DIFFERENTIATION OF FRESHWATER CHARACTERISTICS OF FATTY ACIDS IN MARINE SPECIMENS OF THE ATLANTIC STURGEON, *ACIPENSER OXYRHYNCHUS*

R. G. ACKMAN, C. A. EATON, AND B. A. LINKE[1]

ABSTRACT

Lipids and fatty acids of two marine-caught specimens of the Atlantic sturgeon, *Acipenser oxyrhynchus*, which spawns and also feeds in freshwater, were examined. Specific fat contents, respectively 47.2 and 25.0% in orange-colored dorsal tissue and 8.5% in both livers, were high but not unexpected for sturgeons generally. In each fish a very consistent basic fatty acid composition of depot fats showed that this fat in various parts of the body had a common function. Depot fat from the fatter fish had high iodine values (ca. 190) while in the leaner fish values were lower (ca. 135) and more typical of sturgeons generally. The fatty acid details of depot fats showed some characteristics of marine fats, such as the presence of the unusual $\omega 1$ and $\omega 4$ polyunsaturated fatty acids, the low figure for linoleic acid and relatively high proportions of long chain polyunsaturated fatty acids, but were more typical of freshwater fats in the virtual absence of eicosenoic and docosenoic acids. Broadly speaking, the fatty acids of the Atlantic sturgeon seem to place it in a special class of fish with fats generally resembling freshwater fish fats in composition, despite its marine origin.

The Atlantic sturgeon, *Acipenser oxyrhynchus* Mitchill, is widely distributed along the Atlantic coast of North America and is to be distinguished from *A. sturio*, the common sea sturgeon of Europe (Scott and Crossman 1973). The Atlantic sturgeon is an anadromous fish, spawning in freshwater,[2] whereas some other sturgeon species, such as the lake sturgeon, *A. fulvescens*, are restricted to freshwater. The most recent and detailed study of sturgeon lipids and fatty acids has been based on an *A. sturio* specimen, apparently of freshwater origin, as it showed a fatty acid pattern which is characteristic of lipids in freshwater fish (Reichwald and Meizies 1973).

The standard reference book on fatty acids states that sturgeon fats are "of the freshwater type" (Hilditch and Williams 1964) although this view was based on a single analysis of a specimen of *A. sturio* caught in the North Sea (Lovern 1932). We wish to report that a study of two saltwater *A. oxyrhynchus* shows that, during its marine period, the Atlantic sturgeon deposits fat with some composition details corresponding to marine fatty acid characteristics. However the fat definitely lacks other details characteristic of fats of higher marine organisms and thus reinforces the published viewpoint based on the common sea sturgeon of the Northeast Atlantic.

MATERIALS AND METHODS

Samples

Two *A. oxyrhynchus* were acquired from fish traps located in an area of the entrance to Halifax Harbour known as Eastern Passage. Both were male, that taken on 12 October 1968 (A) being 150 cm in length and that taken 30 August 1973 (B) being 155 cm. Fish A was frozen whole at -40°C until dissected in March 1969. Fish B was held overnight in an aquarium and dissected immediately after sacrifice. In both cases sections were cut transversely through the middle of the fish. In fish A this was done while frozen and the cut section included liver which was recovered for study, while in fish B the liver was removed separately from the fish. Both fish showed a soft fatty orange layer between the dorsal skin and muscle, of one or more centimeters in thickness, but thinning down the flanks. Parts of this layer penetrated the muscle, especially between myotomes, and streaks of similar colored material appeared in the muscle. A section through fish B was observed to have a

[1]Environment Canada, Fisheries and Marine Service, Halifax Laboratory, P.O. Box 429, Halifax, Nova Scotia B3J 2R3 Can.

[2]Sturgeon were once so common that those blocked by the falls in the Hudson river were taken in large quantities and marketed in New York City as "Albany veal." They appear to be returning to their former habitat in large numbers (R. Severo, New York Times, 9 July 1975).

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white layer 2-3 mm in thickness between the epidermis and the soft orange layer.

Lipid from the orange tissue of fish A was extracted by blending with n-hexane in a Waring Blendor.[3] All other lipids were extracted by the method of Bligh and Dyer (1959). For fish A the samples examined, and lipid recoveries, were liver, 8.5%, orange tissue, 47.2%; muscle freed of all visible orange tissue and fat, 2.0%; and whole steak section, 7.2%. Lipid recoveries from fish B samples were liver, 8.5%; orange tissue, 25.0%; muscle freed of all visible orange tissue and fat, 1.2%; and subdermal white layer, 1.3%. Total lipids from the fish A samples were saponified and non-saponifiable materials removed. The recovered fatty acids were converted to methyl esters with boron trifluoride in methanol. White layer and orange tissue samples from fish B were treated similarly, but the muscle and liver lipids were fractionated on a column of divinylbenzene copolymer beads and eluted with benzene. The purity of the various fractions was monitored by thin-layer chromatography on silicic acid. The major fractions, the triglycerides and the polar lipids with the mobility of phospholipids, were transesterified with BF_3-MeOH. Analyses of recovered methyl esters of fatty acids are given in Tables 1 and 2. Further details of these methods, including gas-liquid chromatography of methyl esters on open-tubular polyester columns, will be found elsewhere (Sipos and Ackman 1968; Ackman, Hooper, and Frair 1971; Ackman and Hooper 1973).

