LXXXIX. FAT METABOLISM IN FISHES

XII. SEASONAL CHANGES IN THE COMPOSITION OF HERRING FAT

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It is well known that the fat content of herring varies over a wide range and extreme values may be as low as 1 % or as high as 30 %. Lovern & Wood [1937] made a study of the seasonal nature of these variations and showed that following minimal values about April, there was a rapid rise in fat content during late May and June to maximal values in July. After this point had been reached the length of time that a high fat content was maintained depended on when the fish spawned; relatively high values were maintained until spawning was imminent, when cessation of feeding caused a rapid drop in the fat content. The rapid rise in June was associated with the intensive feeding which then takes place, food organisms being very abundant at that time. In winter, scarcity of food, and possibly lack of appetite, result in a steadily falling fat content to the minimum values in April.

In the present paper it is shown that the fat of herring varies in composition as well as in quantity, and the variations of composition are likewise of a seasonal nature.

EXPERIMENTAL

Herring were obtained at such seasons as seemed likely to be of particular interest from the aspect of fat metabolism. Thus a sample was taken in April, when the fat content should be minimal. Three samples were taken during the period of rapid rise in fat content (June and July) and two samples were obtained in October, one from spent fish and the other from fish only $\frac{1}{2}$ – $\frac{3}{4}$ ripe [cf. Lovern & Wood, 1937]. Of these latter samples the spent fish contained considerably less fat than the others. All the foregoing fish were adults; in addition, immature herring caught in April were examined.

Actually the above samples were selected from a considerable number of batches of herring which were tested for fat content, the choice being guided by the results of this test. Each sample was biologically uniform in itself but it would have been difficult to secure racial uniformity from sample to sample and no attempt was made to do so. Unfortunately, a really lean April sample was not forthcoming, but it seems very doubtful whether such a sample would have yielded any further information.

The fish were gutted and the whole of the remaining tissues, including bones and head, were minced and well mixed and a sample was extracted to give sufficient fat for analysis. Each batch consisted of about 20 herring, selected on a basis of biological uniformity as already mentioned. The particulars of these samples are given in Table I. The fats were examined by the ester fractionation method and the fatty acid compositions are given in Table II. Degrees of average unsaturation are expressed as lack of hydrogen, as in former papers.

Table I. *Particulars of samples of herring*

Sample no.	Month caught	% fat	Iodine value of fat
1	April	8.2	115.5
2	June	10.7	144.2
3	June	15.7	154.3
4	July	20.7	152.5
5	October	18.8	138.6
6	October	12.0	129.9
7*	April	4.6	147.9

* Immature fish.

Table II. *Composition of fatty acids of herring fats (wt. %)*

Sample	Saturated			Unsaturated				
	C ₁₄	C ₁₆	C ₁₈	C ₁₄	C ₁₆	C ₁₈	C ₂₀	C ₂₂
1	8.0	15.7	0.2	—	4.6 (-2.6 H)	22.2 (-2.9 H)	22.0 (-3.9 H)	27.3 (-4.2 H)
2	7.3	16.7	Trace	0.6	7.5 (-2.7 H)	21.1 (-3.3 H)	27.3 (-4.8 H)	19.5 (-5.7 H)
3	7.5	12.8	0.1	0.3	7.0 (-3.0 H)	21.1 (-4.8 H)	30.0 (-5.2 H)	21.2 (-4.8 H)
4	8.3	12.1	0.3	0.5	6.4 (-3.4 H)	21.0 (-4.5 H)	28.3 (-5.5 H)	23.1 (-4.6 H)
5	7.3	13.0	Trace	0.8	4.9 (-2.7 H)	20.7 (-4.2 H)	30.1 (-4.6 H)	23.2 (-4.3 H)
6	6.6	13.7	0.5	0.2	4.9 (-2.8 H)	16.3 (-3.6 H)	28.7 (-4.4 H)	29.1 (-4.1 H)
7	5.8	12.4	0.6	—	4.7 (-3.0 H)	17.8 (-3.9 H)	31.1 (-4.3 H)	27.6 (-4.8 H)

DISCUSSION

Before considering the variations that are evident from sample to sample in Table II, there are several features to be noted which are peculiar to all the herring fats. These features may be regarded as specific peculiarities of the herring. In a previous paper [Lovern, 1937] the average composition of a marine fish fat was arrived at by means of frequency curves. Such a composition would involve the following approximate amounts of unsaturated acids: C₁₆ 10 %, C₁₈ 25 %, C₂₀ 25 %, C₂₂ 15 %. These figures correspond to the maxima on the frequency curves and, of course, a fair variation from them must be allowed before a fat could be described as abnormal. The fats in Table II are quite within the normal range for C₁₈ and C₂₀ acids but they undoubtedly have an abnormally high content of C₂₂ acids and this feature may probably be considered as a characteristic property of herring fat. In this connexion, however, it may be noted that far more liver fats than body fats from marine fish were incorporated in the curves referred to above. There may be a tendency towards higher proportions of C₂₂ acids in the body fats from marine fish, such as, for instance, turbot and halibut [Lovern, 1937]. The content of C₁₆ unsaturated acids is on the low side but the frequency curve for the proportion of these acids in a marine fish fat is unsymmetrical. The true maximum probably corresponds to between 5 and 10 % of the acids. If total C₁₆ acids (both saturated and unsaturated) are considered, the peculiarity of the herring fats is not marked, the average for a marine fish fat being 20-25 %. In the writer's opinion it is doubtful how far a low content of C₁₆ unsaturated acids should be regarded as a specific characteristic of herring fat.

