ビワマスとアマゴの体色の銀白化に伴う脂肪酸組成の変化

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Changes in Fatty Acid Composition Associated with Body Silvering in Biwa Salmon *Oncorhynchus rhodurus* and Amago Salmon *O. rhodurus*[*1]

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Changes in lipid content, lipid class composition, and fatty acid composition in wild and cultured biwa and amago salmon underyearlings were examined during the period of body silvering. Cultured biwa salmon showed slight changes in these components of the muscle during body silvering. Although cultured amago salmon parr showed seasonal fluctuations in the components, the smolts did not show definite difference as compared with the parr in early smolting season. On the other hand, wild biwa salmon displayed a marked difference in the lipid class composition and fatty acid composition between the parr in the river and the silvery fish in the lake. In silvering biwa salmon, depletion of 16: 1, 18: 2n6, 18: 3n3 and increase in 22: 6n3 of nonpolar lipids were observed, the pattern being similar to the marine fish lipid. Since no change was seen in cultured biwa salmon, differences in the lipid class and fatty acid compositions between the parr in the river and the silvery fish in the lake in wild biwa salmon seem to be related to differences in their feeding habit and/or in swimming activity.

Most anadromous salmonids show dramatic changes known as smoltification during seaward migration.[1-3] This phenomenon implies morphological, behavioral, and biochemical changes associated with transformation from parr to smolt stage. One of the important physiological alterations during smoltification is the changes in body composition such as lipid, glycogen, and glucose.[2] These changes seem to be linked to the difference in metabolism between parr and smolt stages.[4] During smoltification, the fatty acid composition has been shown to change from the fatty acid pattern of freshwater fish to that of typical seawater fish, this alteration being considered to be preadaptive to seawater entry.[5,6]

Biwa salmon *Oncorhynchus rhodurus*, which inhabit Lake Biwa located in Mainland of Japan, go downstream into the lake in the early summer of their first life in the river.[7] At the same time, they exibit similar morphological changes as smoltification in other anadromous salmonids.[8,9] Despite these smolt-like changes, they do not acquire seawater adaptability.[10,11]

The present study aims to examine the changes in lipid content and fatty acid composition associated with body silvering in wild and cultured biwa salmon in comparison with the changes in closely related amago salmon *O. rhodurus*.

Materials and Methods

Animals

Wild biwa salmon parr were collected in Shiotsuokawa River on May 30, and silvery bodied juveniles were obtained by trawl net in the lake on August 11, 1986. Cultured biwa and amago salmon were reared in spring fresh water at constant temperature (12±1°C) under natural photoperiod from underyearling April to November 1986 in Samegai Trout Farm. They were from the stocks which had originated from Lake Biwa (biwa salmon) and Gifu Prefecture (amago salmon), respectively. They were fed with a commercial trout diet (2C, Nihon Nosan Kogyo)

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Table 1. Lipid content and fatty acid composition of dietary lipid (%)

Lipid content	5.7
Fatty acid	
14:0	2.5
16:0	18.4
18:0	2.8
16:1	5.2
18:1	17.4
20:1	2.7
22:1	—
18:2n6	21.2
20:2	0.8
18:3n3	1.7
20:3	0.3
18:4	1.0
20:4	0.9
22:4	0.2
20:5n3	10.0
22:5	1.3
22:6n3	11.8
Unknown	1.8

twice daily throughout the experiments. Cultured biwa salmon parr were sacrificed on May 23, and the silvery bodied biwa salmon on July 26 (during body silvering) and November 25 (5 months after body silvering). Cultured amago salmon parrs were sampled on May 23, July 21, and November 27, and the smolts were obtained on November 27 (2 months after smolting). They were stored at −25°C until lipid analyses.

