogenetic and ecomorphological factors. On average, higher EPA  
537 and DHA contents were characteristic of marine planktivorous fast swimming Clupeiformes and  
538 anadromous Salmoniformes. Their high EPA and DHA contents were believed to play the role of  
539 activators for muscle cell metabolism to support fast continuous swimming, especially during  
540 long migrations. Our meta-analysis did not support ideas concerning significant influence of  
541 higher trophic levels (piscivory) and cold environments (homeoviscous adaptation) on EPA and  
542 DHA contents in fish. There was no correlation between EPA and DHA percentages (% of total  
543 FAs) and contents ( $\text{mg g}^{-1}\text{WM}$ ) in fish biomass. Therefore, the meta-analysis confirmed that the  
544 percentages were not a reliable measurement to estimate nutritive value of fish species for  
545 humans. However, many causes of high and low levels of EPA and DHA in different fish species  
546 remained unexplained and should be evaluated in future studies.

547

#### 548 **Acknowledgements**

549

550 The work was supported by a Russian Science Foundation grant (No. 16-14-10001).

551

552

#### 553 **References**

554

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**Table 1** Content of eicosapentaenoic (EPA) and docosahexaenoic (DHA) acids and their sum (mg g<sup>-1</sup>, wet mass) in various wild fish species, types of habitat (H1: p – pelagic, bp – benthopelagic, d – demersal; H2: c – cold waters, t – temperate waters, w – warm waters; H3: m – marine, f – freshwater, b – brackish, a - migratory (anadromous)), types of feeding (F: p – piscivorous, o – omnivorous, pl – planktivorous, b – benthivorous, d – detritivorous, ph – consuming phytoplankton, wp – consuming water plants, pph – consuming periphyton), V - swimming velocity: f – fast, m - medium, s – slow, and common or sampled size (cm). Species within orders are ranged by EPA+DHA content values.

Taxon	EPA	DHA	Sum	H1	H2	H3	F	V	Size	Ref.*
<b>Order Myliobatiformes</b>										
<i>Gymnura spp.</i>	0.03	0.09	0.12	d	w	m	b/p	s	34	[1]
<b>Order Anguilliformes</b>										
<i>Anguilla anguilla</i>	1.6	2.2	3.7	d	t	fbma	p	f	41	[2 <sup>1</sup> ]
<b>Order Clupeiformes</b>										
<i>Sardinops sagax</i>	6.6	19	25.6	p	t	m	pl	f	30	[3]
<i>Hilsa macrura</i>	20.42	1.69	22.11	p	w	m	pl	f	35	[1]
<i>Sardina pilchardus</i>	8.5	8.37	16.87	p	t	m	pl	f	25	[4]
<i>Etrumeus teres</i>	12.34	4.33	16.67	p	t	m	pl	f	25	[5]
<i>Dussumieria acuta</i>	3.43	10.16	13.59	p	w	m	pl	f	20	[6]
<i>Clupea harengus pallasii</i>	4.99	5.76	10.74	p	c	m	pl	f	25	[3,7]
<i>Alosa fallax lacustris</i>	5.83	4.04	9.87	p	t	f	pl	f	50	[8]
<i>Alosa sapidissima</i>	1.33	4.70	6.03	p	t	mb	pl	f	76	[9]
<i>Ethmalosa fimbriata</i>	2.11	2.25	4.36	p	w	mba	ph	f	25	[1]
<i>Chirocentrus dorab</i>	0.24	0.54	0.78	p	w	m	p	f	100	[1]
<b>Order Cypriniformes</b>										
<i>Barbatula = Orthrias toni</i>	2.97	1.73	4.70	d	ct	f	b	s	9	our
<i>Phoxinus czekanowskii</i>	2.64	1.90	4.53	dp	t	f	b	m	6	our
<i>Gobio gobio</i>	2.49	1.64	4.13	d	t	f	b	s	12	our
<i>Leuciscus leuciscus baikalensis</i>	1.66	1.65	3.32	dp	ct	f	b	f	15	our
<i>Cobitis melanoleuca</i>	1.40	1.68	3.08	d	t	f	b	s	13	our
<i>Squalius squalus</i>	0.60	1.96	2.55	dp	t	f	o/p	m	49	[8]
<i>Alburnus alburnus</i>	1.25	1.22	2.47	p	t	f	pl	m	15	[8]
<i>Rutilus rutilus</i>	0.77	1.55	2.32	dp	t	fb	b/pl/wp	m	25	[2 <sup>1</sup> ,8,10]
<i>Catostomus commersonii</i>	0.92	1.36	2.28	d	t	fb	b/wp	m	41	[11]
<i>Tinca tinca</i>	0.87	1.19	2.05	d	t	f	d/wp/b	s	45	[2 <sup>1</sup> ,8]
<i>Scardinius erythrophthalmus</i>	0.68	1.27	1.94	dp	t	f	<b>wp/b</b>	m	20	[2 <sup>1</sup> , 8]
<i>Rutilus pigus</i>	0.65	1.03	1.68	dp	t	f	<b>b/wp/d</b>	m	25	[8]
<i>Leuciscus idus</i>	0.50	1.10	1.60	dp	t	fb	b/wp/p	m	44	[2 <sup>1</sup> ]
<i>Carassius gibelio</i>	0.60	1.00	1.60	dp	t	f	pl/b/wp/d	m	20	[12]
<i>Carassius carassius</i>	0.45	0.97	1.42	d	t	fb	b/wp/d	s	15	[2 <sup>1</sup> ,8]
<i>Blicca bjoerkna</i>	0.40	0.80	1.20	d	t	fb	b	m	16	[2 <sup>1</sup> ]
<i>Abramis brama</i>	0.34	0.67	1.02	d	t	fb	b	m	30	[2 <sup>1</sup> ,10]
<i>Hypophthalmichthys molitrix</i>	0.36	0.48	0.85	dp	w	f	ph	m	18	[13]
<i>Cyprinus carpio</i>	0.34	0.50	0.84	dp	t	fb	o/b/wp	m	31	[8,11,13]
<i>Culter alburnus</i>	0.16	0.48	0.64	dp	t	f	p/b	m	25	[13]
<i>Hypophthalmichthys nobilis</i>	0.19	0.35	0.54	p	w	f	pl/ph/p	m	70	[13]
<b>Order Siluriformes</b>										
<i>Ictalurus punctatus</i>	1.61	1.62	3.98	dp	w	f	p/o	m	57	[14]
<i>Ictalurus melas</i>	1.23	1.42	2.65	d	w	f	o/wp	m	28	[8]
<i>Plotosus spp.</i>	1.46	0.89	2.35	d	w	bmf	o/p	s	80	[1]
<i>Silurus glanis</i>	0.33	1.12	1.44	d	t	f	p	m	300	[8]
<i>Synodontis victoriae</i>	0.2	0.7	0.9	d	w	f	b	s	15	[15]
<i>Bagrus docmas</i>	0.1	0.7	0.8	d	w	f	b/p	s	60	[15]
<i>Clarias gariepinus</i>	0.2	0.5	0.7	d	w	f	o/p	s	125	[15]
<b>Order Osmeriformes</b>										
<i>Hypomesus pretiosus</i>	3.6	5.7	9.3	p	t	mb	pl	f	15	[3]
<i>Mallotus villosus</i>	3.6	4.6	8.2	p	c	mb	pl	f	15	[3]