There is a further peculiarity in all the fats in Table II. Many of the degrees of average unsaturation are abnormal in all the samples, irrespective of variations from sample to sample. Average values for the unsaturation of the different acid groups in a marine fish fat were quoted in the paper already referred to [Lovern, 1937] and may be given again: C_{16} , -2.0 to -2.5 H; C_{18} , -2.6 to -3.3 H; C_{20} , -5.5 to -6.5 H; C_{22} , -7.0 to -9.5 H. It will be seen that all the herring fats have C_{16} acids of abnormally high degrees of unsaturation and C_{22} acids of abnormally low degrees of unsaturation. Most of them have unusually unsaturated C_{18} acids and unusually saturated C_{20} acids. Taking them as a whole it would be fair to say that the specific features of herring fat include abnormality of unsaturation for all the acid groups, unusually high values for C_{16} and C_{18} acids and low values for C_{20} and C_{22} acids.

Apart from these general features there are variations from one sample to another. The variations in the proportions of the different acids are in certain cases significant; C_{20} acids range from 22.0 to 31.1 % and C_{22} acids from 19.5 to 29.1 %. The cause of the variations is not clear. The fact that large amounts of C_{22} acids are found in samples 1, 6 and 7, which are from fish which had undergone partial starvation, is in harmony with previous evidence [Lovern, 1934, 2]. In starving salmon it was shown that fatty acids of low molecular weight were more readily mobilized than those of higher molecular weight, leading to a progressive accumulation of the latter. However, there is no indication of a preferential mobilization of the smaller molecules in this case, e.g. C_{14} acids. The largest amounts of C_{16} unsaturated acids are found in the feeding fish (nos. 2, 3 and 4) and the smallest amounts in the starved fish, but this is not the case with the total C_{16} acids, and, as has been shown previously, it is the total C_{16} acids which must be considered in view of the interconvertibility of saturated and unsaturated derivatives.

Whatever the cause of these variations in the proportions of the various acids, the variations themselves, although real enough, are not of a large order, and do not strikingly differentiate the samples. On the other hand the samples cover a wide range as regards the average degrees of unsaturation of the acids. C_{16} acids range from -2.6 to -3.4 H, C_{18} from -2.9 to -4.8 H, C_{20} from -3.9 to -5.5 H and C_{22} from -4.1 to -5.7 H. These variations are not erratic. They are lowest in starved fish and highest in feeding fish. Sample 7 will be considered separately; in the others the unsaturation of C_{16} acids rises steadily as the fish feed and reaches a maximum when the fat content is at a maximum, after which it falls away. The other groups of fatty acids follow a similar course except that in C_{18} acids and especially in C_{22} acids the maximum unsaturation is reached earlier than the maximum fat content.

During the period of intensive feeding by herring in June, fat is being ingested at a very high level. A major ingredient of the diet is the copepod *Calanus finmarchicus*, which has a high fat content. Moreover, *Calanus* fat is highly unsaturated, especially as regards C_{18} acids (-5.1 H) [Lovern, 1935]. The C_{20} and especially C_{22} acids of herring fat always have such low degrees of unsaturation; even when the herring are rapidly ingesting copepod fat containing highly unsaturated C_{20} and C_{22} acids, that it seems certain that hydrogenation of these acids must have taken place [cf. Lovern, 1937]. If hydrogenation of C_{18} acids also takes place, it does so to a less extent than in C_{20} and C_{22} acids.

In the writer's opinion the observed variations are brought about as follows. The herring prefers a depot fat with comparatively saturated C_{20} and C_{22} acids and to this end ingested C_{20} and C_{22} acids are partially hydrogenated. In June

the fish ingest highly unsaturated fat at an abruptly increased and very high level. It seems only natural that the hydrogenation mechanism should prove temporarily unequal to such a sudden change in diet. The unsaturation of all acid groups would tend to rise. Then the hydrogenation mechanism would function more actively and it seems likely that it would operate preferentially on the C_{22} acids. It is in respect of the C_{22} acids that the specific peculiarity of the herring is most marked when compared with the average marine fish. Thus, long before the period of intensive feeding is over, the rate of saturation of C_{22} acids is sufficient to cope with the ingested fat (the drop from sample 2 to 3, during the period of intensive feeding, is striking). The saturation of the other acids is not so urgent, although steady hydrogenation of C_{20} acids must be going on, as, in spite of the fact that most of the fat in sample 4 must be fat deposited during the intensive feeding period, its unsaturation is only -5.5 H as opposed to -7.8 H in *Calanus* fat [Lovern, 1935]. In this connexion it should be noted that sample 1 with 8.2 % of fat is not representative of the minimum fat content which herring attain before the commencement of intensive feeding. A figure of 2-3 % is much nearer the average. Thus it is clear that the fat of sample 4 is mainly fat which has been recently deposited.

