[Te]chnical Papers

[OF] THE U.S. FISH AND WILDLIFE SERVICE

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UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

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By Donald V. Rottiers
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UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
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Proximate Composition and Caloric Content of Eight Lake Michigan Fishes[1]

by

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Abstract

We measured the proximate composition (percentage lipid, water, fat-free dry material, ash) and caloric content of eight species of Lake Michigan fish: lake trout (*Salvelinus namaycush*), coho salmon (*Oncorhynchus kisutch*), lake whitefish (*Coregonus clupeaformis*), bloater (*Coregonus hoyi*), alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), deepwater sculpin (*Myoxocephalus quadricornis*), and slimy sculpin (*Cottus cognatus*). Except for alewives, proximate composition and caloric content did not differ significantly between males and females. And, for coho salmon, there was no significant difference in composition between fish collected in different years. Lipid and caloric content of lake trout increased directly with age. In all species examined, lipids and caloric contents were significantly lower in small, presumably immature, fish than in larger, older fish. Lipid content of lake trout, lake whitefish, and bloaters (range of means, 16–22%) was nearly 3 times higher than that of coho salmon, sculpins, rainbow smelt, and alewives (range of means, 5.2–7.0%). The mean caloric content ranged from 6.9 to 7.1 kcal/g for species high in lipids and from 5.8 to 6.3 kcal/g for species low in lipids. Although the caloric content of all species varied directly with lipid content and inversely with water content, an increase in lipid content did not always coincide with a proportional increase in caloric content when other components of fish composition were essentially unchanged. This observation suggests that the energy content of fish estimated from the proximate composition by using universal conversion factors may not necessarily be accurate.

Information on the proximate composition and caloric content of Great Lakes fishes is needed to understand energy flow through Great Lakes ecosystems and to evaluate laboratory-derived energy budgets. Such data are also useful for understanding the relation between forage availability, feeding levels, and the general well-being of fish. Because of increasing rates of salmonid stocking in the upper Great Lakes and the instability of the alewife (*Alosa pseudoharengus*), one of the principal prey fishes of these salmonids, forage availability will be a major concern in future fishery management.

Most of the published information on caloric content and proximate composition of freshwater fishes is based on analyses of the edible portion of commercial species (Atwater 1892; Ingalls et al. 1950; Sidwell et al. 1974). Information on the composition of whole freshwater fish – a few species excepted – is unavailable. Since fish usually ingest their prey whole, the whole fish and stomach contents must be analyzed to establish the energetic relations between predator and prey species.

Shul'man (1974) pointed out that information on proximate composition, particularly lipid content, is also useful for evaluating the condition of fish for wintering, migrating, and spawning, and for distinguishing racial and biological differences. Racial differences have been observed, for example, in the proximate composition of subpopulations of Lake Superior lake trout, *Salvelinus namaycush* (Eschmeyer and Phillips 1965; Thurston 1962).

Before direct calorimetry was in wide use, caloric content was estimated from the proximate composition of fish by using either the gross energy constants described by Brody (1945) and Klieber (1961) or constants based on digestibility of dietary components given by Phillips and Brockway (1959) and Phillips (1969). Thus much of the caloric information now available has been based on estimations. Meakins (1976) pointed out that no constants can be used in studies of fish production and energetics for energy incorporated as growth. As a result, direct measurement of the caloric content of individual fish and their prey must be made before data on growth and food intake rates from

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field and laboratory studies can be converted to equivalent energy units and compared. We found no published caloric values for Great Lakes species.

The purpose of this study was to measure the caloric content and proximate composition of eight Lake Michigan fishes and to determine the predictability of one component from another and, where possible, the yearly and seasonal change in composition of these species. The species studied were lake trout, coho salmon (*Oncorhynchus kisutch*), alewife, slimy sculpin (*Cottus cognatus*), deepwater sculpin (*Myoxocephalus quadricornis*), lake whitefish (*Coregonus clupeaformis*), rainbow smelt (*Osmerus mordax*), and bloater (*Coregonus hoyi*).

Materials and Methods

The fish analyzed in this study were collected in Lake Michigan from April through November 1969–71. The location, length, weight, date, and depth of capture were recorded for each fish. Sex was determined for mature lake trout, coho salmon, and alewives. Age was determined for lake trout by relating fin clips and lengths to stocking records (natural reproduction is not known to have occurred in recent decades; all fish stocked have been fin-clipped). Fish of a given species caught on the same date and weighing less than 0.5 kg were usually combined in a single composite sample. Fish were frozen immediately after capture and later transported to the Great Lakes Fishery Laboratory and stored at -30°C.