Lipid Analyses

Lipid of the dorsal muscle was extracted with methanol-chloroform for determination of total lipid contents.[12] Lipid class composition was evaluated by Iatroscan (Iatron TH-10) on silica gel rod using *n*-hexane/ethyl ether/acetic acid (85:15:1, v/v/v) as development solvent. For

Table 2. Body weight, condition factor and lipid content in dorsal muscles of biwa and amago salmon

		Date	Phase*1	Body weight (g)*2	Condition factor*2,3	Lipid content (%)*2
Biwa salmon	Wild	May 30	P	4.86±0.32	1.70±0.07	1.63*4
		Aug. 11	S	15.07±0.59	1.85±0.06	1.13±0.12
	Cultured	May 23	P	4.75±0.24	1.56±0.02	2.15*4
					** (May 23 vs. Jul. 26); ** (May 23 vs. Nov. 25)	
		Jul. 26	S	11.34±0.39	1.36±0.02	1.95±0.12
					** (Jul. 26 vs. Nov. 25)	
		Nov. 25	S	23.21±0.73	1.21±0.02	1.96±0.06
Amago salmon	Cultured	May 23	P	9.98±0.49	1.51±0.03	1.85*4
					** (May 23 vs. Jul. 21)	
		Jul. 21	P	23.41±1.64	1.72±0.03	2.59±0.13
					** (Jul. 21 vs. Nov. 27 P); ** (Jul. 21 vs. Nov. 27 S)	** (Jul. 21 vs. Nov. 27 P); ** (Jul. 21 vs. Nov. 27 S)
		Nov. 27	P*5	28.15±2.53	1.40±0.04	2.04±0.14
		Nov. 27	S	63.90±6.31	1.31±0.13	1.81±0.37

*1 P: parr, S: silvery bodied fish. *2 Mean±S.E.M. (n=5).
*3 Condition factor=body weight(g)×100/[standard length(cm)].[3]
*4 For analysis, 10 individuals were pooled. *5 Immature small parr.
*,** Significantly different at $p<0.05$ and $p<0.01$, respectively.

Table 3. Changes in lipid class composition in dorsal muscles during body silvering in biwa and amago salmon (%)

		Date	Phase*1	TG*2	FFA*3	Cho*4	PL*5
Biwa salmon	Wild	May 30	P	45.4*6	—	3.3	51.3
		Aug. 11	S	25.8±4.90*7	10.8±1.05	5.8±0.75	57.7±4.22
	Cultured	May 23	P	56.3*6	—	3.1	40.7
		Jul. 26	S	56.4±1.17*7	0.2±0.11	2.7±0.10	40.8±1.07
				** (Jul. 26 vs. Nov. 25)		** (Jul. 26 vs. Nov. 25)	** (Jul. 26 vs. Nov. 25)
		Nov. 25	S	63.6±1.55*7	—	1.7±0.17	34.7±1.52
Amago salmon	Cultured	May 23	P	45.7*6	—	2.8	51.5
		Jul. 21	P	70.1±1.40*7	0.3±0.12	1.8±0.19	27.9±1.19
		Nov. 27	P	60.5±2.68*7	—	2.0±0.30	37.6±2.36
		Nov. 27	S	56.1±7.46*7	0.2±0.16	2.3±0.48	41.4±6.88

*1 P: parr, S: silvery bodied fish. *2 TG: Triglycerides. *3 FFA: Free fatty acids.
*4 Cho: Cholesterol. *5 PL: Phospholipids. *6 For analysis, 10 individuals were pooled.
*7 Mean±S.E.M (n=5). ** Significantly different at $p<0.01$.

fatty acid analyses, polar and nonpolar lipids were separated by preparative thin-layer chromatography as in Juaneda and Rocquelin.[13] After saponification and methylation were performed using 2N NaOH-methanol and 2N HCl-methanol, respectivery, the fatty acid composition was determined by a gas chromatograph (Hitachi 263–30) at 230°C using a glass column of 2 m length packed with Unisol 3000. Identification was made by comparing retention time with authentic fatty acid standard. The area percentage of each peak was calculated with Hitachi

