Variations in Muscle Lipid Content of High-Seas Chum and Pink Salmon in Winter

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Abstract: The potential use of lipids for estimating trophic condition of high-seas chum, *Oncorhynchus keta*, and pink salmon, *O. gorbuscha*, was evaluated by examining variations in total lipid content and lipid classes in the white muscle during the winter. Total lipids of both species were low and the total lipid content of the white muscle of pink salmon varied by capture location. Significant differences were observed in the proportions of 22:6n3 (docosahexaenoic acid) in the neutral lipids, and of 22:6 and 18:1n9 (elaidic acid) in the polar lipids. As the total lipid content decreased, the proportions of 22:6n3 and 18:1n9 increased and decreased respectively. The low lipid levels and the changes in fatty acids profiles suggest that chum and pink salmon are starving in winter.

INTRODUCTION

All animals require dietary lipids for metabolic energy and the synthesis of cell membranes. In carnivorous fish like salmonids, which have a limited ability to utilize carbohydrates as an energy source, dietary lipids play a more important role in providing energy and in sparing dietary protein (Watanabe 1982). Despite the common use of biochemical techniques to assess growth and nutrition of fish species since the 1980s, particularly salmonids (Idler and Bitners 1958; Fukuda et al. 1986; Nakano 1988; Shearer et al. 1994), surprisingly little is known about lipid changes in high-seas salmon. Azuma et al. (1998) examined growth characteristics of chum, *Oncorhynchus keta,* pink, *O. gorbuscha*, and sockeye, *O. nerka,* salmon caught on the high-seas and reported the content of triacylglycerol in the muscle of the fish.

Winter in the North Pacific Ocean may be stressful for salmon because water temperatures are low and there is little food available. As an energy source for metabolism, lipids play an important role during periods of stress, especially starvation in fish. Yet there is no information on the lipid contents and fatty acid profiles of chum and pink salmon in winter. Therefore, we examined the total lipid content, lipid classes, and fatty acid composition in the white muscle of chum and pink salmon from the high-seas to gain information on their feeding condition and energy reserves at that season.

MATERIAL AND METHODS

A total of 80 salmon (10 chum and 70 pink salmon), was captured from the eastern North Pacific Ocean (ENPO; 45°N, 179°W), from two stations in the western North Pacific Ocean (WNPO; 45°N, 165°E and 45°N, 160°E) and from the Gulf of Alaska (46°N, 168°W) by the research vessel *Kaiyo maru* in January 1996 (Ueno et al. 1997) and February 1998 (Nagasawa 1999) (Table 1). For comparative purposes, a total of 53 salmon (25 chum and 28 pink salmon), was captured in the Gulf of Alaska (52°N, 145°W) by the research vessel *Oshoro maru* in July of 1998 for use as summer-season reference samples (Table 1). Fish were caught with gill net or trawl net and measured fork length (cm) and body weight (g) for computation of the condition factor (fork length $(cm)^3$/body weight (g) x 1,000). The white muscle tissue for lipid analysis was taken from the lateral part just behind the head. The tissue samples were frozen at -80°C until analyzed. Total lipids in the white muscle were extracted with chloroform/methanol and measured gravimetrically (Bligh and Dryer 1959), separated into polar lipid and neutral lipid fractions with Sep-Pak (Waters Co., MS, U.S.A.), and measured gravimetrically (Juaneda and

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Table 1. Biological characteristics of chum and pink salmon used in this study. Values are mean and (S.D.).

Species	Maturity	Area	Location	Date	No. of Fish	Fork Length (cm)	Body weight (g)	Condition Factor
Chum salmon	Immature	Eastern North Pacific Ocean	45°N,179°W	21 Feb. 1998	10	35.4(1.2)	428 (63)	9.6 (0.7)
	Immature	Gulf of Alaska	52°N,145°W	8 July 1998	25	51.4 (3.7)	1,679 (452)	12.1 (0.7)
Pink salmon	Immature	Western North Pacific Ocean	45°N,165°E	10 Feb. 1998	10	28.9 (1.9)	216 (40)	9.4 (0.3)
	Immature	Western North Pacific Ocean	45°N,160°E	11 Jan. 1996	20	23.8(1.8)	123 (32)	8.9 (0.7)
	Immature	Gulf of Alaska	46°N,168°W	18 Jan. 1996	40	25.1(1.8)	138 (32)	8.5 (0.7)
	Mature	Gulf of Alaska	52°N,145°W	8 July 1998	28	49.3 (2.6)	1,602 (368)	13.1 (1.5)