In the preparation of samples for proximate analysis and caloric determinations, fish were partly thawed, cut into 4- to 6-cm pieces, ground three times, and then mixed by kneading the sample in a plastic bag. Each time the fish were ground, the grinder head was removed and pieces of bone and skin that collected between the cutter blades and perforated plates were removed and mixed in a plastic bag with the portion of the sample that had already been extruded through the perforated plates. Subsamples (300 g) of the ground fish were placed in paper cups, then sealed in Saran bags, and refrozen at -30°C for later analysis. Before analysis, samples were thawed and homogenized in a blender. All samples used for proximate composition and caloric analysis were weighed to the nearest 0.0001 g.

Ash content was determined by placing 2 g of sample (wet weight) in a cool muffle furnace, heating it to 500°C, and holding it at that temperature for 3 h. Slow heating prevented the sudden generation of gases that might have ejected the sample from the crucible if heating had been rapid.

We measured lipids by using analytical procedures described by Reinert et al. (1974). A 10-g portion of ground fish (wet weight) was homogenized for 5 min in a 20-mL mixture (1:1) of isopropanol and benzene, then slowly boiled for 45 min in a water bath. Isopropanol lost through evaporation was replaced with hexane to complete extraction of lipids. After the sample had cooled, it was filtered through a preweighed column packed with glass wool. The remaining solid materials were washed four times with 5 mL of hexane and the recovered solvent was added to the original extract. When the total volume of extract had been reduced by evaporation to 20 mL, the extract was placed in a tared aluminum pan, and the remaining solvent evaporated from the pan at room temperature. Fat-free dry material (FFDM), an approximation of the total carbohydrate and protein in the sample, was defined as the percentage of the original sample weight remaining in the column after water and lipids had been removed and ash subtracted. The residue, FFDM, was dried and weighed. All proximate components were expressed as percentages.

Moisture content was determined by oven-drying 15 g of homogenized fish at 100°C until a constant weight was attained 18–24 h later. Dried samples were stored in a desiccator over silica gel until used for caloric analysis.

Caloric content was determined with a Parr Model 1241 adiabatic calorimeter (Anonymous 1968). Samples weighing 1 g (dry weight) were tamped into a stainless steel cup and combusted with oxygen under 25 atmospheres pressure. (The dried fish was tamped rather than pelletized because compression of the sample during pelletization was found to squeeze out lipids.) Oxygen bombs were standardized with benzoic acid at the beginning and end of each series of analyses. Standard values for the oxygen bombs did not change during these analyses. The heat of combustion was corrected for fuse wire burned and acid formed. No correction was made for sulfur because its concentration in fish is low (mean, 225 mg/100 g of fish) and does not vary widely among species (Gordon and Roberts 1977). Caloric content was expressed as kcal/g, wet and dry weight. We reanalyzed all samples that were incompletely burned in the oxygen bomb (about 4% of the total).

Using computer-generated scatter diagrams, we determined possible trends or relations between energy content, proximate composition, sex, age, season, year, and size for each species for which appropriate data were available. These trends were described by regression lines with standard errors of estimate and correlation coefficients. We used analysis of variance (ANOVA) to determine if the proximate composition and energy content of lake trout, coho salmon, and alewives differed significantly by sex or year. Coho salmon and lake trout were the only species for which we had sufficient data on caloric content, proximate composition, age, weight, and sex of individual fish to measure variability and establish certain trends for prediction. All other species were analyzed as composite samples.

Results

The whole fish of the different species varied in proximate composition; in percentages of water, lipids, and ash; and in FFDM (Table 1; Fig. 1). Statistically significant

linear regressions and correlation coefficients describing the relation between proximate components, caloric values, and other data were found in 33 of 48 apparent trends selected from among 143 computer-generated scatter diagrams representing various combinations of variables for the eight species (Table 2; Figs. 2–5). Although we had insufficient data to establish significant trends for each species, we included the data for all species in Figs. 1–4.

No clear seasonal trends in energy content were observed for any species. Although neither lipid nor caloric content differed significantly between years for lake trout and alewives, both were significantly lower in coho salmon in 1969 than in 1970–71 (ANOVA, $P<0.05$). The mean lipid and caloric contents were lower — but not significantly so — in females than in males in all eight species (Table 1). Caloric content and proximate composition of coho salmon and lake trout varied with size and maturity (Tables 1 and 3; Figs. 4 and 5).

Mean water content by species ranged from 58.5% in lake whitefish to 77.6% in deepwater sculpins. Because water and lipid content were inversely related (Figs. 2a, 2b, and 3a; Table 2), mean lipid content was highest in lake whitefish (22.4%) and lowest in sculpins (5.3%).

