J. Fac. Appl. Biol. Sci.,
Hiroshima Univ. (1997), **36** : 1 ~ 9

Adipose Tissue of Wild and Cultured Ayu, *Plecoglossus altivelis* (Pisces)

Heisuke NAKAGAWA, Tetsuya UMINO,
Michifumi MORI, and Kenji SAKAE

Faculty of Applied Biological Science, Hiroshima University,
Higashi-Hiroshima 739, Japan

Received April 30, 1997

Abstract Intraperitoneal fat body (IPF) was biochemically and morphologically compared between wild and cultured ayu in relation to lipid mobilization.

In vitro lipolysis activity was preliminarily determined using IPF obtained from cultured ayu. IPF preparations (homogenates, fat cells, and slices) were incubated with bovine serum albumin with lipolytic hormones. Lipolytic hormones induced marked fatty acid release from IPF. Although cyclic AMP (c-AMP) did not stimulate the activity, dibutyryl-AMP induced fatty acid liberation. These results suggest the presence of a hormone-sensitive lipase and a possible role of c-AMP in phosphorylation by protein-kinase in lipolysis.

In the *in vitro* lipolytic system, incubation with IPF homogenates from both wild and cultured ayu liberated preferentially C22:6. However, incubation with IPF slices liberated all fatty acids non-selectively. *In vitro* lipolysis activity of cultured ayu was markedly lower than that of wild ayu.

Scanning electronic microscopic observation of IPF of cultured ayu showed significantly larger cell diameter than in that of wild ayu.

Keywords: Adipose tissue, ayu, fatty acids, lipid mobilization, lipid reserves, lipolysis

INTRODUCTION

Cultured ayu characteristically have high lipid reserves in both muscle and intraperitoneal part compared to wild fish (NAKAGAWA *et al.*, 1991b). The merits of ayu culture are high market value, high growth rate, and its favored taste. Over feeding and excessive feed oil supplementation sometimes cause deterioration of carcass quality caused by excessive lipid accumulation in the fish body. The rise in productivity may be accompanied by reductions in the characteristic taste and odor of this fish. Therefore, many studies have been performed in cultured ayu to maintain the low lipid reserves without spoiling growth by controlling the feeding regime (NEMATIPOUR *et al.*, 1988; MUSTAFA *et al.*, 1991; YAO *et al.*, 1994) and environmental conditions (NAKAGAWA *et al.*, 1995).

Lipogenesis and lipolysis should be well balanced. Depression of lipolysis activity occurs as a result of poor nutritional conditions (SAKAMOTO and YONE, 1980; TAKEUCHI and NAKAZOE, 1981). Mobilization of reserved lipids to energy can be evaluated by changes in body components before and after starvation, and *in vitro* lipolysis activity was examined by NEMATIPOUR *et al.* (1990) and NAKAGAWA *et al.* (1995). However, the endocrinical control

and mechanism of lipolysis system in fish are not clear.

This study was designed to establish analytical conditions for determining *in vitro* lipolysis activity and to compare various characteristics of adipose tissue between wild and cultured ayu.

MATERIALS AND METHODS

Experimental animals

Wild and cultured ayu were obtained from the Ohta-gawa Fisherman's Association in Hiroshima Prefecture. The IPF taken from the fish 50–80 g in body weight were used for measurement of *in vitro* lipolysis and were observed using a scanning electronic microscope.

Preparation of IPF homogenate

The IPF obtained from 3 fish (ca. 1 g) were homogenized with 5 m*l* of 0.25 M sucrose at 4° C, according to the method of OKUDA *et al.* (1966). The homogenate was centrifuged at 4000 rpm for 10 min. The top layer and clear middle layer were combined and re-homogenized. The resultant homogenate was assayed to determine the *in vitro* lipolysis activity.

Preparation of fat cells

Fat cells of IPF were prepared according to RODBELL (1964), using siliconized vessels. IPF were washed with a buffer solution (135 mM NaC*l*, 5 mM KC*l*, 1 mM $MgSO_4$, 25 mM Tris: pH 7.4) and cut into small pieces. About 100 mg of IPF was added to a solution consisting of 10 m*l* of the above buffer solution, 10 mg of collagenase (Nitta Gelatin Co.), 5 mg of glucose, and 400 mg of fatty acid-free bovine serum albumin. After incubation at 20° C, pH 7.5, for 30 min, small fragments liberated from the tissue were obtained by gentle centrifugation and used for measurement of lipolysis activity.

