A quantitative comparison between diet and body fatty acid composition in wild northern pike *(Esox lucius L.)*

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Abstract

The fatty acid compositions of wild female northern pike *(Esox lucius* L.) and their principle prey species were compared to assess the extent to which pike modify the relative abundance of dietary fatty acids during assimilation and to indicate the optimum dietary content of essential fatty acids (EFAs) for pike. Only minor differences existed between the estimated whole body fatty acid composition of pike and diet fatty acid composition as calculated from the contribution of each prey species to the pike's diet. Saturated fatty acids comprised a slightly higher percentage of diet lipids (25% wt) than of pike lipids (21% wt) whereas monounsaturated fatty acids were less abundant in diet lipids (26% wt) than in pike (29% wt). Percentages of total polyunsaturated fatty acids (PUFAs), $n-3$ fatty acids, and $n-6$ fatty acids were approximately 43, 30, and 13% wt respectively and differed by less than 1% wt between pike and diet lipids. Among individual PUFAs, the largest differences occurred in $20:5(n-3)$ and $22:6(n-3)$ which comprised, on average, 9.6 and 14.7% wt respectively of diet lipids and 5.9 and 18.3% wt respectively of pike lipids. The close similarity in fatty acid composition between pike and their diet suggests that pike may have limited abilities to elongate and desaturate 18 carbon PUFAs and may require specific long chain PUFAs in the diet. The $n - 3$ PUFA content of the pike's natural diet may exceed the minimum EFA requirements of better studied species such as rainbow trout and turbot.

Introduction

Fatty acid analysis of prey species provides a useful guide to the optimum essential fatty acid (EFA) intake of large piscivorous fish such as adult northern pike *(Esox lucius* L.) which are difficult to feed and maintain in captivity. Furthermore, comparison of fatty acid composition between wild fish and their prey may indicate the degree to which dietary fatty

acids are structurally modified or selectively catabolized during the incorporation of dietary lipids into fish tissues. To date, however, the fatty acid compositions of the natural diets of fish have not been well characterized (Henderson and Tocher 1987; Sargent *et al.* 1989).

Available evidence suggests that the ability to modify dietary fatty acids varies greatly between fish species and is related to diet fatty acid composi-

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tion. Rainbow trout *(Oncorhynchus mykiss)* have a relatively good ability to elongate and desaturate 18 carbon $n - 3$ and $n - 6$ fatty acids (Owen *et al.* 1975; Sellner and Hazel 1982; Watanabe 1982; Christiansen 1984; Bell *et al.* 1986; Hagve *et al.* 1986) and this ability may be an adaptation to their high consumption of insects. Aquatic insects do not appear to contain significant amounts of $22:6(n-3)$ (Hanson *et al.* 1985), the predominant polyunsaturated fatty acid (PUFA) in fish tissues. In contrast, piscivorous marine fish such as plaice and turbot have a poor ability to chain elongate and desaturate 18 carbon $n-3$ and $n-6$ PUFAs, presumably because they normally obtain adequate amounts of long chain PUFAs such as $20:4(n-6)$, $20:5(n-3)$, and 22:6(n - 3) in their diet (Owen *et al.* 1972, 1975; Linares and Henderson 1991).

The poor ability of piscivorous fish to elongate and desaturate 18 carbon EFAs suggests that the relative quantities of individual long chain PUFAs in the body as a whole may be largely determined by diet fatty acid composition. However, this hypothesis has not been tested and it is possible that piscivorous fish have considerable ability to synthesize saturated and $n-7$ and $n-9$ unsaturated fatty acids and to selectively catabolize or retain individual EFAs and thus maintain a whole body fatty acid composition different from that of the diet.

In this study, the fatty acid compositions of female northern pike and their principle prey species were compared to determine the extent to which pike modify the relative abundance of different dietary fatty acids during their incorporation into body tissues and to aid in defining the optimum dietary EFA content for pike. Female pike were analyzed, rather than males, because this study is part of a larger one which examines the role of environmental and physiological factors in the seasonal cycles of fatty acid composition in female pike (Schwalme 1991).