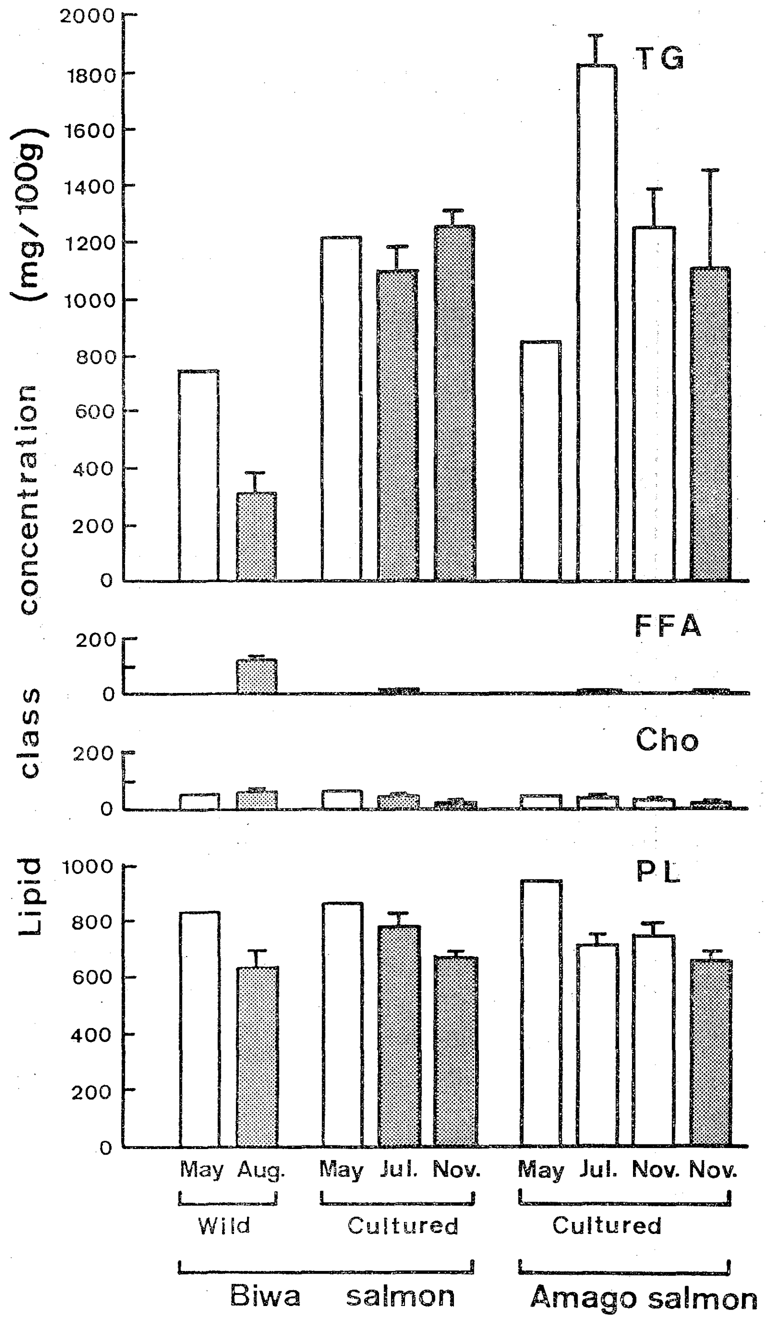

Fig. 1. Changes in the lipid class concentration (mg/100 g muscle). White and dotted columns indicate the parr and silvery bodied fish, respectively. TG, triglycerides; FFA, free fatty acids; Cho, cholesterol; PL, phospholipids.

Table 4. Fatty acid composition of nonpolar lipids in dorsal muscles of biwa and amago salmon (Area %)