Preparation of IPF slices

The IPF obtained from 3 fish were rinsed with a buffer solution (124 mM NaC*l*, 5 mM KC*l*, 3 mM NaH_2PO_4, 12 mM $NaHCO_3$, 1 mM $MgSO_4$, 2 mM $CaCl_2$, 2.5% albumin: pH 7.4). IPF slice of preparations weighing approximately 100 mg were assayed for lipolysis activity.

Assay of lipolysis activity

In vitro lipolitic activity was measured by the method of OKUDA *et al.* (1966). Aliquots of 1 m*l* of IPF homogenate or fat cells were added to glass-stoppered test tubes containing 1 m*l*. Tris buffer with lipolytic hormone, and was incubated for 120 min at 20° C. Then, 1 m*l* of 0.033 M phosphate buffer containing 2.5% fatty acid-free bovine serum albumin was added and incubated for a further 120 min. Methanol-chloroform mixture (1:1 v/v) was added to the incubation mixture to stop the reaction and to extract lipid. Adrenaline (*L*-adrenaline bitartrate) and cortisol were obtained from Nacalai Tesque Co. Vasopressin, glucagon, cyclic 3', 5'-AMP (c-AMP), and dibutyryl cyclic AMP (dbc-AMP) were purchased from Sigma Chemical Co. Lipolysis activity was expressed as the amount of fatty acids released into the incubation media equivalent to 1 g of IPF, measured with a NEFA Test Kit (Wako Chemical Co.) based on the method of DUNCOMB (1964).

Fatty acid composition

The lipids extracted from the incubation media with methanol-chloroform mixture were

subjected to preparative thin layer chromatography (Kieselgel 160F 254G, Merck Co.). Separated fatty acids were converted into their methyl esters with dimethylformamide–dimethylacetal. Fatty acid composition was analyzed with a Hitachi Gas Chromatograph 183 attached to an FID detector. Unisol 3000 was packed in a 2 m glass column, and column temperature was maintained at 230° C.

Scanning electronic (SE) microscopic observation

The IPF washed with 0.9% NaCl were incubated with collagenase for 30 min at room temperature. Then, the samples were pre-fixed in 0.1 M phosphate buffer (pH 7.3) containing 2.5% glutaraldehyde and 4% paraformaldehyde. After rinsing the specimens for 10 min in 0.2 M phosphate buffer, they were post-fixed in 1% osmium oxide solution for 90 min and then dehydrated through a graded ethanol series. The specimens transferred to isoamylacetate were subjected to critical point-dry using liquid CO_2. The dried specimens coated with gold by an ion sputter coater (JFC-1100, JEOL) were observed with a JSM-T20 SE microscope (JOEL).

Statistical analysis

The data were analyzed using student's *t*-test to determined if the differences between means were significant. Probability values of 0.05 or less were considered statistically significant.

RESULTS

Preliminary experiments regarding pH dependence, optimum conditions such as incubation temperature, time course, albumin concentration, and hormone concentration were performed using IPF obtained from cultured ayu. The pH dependence of lipolysis was measured by incubation of IPF slices for 120 min in different pH media containing albumin (2.5%) and adrenaline (10 μg). The medium pH was controlled by addition of HCl and NaOH. The activity showed a broad pH range between 7.0 and 8.0, and the highest activi-

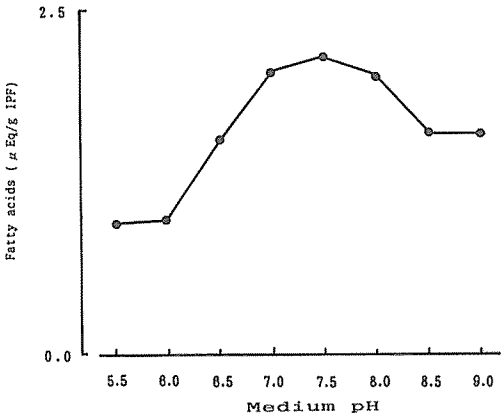

Fig. 1. Effects of pH on lipolysis activity in intraperitoneal fat body (IPF). Incubation time: 60 min, incubation temperature: 20° C, albumin concentration: 2.5%.