Materials and methods

Adult female pike and their principle prey species were collected from Lac Ste. Anne, Alberta (53°, 44' N, 114°, 22' W) in June and August 1989. The diet of adult pike in Lac Ste. Anne consists predominantly of yellow perch *(Perca flavescens),* white sucker *(Catostomus commersoni),* burbot *(Lota lota),* and spottail shiner *(Notropis hudsonius),* which together comprise 94% of total dietary caloric content (Diana 1979). Whitefish *(Coregonus clupeaformis),* walleye *(Stizostedion vitreum),* and other pike comprise the remainder of the diet (Diana 1979). Pike, white sucker, and whitefish were collected using gill nets whereas juvenile perch, spottail shiner and burbot were collected by seining or dip netting in shallow water along shore. A description of the pike and prey species collected and the tissues analyzed for fatty acid content is given in Table 1.

In the case of small prey items such as juvenile perch, spottail shiner, and burbot, lipids were extracted from the whole fish. For each pike, and prey items too large to homogenize whole, the major organs and tissues were sampled and whole body fatty acid composition was calculated after summing the content of each fatty acid in all organs and tissues analyzed.

Fish collected using gill nets were kept in a freezer $(-20^{\circ}C)$ prior to lipid extraction from tissues which was completed within 4 to 5 hours after removal of fish from the nets. Smaller prey species were kept alive in lake water until lipid extraction. Lipid extraction was done by homogenizing whole fish or tissue samples (2 to 4 g) with 40 volumes of a 2:1 mixture of chloroform-methanol (Folch *et al.* 1957) containing butylated hydroxytoluene (BHT) at levels of approximately 0.1% of the lipid content of the extract. Lipid extracts were cleared of particulate matter by filtering through Whatman # 1 filter paper, bubbled with nitrogen, and stored in completely filled glass vials (at -30° C) prior to further processing. The washing procedure of Folch *et al.* (1957) (using 0.58% NaCl) was used to remove nonlipids from the chloroform-methanol extracts.

Fatty acid analyses were performed separately on the neutral and polar lipid fractions of muscle from pike collected in August. Procedures used to separate neutral and polar lipids and the use of internal standards to quantify fatty acids in these fractions are described in Schwalme and Mackay (1992). In all other tissues, fatty acid analyses were

Month	Species sampled	$\mathbf n$	Body weight (g) $(mean \pm SD)$ or range)	Standard length (cm) (mean \pm SD or range)	Tissues analyzed
June	female pike	6	$1,290 \pm 456$	52.3 ± 6.0	liver, white muscle, adipopancreatic tissue
	white sucker	3	88 to 368	17.1 to 26.3	white muscle, viscera (includes gonads, liver, adipose tissue, and digestive tract)
	burbot	$\overline{\mathbf{3}}$	$12 \text{ to } 72$		white muscle, viscera (includes gonads, liver, adipose tissue, and digestive tract)
	spottail shiner	6	2.6 ± 0.5		whole fish
	juvenile perch	8	2.7 ± 0.5	$\qquad \qquad$	whole fish
August	pike	6	789 ± 209	43.9 ± 4.1	liver, white muscle, adipopancreatic tissue
	whitefish	4	214 ± 21	24.3 ± 0.8	liver, white muscle, viscera (includes gonads, adipose tissue, digestive tract)
	burbot	9a	1.7 ± 0.4		whole fish
	spottail shiner	8	2.8 ± 1.1	-	whole fish
	juvenile perch	8	4.4 ± 0.6		whole fish

Table 1. Characteristics of pike and prey items sampled for fatty acid analysis

a To obtain enough tissue for analysis, the six smallest burbot were homogenized in pairs, giving a total of six replicates.

Table 2. Contribution of various prey species to the wet weight and fatty acid content of the northern pike diet in Lac Ste. Anne

Prey species	Sampling date								
		June		August					
	FA concentration ^a $\%$ wet wt $(\text{mean} \pm \text{SEM})$	$\%$ of Diet ^b wet wt	$\%$ of Dietary ^c FA content	FA concentration ^a % wet wt (mean \pm SEM)	% of Diet ^b wet wt	% of Dietary ^c FA content			
Yellow perch	1.09 ± 0.13	51.1	51.1	1.42 ± 0.12	57.7	71.0			
White sucker	0.66 ± 0.04	22.1	13.4		23.9	13.8^{d}			
Spottail shiner	1.45 ± 0.16	12.7	16.9	2.49 ± 0.34	$\mathbf{0}$	0			
Burbot	1.54 ± 0.61	11.9	16.8	0.98 ± 0.01	11.8	10.1			
Whitefish		2.2	1.8 ^d	0.89 ± 0.08	6.6	5.1			
Total		100.0	100.0		100.0	100.0			