Fatty acid	Wild biwa salmon		Cultured biwa salmon			Cultured amago salmon			
	May 30 (P)[*1]	Aug. 11 (S)[*2]	May 23 (P)[*1]	Jul. 26 (S)[*2]	Nov. 25 (S)[*2]	May 23 (P)[*1]	Jul. 21 (P)[*1]	Nov. 27 (P)[*3]	Nov. 27 (S)[*2]
14:0	2.7[*4]	1.3±0.09[*5]	2.5[*4]	2.5±0.04[*5]	2.5±0.03[*6]	2.3[*4]	2.6±0.05[*5]	2.4±0.05[b*6]	2.4±0.04[b*5]
16:0	19.5	17.2±0.67	18.5	18.8±0.29	20.1±0.22[a]	18.7	20.4±0.38	19.2±0.37	20.1±0.39
18:0	4.7	3.1±0.06	3.4	3.7±0.07	3.7±0.08	3.7	3.5±0.27	3.9±0.20	4.1±0.10
16:1	11.2	6.3±0.25	6.1	6.5±0.22	8.0±0.27[a]	7.0	9.3±0.25	7.7±0.29[b]	7.6±0.31[b]
18:1	23.6	26.2±1.09	27.1	24.6±0.55	25.0±0.13	28.3	29.6±0.63	25.9±0.81[b]	25.8±1.12[b]
20:1	0.4	1.3±0.14	4.9	4.1±0.11	3.0±0.13[a]	5.3	3.4±0.14	2.9±0.09[b]	3.0±0.10[b]
22:1	—	—	2.3	1.8±0.06	1.2±0.04[a]	2.3	1.5±0.09	1.1±0.04[b]	1.2±0.06[b]
18:2n6	8.1	4.6±0.26	15.3	15.2±0.34	15.3±0.06	13.6	11.5±0.39	15.8±0.59[b]	15.8±0.70[b]
20:2	0.3	0.9±0.09	0.7	0.8±0.03	1.0±0.08[a]	0.8	0.9±0.06	0.9±0.02	1.0±0.02[c]
18:3n3	11.1	3.3±0.34	1.2	1.2±0.04	1.2±0.05	1.1	0.9±0.09	1.2±0.08[b]	1.2±0.05[b]
20:3	0.4	0.2±0.02	0.3	0.2±0.02	0.2±0.03	0.3	0.2±0.04	0.3±0.04	0.3±0.04
20:4	1.0	4.7±0.14	0.6	0.7±0.00	0.8±0.03[a]	0.4	0.5±0.01	0.7±0.02[b]	0.8±0.02[bc]
22:4	0.1	1.6±0.06	0.1	0.2±0.02	0.2±0.00	0.1	0.1±0.02	0.2±0.00[b]	0.2±0.02[b]
20:5n3	5.1	5.4±0.32	3.1	3.6±0.10	3.1±0.05[a]	2.7	2.6±0.07	2.8±0.11	2.7±0.15
22:5	1.6	2.7±0.12	1.0	1.2±0.06	1.2±0.03	0.9	0.8±0.04	1.2±0.04[b]	1.1±0.06[b]
22:6n3	3.6	16.2±0.74	10.3	11.5±0.17	10.8±0.14[a]	10.3	10.0±0.38	10.9±0.15	10.2±0.56
Unknown	6.6	4.9±0.24	2.6	3.4±0.56	3.0±0.18	2.2	2.1±0.05	2.7±0.13[b]	2.4±0.14
Ts[*7]	26.9	21.7±0.64	24.4	25.1±0.28	26.2±0.16[a]	24.7	26.5±0.52	25.6±0.41	26.7±0.35
Tm[*8]	35.2	33.8±1.17	40.4	37.0±0.59	37.1±0.18	42.9	43.9±0.66	37.6±0.99[b]	37.6±1.19[b]
Tp[*9]	31.3	39.6±1.57	32.6	34.5±0.65	33.8±0.19	30.2	27.5±0.83	34.2±0.88[b]	33.2±1.51[b]

*1 P: parr. *2 S: silvery bodied fish. *3 Immature small parr. *4 For analysis, 10 individuals were pooled. *5 Mean±S.E.M (n=5). *6 N=4. *7 Ts: Total saturated acids. *8 Tm: Total monounaturated acids. *9 Tp: Total polyunsaturated acids. [a] Significantly different from the value of Jul. 26 (S) ($p<0.01$). [b] Significantly different from the value of Jul. 21 (P) ($p<0.01$). [c] Significantly different from the value of Nov. 27 (P) ($p<0.01$).

