FOOD OF SALMONINE PREDATORS IN LAKE SUPERIOR, 1981-87

Great Lakes Fishery Commission

TECHNICAL REPORT 59

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ABSTRACT. Diets of ten species of Lake Superior salmonines are described. Rainbow smelt (Osmerus *mordax)* were the primary prey during all seasons and years for inshore lake trout *(Salvelinus namaycush),* Pacific salmon *(Oncorhynchus* spp.), Atlantic salmon *(Salmo salar),* brown trout *(S. trutta),* brook trout *(Salvelinus fontinalis),* and splake (lake trout x brook trout hybrid). Coregon-ines were the second most-important prey for chinook salmon (0. *tshawytscha),* siscowet trout (S. *namaycush siscowet),* and splake. Invertebrates were important to rainbow trout (0. *mykiss),* coho salmon *(0. kisutch),* and pink salmon (0. *gorbuscha),* especially

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during the summer. Diets of lake trout from inshore and offshore locations differed markedly. Rainbow smelt were the primary food of inshore lake trout, and coregonines were the main food of offshore lake trout. Chinook salmon and inshore lake trout had the most similar diets because they ate similar proportions of rainbow smelt and coregonines. Salmonines generally ate more rainbow smelt and less coregonines in proportion to the abundance of these prey in the lake. If rainbow smelt populations collapse, the ability of salmonines to convert to a diet based on lake herring *(Coregonus artedi)* could be important to the stability of predator populations.

INTRODUCTION

Lake herring *(Coregonus artedi)* and deepwater ciscoes *(Coregonus* spp.) were historically the principal prey of lake trout *(Salvelinus namaycush) in* Lake Superior (Dryer et al. 1965). Beginning in the 1950s, lake herring stocks declined lakewide, mainly from sequential overfishing of discrete stocks (Lawrie and Rahrer 1972, Selgeby 1982, MacCallum and Selgeby 1987). As lake herring stocks declined in the 1950s and early 1960s, the exotic rainbow smelt *(Osmerus mordax),* which invaded Lake Superior in the early 1930s, increased in abundance and replaced coregonines as the major food of lake trout (Dryer et al. 1965). In the early 1950s, up to 90% of lake trout food was coregonines. By 1963, rainbow smelt made up 66% of the diet, and coregonines dropped to only 8% (Dryer et al. 1965).

As the composition of prey populations changed, the total number of predators in Lake Superior increased greatly during the 1960s, 1970s, and 1980s. Annual lakewide stocking of salmonines (lake trout for rehabilitation purposes and exotics for added fishing opportunities) increased from less than 1.0 million fish in 1958 to more than 9.5 million fish in 1986 (MacCallum and Selgeby 1987). Species stocked in addition to lake trout were rainbow trout *(Oncorhynchus mykiss),* brown trout *(Salmo trutta),* Atlantic salmon (S. *salar),* coho salmon (0. *kisutch),* chinook salmon *(0. tshawytscha),* and splake-a lake trout x brook trout *(Salvelinus fontinalis)* hybrid. In addition, wild lake trout were reproducing at many locations (Krueger et al. 1986) and pink salmon *(0. gorbuscha),* coho salmon, chinook salmon, brown trout, and rainbow trout were reproducing in many tributaries (MacCallum and Selgeby 1987).

Concern about stability of prey and predator components of the Lake Superior fish community arose when rainbow smelt biomass declined by more than 90% from 1978 to 1981 (Selgeby 1985, MacCallum and Selgeby 1987, Hansen 1990).

Because a sharp reduction in rainbow smelt biomass occurred simultaneously with increasing predator populations, a study was conducted to evaluate the diets of Lake Superior salmonines. In this paper we describe the diets of ten species of Lake Superior salmonines between 1981 and 1987, and examine the degree of overlap in the diets of various salmonines.

METHODS

Stomachs from adult lake trout and introduced salmonines (all adult-sized fish) were obtained from the Wisconsin, Michigan, Minnesota, and Ontario waters of Lake Superior from 1981-87 - except during 1983 when no stomachs were collected. (Table 1). The main sources were anglers, tribal and state-licensed commercial gillnetters, and government-agency assessments. Angler-caught fish were obtained at fishing tournaments, from charter-boat operators, and from individuals. Most samples of angler-caught fish were from Minnesota and Wisconsin waters with fewer numbers from central Michigan (Keweenaw Peninsula east to Munising) and Ontario waters (Whitefish Bay, Michipicoten Harbor, Black Bay, Nipigon Bay, and Thunder Bay). All siscowet trout (S. namaycush siscowet) and additional lake trout were collected from commercial gillnet catches from Beaver Bay to Grand Portage, Minnesota; the Apostle Islands in Wisconsin waters; and from Michigan waters eastward to Marquette. Stomachs of offshore lake trout were obtained during federal assessment netting at Stannard Rock and Isle Royale, Michigan. In this report, all lake trout taken from along the mainland shore are called “inshore.” Lake trout from Stannard Rock and Isle Royale are called “offshore.” Additional stomach samples of various species were obtained from assessment netting by the U.S. Fish and Wildlife Service (USFWS), Red Cliff Fisheries Department, Great Lakes Indian Fish and Wildlife Commission, and by natural-resources agencies in Minnesota, Wisconsin, Michigan, and Ontario.

Table 1. Sample sizes of Lake Superior salmonines examined for stomach contents by year and location.

Wisconsin = WI, Michigan = MI, Minnesota = MN, Ontario = ON.

