C. FAT METABOLISM IN FISHES

XI. SPECIFIC PECULIARITIES IN DEPOT FAT COMPOSITION

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IN various papers in this series and elsewhere the author has drawn attention to peculiarities of composition characterizing the fats from fish of certain families, such peculiarities usually being more or less specific for a family. It is noteworthy that throughout the animal kingdom as a whole the greatest divergence of fatty acid types in the glycerides of the different species is to be found in the depot fats rather than in the organ (e.g. the liver) fats. Indeed the liver fats of such diverse forms as mammals and fish are not very dissimilar, whereas the depot fats have very little in common. In the case of fish this broad generality is masked to some extent by the fact that the liver is frequently utilized as a fat depot.

The significance of specific compositions from the biological standpoint has been considered by Hilditch & Lovern [1936]. In the present paper this subject is dealt with from a different angle, namely the types of peculiarity that may be encountered, together with suggestions as to the manner in which some of these modifications are brought about. Most of the types studied were suggested by previous work and are now amplified by additional examples, chosen as likely to illustrate these processes.

EXPERIMENTAL

The following fats were examined and the composition of their fatty acid mixtures is recorded in Table I: liver fats of the pollack (*Gadus pollachius*), turbot (*Rhombus maximus*), salmon (*Salmo salar*), catfish (*Anarrhichas lupus*), angel fish (*Squatina angelus*), ratfish (*Chimaera monstrosa*) and spotted dogfish (*Scyllium canicula*): body fats of the turbot, halibut (*Hippoglossus hippoglossus*), sea trout (*Salmo trutta*), brown trout (*S. trutta*), and lampern (*Petromyzon fluviatilis*): mesenteric fat of the salmon.

DISCUSSION

The composition of an animal fat will depend on the particular species studied and to some extent also on the type and quantity of fat taken by that animal in its food. There may be other factors but these two are definite. As far as the majority of fish are concerned, their food is roughly constant on balance, being the smaller specimens of mixed species. The ingested fat will therefore be a sort of "average" fish fat. This "average" fat will be different, however, in fresh or salt water, since it has been shown repeatedly [Lovern, 1932; 1934, 3; 1935, 1] that fresh-water and marine fish fats are of different types even allowing for individual specific variations. The evidence of other workers agrees with this statement [Shorland & McIntosh, 1936; Belopolsky *et al.* 1936]. The final proof

Table I. *Compositions of fatty acids of fish fats (wts. %)*

Source	Saturated			Unsaturated					
	C ₁₄	C ₁₆	C ₁₈	C ₁₄	C ₁₆	C ₁₈	C ₂₀	C ₂₂	C ₂₄
Pollack liver	2.1	13.0	1.4	—	10.9	34.2 (-2.7 H)	25.4 (-5.4 H)	13.0 (- 6.5 H)	—
Turbot liver	7.6	14.9	0.8	1.5	21.4 (-2.1 H)	27.1 (-2.5 H)	14.0 (-6.1 H)	12.7 (- 6.7 H)	—
Turbot body	3.4	15.1	2.1	0.3	8.9 (-2.6 H)	21.7 (-3.4 H)	26.6 (-6.0 H)	21.9 (- 7.7 H)	—
Halibut body	4.0	14.8	0.7	Trace	6.5 (-2.6 H)	23.8 (-3.0 H)	26.9 (-5.2 H)	23.3 (- 6.5 H)	—
Salmon liver	2.7	10.9	1.6	0.7	12.3 (-2.0 H)	32.8 (-2.9 H)	25.8 (-5.7 H)	13.2 (- 7.8 H)	—
Salmon mesentery	3.6	14.4	2.3	0.1	7.1 (-2.4 H)	25.3 (-2.9 H)	28.4 (-4.6 H)	18.8 (- 6.1 H)	—
Sea trout body	2.2	17.0	4.0*	0.1	8.8 (-2.4 H)	26.3 (-3.0 H)	19.7 (-6.6 H)	19.0 (- 9.2 H)	2.5 (-? H)
Brown trout body	3.1	19.0	4.5	0.4	11.5 (-2.6 H)	38.3 (-3.9 H)	15.0 (-7.8 H)	8.2 (-10.1 H)	—
Catfish liver	1.5	17.9	2.3	—	11.7 (-2.2 H)	46.8 (-2.6 H)	12.0 (-6.4 H)	5.9 (- 8.2 H)	1.9 (-? H)
Angel fish liver	1.4	17.0	2.0	—	6.5 (-2.0 H)	20.7 (-3.0 H)	21.9 (-6.0 H)	30.5 (-10.2 H)	—
Ratfish liver	—	8.4	7.2†	—	2.5	50.6 (-2.2 H)	19.6 (-2.9 H)	7.9 (- 3.5 H)	2.1 (-? H)
Spotted dogfish liver	1.7	15.7	3.3	—	4.0 (-2.2 H)	25.3 (-3.0 H)	24.4 (-6.4 H)	24.8 (- 9.2 H)	Trace ?
Lampem body	9.5	17.6	0.7	—	10.9 (-2.1 H)	35.3 (-2.6 H)	15.3 (-6.5 H)	10.7 (-10.3 H)	—