Table 5. Fatty acid composition of polar lipids in dorsal muscles of biwa and amago salmon (Area %)

Fatty acid	Wild biwa salmon		Cultured biwa salmon			Cultured amago salmon			
	May 30 (P)[*1]	Aug. 11 (P)[*2]	May 23 (P)[*1]	Jul. 26 (S)[*2]	Nov. 25 (S)[*2]	May 23 (P)[*1]	Jul. 21 (P)[*1]	Nov. 27 (P)[*3]	Nov. 27 (S)[*2]
14:0	1.3[*4]	1.5±0.25[*5]	2.1[*4]	2.4±0.31[*5]	1.8±0.22[*5]	1.7[*4]	2.0±0.11[*5]	1.4±0.09[*5]	1.8±0.32[*5]
16:0	21.8	19.4±0.55	19.8	19.8±0.37	19.5±0.56	21.3	19.1±0.16	20.6±0.31[b]	19.5±0.42[c]
18:0	3.1	2.1±0.19	1.2	1.6±0.08	1.6±0.14	1.9	1.9±0.12	2.6±0.05[b]	2.0±0.21[c]
16:1	2.7	2.9±0.29	3.6	3.5±0.13	3.3±0.23	3.3	4.5±0.17	2.2±0.12[b]	2.3±0.10[b]
18:1	9.0	13.1±0.60	15.5	13.2±0.40	12.3±0.62	13.6	16.0±0.41	10.0±0.45[b]	10.3±0.07[b]
20:1	0.1	0.8±0.31	1.6	1.3±0.07	0.6±0.02[a]	1.7	1.5±0.19	0.5±0.04[b]	0.5±0.02[b]
22:1	—	—	—	—	—	—	—	—	—
18:2n6	2.9	2.8±1.04	8.0	7.6±0.30	7.1±0.47	6.4	7.0±0.10	5.6±0.16[b]	6.1±0.17[bc]
20:2	0.2	0.5±0.07	0.6	0.5±0.04	0.6±0.04	0.5	0.7±0.11	0.6±0.05	0.6±0.02
18:3n3	4.8	1.0±0.12	0.8	0.7±0.07	0.6±0.04	0.6	0.6±0.02	0.5±0.02[b]	0.6±0.03[c]
20:3	0.4	0.2±0.05	0.7	0.5±0.05	0.6±0.04	0.3	0.6±0.05	0.6±0.05	0.6±0.02
20:4	2.3	4.9±0.79	2.0	1.8±0.02	2.4±0.05[a]	1.3	1.5±0.04	2.2±0.04[b]	2.0±0.04[bc]
22:4	0.4	2.7±0.54	0.5	0.5±0.02	0.6±0.03[a]	0.3	0.5±0.02	0.6±0.02[b]	0.7±0.02[bc]
20:5n3	11.6	5.9±0.30	6.2	6.9±0.32	6.7±0.23	7.0	5.5±0.17	6.9±0.23[b]	6.7±0.18[b]
22:5	2.9	2.3±0.27	1.4	1.5±0.09	1.5±0.12	1.3	1.4±0.02	1.6±0.12	1.6±0.07[b]
22:6n3	33.7	37.0±1.25	33.0	36.0±0.84	38.6±1.07	37.0	35.1±0.39	42.3±0.64[b]	43.0±0.49[b]
Unknown	2.8	2.8±0.17	2.1	2.2±0.07	2.1±0.05	1.8	2.0±0.03	1.6±0.16[b]	1.9±0.06
Ts[*6]	26.2	23.0±0.66	24.0	23.8±0.27	22.9±0.52	24.9	23.1±0.30	24.6±0.34[b]	23.2±0.43[c]
Tm[*7]	11.8	16.8±1.08	20.7	18.0±0.57	16.2±0.84	18.6	22.0±0.73	12.7±0.58[b]	13.1±0.08[b]
Tp[*8]	59.2	57.5±1.35	53.2	56.0±0.72	58.8±0.44[a]	54.7	53.0±0.46	60.9±0.52[b]	61.8±0.34[b]

[*1] P: parr. [*2] S: silvery bodied fish. [*3] Immature small parr. [*4] For analysis, 10 individuals were pooled. [*5] Mean±S.E.M. (n=5). [*6] Ts: Total saturated acids. [*7] Tm: Total monounsaturated acids. [*8] Tp: Total polyunsaturated. [a] Significantly different from the value of Jul. 26 (S) ($p<0.01$). [b] Significantly different from the value of Jul. 21 (P) ($p<0.01$). [c] Significantly different from the value of Nov. 27 (P) ($p<0.01$).