Ash and FFDM were the least variable of the four proximate components (Fig. 1). The mean ash content varied from a high of 3.0% for alewives to a low of 1.7% for lake

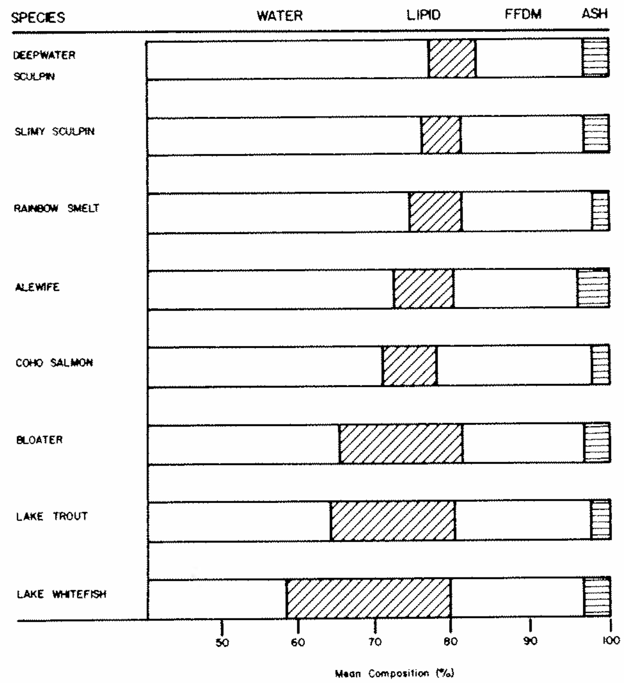

Fig. 1. Mean proximate composition of eight species of Lake Michigan fishes (FFDM + fat-free material).

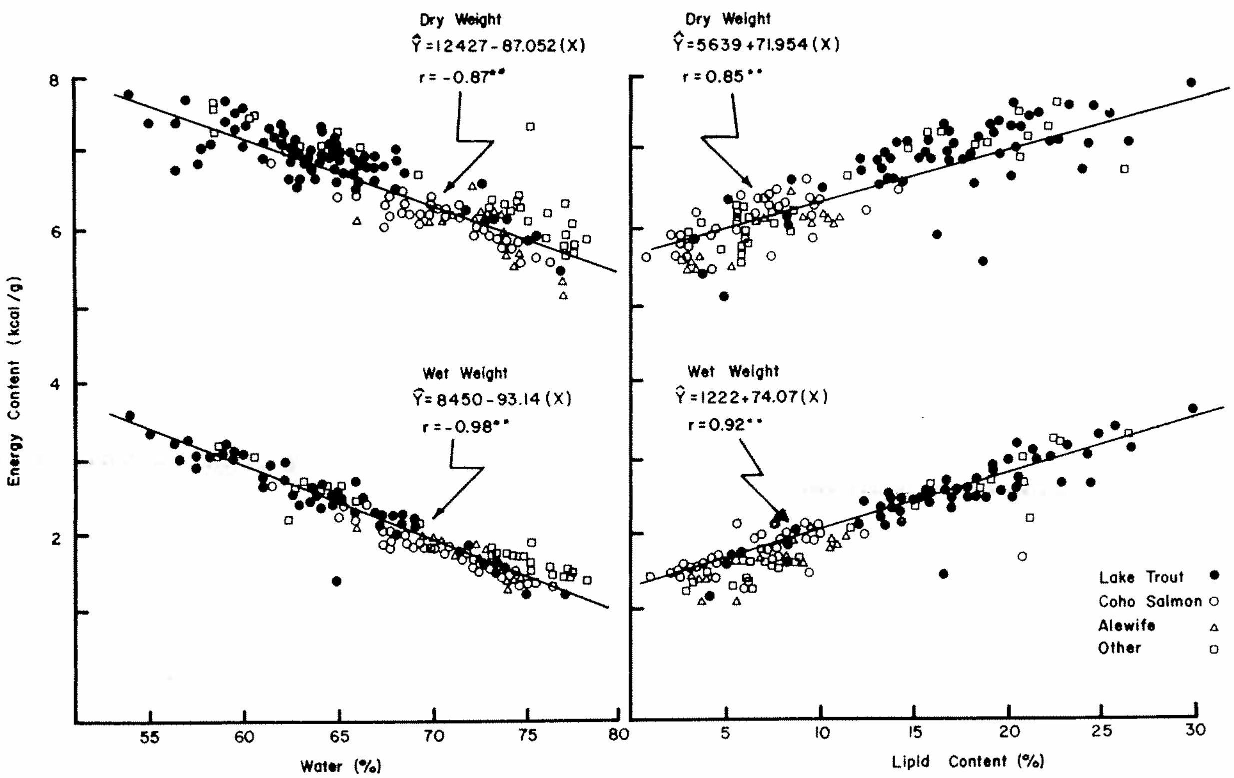

Fig. 2. Relation between dry and wet weight energy content and water and lipid content in lake trout, coho salmon, and alewives, and five other species (data combined).