^a total fatty acid concentration of each prey species; ^b the contribution of each prey species to the pike's diet, expressed as a percentage of diet wet weight and calculated from data given by Diana (1979). In August, walleye and juvenile pike together comprised about 6% of the pike's diet (Diana 1979), but were not included in the analysis; c the contribution of each prey species to the pike's total dietary intake of fatty acids was calculated from the fatty acid concentration of each prey species and that species' percentage contribution to diet wet weight; ^d calculated using the fatty acid concentration of sucker in June and that of whitefish in August because these were the only dates on which sucker and whitefish were caught.

performed on total lipids. A known weight of tri-Otridecanoylglycerol was added to the washed extract of total lipids to serve as an internal standard for quantifying fatty acids. Saponification of lipids, methylation of fatty acids and gas chromatographic determination of tissue fatty acid content and percent composition were performed as

described in Schwalme and Mackay (1992). Quantities of 14:0 could not be accurately measured because that fatty acid co-eluted with BHT during gas chromatography.

The prey species compositions of the diet of female pike in Lac Ste. Anne during June and August as given by Diana (1979) were used to estimate diet fatty acid composition. Diana (1979) presented data on the percentage of the pike's caloric intake contributed by different prey species and each prey species' caloric equivalent (cal/g dry wt) and dry wt:wet wt ratio. Those data were used to calculate the percentage contribution of each prey species to the pike's diet on a wet wt basis (Table 2). The total fatty acid concentration $(\%$ wet wt) of each prey species and its contribution to diet wet wt were used to calculate each prey species' contribution to diet fatty acid content (Table 2). Finally, diet fatty acid composition was calculated by weighting each prey species' fatty acid composition according to that species' contribution to diet fatty acid content.

Results

The various prey species eaten by pike differed considerably in fatty acid content (Table 2). Therefore, the contribution of each prey species to the fatty acid content of the pike's diet differed somewhat from its contribution to the diet calculated on the basis of weight. This was most evident for white sucker, which contributed relatively less to diet fatty acid content than to diet weight, and for yellow perch, which in August contributed relatively more to diet fatty acid content than to diet weight (Table 2).

The prey species collected also differed considerably in fatty acid composition (Tables 3 and 4). For example, $18:1(n-9)$ varied from 10.1% wt in sucker to 22.6% wt in burbot (Table 3) and $22:6(n-3)$ varied from 7.8% wt in spottail shiner (Table 4) to 24.1% wt in sucker (Table 3).

Calculation of diet fatty acid composition from the average fatty acid composition of each prey species (weighted according to each species' contribution to diet fatty acid content) gave only a single estimate for diet fatty acid composition at each collection period. This meant that statistical tests based on the variability in diet fatty acid composition could not be performed. However, the reliability of comparisons between the fatty acid compositions of pike and their diet can be assessed by comparing the data obtained in June and August (Tables 3 and 4).

In both June and August, pike contained percentages of saturated fatty acids (SFAs) which were lower (by 3.2 to 4.3% wt) and percentages of monounsaturated fatty acids (MUFAs) which were higher (by 2.1 to 3.8% wt) than those in diet lipids (Tables 3 and 4). Percentages of $n-3$, $n-6$, and total PUFAs in pike lipids were nearly identical to those in diet lipids (Tables 3 and 4).

Individual fatty acids whose percentages in pike and diet lipids differed by more than 2% wt were, 16:0 (August only), 18:0 (both months), $16:1(n-7)$ (June only), $20:5(n-3)$ (both months), and $22:6(n-3)$ (both months) (Tables 3 and 4). Comparison of Tables 3 and 4 shows that differences in the percent composition of individual fatty acids between pike and diet lipids in June were qualitatively and quantitatively similar to the differences which existed in August. In both months, pike lipids contained lower proportions of 16:0 and 18:0 and higher percentages of $16:1(n-7)$ and $18:1$ $(n - 9)$ compared to diet lipids (Tables 3 and 4). Percentages of $18:2(n-6)$ were greater in pike than in their diet and were offset by similarly large but opposite differences in the percentage of $20:4(n-6)$ (Tables 3 and 4). Compared to diet lipids, pike contained higher percentages of $18:3(n-3)$ and $22:6(n-3)$ which were offset by reductions in the percentage of $20:5(n-3)$ (Tables 3 and 4).