D-2000 Chromato-Integrator.

As shown in Table 1, the lipid content of the commercial trout diet used in the experiment was 5.7%, and fatty acid composition (%) was composed mainly of 16:0, 18:1, 18:2n6, 20:5n3, and 22:6n3 (total 78.8%).

Statistics

All data are presented as mean±SEM. Significant differences were assessed by Duncan's new multiple range test.

Results

Changes in Condition Factor and Lipid Content

In cultured biwa salmon, condition factors of the silvery bodied fish were significantly ($p<0.01$) lower than those of the parr, whereas silvery bodied specimens in wild biwa salmon showed higher values than the parr, although the difference was not significant ($p<0.05$) (Table 2). No significant ($p>0.05$) difference was seen in condition factors of amago salmon between the parr and the smolt in the same season. The lipid contents of dorsal muscles in both wild and cultured silvery bodied biwa salmon and smolts of amago salmon tended to be lower than those in parr. The lipid contents of cultured amago salmon parr in July were 0.5–0.7% higher than those of the parr in May and November, coinciding with higher levels of the condition factor. The total lipid content of wild biwa salmon was lower when compared with the cultured fish.

Changes in Lipid Class Composition

As shown in Table 3, triglycerides (TG), phospholipid (PL), cholesterol (Cho), and free fatty acids (FFA) were the major lipid classes detected in the dorsal muscles. The wild biwa salmon exibited a marked decrease in the TG fraction and an increase in the FFA fraction during body silvering. In cultured biwa salmon, however, there was no definite difference in these fractions between the parr and silvery bodied fish. The TG and PL fractions in cultured amago parr appeared to fluctuate seasonally. No significant ($p>0.05$) difference was observed between parr and silvery bodied fish in November.

When the lipid class composition was expressed as weight per 100 g muscle (Fig. 1), the PL and Cho fractions were maintained at relatively the same levels in both biwa and amago salmon. The TG fraction of wild biwa salmon decreased from 740 mg in parr to 290 mg in silvery bodied fish. On the contrary, FFA, which were not detected in the parr, appeared at 120 mg in the silvery bodied fish. In amago salmon, the TG content of July parr was twice as much as that in May parr (845 mg).

Changes in Fatty Acid Composition

Changes in the fatty acid composition (%) of nonpolar and polar lipids are summarized in Tables 4 and 5, respectively. The nonpolar lipids fractions of both parr and silvery bodied fish or smolts of cultured biwa and amago salmon were composed mainly of 16:0, 18:1, 18:2n6, and 22:6n3. Similarly, the major constituents of the polar lipids fractions were 16:0, 18:1, 18:2n6, 20:5n3, and 22:6n3. In the wild biwa salmon, the dominant fractions of nonpolar lipids changed from 16:0, 16:1, 18:1, 18:2n6, and 18:3n3 of the parr to 16:0, 18:1, and 22:6n3 of the silvery bodied fish, although there was no difference in the major composition of polar lipids fractions (16:0, 18:1, 20:5n3, and 22:6n3).

In cultured biwa and amago salmon, little change was seen in the fatty acid composition of either nonpolar or polar lipid, and also the fatty acid composition of parr was similar to that of silvery bodied fish or smolts. In wild biwa salmon, however, the proportion of 18:1, 20:4, 22:4, and 22:6n3 of both nonpolar and polar lipids in the silvery bodied fish were higher than that in the parr. The 16:1, 18:2n6, and 18:3n3 of the nonpolar lipid and the 18:3n3 and 20:5n3 of the polar lipids in the silvery bodied fish were lower as compared with the parr. The high value of the total polyunsaturated fatty acids of nonpolar lipid in the silvery bodied fish was due primarily to a high proportion in 22:6n3.