* Plus 0.4 % C₂₀.† Plus 1.3 % C₂₀ and 0.4 % C₂₂.

of the genuine nature of this type difference is to be found in the figures for the sea trout and brown trout given in Table I. These fish are now regarded as merely the migratory and non-migratory forms respectively of the same species and yet their fats fall quite definitely into the marine and fresh-water classes respectively. In earlier evidence from the salmon [Lovern, 1934, 3] the young stage was compared with the adult stage. With these trout, however, each variety was adult but one had been feeding in the sea and the other only in fresh water.

This overriding type distinction must obviously be taken into account in considering the nature of specific peculiarities. It is possible to show graphically the difference between marine and fresh-water fish fats, and at the same time to arrive at a conception of the "average" type for each medium, i.e. some idea of the normal food fat of most species. This has been done in Figs. 1-4. The differences of type principally concern the unsaturated acids percentages. Each of the four major component groups, C₁₆, C₁₈, C₂₀ and C₂₂, is considered separately. In Fig. 1, for instance, the abscissae represent percentages of C₁₆ unsaturated acids, approximated in each case to the nearest 5 units. The ordinates represent the frequency (i.e. the percentage of the total number of fats examined) with which that content of C₁₆ acids has been encountered. Fresh-water and marine fats are plotted separately and obviously the respective maxima give an idea of the average composition. Furthermore, the shape of the curve indicates in each case whether or not the majority of samples fall within a narrow range of this average, whilst the relative positions of the two curves on each figure show how sharp a differentiation is to be expected between marine and fresh-water

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 3. Frequency of C₂₀ acids percentages. ○ = marine. △ = freshwater.

Fig. 4. Frequency of C₂₂ acids percentages. ○ = marine. △ = freshwater.

Fig. 5. Frequency of total C₁₆ acids percentages. ○ = marine. △ = freshwater.

fats as regards that particular acid. Figs. 1-4 are for C_{16} , C_{18} , C_{20} and C_{22} acids respectively. Only true fish fats are included (i.e. no invertebrate or aquatic mammal fats) and no fish gonad fats are represented. 17 fresh-water and 44 marine fish fats are represented, some being the author's own analyses and some from other sources.

From Fig. 1 it is evident that whilst a difference in the direction of a higher content of unsaturated C_{16} acids in fresh-water fats is to be expected, there is no sharp distinction (much overlap). This may be due to specific peculiarities often affecting these acids, especially as the author has inferred in several papers a reversible controlling mechanism between saturated and unsaturated C_{16} acids. Actually if total C_{16} (i.e. saturated plus unsaturated C_{16}) acids are plotted there is a rather better differentiation between marine and fresh-water fats as shown in Fig. 5. The two trout fats in Table I show this slight difference in their contents of C_{16} acids (again especially on total C_{16} acids). Incidentally, points well off the smooth curve (as for example in Fig. 1) are obviously due to the method of approximating to the nearest 5 units and are presumably the result of dealing with an insufficient number of samples (17 in this case).

From Fig. 2 it can be seen that a well marked difference exists between the average marine and fresh-water fats as regards C_{18} unsaturated acids. Again the trout figures in Table I show this distinction. At the same time whilst most of the oils fall within a fairly narrow range, there are a few specimens well outside it. These are obvious peculiarities, either specific or due to an unusual diet or other factor. Thus the extreme point on the fresh-water curve (65% C_{18}) represents some tropical carp fed solely on grass [Lovern, 1935, 2].