<i>Osmerus mordax</i>	1.73	2.48	4.21	p	c	f	pl/p	f	14	[9]
<b>Order Salmoniformes</b>										
<i>Coregonus macrophthalmus</i>	6.41	4.34	10.75	p	t	f	pl/o	m	30	[8]
<i>Oncorhynchus keta</i>	4.00	6.00	10.00	p	tc	amf	p/o	f	65	[16]
<i>Salvelinus namaycush</i>	2.71	6.65	9.36	p	t	f	p/o	f	75	[9,11,14]
<i>Oncorhynchus kisutch</i>	2.51	5.95	8.31	p	tc	amf	p	f	71	[9,14]
<i>Oncorhynchus tshawytscha</i>	2.76	4.21	6.96	p	t	a	p/o	f	90	[9,11]
<i>Oncorhynchus gorbuscha</i>	1.97	4.47	6.43	p	tc	amf	o/p	f	50	[3,16,17]
<i>Oncorhynchus nerka</i>	2.12	3.88	6.01	p	tc	amf	pl/o	f	50	[9,16,18]
<i>Oncorhynchus mykiss</i>	1.70	3.96	5.65	dp	tc	amf	o/p	f	45	[9,14,19 <sup>2</sup> ]
<i>Coregonus clupeaformis</i>	2.40	3.23	5.63	d	tc	af	b	m	54	[9,14,20 <sup>2</sup> ]
<i>Salmo trutta</i>	0.9	3.5	4.4	pd	tc	f	pl/b/p	f	29	[19 <sup>2</sup> ]
<i>Salvelinus alpinus</i>	1.3	2.8	4.1	p	tc	f	p	f	29	[19 <sup>2</sup> ]
<i>Salvelinus boganidie</i>	0.98	1.99	2.97	dp	c	f	p/o	f	47	[21]
<i>Thymallus thymallus</i>	0.9	2	2.9	dp	c	fb	o/p	f	25	[2 <sup>1</sup> ]
<i>Thymallus arcticus</i>	0.72	1.92	2.6	dp	c	f	p/o	f	20	[22]
<i>Salvelinus alpinus</i> complex	0.35	1.08	1.43	dp	c	f	b/o	f	31	[21]
<i>Coregonus nasus</i>	0.49	0.81	1.31	d	c	f	b	m	43	[21]
<i>Coregonus sardinella</i>	0.19	0.94	1.13	p	c	f	pl	f	24	[21]
<i>Coregonus pidschian</i>	0.26	0.87	1.13	d	c	f	b	m	35	[21]
<b>Order Esociformes</b>										
<i>Esox lucius</i>	0.40	1.97	2.37	dp	t	f	p	f	95	[2 <sup>1</sup> ,8,14,21]
<b>Order Gadiformes</b>										
<i>Merluccius productus</i>	1.42	1.73	3.15	pd	t	mb	o/p	f	60	[3,9]
<i>Pollachius pollachius</i>	0.69	2.71	3.4	dp	ct	m	p/o	m	75	[9]
<i>Theragra chalcogramma</i>	0.94	1.94	2.88	dp	c	mb	pl/b/p	m	40	[3,9]
<i>Lota lota</i>	1.14	1.35	2.50	d	t	fb	p/b	m	40	[2,8]
<i>Gadus morhua</i>	0.61	1.82	2.42	dp	t	mb	p/o/pl	m	60	[7,9,23]
<i>Merluccius bilinearis</i>	0.36	1.78	2.14	d	c	m	p	m	37	[9]
<i>Gadus macrocephalus</i>	0.62	1.34	1.96	d	t	m	p/b	m	50	[9]
<i>Melanogrammus aeglefinus</i>	0.69	1.1	1.79	d	c	m	b/p	m	35	[9]
<i>Merlangius merlangus</i>	0.08	0.48	0.56	dp	wt	mb	p/b	m	24	[24]
<b>Order Mugiliformes</b>										
<i>Mugil cephalus</i>	1.10	1.36	2.46	dp	w	mbfa	d/pph	f	45	[9,24]
<b>Order Beloniformes</b>										
<i>Belone belone</i>	0.01	0.15	0.16	p	t	mb	p	f	70	[24]
<b>Order Beryciformes</b>										
<i>Hoplostethus atlanticus</i>	0.40	1.12	1.52	d	c	m	o/p	m	40	[9]
<b>Order Scorpaeniformes</b>										
<i>Anoplopoma fimbria</i>	6.53	5.66	12.19	d	c	m	o/p	m	65	[9]
<i>Sebastes pinniger</i>	3.5	5.4	8.9	d	c	m	o/p	m	50	[3]
<i>Sebastes auriculatus</i>	1.07	2.44	3.51	d	c	m	o/p	m	56	[9]
<i>Sebastes entomelas</i>	1.1	2.28	3.38	d	c	m	o/p	m	55	[9]
<i>Ophiodon elongatus</i>	0.99	2.02	3.01	d	t	m	o/p	m	70	[9]
<i>Paracottus knerii</i>	1.83	0.99	2.82	d	c	f	b	s	8	our
<i>Scorpaena plumieri</i>	0.22	2.28	2.5	d	w	m	p/o	s	25	[5]
<i>Scorpaena scrofa</i>	0.29	1.4	1.69	d	tw	m	p/o	s	30	[24]
<b>Order Perciformes</b>										
<i>Trachurus mediterraneus</i>	4.4	5.49	9.89	pd	t	m	p/pl	f	25	[4]
<i>Leiostomus xanthurus</i>	4.85	4.64	9.49	d	w	mb	b/pl	s	28	[9]
<i>Scomberomorus commerson</i>	1.6	7.72	9.32	p	w	m	p	f	90	[6]
<i>Selaroides leptolepis</i>	0.97	7.82	8.79	d	w	m	p/o	f	15	[1]
<i>Trachurus trachurus</i>	1.64	5.86	7.5	pd	t	m	pl/p	f	30	[24]
<i>Pomatomus saltatrix</i>	1.66	5.23	6.89	p	w	mb	p/o	f	60	[9]
<i>Pagellus acarne</i>	3.19	3.41	6.6	dp	w	m	b/pl	m	25	[4]
<i>Ruvettus pretiosus</i>	1.13	5.33	6.46	d	w	m	p/o	f	150	[5]
<i>Euthynnus affinis</i>	0.93	5.51	6.44	p	w	m	p/o	f	47	[6]
<i>Trachinotus carolinus</i>	1.48	4.69	6.17	d	w	mb	b/pl	m	40	[9]
<i>Oligoplites altus</i>	1.05	5.02	6.07	dp	w	mb	p	f	30	[5]
<i>Seriola lalandi</i>	1.57	4.42	5.99	pd	w	mb	p/o	f	85	[9]
<i>Xiphias gladius</i>	0.91	5.04	5.95	p	w	m	p	f	155	[5,9]
<i>Scomberomorus maculatus</i>	1.02	4.61	5.63	p	w	mb	p/o	f	60	[9]