RESULTS AND DISCUSSION

The triglycerides in the two marine *A. oxyrhynchus* were distributed throughout the body in the dorsal fatty layer, in the form of muscle infiltration by this fatty layer, and also in the liver. This is most clearly made evident by comparing the iodine values of the different fats isolated from sturgeon B (Table 2). The white subdermal layer, the orange tissue fat, estimated from thin-layer chromatograms to be >95% triglycerides, and the triglycerides isolated from muscle and liver lipids, all have calculated iodine values in the range 132-139. The two phospholipid fractions have much higher iodine values, as expected for this class of lipids (Ackman 1966). In fish A, the orange tissue fat (a clear oil, estimated to be >95% triglycerides from thin-layer chromatograms) had a calculated iodine value of 186 (Table 1). The liver lipid, also estimated to be mostly

TABLE 1.–Fatty acid composition, in weight percent,[1] for lipids recovered from four tissues of Atlantic sturgeon A.

Fatty Acid[2]	Orange tissue	Muscle (no visible fat)	Whole steak section	Liver
14:0	5.13	2.80	3.61	2.82
Iso 15:0	0.35	0.21	0.27	0.21
Anteiso 15:0	0.16	0.11	0.14	0.10
15:0	0.78	0.53	0.90	0.78
Iso 16:0	0.23	0.12	0.19	0.14
16:0	16.21	17.05	16.34	17.38
Iso 17:0	0.29	0.21	0.31	0.26
Anteiso 17:0	0.15	0.10	0.12	0.09
17:0	0.48	0.39	0.40	0.33
3,7,11,15-TMHD	0.37	0.44	0.46	0.09
Iso 18:0	0.11	0.08	0.14	0.12
18:0	1.65	2.91	1.83	2.58
Total saturates	25.3	25.2	25.0	25.1
16:1ω9	0.42	0.59	0.44	0.39
16:1ω7	7.45	5.61	6.25	6.45
16:1ω5	0.29	0.26	0.17	0.26
17:1ω8	0.42	0.30	0.38	0.45
18:1ω11+9	15.69	15.22	15.11	18.27
18:1ω7	4.04	4.35	3.93	5.49
18:1ω5	0.47	0.45	0.31	0.38
19:1ω9	0.33	0.39	0.32	0.56
20:1ω11	0.35	0.20	0.41	0.16
20:1ω9	1.23	0.96	1.34	1.19
20:1ω7	0.86	0.84	1.25	0.81
22:1ω13+11	0.15	0.05	0.13	0.08
Total monoenes	31.9	29.4	30.2	34.7
16:2ω6	0.26	0.12	0.26	0.04
16:2ω4	1.42	1.03	1.17	0.78
18:2ω6	0.85	0.77	0.85	0.84
18:2ω4	0.28	0.31	0.29	0.57
20:2ω6	0.24	0.15	0.35	0.26
16:3ω4	1.61	0.93	1.47	0.43
18:3ω6	0.08	0.13	0.10	0.13
18:3ω4	0.40	0.20	0.32	0.30
18:3ω3	0.28	0.26	0.30	0.33
20:3ω6	0.18	0.16	0.28	0.21
20:3ω3	0.10	0.10	0.12	0.12
16:4ω3	0.17	0.19	0.15	0.03
16:4ω1	1.40	0.90	1.25	0.15
18:4ω3	2.78	1.62	2.25	1.28
18:4ω1	0.83	0.54	0.64	0.67
20:4ω6	1.37	1.63	1.53	1.72
20:4ω3	1.64	1.41	1.64	1.97
22:4ω6	0.13	0.19	0.20	0.26
20:5ω3	18.37	19.15	19.40	14.33
21:5ω3 or 2	0.99	0.84	0.92	0.94
22:5ω6	0.38	0.74	0.54	0.42
22:5ω3	2.21	3.10	2.82	3.40
22:6ω3	6.85	10.88	7.91	10.94
Total polyenes	42.8	45.4	44.8	40.2
Calc. iodine value	186	199	194	182

[1]NSA = no significant amount. Average percentages for some minor components were: Iso 14:0, 0.07%; 4,8,12-TMTD, 0.03%; 2,6,10,14-TMPD, 0.03%; 19:0, 0.09%; 20:0, 0.04%; 14:1ω7, 0.02%; 15:1ω8, 0.3%; 19:1ω10, 0.07%; 19:1ω8, 0.06%; 20:1ω5, 0.01%; 22:1ω9, 0.04%; 22:1ω7, NSA; 22:1ω9, NSA; 16:2ω7, 0.02%; 18:2ω9, NSA; 20:2ω9, NSA; 16:3ω3, NSA.

[2]3,7,11,15-TMHD (phytanate) = 3,7,11,15-tetramethylhexadecanoic acid. 4,8,12-TMTD = 4,8,12-trimethyltridecanoic acid. 2,6,10,14-TMPD (pristanate) = 2,6,10,14-tetramethylpentadecanoic acid.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Fatty acid composition, in weight percent,[1] for lipids recovered from four tissues of Atlantic sturgeon B.