From Fig. 3 it can be seen that there is good differentiation between marine and fresh-water fats as regards C_{20} acids. Again this is illustrated by the trout fats, although not very strikingly. Furthermore, the fresh-water fats are very uniform but the marine fats show greater variations in their contents of this constituent.

Fig. 4 shows a well marked difference in the C_{22} acids content of marine and fresh-water fats. The trout fats afford a good illustration.

With the aid of these figures it is now easier to consider some actual types of specific peculiarities that have been encountered. For the sake of clarity the bearing of the data in Table I on certain types of peculiarity will be considered, rather than the peculiarities of each fat (or group of fats) by itself. Thus certain of the fats exhibiting more than one type of specific character will be dealt with from several angles in the appropriate places. The types of specific qualities will be grouped under subheadings.

(a) *Peculiarities of unsaturation*

In all the papers in this series and elsewhere the practice of the author has been to express degrees of unsaturation in terms of lack of hydrogen (Table I). At present there is no quantitative method for estimating the proportions of acids of the same number of carbon atoms but of different degrees of unsaturation. Hence average figures are given for each group. Irrespective of any variation in their contents of different (molecular) acid groups some fats show abnormalities in the degrees of average unsaturation of one or more of the acid groups. The values vary considerably from fat to fat (especially those for C_{22} acids) but the majority of samples have values ranging from about -2.0 to -2.5 H for C_{16} acids, -2.6 to -3.3 H for C_{18} acids, -5.5 to -6.5 H for C_{20} acids and -7.0 to -9.5 H for C_{22} acids. Fresh-water fish fats as a whole tend to

have higher figures than marine fish fats. The brown and sea trout fats in Table I are an illustration.

In earlier papers [Hilditch & Houlbrooke, 1928; Guha *et al.* 1930; Lovern, 1930] it has been indicated that the fatty acid compositions of Elasmobranch fish (sharks and rays) fats exhibit peculiarities of unsaturation. In some of them the C_{18} , C_{20} and especially C_{22} acids tend to have higher degrees of average unsaturation than is usual for fish fats. On the other hand certain other Elasmobranch fish are characterized by fatty acids of abnormally low degrees of average unsaturation. The three Elasmobranch fish in Table I (angel fish, spotted dogfish and ratfish) illustrate both these types.

In the above papers suggestions were made that there seemed to be some connexion between the fatty acid composition (in Elasmobranch fish) and the presence or absence of squalene in the unsaponifiable fraction. Squalene-containing oils had acids of low unsaturation, non-squalene-containing oils had acids of high unsaturation. One of the fats used to illustrate this argument was that of the grey dogfish (*Squalus acanthias*) reported by Guha *et al.* [1930] to contain some squalene. This statement was questioned by Tsujimoto [1932] who stated that the liquid part of the unsaponifiable matter of *S. acanthias* is mainly selachyl alcohol, the saturated chimyl and batyl alcohols also being present. Accordingly the author made a further study of the unsaponifiable fraction of *S. acanthias* liver oil and the results agree with those of Tsujimoto. Further, squalene is definitely absent, as no hydrochloride could be obtained. The connexion between squalene and the fatty acid type (which was always difficult to understand) therefore breaks down and is further disproved by the ratfish results. The ratfish liver oil contained 37.5% of unsaponifiable matter which was almost entirely a mixture of chimyl, batyl and selachyl alcohols, squalene being absent. The ratfish acids are of the relatively saturated type. These three alcohols have a rather widespread distribution amongst Elasmobranch fishes and a search of the literature (e.g. Grün & Halden [1929]) shows that wherever they occur the accompanying fatty acids are relatively saturated (indicated by the iodine value of the oil). The genuinely squalene-containing oils examined by Hilditch & Houlbrooke also contain these alcohols. There are, however, a few oils with relatively saturated fatty acids which do not contain any appreciable quantity of these substances (e.g. the oil examined by Tsujimoto [1932]). The angel fish and spotted dogfish oils contained 1.4 and 2.2% of unsaponifiable matter respectively, in each case consisting mainly of cholesterol, and the acids were of the relatively unsaturated type.