<i>Nemipterus japonicus</i>	2.59	2.93	5.52	d	w	m	o/p	m	15	[1]
<i>Morone americana</i>	2.80	2.69	5.49	dp	t	mbf	p/o	m	15	[9,14]
<i>Sebastes alutus</i>	2.72	2.72	5.44	d	tc	m	pl/o	m	30	[9]
<i>Micropogonias undulatus</i>	2.07	2.87	4.94	dp	w	mb	o/b	m	30	[9]
<i>Morone saxatilis</i>	1.78	2.93	4.71	dp	w	mbf	p/o	m	85	[9]
<i>Morone chrysops</i>	1.69	2.64	4.34	dp	t	f	pl/p	m	30	[14]
<i>Acanthocybium solandri</i>	0.45	3.56	4.01	p	w	m	p	f	170	[9]
<i>Lobotes surinamensis</i>	0.68	3.22	3.90	pd	w	mb	p/b	m	80	[5]
<i>Stenotomus chrysops</i>	1.31	2.29	3.60	d	w	m	b/pl	s	22	[9]
<i>Parastromateus niger</i>	0.73	2.77	3.50	p	w	mb	pl	m	30	[1]
<i>Thunnus tonggol</i>	0.53	2.92	3.45	p	w	m	p/o	f	52	[6]
<i>Paralabrax auroguttatus</i>	0.98	2.21	3.19	d	w	m	b/p	m	50	[5]
<i>Trachinotus blochii</i>	1.77	1.23	3.00	d	w	mb	p	m	40	[1]
<i>Epinephelus fasciatus</i>	1.01	1.98	2.99	d	w	m	b/p	m	22	[1]
<i>Sander vitreus</i>	0.99	1.93	2.92	p	t	f	p	f	54	[9,10,14]
<i>Cynoscion nebulosus</i>	0.97	1.92	2.89	pd	w	mb	p/o	f	36	[5,9]
<i>Centropristis striata</i>	0.85	1.93	2.78	d	w	m	b/p	m	30	[9]
<i>Pampus argentus</i>	1.16	1.48	2.64	p	w	mb	pl/p	m	25	[1]
<i>Ocyurus chrysurus</i>	0.37	2.22	2.59	d	w	m	p/o	s	40	[9]
<i>Lutjanus campechanus</i>	0.57	1.96	2.53	d	w	m	b/p	m	60	[9]
<i>Rhomboplites aurorubens</i>	0.32	2.07	2.39	d	w	m	p/b	m	35	[9]
<i>Lutjanus argentimaculatus</i>	0.24	2.1	2.34	d	w	mb	o/p	m	80	[1]
<i>Lates calcarifer</i>	1.39	0.95	2.34	d	w	fbm	p/o	m	150	[1]
<i>Scomberomorus cavalla</i>	0.42	1.86	2.28	p	w	m	p/o	f	60	[9]
<i>Dicentrarchus labrax</i>	0.52	1.75	2.27	d	wt	m	p/o	m	50	[24]
<i>Scomberomorus guttatus</i>	0.37	1.86	2.23	p	w	m	p	f	39	[1,6]
<i>Megalopsis cordyla</i>	0.19	1.96	2.15	p	w	mb	p	f	35	[1]
<i>Micropterus dolomieu</i>	0.36	1.72	2.08	dp	t	f	p/o	m	38	[13]
<i>Sparus aurata</i>	0.45	1.56	2.01	d	w	mb	b	s	35	[24,25]
<i>Atractoscion nobilis</i>	0.27	1.57	1.84	d	w	m	p/o	f	100	[9]
<i>Thunnus albacares</i>	0.23	1.38	1.60	p	w	m	p/o	f	150	[5,9,26]
<i>Boops boops</i>	0.63	0.94	1.57	dp	wt	m	pl/ph/p	m	15	[4]
<i>Coryphaena hippurus</i>	0.17	1.39	1.56	p	w	m	p/o	f	75	[9]
<i>Lopholatilus chamaeleonticeps</i>	0.13	1.41	1.54	d	tw	m	o/p	m	105	[9]
<i>Eleutheronema tetradactylum</i>	0.96	0.53	1.49	p	w	mbfa	p/o	f	50	[1]
<i>Lutjanus griseus</i>	0.45	1.03	1.48	d	w	mb	o/p	m	40	[5]
<i>Perca fluviatilis</i>	0.37	1.09	1.46	dp	t	fb	p/o/pl	m	20	[2 <sup>1</sup> ,8,10]
<i>Perca flavescens</i>	0.37	1.04	1.41	dp	t	fb	p/o	m	19	[9,14]
<i>Mullus barbatus</i>	0.48	0.94	1.42	d	w	m	b/p	s	15	[24]
<i>Lepomis gibbosus</i>	0.27	1.15	1.42	d	tw	fb	o/p	s	10	[14]
<i>Seriola dumerili</i>	0.11	1.25	1.36	p	w	m	p/o	f	100	[9]
<i>Lopholatilus chamaeleonticeps</i>	0.12	1.23	1.35	d	w	m	o/b/p	s	95	[9]
<i>Hyporthodus flavolimbatus</i>	0.12	1.23	1.35	d	w	m	b/p	m	50	[9]
<i>Pomoxis nigromaculatus</i>	0.15	1.11	1.26	dp	t	f	pl/p/o	m	28	[14]
<i>Mycteroperca microlepis</i>	0.12	1.08	1.20	d	w	mb	p/o	m	50	[9]
<i>Gymnocephalus cernuus</i>	0.40	0.80	1.20	d	t	fb	b	s	9	[2]
<i>Makaira nigricans</i>	0.15	1.04	1.19	p	w	m	p	f	290	[5]
<i>Micropterus salmoides</i>	0.13	0.98	1.11	dp	t	f	p/o	m	40	[14]
<i>Alectis indicus</i>	0.24	0.82	1.06	d	w	mb	p/o	m	70	[1]
<i>Lepomis macrochirus</i>	0.17	0.89	1.06	dp	t	f	o/p	m	19	[14]
<i>Epinephelus morio</i>	0.13	0.87	1.00	d	w	m	o/p	m	50	[9]
<i>Sander lucioperca</i>	0.16	0.76	0.92	p	t	fb	p	f	50	[2 <sup>1</sup> ,27]
<i>Rastrelliger kanagurta</i>	0.54	0.23	0.77	p	w	m	pl	f	25	[1]
<i>Tilapia zilli</i>	0.10	0.50	0.70	dp	w	fb	o/ph	s	15	[15]
<i>Oreochromis niloticus</i>	0.10	0.60	0.70	d	w	fb	ph/wp/o	s	30	[15]
<i>Peprilus paru</i>	0.08	0.57	0.65	p	w	mb	p/o	m	18	[5]
<i>Lates niloticus</i>	0.10	0.50	0.60	p	w	f	p	m	85	[15]
<i>Lutjanus johnii</i>	0.07	0.19	0.26	d	w	m	b/p	m	30	[1]
<i>Sciaena umbra</i>	0.05	0.19	0.24	d	t	m	p/o	m	35	[24]
<i>Sarda sarda</i>	0.03	0.15	0.18	p	w	m	p	f	60	[24]
<b>Order Pleuronectiformes</b>										
<i>Pseudopleuronectes americanus</i>	1.79	1.94	3.73	d	t	m	b/wp	s	45	[9]