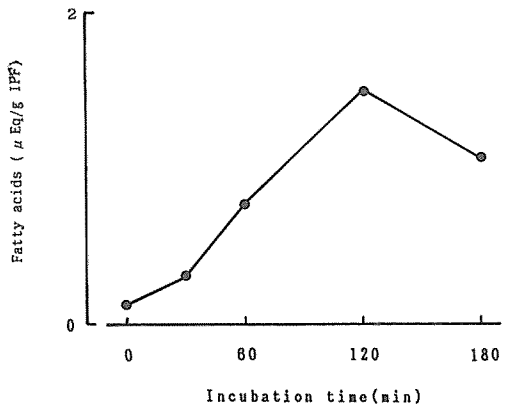

Fig. 2. Effects of incubation time on lipolysis activity in intraperitoneal fat body (IPF). Incubation temperature: 20° C, albumin concentration: 2.5%, pH 7.5.

ty was at pH 7.5 (Fig. 1), which was the same as that for the IPF homogenate.

The time course of fatty acid release from IPF slices is shown in Fig. 2. Fatty acids were linearly liberated from IPF homogenate incubation medium between 30–120 min. However, longer incubation failed to release additional fatty acids. The decreases in fatty acid levels in the media suggest that re-esterification occurred during long-term incubation.

The activity increased linearly with incubation temperature (Fig. 3). Maximum activity was obtained at 40° C, and then decreased with higher temperatures. As high temperature would result in undesirable phenomena in poikilothermal animals, rearing temperature (20° C) was used in the subsequent assays.

No marked activity was detected in the absence of bovine albumin in the incubation medium (Fig. 4). The activity was markedly stimulated by addition of albumin, and reached a maximum at 2.5% albumin. High albumin concentrations, however, depressed the activity.

Table 1 summarizes the *in vitro* lipolysis activities in homogenates, slices, and fat cells of IPF. The hormone used in this experiment strongly stimulated liberation of fatty acids from IPF homogenates and slice preparations. Liberation of fatty acids into the incubation medium was highest from the IPF slices and lowest from the fat cells. Although c-AMP did not stimulate lipolysis activity in IPF homogenates, dbc-AMP which is a derivative of c-AMP markedly stimulated lipolysis activity.

In vitro lipolysis activity was compared between wild and cultured ayu according to the above procedure (Table 2). Free fatty acid levels in intact IPF were higher in wild ayu. The liberation of fatty acids from IPF by incubation with or without lipolytic agents was also higher in wild ayu.

Compositions of fatty acids liberated from the homogenates by lipolysis are shown in

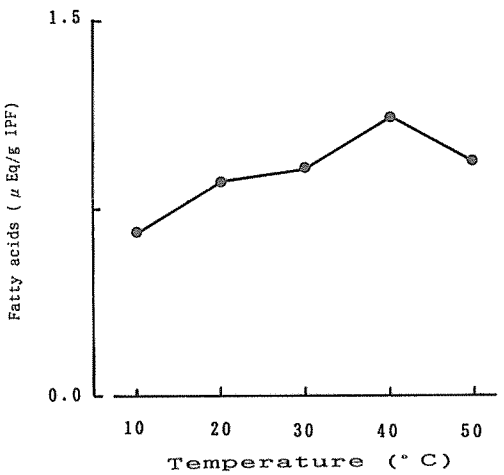

Fig. 3. Effects of incubation temperature on lipolysis activity in intraperitoneal fat body. Incubation time: 60 min., albumin concentration: 2.5%, pH: 7.5.

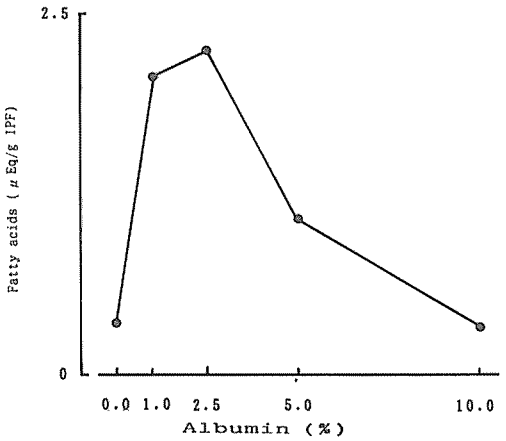

Fig. 4. Effects of albumin concentration on lipolysis activity of intraperitoneal fat body. Incubation time: 60 min, incubation temperature: 20° C, pH: 7.5.