Now the two types of fatty acid mixture found in Elasmobranch fish both differ from the normal in a related manner. One kind is more unsaturated, the other less unsaturated than the average. The writer has in several papers [e.g. 1936] adduced evidence of fat hydrogenation and dehydrogenation processes in fish. The mechanism is presumably enzymic and therefore probably reversible. Thus the enzyme acting one way in certain fish might give an unusually saturated fat whilst in others it could produce an unusually unsaturated fat. It is suggested that this is in fact what happens in Elasmobranch fish. As far as the relatively saturated type is concerned, there is some confirmatory evidence that hydrogenation has been going on. In the case of the ratfish arachidic and behenic acids were present. These acids (especially behenic) are very rare in fish fats and would not be ingested in anything other than minute traces by the fish. Their presence, coupled with such markedly reduced unsaturation of the corresponding unsaturated acids, is strongly suggestive of their origin by hydrogenation. Hilditch & Houlbrooke [1928] also reported

arachidic acid and in one oil a trace of behenic acid in the two relatively saturated shark liver oils which they examined.

An apparent correlation between the presence of chimyl, etc., alcohols and a relatively saturated fatty acid mixture becomes understandable with this conception of hydrogenation. These alcohols, which are the monoglyceryl esters of hexadecyl, octadecyl and octadecenyl alcohols respectively, must have been synthesized by the fish and their production can be most readily pictured by a hydrogenation of the glyceride molecule affecting the carbonyl group. In the oils, moreover, these alcohols are found mainly combined with two fatty acid radicals [André & Bloch, 1932] as would be expected on this theory. The suggestion is, therefore, that these alcohols and the relatively saturated fatty acids which always accompany them are formed by modifications of the same process, and that their association is due to this. There is some evidence from certain marine mammals also of a relationship between the presence of wax alcohols (in this case not coupled to glycerol and presumably derived, therefore, from acids rather than glycerides) and the simultaneous occurrence of a relatively saturated fatty acid mixture [Hilditch & Lovern, 1928].

Several fish fats have been reported where one particular acid group only is abnormal in its degree of unsaturation. Three such are halibut liver oil [Lovern, 1932] and conger eel liver and peritoneal fats [Lovern, 1934, 1]. In the two liver fats the C_{18} acids were exclusively monoethylenic whilst in the conger eel peritoneal fat such was almost the case. For comparison with the halibut liver oil result we may take halibut body oil and turbot liver and body fats from Table I. (Halibut and turbot belong to the same zoological family.) It will be seen that in none of them is so low a degree of unsaturation (of C_{18} acids) reached as in halibut liver oil. Further these four fats vary amongst themselves in a rather regular manner. For reference the degrees of unsaturation of halibut liver oil may be quoted. These are C_{16} -2.0 H, C_{18} -2.0 H, C_{20} -5.5 H and C_{22} -7.6 H. It will be seen that in each fish the C_{16} and C_{18} unsaturated acids of the body fat are more unsaturated than those of the corresponding liver fat. Further, the liver and body fats of the turbot both tend to be more unsaturated throughout than the corresponding halibut fats. The tunny [Lovern, 1936] is another example of a fish having varying degrees of unsaturation (in this case principally affecting the C_{18} acids) in the different fat depots. Such variations from species to species and for different depots within the same animal can most readily be interpreted with the aid of the hydrogenation/dehydrogenation system postulated in previous papers and discussed above. It is suggested, therefore, that abnormal degrees of unsaturation (either high or low) may be ascribed to specific functionings of this reversible system.

(b) *Regular peculiarities in percentage composition*

From Figs. 1-5 a general idea can be obtained of the content of the four main acid groups of most fish fats. Now it sometimes happens that a fat will differ from this "average" type in a regular manner. For instance, C_{16} acids may be markedly below the average, C_{18} slightly below, C_{20} slightly above and C_{22} markedly above the average. Often this peculiarity is evinced in a balanced form among the several depots in a single fish—one depot being unusually rich in the higher acids and another unusually rich in the lower. Examples of this have been dealt with in previous papers [e.g. Lovern, 1934, 1], and the suggestion was made that the controlling mechanism was operated in some manner according to molecular size. Certain depots appeared to be much less permeable

(or otherwise unavailable) than others to larger molecules and a molecular separation was effected.