Between June and August, the pike's principle food, yellow perch, underwent significant changes (t-test, $p < 0.05$) in fatty acid composition of which the most notable were increases in the percentages of $16:1(n-7)$ and total MUFAs, and decreases in $22:6(n-3)$ and total n - 3 PUFAs (Tables 3 and 4). The percentage of $22:6(n-3)$ in pike lipids also declined between June and August (Tables 3 and 4), but this change was not statistically significant (ttest, p < *0.05).*

Discussion

The similarity in fatty acid composition between pike and their diet suggests that pike do not need to, and may not have the ability to, significantly modify the fatty acid composition of dietary lipids during their assimilation. Certainly, percentages of

95

Fatty acid	Pike ^a $(n = 6)$	Pike diet ^b	Yellow perch $(n=8)$	Burbot $(n=3)$	Shiner $(n=6)$	Sucker $(n = 3)$
16:0	15.3 ± 0.15 c	16.4	16.1 ± 0.21	15.5 ± 0.35	16.7 ± 0.46	18.6 ± 0.21
18:0	5.9 ± 0.15	8.0	7.9 ± 0.32	8.4 ± 1.35	8.2 ± 0.28	7.5 ± 0.40
$16:1(n-7)$	11.4 ± 0.46	9.4	9.5 ± 0.66	9.6 ± 1.88	9.9 ± 0.60	8.4 ± 0.22
$18:1(n-9)$	17.6 ± 1.26	15.7	14.9 ± 1.09	22.6 ± 3.15	16.1 ± 0.70	10.1 ± 0.22
$18:2(n-6)$	5.4 ± 0.28	3.7	3.6 ± 0.27	3.9 ± 0.41	4.7 ± 0.50	2.8 ± 0.13
$20:4(n-6)$	5.9 ± 0.22	7.2	6.9 ± 0.25	8.9 ± 1.76	6.6 ± 0.39	7.4 ± 0.33
$22:5(n-6)$	1.7 ± 0.09	1.9	2.4 ± 0.17	1.0 ± 0.14	0.9 ± 0.05	2.1 ± 0.20
$18:3(n-3)$	3.7 ± 0.17	2.7	2.1 ± 0.22	3.6 ± 0.44	4.0 ± 0.53	2.1 ± 0.06
$20:5(n-3)$	5.6 ± 0.12	9.7	9.5 ± 0.30	11.0 ± 1.24	9.7 ± 0.45	9.0 ± 0.50
$22:5(n-3)$	2.0 ± 0.08	2.6	2.2 ± 0.06	2.9 ± 0.20	2.8 ± 0.18	3.8 ± 0.11
$22:6(n-3)$	19.8 ± 1.20	15.7	16.4 ± 1.13	8.0 ± 1.47	14.0 ± 1.24	24.1 ± 0.66
others	5.7 ± 0.14	6.9	8.5 ± 0.37	4.7 ± 0.15	6.4 ± 0.38	4.0 ± 0.25
SFA	21.2 ± 0.14	24.4	24.0 ± 0.48	23.8 ± 1.02	24.9 ± 0.67	26.1 ± 0.19
MUFA	29.0 ± 1.51	25.2	24.5 ± 1.66	32.2 ± 5.02	25.9 ± 1.29	18.6 ± 0.43
PUFA	44.1 ± 1.45	43.5	43.0 ± 1.31	39.3 ± 4.15	42.7 ± 1.04	51.3 ± 0.34
all n–6	13.0 ± 0.42	12.8	12.9 ± 0.28	13.7 ± 1.66	12.2 ± 0.22	12.3 ± 0.11
all $n-3$	31.1 ± 1.09	30.7	30.1 ± 1.16	25.5 ± 2.49	30.5 ± 1.10	38.9 ± 0.34
FA conc. % wet wt	0.93 ± 0.084	1.09	1.09 ± 0.125	1.54 ± 0.607	1.45 ± 0.164	0.66 ± 0.037