	<i>Lepidopsetta bilineata</i>	1.80	1.10	2.90	d	t	m	b/p	s	30	[7]
	<i>Hippoglossoides platessoides</i>	1.6	1.26	2.86	d	tc	m	b/p	s	40	[9]
	<i>Eopsetta jordani</i>	1.02	1.80	2.82	d	tc	m	b/p	s	45	[9]
	<i>Parophrys vetulus</i>	1.30	1.30	2.60	d	tc	m	b	s	35	[9]
	<i>Hippoglossus stenolepis</i>	0.90	1.66	2.56	d	tc	m	p/b	s	65	[9]
	<i>Limanda ferruginea</i>	1.03	1.41	2.44	d	tc	m	b/p	s	40	[9]
	<i>Glyptocephalus zachirus</i>	0.82	1.07	1.89	d	tc	m	b	s	36	[9]
	<i>Paralichthys dentatus</i>	0.30	1.56	1.86	d	tc	mb	p/b	m	45	[9]
	<i>Paralichthys californicus</i>	0.25	1.39	1.64	d	w	mb	p/b	m	40	[9]
	<i>Microstomus pacificus</i>	0.70	0.90	1.60	d	tc	m	b	s	40	[9]
	<i>Glyptocephalus cynoglossus</i>	0.59	0.79	1.38	d	c	m	b/p	s	40	[9]
	<i>Cynoglossus arel</i>	0.08	1.13	1.21	d	w	mb	b	s	30	[1]
	<i>Paralichthys lethostigma</i>	0.13	0.73	0.86	d	w	mb	p/b	s	50	[9]
	<i>Paralichthys albigutta</i>	0.10	0.52	0.62	d	w	mb	p/b	s	35	[9]
	<b>Order Ceratodontiformes</b>										
934	<i>Protopterus aethiopicus</i>	0.10	0.30	0.40	d	w	f	pl/p	s	130	[15]