The halibut and turbot data in Table I afford another illustration of this type of peculiarity. For comparison the data for the unsaturated acids of halibut liver oil may be quoted [Lovern, 1932]; C_{16} 18.7%, C_{18} 34.4%, C_{20} 13.8% and C_{22} 13.6%. The two liver fats are quite different from the corresponding body fats. The liver fat in each case contains much more C_{16} and distinctly more C_{18} unsaturated acids than the body fat, but less C_{20} and C_{22} acids. The main fat depot in these two fish is the body and from Figs. 1–4 it can be seen that the halibut and turbot body fats are within the normal ranges for marine fish fats. The liver fats are not, however. They are too high in C_{16} acids and too low in C_{20} acids. The C_{18} and C_{22} acids are not far from normal. At first sight this looks a rather erratic separation. C_{18} acids would be expected to be about normal (or only slightly higher), as they occupy a medium position in molecular size, but C_{22} acids would be expected to be markedly reduced. Actually there is another type of specific peculiarity found in turbot and halibut fats which will account for this, and it will be discussed in the next section. The total fat of the halibut or turbot is almost of the normal marine type apart from this remaining specific peculiarity and the liver fats afford another illustration of peculiarities brought about by some selection operating according to molecular size.

Some Elasmobranch fish (of which the angel fish and spotted dogfish in Table I are examples) also exhibit peculiarities of this regular type. The contents of lower acids (total C_{14} and C_{16}) are abnormally low whilst at the other end of the chain this is balanced by an unusually high C_{22} content.

(c) *Irregular peculiarities in percentage composition*

Some fats vary from the average type in a manner which cannot quite be classified under the preceding section. In certain cases, however, they approach somewhat closely to it and in these instances we may be dealing with the net result of more than one specific peculiarity in the same fat. For instance many Elasmobranch fish exhibit a modified form of the previous type of effect. Fish having acids of the relatively saturated type, accompanied by chimyl, batyl and selachyl alcohols, are those in question and the ratfish of Table I may be taken as an example. Here also the C_{14} and C_{16} acids are depressed, but there is no rise in C_{22} acids. (In the case of the ratfish there is, in fact, a fall in C_{22} acids.) On the other hand, C_{24} acids make their appearance—only a small amount in the case of the ratfish, but much more in other cases (10 and 12% in the oils examined by Hilditch & Houlbrooke [1928]). Thus there is a kind of reciprocal balance.

A word must be said at this point about the occurrence of C_{24} acids in fish fats. Such acids have been reported to occur in various oils, including cod liver oil [Toyama & Tsuchiya, 1934], whilst Brocklesby [1936] states that pilchard body oil contains 15.2% of highly unsaturated C_{24} acids. The experience of the author, however, has been that C_{24} acids only occur in appreciable amounts in a limited range of fish fats. In other cases, whilst traces may well be present these are too small to be estimated. Thus Elasmobranch fish will ingest only very small quantities of C_{24} acids and those which deposit them in appreciable amounts in their depot fat must either have concentrated or synthesized them.

The ratfish oil is a good illustration of another type of irregular peculiarity. It sometimes happens that the content of a certain acid (or acids) is greatly enhanced or diminished (compared with the normal) in the fat of a certain species. The ratfish and the catfish of Table I are examples of the former. C_{18} acids are notably in excess of the average for marine fish. The reason for this is obscure

with the data at present available. The catfish (like the sea trout) is also noteworthy in having accumulated C_{24} acids. As far as the catfish is concerned, the unusual diet may be a factor to be taken into consideration. This fish lives almost entirely on molluscs and, until data are available on a range of mollusc fats, we do not know whether the catfish ingests fat of the "average" marine type or not.

The tunny fats quoted in a previous paper [Lovern, 1936] are instances of a species in which certain acids are suppressed, rather than enhanced. C_{14} acids are almost entirely eliminated. The C_{16} unsaturated acids are reduced in amount but this is due to conversion into saturated acid rather than to elimination.