Fatty acid[2]	White subdermal layer	Orange tissue	Muscle (no visible fat)		Liver	
			Triglyceride	Polar lipid	Triglyceride	Polar lipid
14:0	3.75	3.81	3.50	0.75	2.42	1.53
Iso 15:0	0.37	0.35	0.31	0.21	0.20	0.14
Anteiso 15:0	0.20	0.26	0.22	0.11	0.09	0.04
15:0	0.71	0.66	0.52	0.43	0.62	0.72
Iso 16:0	0.18	0.20	0.14	ND[3]	0.16	0.11
16:0	15.46	15.24	14.75	22.42	18.32	25.72
7-MHD	0.33	0.25	0.22	0.11	0.19	0.20
2,6,10,14-TMPD	0.22	0.28	0.18	ND	0.16	NSA
Iso 17:0	0.35	0.29	0.28	0.10	0.33	0.24
Anteiso 17:0	0.19	0.25	0.18	0.07	0.20	0.16
17:0	0.27	0.31	0.27	0.27	0.32	0.74
3,7,11,15-TMHD	1.08	1.38	0.55	0.14	0.05	0.27
Iso 18:0 ?	0.14	0.20	0.20	0.08	0.23	0.35
18:0	2.17	1.98	3.14	8.71	2.67	11.77
19:0	0.15	0.13	0.12	0.33	0.07	0.43
20:0	0.18	0.19	0.14	0.09	0.08	0.31
Total saturates	25.9	26.1	25.1	33.9	26.3	43.0
16:1ω9	0.20	0.25	0.21	0.03	0.20	0.61
16:1ω7	6.22	6.08	5.47	1.01	4.50	1.13
17:1ω8	0.75	0.70	0.63	0.31	0.52	0.09
18:1ω9	25.94	25.67	25.75	11.81	31.16	9.03
18:1ω7	4.00	3.91	5.94	3.94	4.46	4.44
18:1ω5	0.43	0.49	0.71	0.21	0.56	0.21
19:1ω10+8	0.54	0.32	0.61	0.10	0.43	0.14
19:1ω6	0.20	0.22	0.48	0.05	0.21	0.07
20:1ω11	1.27	1.29	1.05	0.13	0.31	0.80
20:1ω9	2.76	2.70	2.40	0.55	2.44	2.00
20:1ω7	2.41	2.40	1.72	0.27	1.41	0.89
20:1ω5	0.22	0.23	0.17	0.02	0.13	0.10
22:1ω13+11	0.51	0.46	0.18	0.10	0.14	0.62
22:1ω9	0.26	0.36	0.16	0.01	0.19	0.13
22:1ω7	0.15	0.16	0.05	ND	0.10	0.09
Total monoenes	46.0	45.5	45.7	18.7	46.9	20.8
16:2ω6	0.15	0.21	0.16	ND	0.04	0.16
16:2ω4	0.95	0.85	0.84	0.12	0.52	0.24
18:2ω6	0.84	0.84	0.77	0.22	0.68	0.52
18:2ω4 ?	0.21	0.20	0.26	0.10	0.51	ND
20:2ω9	0.12	0.07	0.15	Trace	0.19	0.03
20:2ω6	0.52	0.56	0.48	0.19	0.35	0.27
20:2ω4	0.25	0.18	0.18	Trace	0.12	ND
NMID [20:2]	0.44	0.48	0.24	0.03	0.10	0.03
NMID [22:2]	0.50	0.52	0.18	0.01	0.20	0.05
16:3ω4	0.65	0.64	0.70	Trace	0.32	ND
18:3ω6	0.26	0.29	0.19	Trace	0.07	Trace
18:3ω4	0.74	0.68	0.52	ND	0.48	ND
18:3ω3	0.48	0.41	0.38	0.11	0.24	0.18
20:3ω6	0.26	0.19	0.12	0.05	0.14	0.06
20:3ω4	0.16	0.30	0.15	ND	0.35	ND
20:3ω3	0.18	0.27	0.13	0.05	0.31	0.08
16:4ω1	0.61	0.60	0.52	0.02	0.08	0.01
18:4ω3	1.29	1.18	1.12	0.07	0.51	0.09
18:4ω1 ?	0.38	0.37	0.47	0.03	0.33	0.01
20:4ω6	1.40	1.28	1.37	4.78	0.84	6.90
20:4ω3	1.42	1.41	1.18	0.26	1.24	0.37
22:4ω6	0.17	0.51	0.20	0.20	0.29	0.32
20:5ω3	0.62	10.21	10.19	18.61	6.95	7.35
21:5ω2 or 3	0.64	0.66	0.67	0.06	0.62	0.05
22:5ω6	0.56	0.44	0.44	0.26	0.56	0.64
22:5ω3	2.44	2.52	2.57	2.02	4.87	2.86
22:6ω3	3.85	3.32	4.40	18.77	5.10	16.46
Total polyenes	28.1	28.4	29.2	47.4	26.8	36.2
Calc. iodine value	139	136	136	201	132	161