The nonpolar lipid in wild biwa parr was higher in 16:1 and 18:3n3 and lower in 20:1, 22:1, 18:2n6, and 22:6n3 than in cultured biwa parr. On the other hand, 18:3n3 and 20:5n3 of the polar lipids in wild biwa parr were 4 and 5.4% more, respectively, than the values of cultured biwa parr. The nonpolar lipid fraction of wild silvery bodied fish contained several higher polyunsaturated fatty acids than did the cultured silvery bodied fish. The 18:2n6 in the cultured fish was higher than that of the wild fish in both nonpolar and polar lipids.

Discussion

A marked decrease in total body or muscle lipid has been shown during parr-smolt transformation in steelhead trout, coho and masu salmon,[14-20] independent on changes in activity or temperature.[4] The reduction in the lipid of the smolt occurs mainly in the TG, which seems to be utilized as energy sources, and little change is seen in the other lipid classes.[17,18,20] Furthermore, the smolt has more polyunsaturated fatty acid in liver and muscle than the parr.[6] These changes are considered as a shift from a freshwater fish pattern to typical marine fish pattern.[6,17] As shown in the present study, there were slight changes in the lipid content, lipid class composition and fatty acid composition of muscle during body silvering in cultured biwa salmon fed the same diet throughout the experiment. On the other hand, wild biwa salmon showed marked differences in these parameters between parr in the river and silvery bodied fish in the lake. The wild biwa salmon indicated a definite decrease in the TG and an increase in the FFA during body silvering. Similar results were reported in the flesh of wild masu salmon[17] and in the plasma of cultured masu salmon.[19] The loss of TG and the presence of FFA in the wild biwa salmon may be related to the enhanced TG utilization and fatty acid mobilization associated with increased swimming activity in the lake. In silvery bodied fish had markedly low 16: 1, 18: 2n6, 18: 3n3, and high 22: 6n3 in the fatty acids of nonpolar lipid, similar to the pattern in marine fish, whereas changes were scarcely seen in the polar lipid. The changes in the lipid of smolting salmon seem to be related to preadaptation processes to the marine habitat.[3,4] In nature, biwa salmon go downstream to the lake in May and June as underyearlings and inhabit the offshore zone of the lake deeper than 20 m.[7] They are known to feed on mainly aquatic insects in the river and crustaceans in the lake.[21] Since fatty acid composition is readily influenced by dietary fatty acids,[22,23] changes in the fatty acid composition of the wild biwa salmon between parr and silvery bodied fish, which are similar to those of smolting salmon, is likely to be related to the different feeding habit and water temperature.

It has been reported that biwa salmon displays similar morphological alternations as smoltification, coinciding with the downstream migration, although they do not acquire seawater adaptability.[8,9,11] Recent studies have revealed that thyroid hormones, growth hormone, prolactin, and cortisol play an important role in the smolting processes.[1-3] Growth hormone and thyroid hormones, especially, are suggested to enhance the seawater adaptability.[1-3] At the same time, these hormones are considered to be involved in the lipid depletion associated with smoltification.[24] Sheridan *et al.*[6] suggest that alterations in fatty acid composition towards a more polyunsaturated pattern may serve an osmoregulatory role by either directly or indirectly influencing ion movement across the cell membrane. In the present study, the fatty acid pattern of the cultured biwa salmon during body silvering did not shift from the freshwater fish pattern to the marine fish pattern. These results suggest that changes in the lipid metabolism during smoltification of anadromous salmonids differed from those during the body silvering of biwa salmon without acquiring hypo-osmoregulatory ability.

In the present study, cultured amago salmon smolts did not indicate definite differences in the lipid content, lipid class composition and fatty acid composition when compared with the parr in the same season. Body silvering of amago salmon used in the experiment began at the end of September and peaked towards the end of November, and their seawater adaptability developed in Janualy.[11] According to Ota and Yamada,[16,17] greater differences in the lipid contents and the fatty acid compositions are observed between parr and smolt of masu salmon in latter period of smoltification during fresh water habitation. Thus, characteristics of the lipid level and fatty acid composition in amago smolts may be variable in the latter smolting season. Further studies are need to clarify the changes in the lipid composition during amago salmon smoltification.

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