It has been mentioned that *Calanus* fat has particularly highly unsaturated C_{18} acids (-5.1 H). It seems from what has already been said that the herring does not require a relatively saturated C_{18} acid mixture—in fact from the high state of unsaturation of C_{18} acids in sample 5, long after the period of intensive feeding has passed, it appears that an unusually high degree of unsaturation of these acids can be tolerated. However, there is presumably a limit above which the unsaturation cannot rise without an attempt being made to modify it. In sample 3, when rapid ingestion of fat has gone on some time and is still going on, the C_{18} acids of the herring fat have almost reached the state of unsaturation of *Calanus* fat. Evidently there has been no attempt so far to hydrogenate them. After this level has been attained, however, there is a drop (sample 4), whilst still more fat is being ingested. The limit appears to have been reached in sample 3 and hydrogenation of the C_{18} acids has then commenced.

The C_{16} unsaturated acids are unique in that they have a higher level of unsaturation than *Calanus* fat (-2.4 H). Their increase in unsaturation during the feeding period cannot, therefore, be due to ingestion of food fat at a higher level than the herring metabolism can deal with. In a previous paper [Lovern, 1937] it has been suggested that hydrogenation and dehydrogenation of fats in fish are brought about by a reversible enzyme system. The writer's opinion is that dehydrogenation of C_{16} acids goes on during intensive feeding at the same time as hydrogenation of the other acids. The C_{16} acids may indeed provide part of the hydrogen required for hydrogenation of the other acids.

The compositions of samples 5 and 6 are suggestive. Both of these are from fish caught at the same period, long after intensive feeding has ceased. The herring of sample 6, however, having recently spawned, had undergone partial starvation through loss of appetite, whilst the fish of sample 5 had gone on feeding at the normal summer and autumn level. Sample 5 had not lost much fat but sample 6 had been considerably depleted. Both sets of fish had had the same period in which hydrogenation could go on, yet in sample 6 the acids (apart from C_{16}) are more saturated than in sample 5. This suggests a preferential utilization of the more unsaturated acids. There is a long gap in time between samples 4 and 5. In view of the rapidity with which hydrogenation must have been taking place to cope with the high rate of fat ingestion, it seems likely that when intensive feeding ceased in July the herring fat would soon

reach the required degree of saturation. Probably the degree of saturation found in sample 5 was attained long before October and then remained more or less stationary. The fall in sample 6 compared with sample 5 can only be associated with the lower fat content and not with the length of time that hydrogenation has gone on—hence the conclusion that selective utilization of the more unsaturated constituents has taken place. The C_{16} acids are interesting in this respect. The extra unsaturation acquired during the intensive feeding period seems to be lost very rapidly and these acids have reached the minimum unsaturation required by the herring in sample 5. Any further drop would be prevented either by dehydrogenation or by a cessation of selective utilization. If there is a tendency (as found in the salmon) for fatty acids of smaller molecular size to be most readily utilized as fuel, and if in addition the herring preferentially utilizes the more unsaturated constituents of the fat, then the very sudden drop in unsaturation of the C_{16} acids is readily understandable.

The degree of unsaturation is still lower in sample 1 than in sample 6, except in the case of the C_{16} and C_{22} acids which show little change. The lower limit of unsaturation for both these acids seems to have been almost reached in sample 5.

It should be noted that in the case of starving salmon already referred to there was no evidence of a preferential utilization of the more unsaturated acids.

The immature herring of sample 7 should be compared with those of sample 1, caught at the same period. It will be seen that the degrees of unsaturation are higher throughout. This condition of higher unsaturation in young specimens may be true for many species. For instance, young salmon have much more highly unsaturated fat than adult salmon [Lovern, 1934, 3], and the fat of the foetus of a porpoise was found to be much more highly unsaturated than the maternal fat [Lovern, 1934, 1].

SUMMARY

The fats from samples of herring caught at different seasons have been analysed and the fatty acid compositions recorded.

An abnormally high content of C_{22} acids, unusually unsaturated C_{16} and C_{18} acids and unusually saturated C_{20} and C_{22} acids are considered as characteristic features of the fats of the species.

Unsaturation of the different acid groups varies progressively from sample to sample. It is suggested that rapid ingestion of highly unsaturated fat during June causes a temporary unbalancing of fat hydrogenation in the herring. A temporary rise in unsaturation results, but hydrogenation is soon modified to meet the situation. C_{16} acids are dehydrogenated instead of being hydrogenated whilst C_{18} acids are not markedly affected over a large range.

It is suggested that in fasting herring the more highly unsaturated constituents of the fat are preferentially utilized.

Immature herring had a more unsaturated fat than adult herring caught at the same period.

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