[1]NSA = no signficant amount. Average percentages for some minor components from subdermal layer, orange tissue, and triglycerides were: 12:0, 0.04%; 13:0, 0.01%; iso 14:0, 0.04%; 4,8,12-TMTD, 0.05%; anteiso 16:0, 0.02%; anteiso 18:0, 0.02%; iso 19:0, 0.05%; anteiso 19:0, 0.02%; 22:0, 0.01%; 14:1ω7, 0.02%; 14:1ω5, 0.01%; 16:1ω11, NSA; 16:1ω5, 0.08%; 17:1ω6, 0.03%; 18:1ω13, NSA; 18:1ω11, trace; 20:1ω15(?), 0.06%; 22:1ω5, NSA; 18:2ω9, 0.05%; 22:2ω6, 0.11%; 16:3ω3, trace in TG; 20:3ω9, 0.03%; 16:4ω3, 0.01%; 22:4ω3, 0.06%.

[2]7-MHD = 7-methylhexadecanoic acid from 7-methylhexadecenoic acid (Hooper et al. 1973), measured in hydrogenated esters. 2,6,10,14-TMPD (pristanate) = 2,6,10,14-tetramethylpentadecanoic acid. 3,7,11,15-TMHD (phytanate) = 3,7,11,15-tetramethylhexadecanoic acid. NMID=non-methylene-interrupted dienoic acids. 4,8,12-TMTD = 4,8,12-trimethyltridecanoic acid.

[3]ND = not determined.

triglyceride by thin-layer chromatography, had a similar iodine value, as did the lipid from the steak section of high fat content. This high fat content appears to be normal as Fraser et al. (1961) reported 6.2% fat in a steak from this species. Evidently, the fatty acid compositions of triglycerides for fish A would give high iodine values similar to those for phospholipids, for example in the lean muscle extract which would include about half of each type of lipid. The actual iodine value of the triglyceride of sturgeon A is unusually high for marine fish triglycerides (Ackman 1966) but a considerable range of iodine values appears possible for sturgeon depot fats. The "peritoneal cavity" depot fat of the *A. sturio* examined by Lovern (1932) had an iodine value of 126.5, and that of the corresponding liver lipids was 125. A Pacific coast sturgeon (species unknown) had body and liver oils with respective iodine values of 90 and 95 (Bailey et al. 1952), and the iodine values of fats of three types of flesh from the freshwater *A. sturio* of Reichwald and Meizies (1973) were also low. Two *A. baeri* kept in captivity for several years in the Freshwater Fisheries Research Laboratory in Tokyo were slightly different from each other in fatty acid compositions (Table 3) but the fats in each body sample, dorsal flesh and ventral flesh, were respectively quite similar in each fish although they differed in some details from the liver fatty acids (Shimma and Shimma 1968). These authors specifically note the absence of mesentary fat (cf. Lovern 1932), although they found the testes to be unexpectedly high in fat. Oil from American sturgeon of unspecified origin had an iodine value of 125.3 (Bull 1899) and the liver oil from *A. mikadoi* an iodine value of 157.7 (Tsujimoto 1926). Russian data shows Caspian and Atlantic sturgeon fats as having respective iodine values of 122 and 125 (Zaitsev et al. 1969).

In comparative detail, the fatty acid analyses from sturgeon A show little differences between the fat from steak section, orange tissue, lean muscle, and liver (Table 1). However, the high proportions of 22:6ω3 in the lean muscle and in the liver may reflect inclusion of phospholipids which contained relatively high proportions of 22:6ω3 (compare fish B, polar lipids, Table 2). The analysis of particular lipids from fish B is more appropriate for detailed discussion. The fatty acid composition shows that fat from the subdermal white layer, the orange tissue fat, and the muscle triglycerides are all essentially the same fat. Hake skin fats (*Merluccius capensis* and *M. paradoxus*) resemble adjacent dark muscle fat in fatty acid composition (Wessels and Spark 1973). The fatty acid composition of triglycerides in the liver of sturgeon B is also basically similar but has a few fatty acid characteristics shared with the liver phospholipids. Thus the level of 14:0 is lower and the proportion of 16:0 is higher. However 18:0 is not affected in the liver triglyceride, relative to the other triglycerides, so there is no effect on the total of saturated acids. The total for monoethylenic acids in the liver triglycerides is also nearly the same as in the other triglycerides. Although in detail the 16:1 acids are less in parallel to the phospholipid composition, the 18:1 acids are unexpectedly higher, a characteristic confirmed by fish A liver (Table 1). This intermediate status of the liver triglycerides is also apparent in many details and subtotals among the polyunsaturated acids. A singular exception lies in the low proportion of 20:4ω6, which does not seem to extend to any other "ω6" acid. On the other hand, the observation that 20:5ω3 in the liver triglyceride is not intermediate between the other triglycerides and the liver phospholipid is offset by the higher level of the homologous 22:5ω3. In fish A it is possible that 20:4ω6 is also low in liver lipid (of which a large proportion would be triglyceride) but the lower level of 20:5ω3 is less marked in the fatty acid

TABLE 3.—Some fatty acid details, in weight percent, for fats from tissues of three sturgeon examined in Japan (from Shimma and Shimma 1968).