935 Ref.\*: [1] Abd Aziz et al. 2013; [2] Ahlgren et al. 1994; [3] Huynh & Kitts 2009; [4] García-Moreno et al. 2013; [5]

936 Castro-Gonzalez et al. 2013; [6] Sahari et al. 2014; [7] Gladyshev et al. 2007; [8] Vasconi et al. 2015; [9] Cladis et  
 937 al. 2014; [10] Sushchik et al. 2017; [11] Neff et al. 2014a; [12] Rogozin et al. 2011; [13] Zhang et al. 2012; [14]  
 938 Neff et al. 2014b; [15] Kwetegyeka et al. 2008; [16] Henriques et al. 2014; [17] Gladyshev et al. 2006; [18]  
 939 Gladyshev et al. 2012b; [19] Heissenberger et al. 2010; [20] Wagner et al. 2010; [21] Gladyshev et al. 2017; [22]  
 940 Sushchik et al. 2007; [23] Sioen et al. 2006; [24] Chuang et al. 2012; [25] Amira et al. 2010; [26] Al-Busaidi et al.  
 941 2015; [27] Gladyshev et al. 2014.

942 <sup>1</sup>Converted from dry mass, given in Table III of the source (Ahlgren et al., 1994) to wet mass using species-specific  
 943 dry mass / wet mass ratios given in Table I of the source.

944 <sup>2</sup>The data were recalculated from dry mass using mean moisture content in Salmoniformes 72.5% (Gladyshev et al.  
 945 2006, 2007; Sushchik et al. 2006, 2007).

946 **Table 2.** Results from the forward selection procedure, showing significant phylogenetic,  
 947 ecomorphological and abiotic environmental variables.  
 948

Variables retained for variation partitioning from forward selection	adjR2cum	F	P-value
<b>Phylogenetic</b>			
<i>Clupeiformes</i>	0.15	35.96	0.002
<i>Salmoniformes</i>	0.24	25.65	0.002
<i>Scorpaeniformes</i>	0.26	07.99	0.004
<i>Osmeriformes</i>	0.28	04.99	0.030
<b>Ecomorphological</b>			
Planktivorous	0.17	42.79	0.002
Swimming Velocity	0.25	22.29	0.002
Migratory	0.26	06.02	0.014
<b>Abiotic environments</b>			
Temperature	0.03	06.63	0.008
Salinity	0.07	10.93	0.002

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### Figure legends

952 **Fig. 1** Contents of the sum of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA),  
953 minimum, maximum and median values and quartiles in fish orders: Clupeiformes (Clu, in  
954 parentheses – number of species); Scorpaeniformes (Scorp); Salmoniformes (Salm); Perciformes  
955 (Perc); Osmeriformes (Osm); Cypriniformes (Cyp); Siluriformes (Silur); Pleuronectiformes  
956 (Pleur); Gadiformes (Gad); and miscellaneous (Miscellan, Anguilliformes, Beloniformes,  
957 Beryciformes, Esociformes, Ceratodontiformes, Mugiliformes and Myliobatiformes). Bars –  
958 minimum and maximum; boxes – 25% - 75%; black squares – median.

959

960 **Fig. 2** Sum of eicosapentaenoic (EPA) and docosahexaenoic (DHA) fatty acids: levels (% of  
961 total fatty acids, grey bars) and contents ( $\text{mg g}^{-1}$  wet mass, black bars) in muscle tissue of 88 fish  
962 species ranged by levels. (See Table 1 for full fish names).

963

964 **Fig. 3** Plot of correlations between DHA percentage and total FA content ( $\text{mg g}^{-1}$  wet mass) in  
965 88 fish species: dots – experimental data, line – linear approximation.

966

967 **Fig. 4** Results of the partial redundancy analysis (pRDA): A – the Venn diagram of variation  
968 partitioning of EPA, DHA and EPA+DHA fish content, representing unique and shared  
969 contributions of three sets of explanatory variables: phylogenetic, ecomorphological and abiotic  
970 environments. The significance of each testable fraction was expressed as \* $P < 0.05$ , \*\* $P <$   
971  $0.01$ , \*\*\* $P < 0.001$ ; B – the redundancy analysis (RDA) ordination triplot of the first two  
972 canonical axes showing response (EPA, DHA and EPA+DHA) and explanatory variables:  
973 arrows and centroids for nominal variables (black triangles). Gray dots represent species. The  
974 triplot has 1-st type scaling.