Table 1. *Mean caloric and proximate analysis data (SD in parentheses) for eight Lake Michigan fishes.*[a]

Species	Number of samples[b]	Mean no. fish per sample	Mean length (mm)[c]	Mean weight (g)		Mean proximate composition (%)				Mean caloric content (kcal/g)	
				Wet	Dry	Water	Lipid	Ash	FFDM[d]	Dry wt	Wet wt
Alewife	5 ♂	57	ND	41.3	11.8	71.5 (1.80)	10.1 (1.0)	2.8 (0.35)	15.6 (0.35)	6.138 (0.038)	1.733 (0.130)
	6 ♀	58	ND	41.6	11.6	72.1 (3.70)	7.9 (2.0)	3.0 (0.16)	16.9 (2.1)	6.012 (0.273)	1.682 (0.262)
	6 Im	60	ND	46.0	11.8	74.4 (1.74)	5.0 (2.4)	3.1 (0.50)	17.4 (4.2)	5.822 (0.398)	1.495 (0.193)
Mean				43.2	11.8	72.8 (2.67)	7.5 (2.8)	3.0 (0.38)	16.7 (1.76)	5.982 (0.302)	1.636 (0.216)
Lake trout	54 ♂	1	584	2,354.9	885.4	62.4 (3.15)	19.0 (4.2)	1.7 (0.26)	16.8 (2.30)	7.103 (0.334)	2.674 (0.307)
	23 ♀	1	619	2,560.3	939.6	63.3 (2.64)	17.2 (3.6)	1.8 (0.26)	17.7 (1.53)	6.999 (0.286)	2.576 (0.262)
	36 Im	2	507	1,206.5	451.2	68.6 (5.00)	12.0 (4.6)	1.9 (0.31)	17.6 (2.52)	6.486 (0.462)	2.059 (0.453)
Mean			570	2,030.9	718.9	64.6 (4.64)	16.4 (5.5)	1.8 (0.28)	17.3 (2.27)	6.885 (0.406)	2.458 (0.446)
Coho salmon	25 ♂	1	602	2,848.9	868.9	69.5 (3.73)	8.7 (4.9)	2.0 (0.37)	19.8 (1.86)	6.227 (0.276)	1.931 (0.353)
	25 ♀	1	576	2,392.1	708.1	70.4 (3.22)	7.8 (4.2)	1.9 (0.20)	20.0 (3.84)	6.157 (0.346)	1.866 (0.324)
	26 Im	1	503	1,380.6	381.0	72.4 (2.99)	5.6 (4.2)	1.9 (0.26)	20.1 (1.90)	6.003 (0.307)	1.664 (0.270)
Mean			560	2,196.3	641.3	70.8 (3.50)	7.3 (4.6)	1.9 (0.28)	20.0 (2.66)	6.123 (0.321)	1.818 (0.333)
Ra ıbow smelt	10	79	ND	19.2	4.9	74.6 (1.24)	6.6 (1.0)	1.8 (0.21)	16.9 (1.26)	6.261 (0.388)	1.590 (0.120)
Lake whitefish	5	1	564	2,420.8	997.4	58.8 (4.33)	22.4 (2.7)	1.7 (0.27)	17.2 (1.73)	7.092 (0.323)	2.919 (0.256)
Bloater	8	45	ND	142.4	48.8	65.7 (3.94)	16.0 (4.3)	2.1 (0.24)	16.3 (1.05)	6.884 (0.453)	2.360 (0.430)
Slimy sculpin	6	390	ND	6.7	1.6	76.2 (0.99)	5.3 (1.7)	2.6 (0.17)	15.9 (1.52)	5.766 (0.204)	1.372 (0.097)
Deepwater sculpin	4	164	ND	14.6	3.2	77.6 (0.57)	5.4 (1.5)	2.6 (0.17)	14.4 (1.69)	5.775 (0.175)	1.295 (0.049)

[a]Data on caloric content and proximate composition of individual fish are available from the senior author.
[b]Im = immature.
[c]ND = no data.
[d]Fat-free dry material, ash-free.