Sample		Fat (%)	Percentages of some important fatty acids in fat								Calc. iodine value
			4:0	16:0	16:1	18:1	18:2	20:1	20:5	22:6	
A. baeri (A)	dorsal	7	2.5	18.5	7.5	29.8	1.4	3.3	8.0	16.9	171
	ventral	71	2.3	16.6	9.0	31.0	1.4	4.0	6.9	13.8	160
	liver	38	2.6	15.5	7.6	44.1	1.6	3.5	3.8	9.9	130
A. baeri (B)	dorsal	14	3.7	21.6	10.5	33.1	1.3	2.8	6.5	11.4	140
	ventral	76	3.7	19.7	9.7	29.5	1.7	3.5	6.6	13.6	154
	liver	51	1.6	23.7	6.7	54.4	—	1.9	2.7	5.3	95
A. shrenki	liver	41	1.1	18.5	9.8	45.1	7.9	2.2	2.5	1.8	99

composition of the total lipids of the liver. The significance of these observations is obscure but it is probable that the liver is active in de novo biosynthesis of 16:0 and 18:0 acids. If 18:0 is desaturated to 18:1ω9, it could explain the higher level of the latter in the liver triglyceride in terms of a temporary storage function before distribution elsewhere. The same role could result in the liver triglyceride accumulating 22:5ω3 at an intermediate stage between 20:5ω3 and 22:6ω3 for either conversion or catabolism. The two Atlantic sturgeon do not appear to have as much fat in the liver as observed in other species or perhaps in animals from other habitats. Zaitsev et al. (1969) show 8-16% oil in livers of other than Danube sturgeon, and 8-20% in the latter. The liver of an *A. mikadoi* taken at sea near Hokkaido yielded 52% oil by boiling (Tsujimoto 1926) and Shimma and Shimma (1968) report 38 and 51% lipid in livers of two *A. baeri*.

Among the unusual fatty acids observed in the fat of fish B, special mention should be made of the NMID (nonmethylene-interrupted dienes) [20:2] and [22:2] (Ackman and Hooper 1973; Paradis and Ackman 1975). In vertebrate lipids these unusual fatty acids are apparently deposited in parallel with 20:1 and 22:1. The generally lower levels of the latter in the lipids of fish A resulted in the NMID [20:2] and [22:2] being barely detectable (≤0.01%) and they are not included in Table 1. The food of sturgeons on the Nova Scotian shelf is probably basically bottom invertebrates (Scott and Crossman 1973). Many of these organisms are potential sources of these unusual acids (Ackman and Hooper 1973; Watanabe and Ackman 1974; Ackman et al. in press). These acids do not appear to occur significantly in the oils from pelagic fish and it can be assumed that their occurrence in the sturgeon is a food web effect rather than a peculiarity of the species. The absence of 16:1ω11 and 18:1ω13 suggests that indigenous biosynthesis is unlikely.

The levels of isoprenoid acids in triglycerides of fish B, especially 3,7,11,15-tetramethylhexadecanoic acid (phytanic), are unusually high for marine fish oils (Ackman and Hooper 1968), but the exclusion of these acids from the biospecific phospholipids of animals higher than molluscs has been observed previously (Ackman et al. 1970; Ackman and Eaton 1971; Ackman and Hooper 1973; Hooper et al. 1973). The properties of phytanic acid resemble those of 18:0 and a possible unusual low turnover rate for C_{18} acids (see below) could explain the accumulation of phytanic acid. On the other hand, the relatively lower levels of 4,8,12-trimethyltridecanoic acid and 2,6,10,14-tetramethylpentadecanoic acid (pristanic) are not easily reconciled with this explanation. Some gas-liquid chromatographic evidence based on calculation of retention times indicated the presence of the chain extension product of phytanic acid, 5,9,13,17-tetramethyloctadecanoic, and of 6,10,14-trimethylpentadecanoic acid derived from 4,8,12-trimethyltridecanoic acid (Maxwell et al. 1973). However, these components were only present in trace amounts ≥0.01% and identifications are speculative.

The importance of marine algae (the primary source of phytol from which phytanic acid is derived) in the diet of sturgeons is not known (Scott and Crossman 1973). In freshwater, Atlantic sturgeon do eat algae (Leim and Scott 1966). The unusually high levels of 16:2ω4, 16:3ω4, and 16:4ω1, all of which are primarily algal in origin (Ackman et al. 1968), indicate that plants provide a significant proportion of dietary lipids. The tentatively identified higher homologues 18:2ω4, 18:3ω4, and 18:4ω1 behaved as appropriate polyunsaturated fatty acids on nitromethane enrichment (Jangaard 1965) and on thin-layer chromatography on silver nitrate impregnated silicic acid (Morris 1966), and were eliminated (probably converted to 18:0) on hydrogenation. The retention times in gas-liquid chromatography were appropriate to the proposed structure (Ackman et al. 1974). All of these acids may be found in trace amounts in many marine oils, but in both of the sturgeon oils were of much greater importance than usual. As far as we are aware, these acids originate in marine and not freshwater plant lipids. Their exclusion from the polar lipids indicates that they are biochemically functional. It is known that 16:4ω1 does not chain extend to 18:4ω1 in the rat (Klenk 1963) and the reason for the apparent facile chain extensions in sturgeon could be due to a steady intake of the unusual C_{16} acids or their C_{18} homologues from primary plant lipids, or from the fats of marine invertebrates feeding on macrophytes or unicellular algae, or to a general tendency of sturgeons to chain extend C_{16} acids to a stable accumulation of C_{18} acids. The latter possibility, suggested to explain the accumulation of phytanic acid, is part of the larger question of turnover rates for fatty acids in the marine sturgeon and is linked in turn to the freshwater aspects of their lipid biochemistry. It is probable that