Table 3. Fatty acid compositions of pike, the pike's diet, and prey species in June

Data shown as mean \pm SEM; ^a fatty acid compositions of pike and prey species were estimated from weighted averages of the compositions of the individual organs and tissues identified in Table 1; b the fatty acid composition of the pike's diet was calculated from the</sup> contribution of each prey species to the pike's dietary fatty acid intake as indicated in Table 2; c fatty acid compositions are the mean weight $\%$ of the indicated fatty acids in total lipids of pike, the pike's diet, and prey species; Abbreviations: SFA - total saturated fatty acids, MUFA - total monounsaturated fatty acids, PUFA - total polyunsaturated fatty acids, $n-3 - \omega 3$ fatty acids, $n-6 - \omega 6$ fatty acids, FA conc. - total fatty acid concentration.

Data shown as mean **±** SEM; Footnotes and abbreviations are given in Table 3.

 $20:4(n-6)$ and $20:5(n-3)$ which are 1.2 to 4.1% wt lower in pike than in diet lipids (Tables 3 and 4) provide no evidence of significant elongation and desaturation of $18:2(n-6)$ or $18:3(n-3)$ by pike. Although amounts of $22:6(n-3)$ were 3.0 to 4.1% wt higher in pike than in their diet (Tables 3 and 4), this is not sufficient to indicate that pike are actively elongating and desaturating $20:5(n-3)$ to 22:6 $(n-3)$. Because the gross dietary conversion efficiency of pike is about 30% (Diana 1982), pike probably consume considerably more $22:6(n-3)$ (and other nutrients) than they accumulate in their tissues. Therefore, higher percentages of 22:6 $(n-3)$ in pike compared to their diet can be due to selective retention of this fatty acid and does not necessarily imply that pike are synthesizing 22:6 $(n-3)$ from $20:5(n-3)$.

Quantities of $n - 3$ PUFAs present in the pike's diet equal or exceed the minimum dietary requirements for these essential fatty acids which have been established experimentally in better studied species such as rainbow trout and turbot. Assuming the water content of the pike's diet to be similar to that of yellow perch (78% of wet wt; Tanasichuk and Mackay 1989), the total $n-3$ PUFA content of the pike's diet is about 1.5% of dry weight. This corresponds well with the dietary $n-3$ PUFA requirements established experimentally in rainbow trout (0.5 to 1.7% of diet dry wt) (Castell *et al.* 1972; Watanabe *et al.* 1974; Takeuchi and Watanabe 1977) and turbot $(0.57 \text{ to } 1.3\% \text{ of diet dry wt})$ (Gatesoup *et al.* 1977; Leger *et al.* 1979; Le Milinaire *et al.* 1983). However, the EFA requirements of fish vary according to the quantity of lipid and the type of fatty acid *(i.e.,* 18 carbon vs long chain PUFA) supplied in the diet. Accordingly, the $n-3$ PUFA requirements of rainbow trout have also been expressed as 20% of diet fatty acids if supplied as $18:3(n-3)$ and as 10% of diet fatty acids if supplied as $20:5(n-3)$ plus $22:6(n-3)$ (Takeuchi and Watanabe 1977). Percentages of total $n - 3$ PUFAs (29.1 to 30.7; Tables 3 and 4) in the pike's diet thus exceed the requirements of rainbow trout expressed as $18:3(n-3)$ and percentages of 20 and 22 carbon $n - 3$ PUFAs in the pike's diet (25.5) to 28.0; Tables 3 and 4) are double to triple the requirements established for trout. Although quantities of $n-3$ PUFAs four times in excess of dietary requirements suppress growth in trout (Takeuchi and Watanabe 1979), the high percentage of $n-3$ PUFAs in the diet of pike does not appear to be detrimental because pike in Lac Ste. Anne exhibit normal growth rates (Mackay 1989) and otherwise appear healthy. This suggests that the optimum dietary intake of long chain $n-3$ PUFAs for pike may be higher than the minimum $n-3$ PUFA requirements established experimentally for rainbow trout. On the whole, the good agreement between the $n-3$ PUFA content of the pike's natural diet and experimentally derived $n-3$ requirements of fish suggests that natural foods can be useful indicators of the optimal fatty acid composition of fish diets.