Condition factor = (Fork length (cm)^3/Body weight (g)) × 1,000

Rocquelin 1985). Each of the polar and neutral lipids was dissolved in 2 ml of absolute methanol containing 2N of potassium hydroxide and saponified at 80°C for 10 min. The non saponifiable material was then removed by an initial petroleum ether extraction of the alkaline saponification mixture and discarded. Fatty acids were converted to their methyl esters by refluxing for 1hr in 5% HCl-methanol solution at 100°C and the fatty acid methyl esters were extracted with hexane (Ichihara et al. 1996). The fatty acid compositions were analyzed with Hewlett-Packard model 6890 gas chromatography (Hewlett-Packard Co., WA, USA) on PUFA capillary column (Supelco Inc., PA, USA). A flame ionization detector was employed to detect mass peaks, and peak areas were integrated electronically with Hewlett-Packard GC ChemStation Rev. A.03.05 (Hewlett-Packard Co., WA, USA); % by weight was estimated from peak areas of each fatty acid. The resulting values were tested for significant differences using the Student's *t*-test.

A short hand designation for fatty acids was used throughout where the carbon number identified the position of the first double bond counting from the methyl end. The first number identified the number of carbon, the second number, the number of double bonds and last number the position of the double bond.

RESULTS

Total Lipid Content

Chum salmon

Total lipid content in chum salmon captured in February 1998 in the ENPO (45°N, 179°W) was low in white muscle (< 1.7%, mean = 1.1%). Total lipid contents in the white muscle of chum salmon caught in the Gulf of Alaska (52°N, 145°W) in July of 1998 was high (< 18.6%, mean = 12.3%). Polar lipids in the white muscle were unchanged in winter (mean = 0.7%) and summer (mean = 0.9%), but neutral lipids varied (mean = 0.3% in winter and 11.4% in summer) (Table 2, Fig. 1).

Pink salmon

Total lipid content in pink salmon captured in WNPO (45°N, 165°E), was also low in white muscle (< 1.7%, mean = 1.4%) (Table 2). Total white muscle lipid content in pink salmon captured in January 1996 in WNPO (45°N, 160°E) (< 6.9%, mean = 3.3%) was significantly higher ($p < 0.001$) than in pink salmon captured in the Gulf of Alaska (46°N, 168°W) (< 1.8%, mean = 1.0%) in the winter of 1996 (Table 2). The lipid contents were correlated with body weight (Fig. 2). As in chum salmon, total lipid contents in pink salmon captured in July of 1998 in the Gulf of Alaska (52°N, 145°W) was also high in white muscle (< 18.5%, mean = 11.3%). The lipid contents were correlated with body weight (Figs. 2 and 3). Polar lipids in the white muscle were unchanged in winter and summer, but neutral lipids varied seasonally (Table 2, Fig. 3) as in chum salmon.

Composition of Fatty Acids

Eighteen fatty acids were identified in all samples of chum and pink salmon (Tables 3, 4, and 5). In addition, we were able to resolve some minor unidentified fatty acids and an unknown substance. Of the neutral lipids in summer samples of chum and pink salmon, 16:0, 18:1n9, 20:1n11, 20:5n3, 22:1n11 and 22:6n3 were present in significant amounts. Among polar lipids from summer sampled chum and pink salmon, 16:0, 18:1n9, 20:5n3 and 22:6n3 were also present in significant amounts. There was no difference between species in the more abundant fatty acids present in winter and summer samples. However, a significant seasonal difference ($p < 0.05$) was observed in the proportion of 22:6n3 among neutral lipids of chum (Fig. 4), and pink salmon (Fig. 5) and 18:1n9 among polar lipids of chum salmon. As the total lipid content decreased, the proportion of 22:6n3 increased among neutral lipids, and 22:6n3 and 18:1n9 increased and decreased respectively among polar lipids. In pink salmon, significant differences ($p < 0.05$) in the proportion of 22:6n3 were observed in both neutral lipids and polar lipids fatty acid composition between the winter and summer samples (Tables 4 and 5).