975

976 **Fig. 5** Mean values of the sum of eicosapentaenoic and docosahexaenoic acid content  
 977 (EPA+DHA, mg g<sup>-1</sup> wet mass) in muscle tissue of fish.

978 A Swimming velocity ( $V$ , m s<sup>-1</sup>): fast ( $V > 2$ ), medium ( $1 \leq V \leq 2$ ) and slow ( $V < 1$ ).

979 B Salinity of habitats: anadr – migratory (anadromous), fresh – freshwater, fr-br – freshwater-  
 980 brackish, marine, mar-br – marine-brackish.

981 C Types of feeding: ben – benthivorous, ben/pis – benthivorous/piscivorous (in Table 1, b/p and  
 982 p/b), pis – piscivorous, omn/pis – omnivorous/piscivorous (in Table 1, p/o, o/p, p/o/pl, o/b/p and  
 983 pl/p/o), pla – planktivorous, omn/pla – omnivorous/planktivorous (in Table 1, b/pl, pl/b/p,  
 984 pl/b/wp/d, pl/o, pl/p and pl/ph/p), omn/wp – omnivorous/consuming water plants (in Table  
 985 1, b/pl/wp, b/wp, b/wp/d, b/wp/p, d/wp/b, o/b/wp, o/wp, ph/wp/o and wp/b), pla/omn –  
 986 planktivorous/omnivorous.

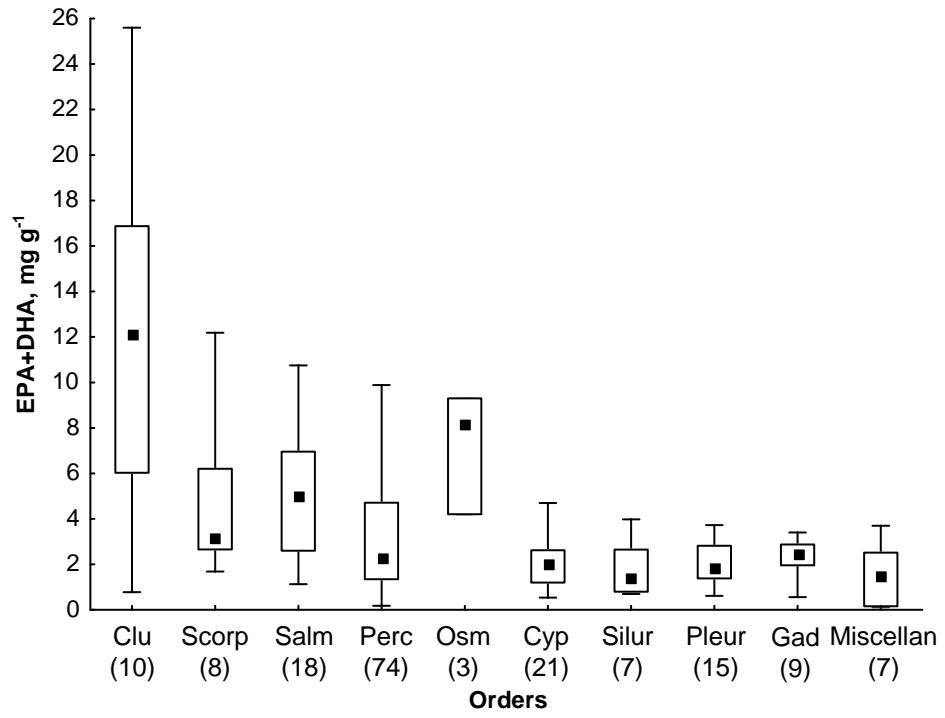
987 D Habitat temperature: cold – cold waters, tem – temperate waters, tem/cold – temperate/cold  
 988 waters, tem/warm – temperate/warm waters, warm – warm waters.

989 E Types of habitat: dem – demersal, dem-pel – demersal-pelagic, pel – pelagic.

990 Bars represent standard errors. Means labeled with the same letter are not significantly different  
 991 at  $P < 0.05$  after Kruskal–Wallis  $H$  test.