marine sturgeon, migrating into freshwater to spawn, live off fat reserves (Scott and Crossman 1973).

The subject of freshwater versus marine fatty acid composition for fish oils and fats has been discussed by various authors (Ackman 1967; Farkas 1971; Ikekawa et al. 1972; Reichwald and Meizies 1973), but not always from the same viewpoint. There is, however, clear agreement that in the depot fats of the sturgeon, from either the freshwater or marine milieu, 18:2ω6 (linoleic acid) is a minor (≤1-2%) component and 20:4ω6 (arachidonic acid) is also of limited significance. The low level of 18:2ω6 is probably a "marine" fat characteristic as most freshwater fish have fats with 5% or more of this acid (Ackman 1967; Farkas and Herodek 1967; Mangold 1973; Reichwald and Meizies 1973). In some other animals such as the turtles, freshwater species freely deposit 18:2ω6 and marine forms do not (Ackman, Hooper, and Frair 1971). Unfortunately, many reports on the composition of freshwater fish fats are confused by fatty acid depositions from rearing on artificial diets exceptionally rich in 18:2ω6 and the normal species pattern may be masked by this factor (Albrecht and Breitsprecher 1969). The higher polyunsaturated acids in depot fats of all sturgeons studied to date are dominated by the C_{20} and C_{22} polyunsaturated fatty acids of the "ω3" (linolenic) family, in all analyses. The figures for total C_{20} and C_{22} polyunsaturated acids in Atlantic sturgeon A correspond fairly closely to those for the marine *A. sturio* examined by Lovern (1932). The tissues sampled by various authors are not always clearly comparable. The "pink calf-like" tissue (3.3% fat) of the sturgeon examined by Reichwald and Meizies (1973) occurs dorsally above the abdominal cavity and is also the main caudal tissue, with the "white lard-like" tissue (52.9% fat) interposed in an arrowhead fashion when viewed in longitudinal section (I. Reichwald, pers. commun.). The location of a transverse section could show quite different relative locations for either tissue. From the fat contents, it appears that our "orange" layer corresponds to the "white" layer of an European sturgeon (Reichwald and Meizies 1973) and possibly to the ventral layer of a Japanese sturgeon (Shimma and Shimma 1968), and our "muscle" corresponds to the "pink" tissue of the former. Among differences in fatty acids of interest listed for different animals may be mentioned 20:5ω3 = ½ 22:6ω3 for two animals kept in captivity on a marine fish diet (Shimma and Shimma 1968, see Table 3) and the virtual absence of 20:5ω3 in the fat of the "white" tissue described by Reichwald and Meizies (1973), although in the "pink" tissue 20:5ω3 > 22:6ω3 agrees with our data, as also reported in less comprehensive studies of European sturgeon (Mangold 1973; Meizies and Reichwald 1973). The depot fats of the marine sturgeon we have investigated had 22:6ω3 at about half the level of 20:5ω3, and we interpret the analysis of the marine *A. sturio* by Lovern (1932) to agree with our data. It appears that at some point in the animals' spawning migration the proportions of these two fatty acids could reverse. Interestingly enough, only one out of four freshwater fish oils (from maria or *Lota lota*) examined earlier contained larger proportions of 22:6ω3 than of 20:5ω3 (Ackman 1967).

The spawning period for Canadian Atlantic sturgeon is presumably in early summer. The two male fish examined showed no gonad development and, therefore, if mature presumably they had spawned and returned to the ocean. Oleic acid (Σ18:1) at 44-49% and palmitic acid (16:0) at 21-23% are indicated by Reichwald and Meizies (1973) and other studies (see above) to be the major components of freshwater sturgeon fats. The depot fats of the two marine Atlantic sturgeon we have investigated differ in that both 18:1 totals are 20-30% (magnitude inversely related to iodine value) and 16:0 is about 15%. The original marine *A. sturio* had about 36% 18:1 and 16-19% 16:0, or in other words, the fats examined by Lovern (1932) displayed a composition for these two fatty acids intermediate to two more recent studies.