Table 2. Total lipid (TL), polar lipid (PL) and neutral lipid (NL) contents in the white muscle of chum and pink salmon caught in the North Pacific Ocean in the winter of 1996 and 1998, and the summer of 1998. Values are mean and (S.D.)

Species	Maturity	Area	Location	TL(%)	PL (%)	NL (%)
Chum salmon	Immature	Eastern North Pacific Ocean	45°N,179°W	1.1 (0.3)	0.7 (0.1)	0.3 (0.2)
	Immature	Gulf of Alaska	52°N,145°W	12.3 (3.5)	0.9 (0.3)	11.4(3.4)
Pink salmon	Immature	Western North Pacific Ocean	45°N,165°E	1.4 (0.2)	0.7 (0.1)	0.5 (0.2)
	Immature	Western North Pacific Ocean	45°N,160°E	3.3(0.3)	0.9(0.2)	2.3(1.3)
	Immature	Gulf of Alaska	46°N,168°W	1.0(0.4)	0.5(0.1)	0.4(0.2)
	Mature	Gulf of Alaska	52°N,145°W	11.3 (4.1)	0.9(0.3)	10.2(4.0)

Fig. 1. Percentage of total lipid content in the white muscle of chum salmon of various sizes (body wt.) caught in the western North Pacific Ocean in winter (solid circles, 45°N, 179°W) and the Gulf of Alaska in summer, 1998 (open circles, 52°N, 145°W).

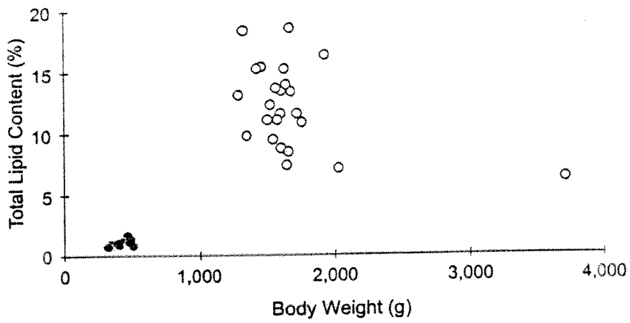


Fig. 2. Percentage of total lipid content in the white muscle of pink salmon of various sizes (body wt.) caught in the western North Pacific Ocean in the winter of 1996 (solid circles, 45°N, 160°E), the western North Pacific Ocean in the winter of 1998 (solid squares, 45°N, 165°E), Gulf of Alaska in the winter of 1996 (open squares; 46°N, 168°W) and Gulf of Alaska in the summer of 1998 (open circles, 52°N, 145°W).

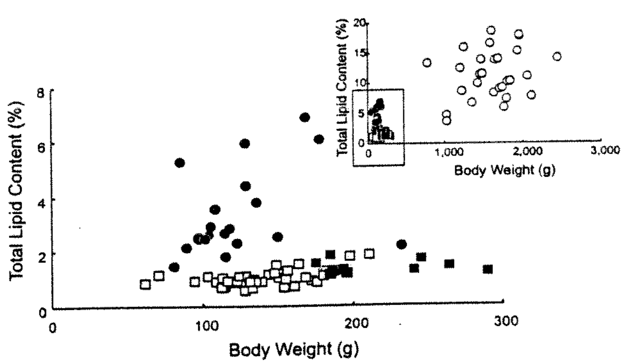
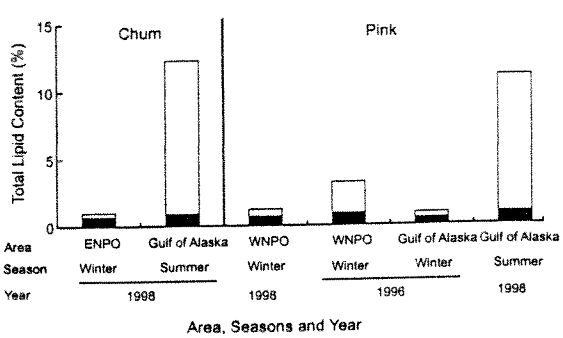


Fig. 3. Polar lipid (solid bars) and neutral lipid (open bars) content of the muscle in chum and pink salmon caught in the Gulf of Alaska, western North Pacific Ocean (WNPO) and eastern North Pacific Ocean (ENPO) in the winter and summer of 1996 and 1998.