Table 1. Effects of lipolytic hormones or cyclic-AMP on *in vitro* liberation of fatty acids from intraperitoneal fat body of cultured ayu

		Homogenate		Slice		Fat cell	
		FFA*1	Effect	FFA*1	Effect	FFA*1	Effectc
None		0.29	—	1.63	—	0.58	—
Adrenaline	(10 μg/ml)	0.43	0.14	3.32	1.69	0.58	0.00
Cortisol	(10 μg/ml)	0.37	0.18	4.83	3.20	0.50	-0.80
Vasopressin	(9.1 IU)	0.22	-0.07			0.37	-0.21
Glucagon	(10 μg/ml)					0.72	0.24
Cyclic-AMP	(0.02 mM)	0.29	0				
Dbc-AMP*2	(5 mM)			5.80	4.17		

*1 free fatty acids released from IPF (μEq/g IPF)
*2 dibutyryl cyclic-AMP

Table 2. Comparison of *in vitro* lipolysis activity of intraperitoneal fat body between wild and cultured ayu

	Wild ayu				Cultured ayu			
	Homogenate		Slice		Homogenate		Slice	
	FFA*1	Effect	FFA*1	Effect	FFA*1	Effect	FFA*1	Effect
Initial	1.34	0	1.80	0	0.69	0	1.04	0
None	1.63	0.29	3.94	2.14	1.14	0.45	2.37	1.33
Adrenaline (10 μg/ml)	3.32	1.98	5.58	3.78	1.13	0.44	2.20	1.16
Cortisol (10 μg/ml)	4.83	3.49	3.38	1.58	0.85	0.16	1.23	0.19
Dbc-AMP*2 (5 mM)	5.80	4.46	6.29	4.49	1.18	0.49	1.85	0.81

*1 free fatty acids released from IPF (μEq/g IPF)
*2 dibutyryl cyclic-AMP

Table 3. There were marked differences in the compositions of fatty acids liberated between homogenates and slices. While the highly unsaturated fatty acid C22:5 was preferentially liberated from the homogenates, fatty acids were equally liberated from the slice preparations. The fatty acid C16:1 which was characteristically higher in cultured ayu, was not liberated by incubation under these conditions. The lipolytic hormones did not affect liberation of C18:1 from wild ayu IPF homogenates.

SE microscopic observation of IPF was carried out in wild and cultured ayu (Fig. 5). The amounts of adipose tissue in the intraperitoneal cavity were fairly high in cultured ayu, but some wild ayu had trace amounts. There were no marked differences in external appearance of IPF between wild and cultured ayu with the exception of cell diameter, which was significantly larger in cultured ayu (Table 4).

DISCUSSION

It has been established that the adipose tissue of ayu contains a lipolytic system (NAKAGAWA *et al.*, 1995; NEMATIPOUR *et al.*, 1990). This study showed that the *in vitro* lipolytic system had optimum activity at pH 7.5, which was the same as that reported for rainbow trout (*Salmo gairdneri*; BILINSKI and LAU, 1969) and steel head trout (*Salmo gaird-*

Table 3. Comparison of fatty acids released from intraperitoneal fat body homogenate between wild and cultured ayu by *in vitro* lipolysis