The very different iodine values for sturgeon A and B are accounted for mainly by the differences in percentages of 20:5ω3, 22:5ω3, and 22:6ω3 in lieu of 18:1 and other monoethylenic acids, as total saturated acids are in the same proportion of fat in both fish and the proportions of most minor unsaturated acids are not important enough to matter. The monoethylenic fatty acids of fish B (total about 45%) probably are more normal as judged by the various low iodine values in the literature for sturgeon fat. The resolving power of open-tubular gas-liquid chromatograph for methyl esters of monoethylenic fatty acids extends our knowledge of the fatty acid biochemistry of the two Atlantic sturgeon in this study. Virtually no 18:1ω11, which could only come from 20:1ω11, was observed. This indicates that the fish were depositing fat and not catabolizing it. On the other hand, the percentage of 20:1ω7 was about the same as that of 20:1ω9 in

the body fats of both sturgeon A and B. Therefore, the pathway 16:1ω7→18:1ω7→20:1ω7 appears to be important, suggesting a period of fatty acid biosynthesis rather than of deposition of exogenous fatty acids. Both fish had about the same percentages of 16:1. Fish A had higher proportions of fat in the muscle than Fish B, and 18:1ω7 was about a quarter of 18:1ω9 in this fat. In the leaner fish B, 18:1ω7 was only about one-fifth of 18:1ω9, suggesting less activity in de novo biosynthesis. It is possible that the diet of fish A was rich in the polyunsaturated fatty acids, the deposition of which was disturbing the typical species-fat composition. Accordingly, fish A may have been more actively engaged in synthesizing monoethylenic fatty acids, via 16:0→16:1ω7→18:1ω7, to achieve this composition. Seals, whose depot fat has a higher iodine value than that of most whales, may show the same monoethylenic fatty acid activity (Ackman, Epstein, and Eaton 1971).

Earlier work on oils from four freshwater fish showed 1-3% 20:1 and about 0.3-0.4% 22:1 (Ackman 1967). Marine fish oils, in our experience, usually show 10% or more of 20:1 and 5% or more of 22:1. The absence of large proportions of 20:1 and 22:1 acids in the marine sturgeon depot fat, even in fish B with the less unsaturated fat, is the key reason for our placing the fat of the marine Atlantic sturgeon in a rather special class of marine fat, or more broadly, in the generally freshwater class of fish fats, as recorded by Hilditch and Williams (1964).

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LITERATURE CITED

ACKMAN, R. G.
1966. Empirical relationships between iodine value and polyunsaturated fatty acid content in marine oils and lipids. J. Am. Oil. Chem. Soc. 43:385-388.
1967. Characteristics of the fatty acid composition and biochemistry of some fresh-water fish oils and lipids in comparison with marine oils and lipids. Comp. Biochem. Physiol. 22:907-922.

ACKMAN, R. G., AND C. A. EATON.
1971. Investigation of the fatty acid composition of oils and lipids from the sand launce (*Ammodytes americanus*) from Nova Scotia waters. J. Fish. Res. Board Can. 28:601-606.

ACKMAN, R. G., C. A. EATON, J. C. SIPOS, S. N. HOOPER, AND J. D. CASTELL.
1970. Lipids and fatty acids of two species of North Atlantic krill (*Meganyctiphanes norvegica* and *Thysanoessa inermis*) and their role in the aquatic food web. J. Fish. Res. Board Can. 27:513-533.

ACKMAN, R. G., S. EPSTEIN, AND C. A. EATON.
1971. Differences in the fatty acid compositions of blubber fats from Northwestern Atlantic finwhales (*Balaenoptera physalus*) and harp seals (*Pagophilus groenlandica*). Comp. Biochem. Physiol. 40B:683-697.

ACKMAN, R. G., S. EPSTEIN, AND M. KELLEHER.
In press. A comparison of lipids and fatty acids of the ocean quahaug (*Artica islandica*) from Nova Scotia and New Brunswick. J. Fish. Res. Board Can.

ACKMAN, R. G., AND S. N. HOOPER.
1968. Examination of isoprenoid fatty acids as distinguishing characteristics of specific marine oils with particular reference to whale oils. Comp. Biochem. Physiol. 24:549-565.
1973. Non-methylene-interrupted fatty acids in lipids of shallow-water marine invertebrates: A comparison of two molluscs (*Littorina littorea* and *Lunatia triseriata*) with the sand shrimp (*Crangon septemspinosus*). Comp. Biochem. Physiol. 46B:153-165.

ACKMAN, R. G., S. N. HOOPER, AND W. FRAIR.
1971. Comparison of the fatty acid compositions of depot fats from fresh-water and marine turtles. Comp. Biochem. Physiol. 40B:931-944.

ACKMAN, R. G., J. D. JOSEPH, AND A. MANZER.
1974. Tentative identification of an unusual naturally-occurring polyenoic fatty acid by calculations from precision open-tubular GLC and structural element retention data. Chromatographia 7:107-114.

ACKMAN, R. G., C. S. TOCHER, AND J. MCLACHLAN.
1968. Marine phytoplankter fatty acids. J. Fish. Res. Board Can. 25:1603-1620.

ALBRECHT, M. L., AND B. BREITSPRECHER.
1969. Untersuchungen uber die chemische Zusammensetzung von Fischnährtieren und Fischfuttermitteln. Z. Fischerei N. F. 17:143-163.

BAILEY, B. E., N. M. CARTER, AND L. A. SWAIN (editors).
1952. Marine oils with particular reference to those of Canada. Bull. Fish. Res. Board Can. 89, 413 p.