Table 3. *Mean caloric and proximate analysis data (SD in parentheses) for Lake Michigan lake trout of different ages.*

Age	Number of samples	Mean no. fish per sample	Mean length (mm)[a]	Mean weight (g)		Proximate composition (%)				Calories (kcal/g)	
				Wet	Dry	Water	Lipid	Ash	FFDM[b]	Dry wt	Wet wt
I	1	4	ND	35.0	8.1	77.0	4.2	2.15	16.7	5.421	1.247
II	10	4	304	388.3	103.7	73.3 (2.92)	6.7 (3.42)	1.78 (0.27)	18.2 (1.60)	6.101 (0.307)	1.637 (0.269)
III	13	2	510	1,422.5	428.2	66.9 (2.90)	13.3 (3.23)	1.97 (0.23)	17.8 (1.02)	6.721 (0.301)	2.235 (0.292)
IV	43	1	566	2,220.0	834.7	62.4 (3.02)	18.7 (3.95)	1.71 (1.80)	17.2 (1.80)	7.050 (0.253)	2.652 (0.271)
V	38	1	607	2,468.1	900.0	63.5 (3.18)	17.6 (4.43)	1.79 (0.32)	17.1 (2.46)	7.014 (0.384)	2.569 (0.330)
VI	7	1	644	2,976.4	1,117.1	61.1 (1.42)	19.3 (3.32)	1.78 (0.19)	17.2 (2.43)	7.140 (0.299)	2.739 (0.209)

[a]ND = no data.
[b]Ash-free, fat-free dry material.

Table 2. *Regression equations describing significant relations between proximate composition and caloric content for various Great Lakes fishes.*

Species and equations[a] (Y	=	a	+	b	X)	Degrees of freedom	Standard error of estimate	Correlation coefficients[b]
Lake trout								
Calories/g (dry)	=	12,146	–	81.492	(% water)	112	264.32	–0.82
	=	5,854	+	62.838	(% lipid)	112	306.82	0.75
	=	8,111	–	683.95	(% ash)	112	421.57	–0.41
	=	6,206	+	0.334	(mean weight, g)	112	342.75	0.67
Calories/g (wet)	=	8,519	–	93.875	(% water)	112	93.28	–0.98
	=	1,264	+	72.757	(% lipid)	112	198.18	0.90
	=	3,520	–	592.62	(% ash)	112	415.89	–0.37
	=	1,713	+	0.367	(mean weight, g)	112	289.59	0.76
Water (%)	=	77.15	–	0.767	(% lipid)	112	1.95	-0.91
	=	72.39	–	0.00386	(mean weight, g)	112	2.98	–0.77
	=	71.16	–	1.573	(age)	112	4.29	–0.39
Oil (%)	=	8.063	+	0.00411	(mean weight, g)	112	3.98	0.69
FFDM (%)	=	20.750	–	0.213	(% lipid)	112	1.95	–0.52
Coho salmon								
Calories/g (dry)	=	11,601	–	77.336	(% water)	75	173.02	–0.84
	=	5,752	+	51.064	(% lipid)	75	220.87	0.73
	=	5,856	+	0.1238	(mean weight, g)	75	227.82	0.51
Calories/g (wet)	=	8,104	–	88.814	(% water)	75	119.33	–0.93
	=	1,397	+	57.364	(% lipid)	75	205.58	0.79
	=	1,503	+	0.1434	(mean weight, g)	75	275.58	0.57
Water (%)	=	75.316	–	0.618	(% lipid)	75	2.07	–0.81
	=	74.135	–	0.0015	(mean weight, g)	75	2.88	–0.58
FFDM (%)	=	22.68	–	0.369	(% lipid)	75	2.06	–0.64
Oil (%)	=	4.328	+	0.00137	(mean weight, g)	75	4.24	0.39
Alewives								
Calories/g (dry)	=	11,172	–	71.313	(% water)	16	242.15	–0.63
	=	5,305	+	89.844	(% lipid)	16	174.64	0.83
	=	7,538	–	522.03	(% ash)	16	236.65	–0.65
Calories/g (wet)	=	7,295	–	77.801	(% water)	16	64.44	–0.96
	=	1,131	+	66.702	(% lipid)	16	114.21	0.86
	=	2,493	–	288.36	(% ash)*	16	192.98	–0.50*
Water (%)	=	78.259	–	0.727	(% lipid)	16	1.79	–0.76
Lake whitefish								
Calories/g (wet)	=	1,021	+	84.87	(% lipid)*	4	132.50	0.89*
Bloater								
Calories/g (dry)	=	5,527	+	85.12	(% lipid)*	7	293.45	0.80*
Calories/g (wet)	=	977	+	87.30	(% lipid)	7	169.99	0.93

[a]Dry = dry weight; wet = wet weight.