992

993 **Fig. 1.**

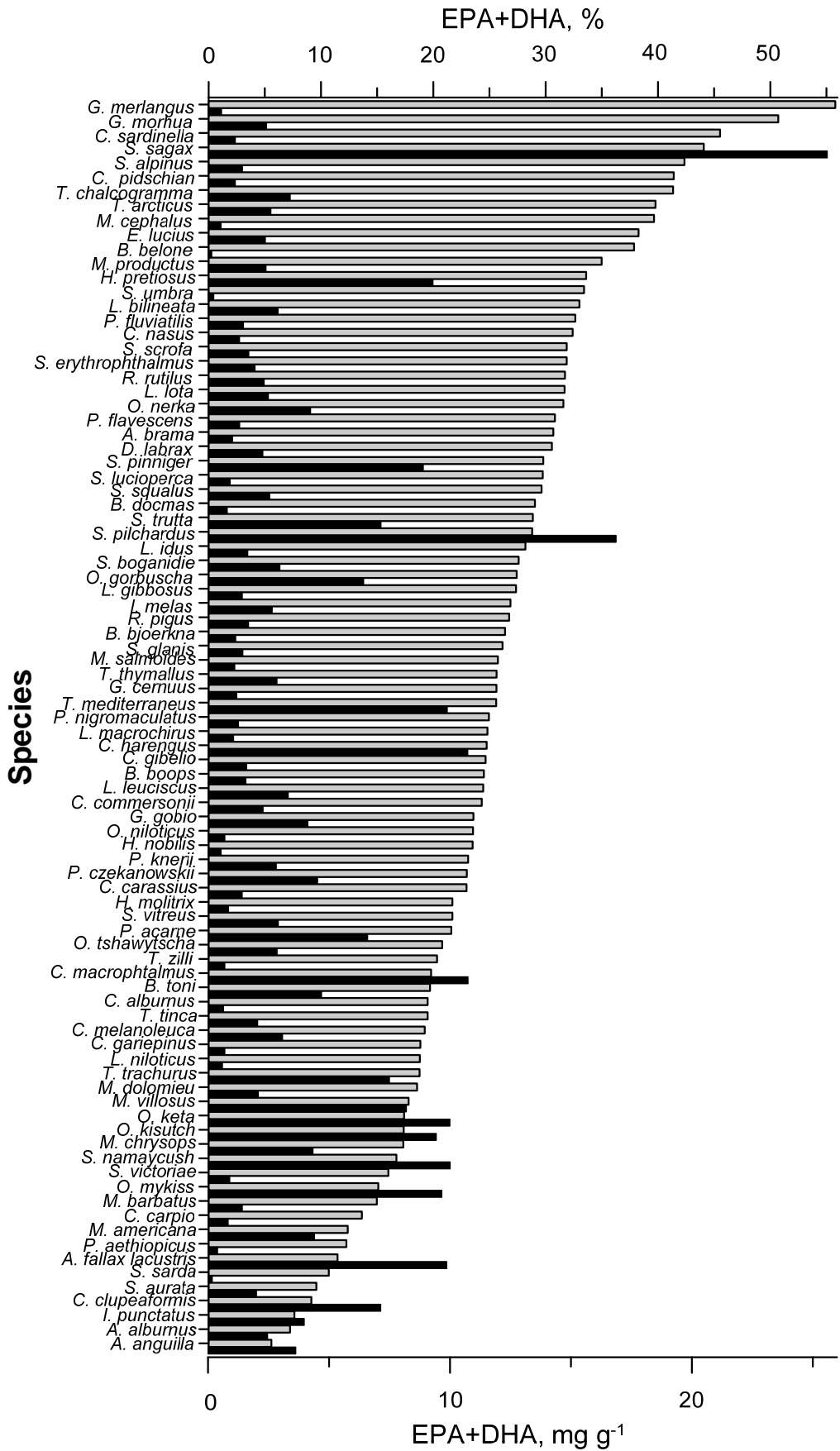


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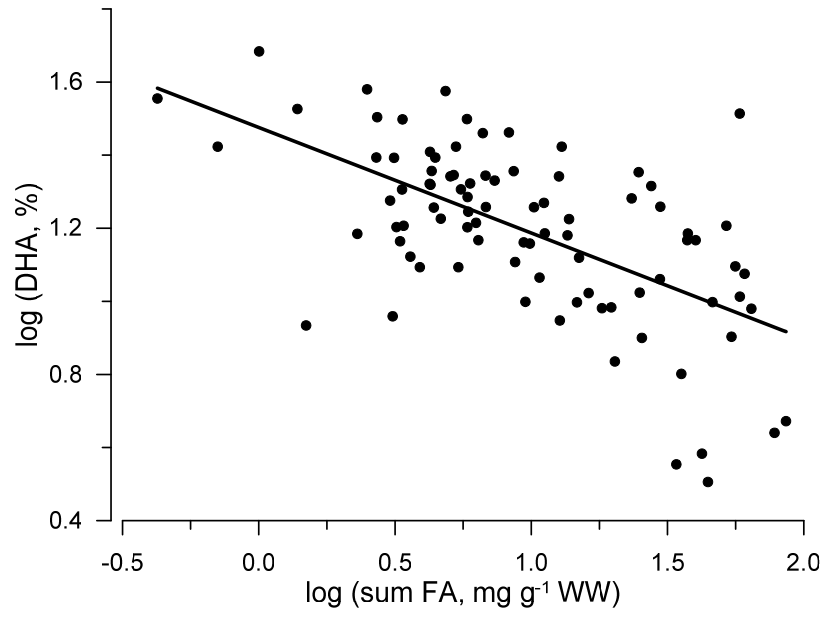
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Fig. 2.