Total fatty acid content and percent composition exhibited considerable variation between different prey species and temporal variation within a single species (Tables 3 and 4). The potential exists for pike to experience similarly large temporal variations in diet composition if they feed exclusively on a single prey species or if they switch from eating predominantly juvenile yellow perch to eating one of the other prey species. However, the strategy of feeding on several prey species may allow pike to reduce the amount of temporal variation in diet fatty acid composition they have to deal with.

One would expect that pike, and other northtemperate fish, might be able to increase their dietary lipid intake in winter, and thus help satisfy the requirements of fatty acids for ovary growth, by feeding on adult females of prey species such as burbot and yellow perch which also undergo ovarian maturation over winter. However, lipids of mature ovaries of yellow perch and burbot consist predominantly of wax esters which are considerably less digestible than triacylglycerols and polar lipids (Henderson and Tocher 1987). The low digestibility of wax esters, together with the low fatty acid content (0.56% wet wt) of the combined somatic tissues of yellow perch from Lac Ste. Anne in January (Schwalme 1991), suggests that female perch with mature ovaries may not provide greatly increased quantities of fatty acids to pike over winter.

In summary, it appears that pike in Lac Ste. Anne have acquired a fatty acid composition which closely resembles that of dietary lipids. This suggests that pike may resemble piscivorous marine fish and terrestrial carnivores such as the cat (Davidson *et al.* 1990) in having relatively poor abilities to elongate and desaturate 18 carbon EFAs and in requiring specific long chain $n - 3$ and $n - 6$ PU-FAs in the diet. Furthermore, seasonal or age related changes in diet fatty acid composition can be expected to significantly influence the fatty acid composition of pike. Interestingly, adult pike in a few Alberta lakes consume considerable quantities of insects such as dragonfly nymphs (Chapman and Mackay 1990). In those waters, pike may need to convert dietary $20:5(n-3)$ to $22:6(n-3)$ and, if unable to do so, may experience a deficiency of $22:6(n-3)$.

References cited

- Bell, M.V., Henderson, R.J. and Sargent, J.R. 1986. The role of polyunsaturated fatty acids in fish. Comp. Biochem. Physiol. 83B: 711-719.
- Castell, J.D., Sinnhuber, R.O., Wales, J.H. and Lee, D.J. 1972. Essential fatty acids in the diet of rainbow trout *(Salmo gairdneri*): growth, feed conversion and some gross deficiency symptoms. J. Nutr. 102: 77-86.
- Chapman, L.J. and Mackay, W.C. 1990. Ecological correlates of feeding flexibility in northern pike *(Esox lucius). J.* Freshw. Ecol. 5: 313-322.
- Christiansen, J.A. 1984. Changes in phospholipid classes and fatty acids and fatty acid desaturation and incorporation into phospholipids during temperature acclimation of green sunfish *Lepomis cyanellus* R. Physiol. Zool. 57: 481-492.
- Davidson, B.C., Giangregorio, A. and Girao, L.A.F. 1990. Essential fatty acids in cheetah and in domestic cats. *In* Omega-6 essential fatty acids: Pathophysiology and roles in clinical medicine. pp. 99-112. Edited by Alan R. Liss, Inc., New York.
- Diana, J.S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike *(Esox lucius).* Can. J. Zool. 57: 2121-2127.
- Diana, J.S. 1982. An experimental analysis of the metabolic rate and food utilization of northern pike. Comp. Biochem. Physiol. 71A: 395-399.
- Folch, J., Lees, M. and Sloane Stanley, G.H. 1957. A simple method for the isolation and purification of total lipides from animal tissues. J. Biol. Chem. 226: 497-509.
- Gatesoupe, F.-J., Léger, C., Métailler, R. and Sargent, J.R. 1977. Alimentation lipidique du turbot *(Scophthalmus maximus* L.) I. Influence de la longueur de chaine des acides gras de la série ω 3. Ann. d'Hydrobiol. 8: 89-97.
- Hagve, T., Christophersen, B.O. and Dannevig, B.H. 1986. Desaturation and chain elongation of essential fatty acids in

isolated liver cells from rat and rainbow trout. Lipids 21: $202 - 205$.

