BIOCHEMISTRY, BIOPHYSICS, AND MOLECULAR BIOLOGY

Polyunsaturated Fatty Acid Content in Muscle Tissue Is Associated with the Duration of Embryo Development in Salmonoid Fishes (Salmonoidei)

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Abstract—A hypothesis was advanced and grounded that the total content of eicosapentaenoic (EPA, 20:5n-3) and docosahexaenoic (DHA, 22:6n-3) acids in fish muscle tissue is associated with the species-specific (taxon-specific) duration of embryo development. A meta-analysis of the original and published data was performed using fishes of the families Coregonidae and Salmonidae as an example. Fishes with longer embryo development times, which are observed at lower temperatures, were found to have significantly higher EPA + DHA contents in muscles as compared with the species that belong to the same families but have shorter embryo development times. This association was explained by the fact that an embryo forms more cells per unit tissue volume at lower temperatures, which requires a greater specific amount of cell membranes and, therefore, greater amounts of EPA and DHA to produce them.

Keywords: salmonid fishes of families Coregonidae and Salmonidae, polyunsaturated fatty acids, eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), embryogenesis

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It is known that long-chain polyunsaturated fatty acids of the omega-3 family (PUFAs) such as eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) are essential components of the human diet. The main dietary source of EPA and DHA is fish. However, the content of PUFAs in the edible biomass (muscle tissue) of different species differs in almost 300 times, and the causes of these differences are not fully understood [1].

There is reason to believe that normal functioning of fish muscle tissue requires a relatively small amount of species-specific PUFAs, which are an important component of cell membranes and determine the activity of membrane-bound proteins [2].

One of the causes of PUFA accumulation in muscle tissue above the threshold level, which ensures the functioning of muscles themselves, obviously, is the necessity to provide developing milt and eggs with these essential substances [3]. Indeed, the proportion of PUFAs in the total amount of fatty acids in eggs of fish (e.g., salmonids) is very high [3-5], and PUFA deficiency in the diet of spawners causes significant disturbances in the embryogenesis in offspring [6, 7].

If the storage of PUFAs in muscle, indeed, serves mainly for subsequently transporting these substances to the eggs and milt, it is logical to assume that the content of EPA and DHA in fish muscles must be directly correlated with the need for these fatty acids for the normal development of eggs and prelarvae.

Thus, the content of PUFAs in muscles should directly depend on the duration of embryogenesis in a given species of fish. To test this assumption, we performed a meta-analysis of the published and our own data on the content of the sum EPA + DHA (mg g⁻¹ wet weight) in the muscle tissue in the representatives of two families of orders Salmoniformes—salmonids (Salmonidae) and coregonids (Coregonidae).

The published data were taken from [1, 2, 8]. Our own previously unpublished data were obtained by the method described in the above-cited papers. The taxonomic affiliation of fishes is given in accordance with the synopsis [9]. Information about the duration of embryogenesis was taken from the reports on freshwater fishes of Russia [9–11].

As can be seen from the data summarized in Table 1, the average content of EPA + DHA in the coregonids in the group that included the species with long

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Species	Content of EPA + DHA	SE	п	Duration of embryogenesis
Omul, Coregonus autumnalis	17.60	3.36	7	190-210
Least cisco, Coregonus sardinella	7.34	1.20	15	220-240
Inconnu, Stenodus leucichthys	6.40	1.39	5	250-260
On average, in the group with long embryogenesis	10.4	3.6	3*	190-260
Muksun, Coregonus muksun	5.97	1.21	13	150-180
Tugun, Coregonus tugun	5.63	0.28	15	183
European whitefish, Coregonus lavaretus	4.74	0.65	67	169-186.5
Broad whitefish, Coregonus nasus	4.27	0.64	23	80-170
Vendace, Coregonus albula	3.31	0.27	6	171.7
Peled, Coregonus Peled	3.25	0.26	7	150-170
On average, in the group with short embryogenesis	3.9	0.4	6*	80-186.5

Table 1. Content of EPA + DHA (mg g^-	⁻¹ wet weight \pm standard error SE) and the duration of embryogenesis (in days) in
coregonid fishes (n is the number of sample	ples or variables in meta-analysis)

* According to the rules of meta-analysis, each species should be presented in the overall (group) mean value by one variable (particular mean value), which is necessary to provide an equal contribution of each species in the overall mean value and level the differences in sample volumes (Gladyshev et al., 2018).

Table 2. Content of EPA + DHA (mg g^{-1} wet weight \pm standard error SE) and the duration of embryogenesis (in days) in salmonids

Species	Content of EPA + DHA	SE	п	Duration of embryogenesis
Chum salmon, Oncorhynchus keta	10.0	0.7	2	70-100 (45-196)
Coho salmon, Oncorhynchus kisutch	8.31	1.13	9	86-100 (34-158)
Chinook salmon, Oncorhynchus tshawytscha	6.96	3.35	10	36-150
Pink salmon, Oncorhynchus gorbuscha	6.43	1.63	23	64-70
Sockeye salmon, Oncorhynchus nerka	6.01	1.70	18	50-150 (62-177)
On average, in the group with long embryogenesis	7.5	0.7	5*	34-196
Rainbow trout, Parasalmo mykiss	5.65	2.02	10	21-35
Brown trout, Salmo trutta	4.4	1.0	3	42-56
Lenok, Brachymystax lenok	3.03	0.39	3	15-49
Siberian taimen, Hucho taimen	1.94	0.19	2	28-38
On average, in the group with a short embryogenesis	3.8	0.8	4*	15-56

* See the note to Table 1.

embryogenesis is almost 2.7 times higher than in the group that included the species of fishes with short embryogenesis.

The estimates made on the basis of the nonparametric Wald-Wolfowitz test show that the differences between the groups were statistically significant (Z = 2.06, p = 0.0392). Similar data were obtained for salmonids (Table 2). The average content of EPA + DHA was significantly higher in the group formed by the species with long embryogenesis (Z = 2.49, p = 0.0128).

However, the experiments described in the literature in which the embryogenesis rate was regulated by changing the egg incubation temperature showed that the lower the temperature (and the slower the development), the greater the number of cell nuclei per unit muscle tissue volume in the prelarvae of the European whitefish and the greater the number of muscle fibers per unit section area [12]. A similar pattern (an increase in the number of cells in the eye and in the pectoral fin at the time of hatching) was observed in the brown trout that developed at low temperature; under these conditions, the embryogenesis of the brown trout also lengthened [13]. Apparently, the tendency to increase the number of myomers at low temperatures of embryogenesis, described in many fishes including salmonids (for review, see [14]) is the consequence of the same pattern. In other words, at low temperatures (and decelerated development), many small cells are formed from the nutrients accumulated in eggs, whereas at high temperatures (and accelerated development), a smaller number of larger cells is formed. This means, in turn, that the embryos with a long period of development need more PUFAs for the synthesis of cell membranes.

This assumption allows, for example, explaining the fact that the development of the eggs obtained from the spawners with PUFA-deficient diet was accompanied by cleavage disorders [6].

Thus, this is the first study to advance the hypothesis about the relationship of the content of EPA and DHA in fish muscles with the species-specific (taxonspecific) duration of embryogenesis. This hypothesis is confirmed by the example of fishes belonging to the families Coregonidae and Salmonidae. The speculations on the causes and mechanisms of this relationship, proposed in this study, require further investigation.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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