Fatty acid	Wild ayu					Cultured ayu				
	Init.	None	Adr.	Cort.	Vas.	Init.	None	Adr.	Cort.	Vas.
14:0	1.6	1.0	5.2	4.7	1.9	0.6	1.7	4.6	2.6	1.0
16:0	39.7	29.8	12.5	16.3	8.0	26.0	25.6	21.9	26.5	29.1
18:0	tr	tr	tr	tr	tr	3.1	tr	tr	tr	tr
14:1	4.2	3.1	1.4	2.3	0.7	7.2	2.5	2.0	2.6	2.7
16:1n7	0.6	tr	tr	tr	tr	16.1	1.9	tr	1.2	tr
18:1n9	30.8	25.9	7.5	9.5	8.9	31.0	20.1	18.6	25.8	25.0
14:2	tr	tr	0.6	1.4	1.3	tr	tr	tr	tr	tr
18:2n6	1.0	tr	tr	tr	tr	3.3	3.1	tr	tr	tr
18:3n3	1.7	2.3	tr	0.8	4.6	tr	1.9	2.4	3.6	2.4
20:3n3, 6	4.5	3.1	0.6	0.8	0.7	5.7	2.3	1.6	2.3	3.4
20:4n3, 6	0.6	tr	tr	tr	tr	tr	tr	tr	tr	tr
20:5n3	6.7	6.5	4.2	tr	tr	3.5	2.5	2.6	3.1	tr
22:5n3	tr	tr	tr	3.1	0.5	tr	tr	0.9	tr	tr
22:6n3	8.6	28.2	68.1	61.3	73.3	3.2	38.4	45.5	32.4	36.4

Initial: before incubation, None: no addition, Adr.: adrenaline, Cort.: cortisol, Vas.: vasopressin

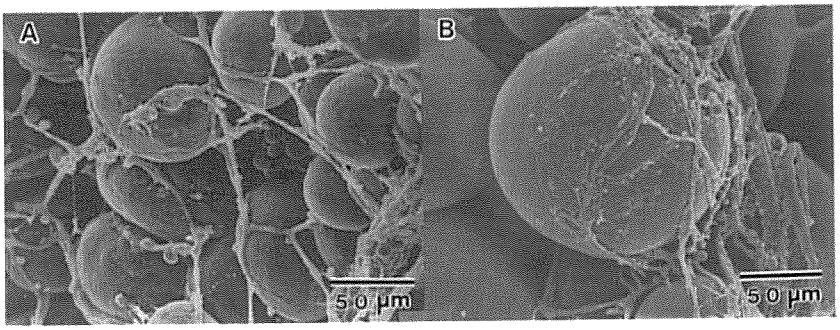

Fig. 5. SE micrographs of intraperitoneal fat body cells of wild (A) and culture ayu (B).

Table 4. Intraperitoneal fat body cell diameter (μm) in wild and cultured ayu

	Wild ayu	Culture ayu
Mean±SD	74.2±16.2	85.9±25.1*
Range	40−115	30−120

n=30,
* significantly different from wild ayu ($p<0.05$)

neri; SHERIDAN and ALLEN, 1984). The value was consistent with that measured in homogenates. However, the optimum pH of the lipolysis activity was different from that of purified lipase (BILINSKI *et al.*, 1971; GJELLESVIK *et al.*, 1989; MUKUNDAN *et al.*, 1985; PAT-

TON *et al.*, 1977; SUZUKI *et al.*, 1981). The optimum temperature was almost the same as those of other lipases reported previously. Inactivation of lipolysis at 50°C was higher than that of oil sardine lipase (*Sardirella longiceps*; MUKUNDAN *et al.*, 1985). The use of 2.5% fatty acid-free albumin favored the release of fatty acids from IPF by blocking re-esterification.

FARCAS (1969) found that lipid reserves in fish adipose tissue could be mobilized by a mechanism similar to that in mammals. SHERIDAN and ALLEN (1984) isolated lipolytic enzymes from trout adipose tissue, and SHERIDAN (1987) found the presence of hormone-sensitive lipase in coho salmon liver. NEMATIPOUR *et al.* (1990) reported that fatty acid release was induced by lipolytic hormones, suggesting the presence of a hormone-sensitive lipolytic system in IPF. However, the present results showed that adrenaline did not effectively promote fatty acid liberation in IPF homogenate, in comparison to other hormones. The hormone-sensitive lipolytic system is mediated by c-AMP-dependent protein-kinase in mammals. The lipolytic hormones enhanced c-AMP production and phosphorylase activity without triglyceride breakdown in pike perch (*Lucioperca lucioperca*; FARCAS, 1969). Although c-AMP did not stimulate the lipolytic activity in ayu, dbc-AMP effectively stimulated the reaction. Accordingly, the lipolytic system appears to be mediated through c-AMP, as suggested by SHERIDAN (1988).