BLIGH, E. G., AND W. J. DYER.
1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37:911-917.

BULL, H.
1899. Ueber die Bestimmung stark ungesättiger Fettsauren in den Thranen. Chemiker-Zeitung 23:1043-1044.

FARKAS, T.
1971. A possible explanation for the differences in the fatty acid composition of freshwater and marine fishes. Ann. Biol. Tihany 38:143-152.

FARKAS, T., AND S. HERODEK.
1967. Investigations of the fatty acid composition of fishes from Lake Balaton. Ann. Biol. Tihany 34:3-13.

FRASER, D. I., A. MANNAN, AND W. J. DYER.
1961. Proximate composition of Canadian Atlantic fish. III. Sectional differences in the flesh of a species of *Chondrostei*, one of *Chimaerae*, and of some miscellaneous teleosts. J. Fish. Res. Board Can. 18:893-905.

HILDITCH, T. P., AND P. N. WILLIAMS.
1964. The chemical constitution of natural fats. 4th ed. Wiley, N.Y., 745 p.

HOOPER, S. N., M. PARADIS, AND R. G. ACKMAN.
1973. Distribution of *trans*-6-hexadecenoic acid, 7-methyl-7-hexadecenoic acid and common fatty acids in lipids of the ocean sunfish *Mola mola*. Lipids 8:509-516.

IKEKAWA, N., M. MATSUI, T. YOSHIDA, AND T. WATANABE.
1972. The composition of triglycerides and cholesteryl esters in some fish oils of salt, brackish and fresh water origins. Bull. Jap. Soc. Sci. Fish. 38:1267-1274.

JANGAARD, P. M.
1965. A rapid method for concentrating highly unsaturated fatty acid methyl esters in marine lipids as an aid to their identification by GLC. J. Am. Oil Chem. Soc. 42:845-847.

KLENK, E.
1963. Uber die Bildung von C_{20}- und C_{22}- Polyensauren aus $\Delta^{4.7.10.13}$-Hexadecate-traensäure bei der Ratte. Hoppe-Seyler's Z. Physiol. Chem. 331:50-55.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

LOVERN, J. A.
1932. Fat metabolism in fishes. II. The peritoneal, pancreatic and liver fats of the sturgeon (*Acipenser sturio*). Biochem. J. 26:1985-1988.

MANGOLD, H. K.
1973. «Unsichtbare" Fette und andere Lipide in Susswasserfischen, Wissenschaftliche Veröffentlichungen der Deutschen Gesellschaft für Ernährung, Band 24, «Unsichtbare" Fette und Lipoide in Lebensmitteln. (Dr. Dietrich Steinkopff Verlag, Darmstadt 1973.) p. 32-38.

MAXWELL, J. R., R. G. COX, G. EGLINTON, C. T. PILLINGER, R. G. ACKMAN, AND S. N. HOOPER.
1973. Stereochemical studies of acyclic isoprenoid compounds. II. The role of chlorophyll in the derivation of isoprenoid-type acids in a lacustrine sediment. Acta Geochim. Cosmochim. 37:297-313.

MEIZIES, A., AND I. REICHWALD.
1973. Die Lipide im Fleisch und im Rogen frischer und geräucherter Fische. Z. Ernährungswissenschaft 12:248-251.

MORRIS, L. J.
1966. Separations of lipids by silver ion chromatography. J. Lipid Res. 7:717-732.

PARADIS, M., AND R. G. ACKMAN.
1975. Occurrence and chemical structure of nonmethylene-interrupted dienoic fatty acids in the American oyster *Crassostrea virginica*. Lipids 10:1-8.

REICHWALD, I., AND A. MEIZIES.
1973. Die Fettsauren der Lipide im Fleisch von Süsswasserfischen und Seefischen. Z. Ernährungswissenschaft 12:86-91.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.

SHIMMA, Y., AND H. SHIMMA.
1968. Fatty acid composition of *Acipenser baeri* cultivated in Tokyo. Bull. Freshwater Fish. Res. Lab. (Tokyo) 18:179-184.

SIPOS, J. C., AND R. G. ACKMAN.
1968. Jellyfish (*Cyanea capillata*) lipids: Fatty acid composition. J. Fish. Res. Board Can. 25:1561-1569.

TSUJIMOTO, M.
1926. Aquatic animal oils. J. Chem. Soc. Jap. Ind. Chem. Sect. 29:71-75.

WATANABE, T., AND R. G. ACKMAN.
1974. Lipids and fatty acids of the American (*Crassostrea virginica*) and European flat (*Ostrea edulis*) oysters from a common habitat, and after one feeding with *Dicrateria inornata* or *Isochrysis galbana*. J. Fish. Res. Board Can. 31:403-409.

WESSELS, J. P. H., AND A. A. SPARK.
1973. The fatty acid composition of the lipids from two species of hake. J. Sci. Food Agric. 24:1359-1370.

ZAITSEV, V., L. KIZEVETTER, L. LAGUNOV, T. MAKAROVA, L. MINDER, AND V. PODSEVALOV.
1969. *In* Fish curing and processing. Mir Publishers, Moscow (translated by A. de Merindol), p. 68, 562.