DISCUSSION

In carnivorous fish like salmonids, which have a limited ability to utilize carbohydrates as an energy source, dietary lipids play an important role in providing energy (Watanabe 1982).

Our current knowledge of lipids in salmonids was based largely on mature fish in freshwater or adult salmon caught in coastal areas. There are few reports of lipid content in high sea salmonids (Azuma et al. 1998). One of the most important findings in this report is that the lipid content in the muscle of pink and chum salmon in winter was low, and among classes of lipids, neutral lipids were much lower in winter than in summer. In general, the polar lipid content, which is a component of the cell membrane, did not vary significantly with species or time of year, and remained approximately at 1% in fish muscle. There was no difference in polar lipid content between winter and summer in either chum or pink salmon muscle. Neutral lipids, which are used by salmon as an energy source, in the muscle of winter salmon were low, about 2.6% of that in summer in chum salmon and 3.9–22.5% of the summer in pink salmon (Table 2). Lipids in the food of fish are digested and absorbed. Following digestion, the free fatty acids in the food are reconstructed as neutral and polar lipids. The low lipid content in the muscle in the winter suggests that chum and pink salmon have inadequate food at that season. Such a low lipid content jeopardizes survival of salmon in high-seas during winter. Nagasawa (this volume) reported that in all of the western and central Pacific, Gulf of Alaska and Bering Sea, the winter zooplankton biomass was low, being, in January or February, about 10% of the summer biomass. Zooplankton biomass was higher in the western Pacific Ocean than in the central Pacific Ocean and Gulf of Alaska in November (Nagasawa this volume). There was a similarity between the regional difference in zooplankton reported by Nagasawa (this volume) and the regional and seasonal variation in lipid content in muscle of pink salmon described this report (Table 2, Fig. 2).

Sasaki et al. (1989) examined the composition of fatty acids in the total lipids of chum salmon during

Table 3. Fatty acid percentage of neutral lipids (NL) and polar lipids (PL) in the muscle of chum salmon caught in the winter and summer of 1998. Values are mean of fatty acids and (S.D.).

	NL		PL	
Fatty Acids	Feb. 1998 WNPO	July 1998 Gulf of Alaska	Feb. 1998 WNPO	July 1998 Gulf of Alaska
14:0	3.37(1.33)	7.21(1.03)	0.89(0.25)	4.35(1.90)
16:0	13.33(1.89)	15.07(2.06)	23.14(5.09)	25.93(5.46)
16:1n7	4.46(2.12)	4.84(0.88)	1.12(0.14)	1.42(0.75)
18:0	3.90(0.75)	4.50(0.84)	4.62(1.24)	5.59(1.32)
18:1n9	18.39(6.65)	18.85(3.39)	5.04(0.77)	10.99(3.52)
18:1n7	2.97(1.38)	1.63(0.29)	1.92(0.53)	1.46(0.39)
18:1n5	0.91(0.39)	0.61(0.08)	0.50(0.14)	0.47(0.17)
18:2n6	1.61(0.53)	1.56(0.18)	0.43(0.16)	0.77(0.10)
18:3n3	1.30(0.66)	1.15(0.24)	0.39(0.08)	0.45(0.03)
18:4n3	1.39(0.96)	2.24(0.79)	0.22(0.05)	0.55(0.08)
20:1n11	2.19(1.08)	3.97(1.72)	0.21(0.16)	1.42(0.83)
20:1n9	2.95(2.16)	1.63(0.30)	0.46(0.49)	0.88(0.59)
20:4n3	1.30(0.58)	1.64(0.29)	0.67(0.12)	0.94(0.14)
20:5n3	5.18(2.44)	6.25(1.57)	7.26(1.27)	7.74(1.84)
22:1n11	2.65(1.69)	4.05(1.58)	0.06(0.05)	2.01(1.05)
22:1n9	1.94(1.09)	2.85(1.32)	0.05(0.03)	1.03(0.47)
22:5n3	1.97(0.60)	1.54(0.27)	2.25(0.62)	2.08(0.32)
22:6n3	13.39(8.70)	10.89(3.09)	41.89(7.02)	30.67(12.51)