[b]All slopes and correlation coefficients highly significant (0.01), except those marked with an asterisk, which are significant (0.05). When r is 0.05 or less, only a small portion of the variation in Y can be attributed to its linear regression on X; however, such statistical significance does indicate a linear relation with non-zero slope (Snedecor and Cochran 1967).

whitefish. Among adult fish, ash content was generally higher in small species (alewives, rainbow smelt, and sculpins) than in larger species (lake trout, lake whitefish, coho salmon, and bloaters). Caloric content of lake trout and alewives decreased, however, with increasing ash content (Table 2). Mean FFDM ranged from 14.4% for sculpins to 20.0% for coho salmon. In coho salmon, FFDM content decreased with increasing lipid content (Table 2), but averaged 2.3 to 5.6 percentage points higher than in any of the other species (range, 14.4–17.7%).

The mean caloric content (dry weight) ranged from 5.77 kcal/g in slimy sculpins to 7.09 kcal/g in lake whitefish (Table 1). The eight species studied can be divided into two groups according to their caloric content: those with a low caloric content were young lake trout, rainbow smelt, alewives, both sculpins, and coho salmon; and those with a high caloric content (usually above 6.5 kcal/g) were adult lake trout, lake whitefish, and bloaters (Fig. 2b). Fish high in calories had 2 to 5 times as much lipid as did fish containing fewer calories. In all species, energy content

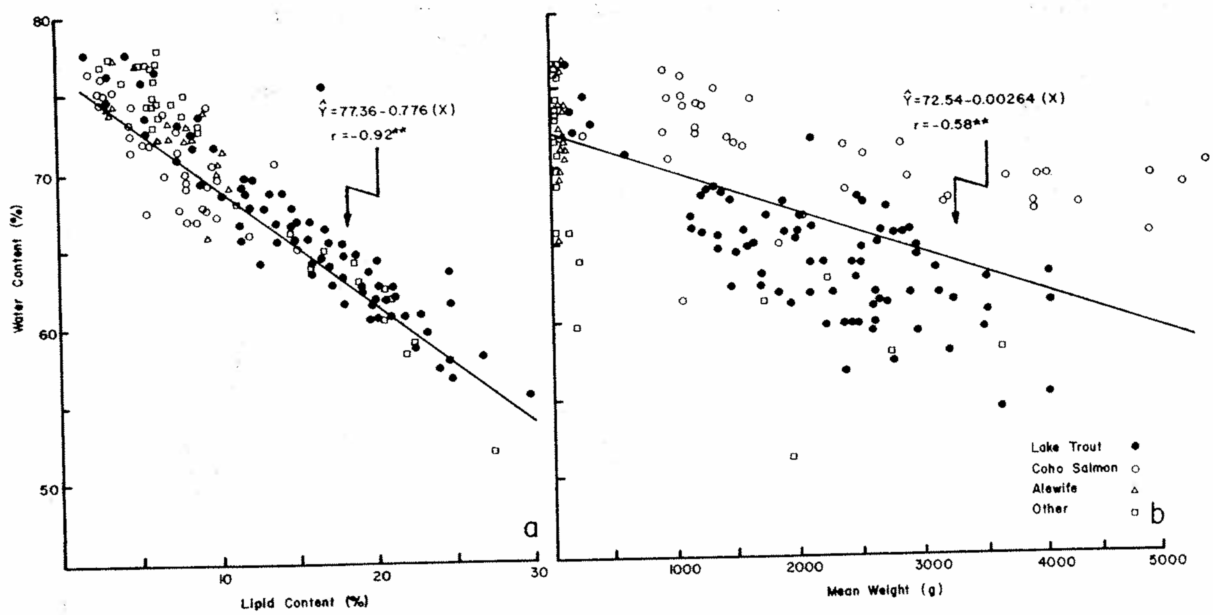

Fig. 3. Relation between water content and lipid content and mean weight of lake trout, coho salmon, alewives, and five other species (data combined).

increased as lipid content increased and decreased as water content increased (Fig. 2). In coho salmon and lake trout, the only species for which individual weights were available, caloric and lipid content increased and water content decreased as mean weight increased (Figs. 3a and 4). Caloric content of lake trout and alewives decreased with increasing ash content (Table 2). In lake trout, the only species for which age information was available, caloric and lipid content increased (Figs. 5a and 5b) and water content decreased with increasing age (Table 3). Although the slopes of the lines describing the relation between caloric content expressed on a wet- and dry-weight basis and the other variables were similar, the correlation coefficients were usually higher and the standard errors lower for caloric values based on wet weights (Figs. 2a and 2b; Table 2).