The composition of the fatty acids released from IPF homogenates was not in agreement with that released from IPF slice preparations. Incubation of IPF homogenate preferentially released C22:6. NEMATIPOUR *et al.* (1990) reported preferential liberation of C20:5 from IPF homogenates. Polyunsaturated fatty acid-rich triglycerides might therefore easily undergo lipid mobilization. In contrast, preferential release of polyunsaturated fatty acids was not found in IPF slices. GAVINO and GAVINO (1992) reported that hormone-sensitive lipase in rat adipose cell preferentially released polyunsaturated fatty acids. Accordingly, preferential release of fatty acids might be due to re-esterification in the incubation medium.

Exercise has been shown to reduce adipose cell size and enhance lipolysis in rats (BUKOWIECKI *et al.*, 1980). Adipose tissue cell size is closely related to lipolysis activity in rats (ASKEW and HECKER, 1976). Wild ayu showed active *in vitro* lipolysis and had smaller adipose cells than cultured ayu. The adipose tissue of ayu is strongly sensitive to feeding regime and environmental impact (NAKAGAWA *et al.*, 1991a, 1995; NEMATIPOUR *et al.*, 1988; YAO *et al.*, 1994). Thus, adipose cell diameter may be a useful indicator to evaluate lipolysis activity.

REFERENCES

E. W. ASKEW and A. L. Hecker, 1976, Adipose tissue cell size and lipolysis in the rat: response to exercise intensity and food restriction. *J. Nutr.*, **106**, 1351-1360.

E. BILINSKI and Y. C. LAU, 1969, Lipolytic activity toward long-chain triglycerides in lateral muscle of rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd. Canada*, **26**, 1837-1866.

E. BILINSKI, R. E. E. JONAS, and Y. C. LAU, 1971, Lysosomal triglyceride lipase from the lateral line tissue of rainbow trout (*Salmo gairneri*). *J. Fish. Res. Bd. Canada*, **28**, 1015-1018.

L. BUKOWIECKI, J. LUPIEN, N. FOLLEA, A. PARADIS, D. RICHARD, and LE-BLANCE, 1980, Mechanism of

enhanced lipolysis in adipose tissue of exercised-trained rats. *Am. J. Physiol.*, 239, E422-E429.

W. G. DUNCOMBE, 1964, The colorimetric micro-determination of non-esterified fatty acids in plasma. *Clin. Chim. Acta*, 9, 122-125.

T. FARCAS, 1969, Studies on mobilization of fats in lower vertebrates. *Acta Biophys. Acad. Sci. Hung.*, 4, 237-249.

V. C. GAVINO and G. R. GAVINO, 1992, Adipose hormone-sensitive lipase preferentially releases polyunsaturated fatty acids from triglyerides. *Lipids*, 27, 950-954.

D. R. GJELLESVIK, A. J. RAAE, and B. TH. WALTHER, 1989, Partial purification and characterization of a triglyceride lipase from cod (*Gadus morhua*). *Aquaculture*, 79, 177-184.

E. K. MUKUNDAN, K. GOPAKUMAR, and M. R. NAIR, 1985, Purification of a lipase from the hepatopancreas of oil sardine (*Sardinella longiceps* Linnaeus) and its characteristics and properties. *J. Sci. Food Agric.*, 36, 191-203.

Md. G. MUSTAFA, H. NAKAGAWA, S. OHYA, T. SHIMIZU, Y. HORIKAWA, and S. YAMAMOTO, 1991, Effects of various level of dietary medium chain triglycerides on growth and lipid reservation in ayu. *Nippon Suisan Gakkaishi*, 57, 2327-2331.

H. NAKAGAWA, H. NISHINO, GH. R. NEMATIPOUR, S. OHYA, T. SHIMIZU, Y. HORIKAWA, and S. YAMAMOTO, 1991a, Effects of water velocities on lipid reserves in ayu. *Nippon Suisan Gakkaishi*, 57, 1737-1741.

H. NAKAGAWA, Y. TAKAHARA, and GH. R. NEMATIPOUR, 1991b, Comparison of lipid properties between wild and cultured ayu. *Nippon Suisan Gakkaishi*, 57, 1965-1971 (in Japanese, with English summary).