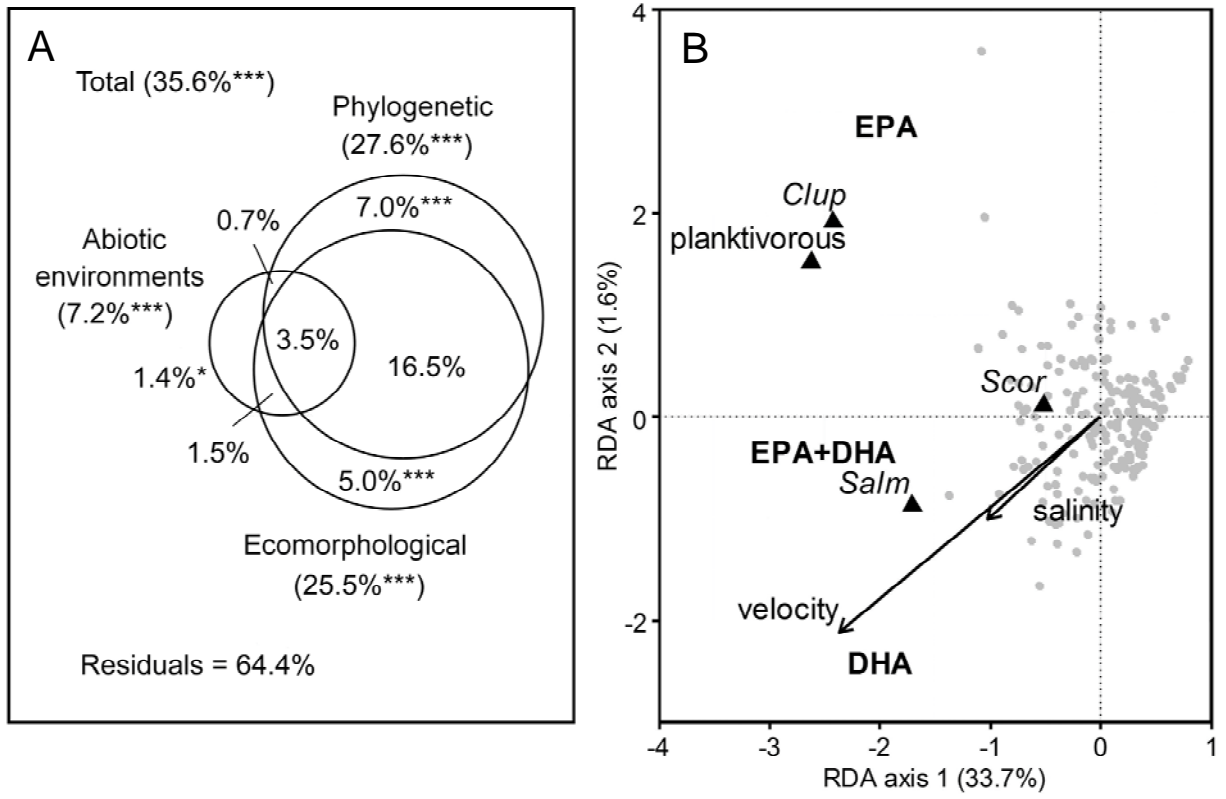
997

998  
999 **Fig. 3.**  
1000



1001

1002  
 1003 **Fig.**  
 1004 **4.**

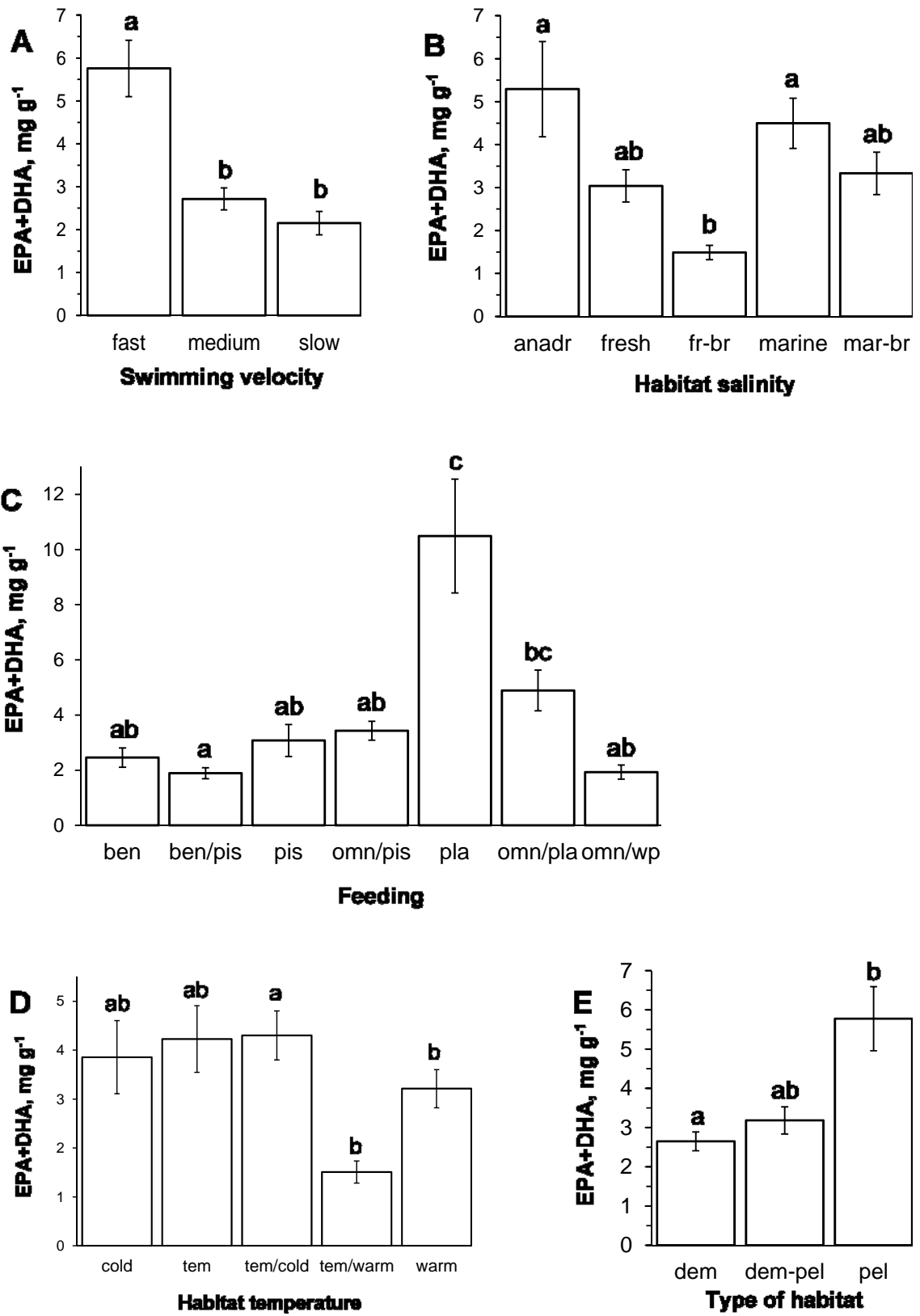


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1008

Fig. 5.



1009