Discussion

Atwater (1892) provided proximate compositions of edible portions for 52 species of American fishes (including lake trout, alewives, rainbow smelt, and lake whitefish). His data cannot be converted accurately to a whole-fish basis, however (even though he gave information on the percentage of fish discarded as inedible), and thus are of little value in evaluating fish energetics. Dugal (1962) presented data for whole alewives and rainbow smelt from Lake Erie. His values for alewives were within the range we found, except for lipids (his range, 11.8–25.7%), which were higher than those reported here. His values for lipids in rainbow smelt were lower than those we recorded. He observed that composition seemed uniform in some species regardless of season or location of capture, whereas in others there was variation. He suggested that these differences were probably related to habitat and diet.

Because we sampled few ripe fish, detection of sexual differences in energy and proximate composition was difficult. Thurston (1962) found no sexual difference in proximate composition in lake trout fillets. Meakins (1976) noted, however, that in threespine sticklebacks (*Gasterosteus aculeatus*) the caloric content of whole gravid females was 23% higher than that of males of similar size. We observed significant sexual differences in composition only between composite samples of male and female alewives after immature fish had been removed. Sexual differences in mature fish are probably greatest just before the spawning season. Because of seasonal changes in fish composition and gonadal development, sexual differences may not always be detectable when all the data for fish collected in a single year are separated by sex and compared, as in the present study. Sexual differences may be detected for most species only when samples of whole fish are compared after they are stratified by age and date of capture.

Stansby (1947) observed that the greatest variation in fish composition was in lipid content, which varied as much as 11-fold in the mackerel (*Scomber scombrus*). He noted that season was a major factor in variation and that diet, locality of collection, size, and age were also important factors. Although we observed little evidence of a seasonal change in the composition of the fish we examined, a sea-

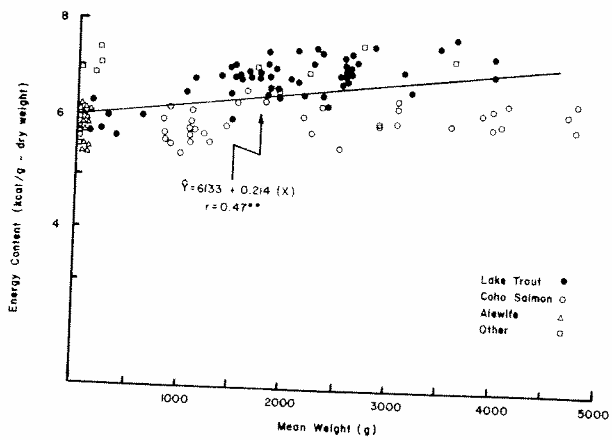

Fig. 4. Relation between energy content and mean weight of lake trout, coho salmon, alewives, and five other species (data combined).

sonal change in the lipid content of yellow perch (*Perca flavescens*), rainbow smelt, and lake trout was observed in samples analyzed recently at the Great Lakes Fishery Laboratory (M. J. Mac, personal communication). The expected seasonal changes in lipid content of the fishes examined were probably not detectable because sampling was inadequate at certain times of the year and variations in lipid content were large among fish of different sizes and ages. Stansby (1947) noted that variations in lipid content increased as fish grew larger. We observed that lipid content of lake trout varied more with age than with size. The decreased rate of lipid accumulation with increasing age, observed in lake trout, is probably related to the slowing of growth rate as the fish grows older and approaches sexual maturity. Lake trout older than those collected for this study were unavailable in Lake Michigan during 1969–71; however, it is likely that the lipid content would have continued to increase at a decreasing rate with age. Love (1980) stated that as fish mature repeatedly in successive years they appear to accumulate progressively larger stores of lipid, presumably to supply gonads which, at least in some species, increase in size with the years disproportionately to the body size of the fish. Therefore, lipid accumulation seems to us to be more logically associated with age than with size of fish, even though the variation is generally greater within age groups than within size groups.

Even though caloric contents based on dry weight are generally accepted as being more accurate than those based on wet weight, the higher correlation coefficients and lower standard errors for caloric values based on wet weight suggest that wet-weight values may be the better form in which to express these data. The apparent improvement in the correlation coefficients and standard error terms is due to the method of computation (wet-weight caloric content was equal to the dry-weight caloric content multiplied by 100, and then divided by 100 minus the percentage of water in