H. NAKAGAWA, T. UMINO, M. MORI, K. SAKAE, and S. OHYA, 1995, Nature of adipose tissue of ayu associated with water velocity. *Fisheries Sci.*, 61, 87-90.

GH. R. NEMATIPOUR, H. NAKAGAWA, S. KASAHARA, and S. OHYA, 1988, Effects of dietary lipid level and *Chlorella*-extract on ayu. *Nippon Suisan Gakkaishi*, 54, 1395-1400.

GH. R. NEMATIPOUR, H. NAKAGAWA, and S. OHYA, 1990, Effect of *Chlorella*-extract supplementation to diet on *in vitro* lipolysis in ayu. *Nippon Suisan Gakkaishi*, 56, 777-783.

H. OKUDA, I. YANAGI, and S. FUJII, 1966, The mechanism of *in vitro* stimulation of lipolysis by adrenaline. *J. Biochem.*, 59, 438-442.

I. S. PATTON, T. G. WARNER, and A. A. BENSON, 1977, Partial characterization of the bile salt-dependent triacylglycerol lipase from the leopard shark pancreas. *Biochim. Biophys. Acta*, 486, 322-330.

M. RODBELL, 1964, Metabolism of isolated fat cells. I. Effects of hormones on glucose metabolism and lipolysis. *J. Biol. Chem.*, 239, 375-380.

S. SAKAMOTO and Y. YONE, 1980, A principal source of deposited lipid in phosphorus deficient red sea bream. *Bull. Jpn. Soc. Sci. Fish.*, 46, 1227-1230.

M. A. SHERIDAN, 1987, Effects of epinephrine and norepinephrine on lipid mobilization from coho salmon liver incubated *in vitro*. *Endocrinology*, 120, 2234-2239.

M. A. SHERIDAN, 1988, Lipid dynamics in fish: aspects of absorption, transportation, deposition and mobilization. *Comp. Biochem. Physiol.*, 90B, 679-690.

M. A. SHERIDAN and W. V. ALLEN, 1984, Partial purification of triacylglycerol lipase isolated from steel head trout (*Salmo gairdnerii*) adipose tissue. *Lipids*, 19, 347-352.

M. SUZUKI, T. TSUJITA, and H. OKUDA, 1981, Studies on lipase activity in post-heparin plasma of fish *Tilapia nilotica*. *Bull. Jpn. Soc. Sci. Fish.*, 47, 1515-1520.

M. TAKEUCHI and J. NAKAZOE, 1981, Effect of dietary phosphorus on lipid content and its composition in carp. *Bull. Jpn. Soc. Sci. Fish.*, 47, 347-352 (in Japanese, with English summary).

S.-J. YAO, T. UMINO, and H. NAKAGAWA, 1994, Effect of feeding frequency on lipid accumulation in ayu. *Fisheries Sci.*, 60, 667-671.

天然および養殖アユの脂肪組織の性状

中川　平介・海野　徹也
森　　道史・栄　　研二

広島大学生物生産学部，東広島市 739

脂質代謝を比較する目的で天然と養殖アユの脂肪組織の性状を生化学的，形態学的に観察した。養殖アユより腹腔内脂肪組織 (IPF) をとり，ホモジェネート，脂肪細胞，スライスで *in vitro* で脂肪分解活性を比較した。活性は IPF を含む反応液に脂質動員ホルモン，牛血清アルブミンを添加して孵置して遊離した脂肪酸量で示した。Cyclic-AMP の添加は脂肪分解の活性化に無効であったが，di-butyryl-AMP は有効であった。これらの結果から，脂肪分解反応系にホルモン感受性リパーゼの存在と protein-kinase によるリン酸化への cyclic-AMP の関与が示唆された。

In vitro 脂肪分解では，天然，養殖アユ共 IPF ホモジェネートから C20:6 の脂肪酸が選択的に遊離したが，スライスでは遊離脂肪酸に選択性はなく均等に遊離した。養殖アユは天然アユと比較して脂肪分解能が著しく低い。

IPF の走査電顕像は天然と養殖アユでは形状に差異はなかったが，養殖アユの脂肪細胞が有意に大きかった。

キーワード：アユ，脂肪細胞，脂肪酸，脂質動員，脂質分解能，貯蔵脂肪