WNPO; Western North Pacific Ocean

Table 4. Fatty acid percentage of neutral lipid in the muscle of pink salmon caught in the western North Pacific Ocean (WNPO) and Gulf of Alaska in the winter of 1996 and 1998, and the summer of 1998 in the Gulf of Alaska. Values are mean percentages of fatty acids and (S.D.).

Fatty Acids	Jan. 1996 WNPO	Jan. 1996 Gulf of Alaska	Feb. 1998 WNPO	Jul. 1998 Gulf of Alaska
14:0	4.93(0.98)	1.67(1.09)	2.86(1.34)	4.49(0.82)
16:0	13.53(1.69)	19.53(3.28)	12.46(2.95)	11.83(1.73)
16:1	3.73(0.71)	2.03(1.11)	3.36(1.62)	3.41(0.88)
18:0	2.06(0.63)	4.57(0.96)	4.63(1.30)	2.63(0.56)
18:1n7	1.88(0.55)	2.86(0.66)	2.32(0.35)	1.04(0.37)
18:1n9	12.82(3.73)	9.67(4.28)	13.87(5.52)	10.65(3.25)
18:2n6	1.48(0.50)	0.69(0.23)	1.90(0.45)	1.59(0.25)
18:3n3	1.97(0.38)	1.35(0.82)	1.07(0.53)	1.04(0.19)
18:4n3	3.71(1.20)	0.74(0.53)	0.99(0.42)	1.79(0.44)
20:1n11	9.25(2.73)	2.47(2.52)	5.16(2.94)	13.95(2.37)
20:1n9	2.10(0.27)	2.24(1.69)	1.88(0.94)	1.45(3.92)
20:5n3	5.89(1.29)	6.68(1.55)	5.67(2.29)	5.71(3.92)
22:1n11	9.04(2.69)	2.54(2.65)	4.18(2.02)	11.61(2.63)
22:5n3	1.25(0.25)	1.74(0.36)	1.80(0.45)	1.59(0.24)
22:6n3	9.83(2.40)	28.72(8.99)	21.64(11.71)	9.89(1.62)

Table 5. Fatty acid percentage of polar lipid in the muscle of pink salmon caught in the western North Pacific Ocean and Gulf of Alaska in the winter of 1996 and 1998, and the summer of 1998 in the Gulf of Alaska. Values are mean of percentages of fatty acids and (S.D.).

Fatty Acids	Jan. 1996 WNPO	Jan. 1996 Gulf of Alaska	Feb. 1998 WNPO	Jul. 1998 Gulf of Alaska
14:0	1.12(0.25)	0.59(0.13)	1.13(0.42)	1.48(0.22)
16:0	20.23(2.15)	17.61(2.64)	20.40(1.11)	16.36(2.32)
16:1	1.02(0.24)	0.71(0.16)	0.9(0.16)	1.07(0.26)
18:0	3.75(0.25)	4.49(0.84)	4.59(0.41)	4.71(1.34)
18:1n9	5.10(0.66)	5.88(1.18)	4.23(0.28)	5.30(1.25)
18:1n7	1.61(0.23)	1.76(0.25)	1.19(0.13)	1.41(0.22)
18:1n5	0.69(0.18)	0.35(0.38)	0.37(0.37)	tr
18:2n6	0.54(0.12)	0.40(0.11)	0.68(0.68)	0.58(0.19)
18:3n3	0.52(0.14)	0.25(0.08)	0.44(0.44)	0.55(0.21)
18:4n3	1.00(0.32)	0.50(0.41)	0.32(0.32)	0.45(0.10)
20:1n11	0.43(0.13)	0.52(0.25)	0.22(0.22)	1.49(1.41)
20:1n9	1.40(2.11)	0.73(0.60)	0.50(0.20)	tr
20:5n3	7.79(1.88)	7.00(1.09)	8.82(1.31)	4.74(2.55)
22:1n11	0.42(0.20)	0.17(0.11)	tr	tr
22:5n3	1.57(0.22)	1.76(0.22)	1.76(0.20)	1.99(0.28)
22:6n3	44.57(3.73)	47.20(1.55)	47.11(2.00)	33.99(7.13)

tr=trace

Fig. 4. Proportion of 22:6n3 in the neutral lipid content of chum salmon caught in the winter (open circles) and the summer (solid circles).