The halibut and turbot fats show a peculiarity in the relative contents of C_{20} and C_{22} acids. As can be seen from Figs. 3 and 4 the usual content of C_{22} acids in a marine fish fat is considerably less than the C_{20} content. (This is even more markedly the case for fresh-water fish fats.) A peculiarity of all the halibut and turbot fats (especially the liver fats) is that the C_{22} acid content is nearly as high as the C_{20} acid content. It is probably this irregularity which accounts for the C_{22} acid content of the liver fats being higher than would be expected on the molecular size separation, as indicated in the preceding section. These liver fats, in fact, are an instance of the joint effect of two opposing specific requirements resulting in some sort of compromise.

The brown trout is another instance of a fish in which opposing requirements have led to compromise, giving an irregular specific character to the fat. The requirements of the Salmonidae family include a rather low content of C_{16} unsaturated acids and a rather high C_{22} acids content in the body fat [Lovern, 1934, 2]. In Table I this can be seen for the salmon mesenteric fat but is not apparent for the salmon liver fat. The sea trout body fat exhibits these characteristics very well, with a C_{22} acids content almost equal to that of C_{20} acids. Now the brown trout, a purely fresh-water form, should in consequence of its habitat and/or food supply have fat of the fresh-water type which would involve a high C_{16} unsaturated acids content and a low C_{22} acids content. In addition, of course, the C_{18} acids should be increased in amount and the C_{20} acids reduced. All these differences are, in fact, to be observed between the two fats, as mentioned earlier in the paper. On the other hand the brown trout fat is a poor example of a fresh-water fish fat as regards the C_{16} and C_{22} acids percentages, as can be seen from Figs. 1 and 4. It is, as stated, probably one result of an equilibrium between two opposing sets of requirements.

The lampern fat is of interest as an example of the partially neutralizing effect of two opposing factors. The precise habits of these fish are not certain but it is known that they visit both salt and fresh water. The specimens examined were obtained from tidal reaches of the River Severn, but almost certainly had some time previously been feeding in the sea. Part of their fat would be deposited whilst feeding in fresh water (before and perhaps after the sea migration also) and part whilst feeding in the sea. The lampern fat is actually a sort of compromise between a fresh-water and a marine fish fat, as can be seen by comparing the data in Table I with Figs. 1-5.

There are quite a number of fish which exhibit no definite species peculiarities, and of these the pollack (Table I) is an example. It has fat closely resembling the "average" type as indeed have the members of the Gadidae family as a whole.

SUMMARY

From time to time in previous papers specific peculiarities in fatty acid composition characterizing the fats of certain species and families of fish have been pointed out. It has also been demonstrated that the fats of fresh-water

and marine species as a whole form two distinct types. The differences between these types have now been expressed graphically. These graphs also give a clue to the probable average composition of the fat ingested by most species of fish.

The degrees of average unsaturation of one or more of the acid groups may be characteristically abnormal in certain fish. In Elasmobranch fish, for instance, certain acids may be either unusually saturated or unusually unsaturated. It is suggested that both these types of peculiarity are brought about by appropriate modification of a reversible hydrogenation/dehydrogenation enzymic system. In many cases the acids of the relatively saturated type are accompanied by chimyl, batyl and selachyl alcohols, and it is further suggested that these have been produced by different modifications of the hydrogenation system. Halibut and turbot are other fish illustrating this unsaturation aspect of specific peculiarities.

Certain fish evince a kind of regular abnormality in the proportions of their various fatty acids. Acids of lower molecular weight are either suppressed or increased in amount with corresponding increase or suppression of the higher acids. Instances given are certain Elasmobranch fish, halibut and turbot. This type of peculiarity is apparently controlled in some way by molecular size.

There are other fish which exhibit peculiarities of an irregular nature, the content of a certain acid or acids being increased or decreased apparently without reference to the other acids. Examples are the high content of C_{18} acids in rat-fish and catfish, and the virtual absence of C_{14} acids from the tunny.

It sometimes happens that two opposing sets of specific requirements are found in the same fish and where this occurs a compromise is the result. Examples given include the case of the brown trout in which the characteristics of the Salmonidae family clash with the effects of the fresh-water habitat of the fish. The lampren affords an illustration of the partially neutralizing effect on the fat of sea feeding and fresh-water feeding by the same animal.

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