- Hanson, B.J., Cummins, K.W., Cargill, A.S. and Lowry, R.R. 1985. Lipid content, fatty acid composition, and the effect of diet on fats of aquatic insects. Comp. Biochem. Physiol. 80B: 257-276.
- Henderson, R.J. and Tocher, D.R. 1987. The lipid composition and biochemistry of freshwater fish. Prog. Lipid. Res. 26: $281 - 347.$
- Léger, C., Gatesoupe, F.-J., Métailler, R., Luquet, P. and Fremont, L. 1979. Effect of dietary fatty acids differing by chain lengths and ω series on the growth and lipid composition of turbot *Scophthalmus maximus* L. Comp. Biochem. Physiol. 64B: 345-350.
- Le Milinaire, C., Gatesoupe, F.-J. and Stephan, G. 1983. Approche du besoin quantitatif en acides gras longs polyinsaturatés de la série $n-3$ chez la larve de turbot *(Scophthalmus maximus).* C. R. Acad. Sci., Paris 296: 917-920.
- Linares, F. and Henderson, R.J. 1991. Incorporation of ¹⁴Clabelled polyunsaturated fatty acids by juvenile turbot, *Scophthalmus maximus* (L.) *in vivo.* J. Fish Biol. 38: 335-347.
- Mackay, W.C. 1989. Growth, feeding, and reproductive biology of freshwater fish in northern Canada. *In* Northern Lakes and Rivers. pp. 75-92. Edited by W.C. Mackay. Boreal Institute for Northern Studies Special Publication, University of Alberta.
- Owen, J.M., Adron, J.W., Middleton, C. and Cowey, C.B. 1975. Elongation and desaturation of dietary fatty acids in turbot *Scophthalmus maximus* L., and rainbow trout, *Salmo gairdneri.* Lipids 10: 528-531.
- Owen, J.M., Adron, J.W., Sargent, J.R. and Cowey, C.B. 1972. Studies on the nutrition of marine flatfish. The effect of dietary fatty acids on the tissue fatty-acids of the plaice *Pleuronectes platessa.* Mar. Biol. 13: 160-166.
- Sargent, J.R., Henderson, R.J. and Tocher, D.R. 1989. The Lipids. *In* Fish Nutrition, 2nd Edition. pp. 153-218. Edited by J.E. Halver. Academic Press Inc, New York.
- Schwalme, K. 1991. The role of environmental and physiological factors in the seasonal cycle of fatty acid composition in female northern pike *(Esox lucius* L.). Ph.D. Thesis, Department of Zoology, University of Alberta.
- Schwalme, K. and Mackay, W.C. 1992. Seasonal changes in the neutral and polar lipid fatty acid content of female northern pike *(Esox lucius* L.). Can. J. Zool. (In press).
- Sellner, P.A. and Hazel, J.R. 1982. Desaturation and elongation of unsaturated fatty acids in hepatocytes from thermally acclimated rainbow trout. Arch. Biochem. Biophys. 213: 58-66.
- Takeuchi, T. and Watanabe, T. 1977. Dietary levels of methyl laurate and essential fatty acid requirement of rainbow trout. Bull. Jap. Soc. Sci. Fisheries. 43: 893-898.
- Takeuchi, T. and Watanabe, T. 1979. Effect of excess amounts of essential fatty acids on growth of rainbow trout. Bull. Jap. Soc. Sci. Fisheries. 45: 1517-1519.
- Tanasichuk, R.W. and Mackay, W.C. 1989. Quantitative and

qualitative characteristics of somatic and gonadal growth of yellow perch *(Percaflavescens)* from Lac Ste. Anne, Alberta, Can. J. Fish. Aquat. Sci. 46: 989-994.

Watanabe, T., Ogino, C., Koshiishi, Y. and Matsunaga, T.

1974. Requirement of rainbow trout for essential fatty acids. Bull. Jap. Soc. Sci. Fisheries. 40: 493-499.

Watanabe, T. 1982. Lipid nutrition in fish. Comp. Biochem. Physiol. 73B: 3-15.