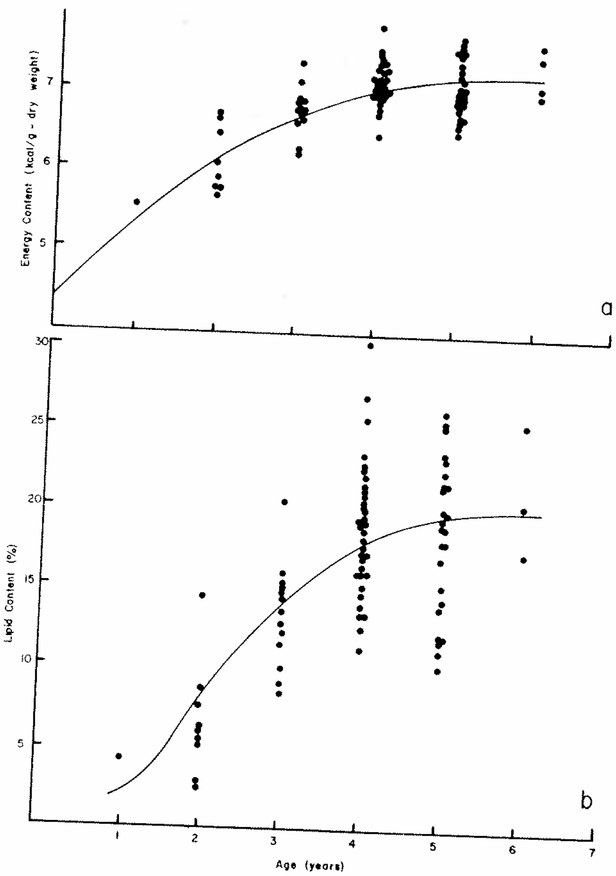

Fig. 5. Relation between lipid and energy content and age of lake trout.

the sample). When variation is calculated as a percentage of the mean (coefficient of variation), however, dry-weight caloric values, as expected, have the lowest percent variation. The distances between the data points and the lines describing the relation between caloric content and other variables in Fig. 2 are not the same for wet- and dry-weight data. The main cause of this variation is the use of individual conversion factors for each wet-weight computation.

The inverse relation between lipid and water content is well known (Love 1970, 1980; Denton and Yousef 1976). However, little information exists on the relation between ash and caloric content observed in lake trout and alewives and a similar relation between lipids and FFDM observed in coho salmon and lake trout (see footnote 2 of Table 2). Groves (1970) derived an equation that enables an accurate estimation of total water, protein, and FFDM in young sockeye salmon (*Oncorhychus nerka*) when either water content or fork length are known. He pointed out that, except for small amounts of lipid materials normally found in lean tissue, no necessary physiological relation exists between lipids and FFDM. The observed relation between caloric content and ash may be a simple replacement or

dilution of energy-containing materials by inorganic materials during growth, resulting in fewer calories per unit weight. Similarly, FFDM may also be displaced or diluted as lipid content increases. Thurston (1962) observed that siscowets (a variety of lake trout) with a lipid content of 21.0–67.2% had a protein content of 6.1–15.9%, whereas "lean" lake trout, with a lower lipid content (1.9–22.5%), contained more protein (14.8 to 20.8%). He also observed that ash was 0.77–1.3% in "lean" lake trout and 0.38–0.85% in siscowets. These data support our contention that the changes observed were caused by replacement or dilution of energy-containing materials by ash-producing materials and FFDM by lipids. The relation between FFDM and ash, lipids, and caloric content in coho salmon appears to be the reverse of that observed for lake trout. Since less of the total body composition of coho salmon consists of lipids, a large percentage of the fish's energy must be stored as protein. The protein content of the edible portions of coho salmon from the Pacific Coast ranges from 20.0 to 22.8% (Karrick and Thurston 1964) – well within the range of values obtained for whole coho salmon from the Great Lakes.

Information on the proximate composition and caloric content of Great Lakes fishes can be used to adjust energy equivalents of growth and food intake rates derived from laboratory growth and food conversion studies to energy levels observed for these species in the lake. Since the mean caloric contents of the major salmonid forage species in Lake Michigan were similar – 5.7 ± 0.2 kcal/g (mean caloric content $\pm$ SD) for sculpins, 6.1 ± 0.3 kcal/g for rainbow smelt, and 6.0 ± 0.3 kcal/g for alewives – a shift in the species composition of the forage would not be expected to significantly alter the energy budget of salmonids.

The mean caloric content of yearling lake trout fed Lake Michigan alewives for 12 weeks in a laboratory study was 6.1 ± 0.24 kcal/g, compared with 6.1 ± 0.3 kcal/g for 2-year-old lake trout in the lake (Rottiers 1980). This similarity of energy content of fish reared in different environments, but on forage of similar composition, suggests that the caloric content and proximate composition of forage are the major factors affecting the proximate composition of the predator fish.

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