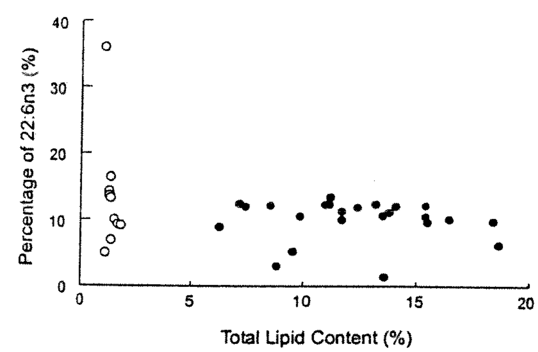
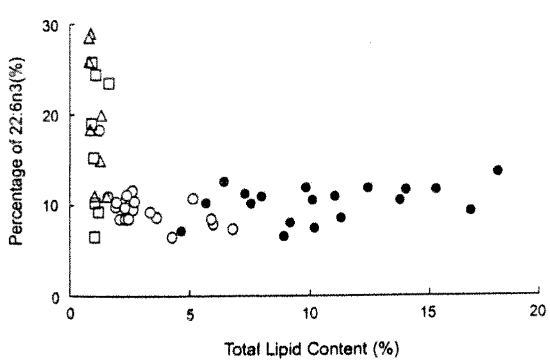


Fig. 5. Proportion of 22:6n3 in neutral lipid contents of pink salmon caught in the western North Pacific Ocean (open circles, 45°N, 160°E) in the winter of 1996, the western North Pacific Ocean (open squares, 45°N, 165°E) in the winter of 1998, Gulf of Alaska (open triangles, 46°N, 168°W) in the winter of 1996, and Gulf of Alaska (solid circles, 52°N, 145°W) in the summer of 1998.



their coastal spawning migration and reported that the major fatty acids in the muscle were 16:0 (15.3%), 18:1n9 (12.01%), 20:1n11 (7.5%), 20:5n3 (7.0%), 22:1n11 (including n13) (5.8%) and 22:6n3 (20.2%). We found that the fatty acids of both pink and chum salmon caught in summer in the Gulf of Alaska were similar, but in winter, when lipid content was less than 1.1 %, the percentages of some fatty acids were altered from those in summer. The proportion of 22:6n3 was increased in neutral lipids in winter, and reached 30% of total fatty acids in pink salmon neutral lipids (Table 4). Docosahexaenoic acid (22:6n3) is the major n-6 polyunsaturated fatty acid in fish, and plays an important role in metabolism. The increasing proportion of 22:6n3 in the samples occurred for one or both of two reasons: an increase in 22:6n3 acid or a decrease in other major fatty acids. Indeed, the proportion of 16:0 and 18:1n9 decreased. We think that the increasing proportion of 22:6n3 was the result of utilization and depletion of 16:0 and 18:1n9.

The uptake of fatty acids in the fish intestine appears to be non-selective, owing to the presence of lipase capable of hydrolyzing fatty acids from triacylglycerol molecules in the three positions (Patton et al. 1975; Lie and Lambertsen 1985). These fatty acids are transported in the blood to either fat depots or target organs, as in mammals. Similar fatty acid profiles of dietary lipids and triacylglycerol rich organs suggest that fatty acid deposition in fish lipids is a nonselective process. Fatty acids are then specifically mobilized from lipid reserves during periods of starvation or low food intake as noted in rainbow trout (*O. mykiss*) and chum salmon (Ando et al. 1985; Sasaki et al. 1989). Kiessling and Kiessling (1993) studied the oxidation rate of 10 major fatty acids with CoA of rainbow trout white muscle. Two fatty acids (14:0 and 16:0) were oxidized as rapidly as pyruvate. Another six acids (16:1n7, 18:0, 18:1n9, 20:1n9, 22:1n9 and 226n3) were oxidized at about three-quarters to one half the rate of pyruvate. The unsaturated fatty acid 22:6n3 was oxidized at a comparable rate to 22:1n9, which is half the rate of palmitic acid oxidation. The change of fatty acids profile in winter as related to changes in total lipids also suggests that salmon had little food during winter. The low lipid contents and changes in fatty acid profiles in winter suggest that chum and pink salmon are confronted with difficult conditions during this season.

Further study of the seasonal and spatial variation in lipid content among North Pacific salmonids is needed to better estimate changes in feeding conditions of salmon during their high seas residency.

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REFERENCES

Ando, S., M. Hatano, and K. Zama. 1985. A consumption of muscle lipid during spawning migration of chum salmon *Oncorhynchus keta*. Bull. Japan. Soc. Sci. Fish. 51: 1817–1824.

Azuma T., T. Yada, Y. Ueno, and M. Iwata. 1998. Biochemical approach to assessing growth characteristics in salmonids. N. Pac. Anadr. Fish Comm. Bull. No. 1: 103–111.

Bligh, E.G., and W.J. Dryer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

Fukuda, M., H. Nakano, and K. Yamamoto. 1986. Biochemical changes in Pacific herring during early developmental stages. Bull. Fac. Fish., Hokkaido Univ. 37: 30–37.

Ichihara, K., A. Shibahara, K. Yamamoto, and T. Nakayama. 1996. An improved method for rapid analysis of the fatty acids of glycerolipids. Lipids 31: 535–539.

Idler, D.R., and I. Bitners. 1958. Biochemical studies on sockeye salmon during spawning migration. II Cholesterol, fat, protein, and water in the flesh of standard fish. Can. J. Biochem. Physiol. 36: 793–798.

Juaneda, P., and G. Rocquelin. 1985. Rapid and convenient separation of phospholipids and non phosphorus lipids from rat heart using silica cartridges. Lipids 20: 40–41.

Kiessling, K.-H., and A. Kiessling. 1993. Selective utilization of fatty acids in rainbow trout (*Oncorhynchus mykiss* Walbaum) red muscle mitochondria. Can. J. Zool. 71: 248–251.

Lie, Q., and G. Lambertsen. 1985. Digestive lipolytic enzymes in cod (*Gadus morhua*): fatty acid specificity. Comp. Biochem. Physiol. B. 80: 447–450.

Nagasawa, K. This volume. Winter zooplankton biomass in the subarctic North Pacific, with a discussion on the survival strategy of Pacific salmon (*Oncorhynchus spp.*) overwintering in the open sea. N. Pac. Anadr. Fish Comm. Bull. No. 2.

Nakano, H. 1988. Qualitative analysis of nucleic acid for studying juvenile fishes. Kaiyou-to-Seibutsu 10: 23–26.

Patton, J.S., J.C. Nevenzel, and A.A. Benson. 1975. Specificity of digestive lipases in hydrolysis of wax esters and triglycerides studied in anchovy and other selected fish. Lipids 10: 575–583.

Sasaki, S., T. Ota, and T. Takagi. 1989. Composition of fatty acids in the lipids of chum salmon during spawning migration. Nippon Suisan Gakkaishi 55: 2191–2197.

Shearer, K.D., T. Asgard, G. Androsdottir, and G.H. Aas. 1994. Whole body elemental and proximate composition of Atlantic salmon (*Salmo salor*) during the life cycle. J. Fish Biol. 44: 785–797.

Ueno, Y., Y. Ishida, A. Shiomoto, S. Urawa, K. W. Myers, J. Morris, and M.V. Koval. 1997. Summary of wintering salmon research aboard the research vessel *Kaiyo-maru* in January 1996. Salmon Rep. Ser. 42: 38–59. (In Japanese and English) [Available from the National Research Institute of Far Seas Fisheries, Shimizu-shi, Shizuoka 424-8633, Japan]

Watanabe, T. 1982. Lipid nutrition in fish. Comp. Biochem. Physiol. B. 73: 3–75.