	Year and location											
	1981				1982				1984			
	WI	MI	MN	ON	WI	MI	MN	ON	WI	MI	MN	ON
Lake trout	22.5	241	30	-	466	20	90	-	16	-	1,161	-
Chinook salmon	10	1	-	-	11		-	-	-	-	74	-
Coho salmon	9	6	39	-	25		1	-	-	-	248	-
Siscowet trout		-	-	-			-	-	-	-	194	-
Rainbow trout	4	5	5	-	2		-	-	-	-	17	-
Brown trout	27	-	-	-	8		-	-	-	-	4	-
Atlantic salmon		-	-	-	-		-	-	-	-	3	-
Pink salmon	5	-	-	-			-	-	-	-	-	-
Brook trout	1	-	-	-	1		-	-	-	-	-	-
Splake	27	-	-	-	11		-	-	-	-	-	-

	Year and location											
	1985				1986				1987			
	WI	MI	MN	ON	WI	MI	MN	ON	WI	MI	MN	ON
Lake trout	836	-	838	-	6.57	-	587	-	695	140	-	-
Chinook salmon	-	-	82	-	-	-	69	-	18	3	37	105
Coho salmon	-	-	138	-	-	-	312	-	37	13	26	-
Siscowet trout	-	-	146	-	-	-	46	-	28	476	-	-
Rainbow trout	-	-	37	-	-	-	13	-	2	1	8	32
Brown trout	-	-	4	-	-	-	2	-	25	-	-	-
Atlantic salmon	-	-	2	-	-	-	8	-	-	-	-	-
Pink salmon	-	-	-	-	-	-	-	-	-	-		1
Brook salmon	-	-	-	-	-	-	-	-	-	-	-	19
Splake	-	-	-	-	-	-	-	-	2	-	-	-

All predators examined for diet were processed similarly. Total length (mm) and weight (g) were measured for each predator. Digestive tracts were excised and either placed in plastic bags and frozen, or preserved in jars with 10% formalin. In the laboratory, stomach contents were identified by species when possible and sorted into the following prey categories:

1) rainbow smelt,

2) coregonines-primarily lake herring with smaller numbers of deepwater ciscoes *(Coregonus* spp.),

3) sculpins *(Cottidae* spp. and *Myoxocephalus thompsoni),*

4) other fish prey,

5) aquatic insects,

6) terrestrial insects,

7) opossum shrimp *(Mysis relicta),* and

8) other invertebrates.

The collective weight of all organisms within a prey category was measured to the nearest 0.1 g. Total lengths were measured for undigested prey fish and estimated for partially digested fish.

Results are reported as the percent contribution to the total food weight. by each prey category. All analyses were structured to yield an unweighted mean percent by weight on a monthly or yearly basis. The percent-frequency-of-occurrence data by prey category is reported for all combined samples of a given species. Except where noted, data were pooled over all locations.

Diet summaries are presented for all predator species sampled. Lake trout was the primary target predator, and sample sizes were routinely large. Therefore, lake trout diets were examined in detail. Samples of chinook salmon and coho salmon were smaller, but were considered adequate for a description of seasonal diet trends.

Regression analysis was used to investigate the relationship between predator length and rainbow smelt length in the stomachs of lake trout, chinook salmon, and coho salmon. The relationship between lake trout length and coregonine length was also investigated. Differences among the non-normal size distributions of rainbow smelt eaten by lake trout, chinook salmon, and coho salmon with a total length of 450-600 mm were tested using a Kruskal-Wallis test (Zar *1974).*

Diet similarity indices were calculated between pairs of predators with the method of Shorygin (Windell 1971). Index values range from 0 for non-overlapping diets to 100 for identical diets. Data from all months and years were combined for the comparisons. No attempt was made to compare diets of predators of different sizes within each species because samples of smaller fish were few.

RESULTS

Rainbow smelt were the principal prey for seven of the ten species examined. Rainbow smelt composed from 46%-77% by weight of the diets of inshore lake trout, chinook salmon, Atlantic salmon, brown trout, brook trout, and splake (Table 2). Invertebrates (primarily terrestrial insects) dominated the food of coho salmon, pink salmon, and rainbow trout. Coregonines were the major food of offshore lake trout, but were of secondary importance to inshore lake trout, siscowet trout, chinook salmon, and splake. Siscowet trout consumed principally sculpins, mostly deepwater *(Myoxocephalus thompsoni)* and slimy (Cottus *cognatus).* Other food items eaten by salmonines were burbot *(Lota lota),* alewife *(Alosa pseudoharengus),* ninespine stickleback *(Pungitius pungitius),* white sucker *(Catostomus commersoni),* opossum shrimp, and burrowing amphipods *(Diporeia* spp.), but all were of minor importance.

Spiny water fleas *(Bythotrephes cederstroemi)* were found in salmonine stomachs collected in October and November, 1987, near Houghton Point, Wisconsin, and from Whitefish Bay, Ontario. The spiny water flea is a large, predatory cladoceran native to northern European lakes that has recently invaded the Great Lakes (Bur et al. 1986, Cullis and Johnson 1988). Salmonines that ate B. *cederstroemi* were chinook salmon, coho salmon, pink salmon, splake, brown trout, and rainbow trout. Generally, large numbers of the cladoceran were eaten, and as many as 900 specimens were found in an individual stomach.

The frequency of occurrence of rainbow smelt was higher than any other prey in the stomachs of inshore lake trout, chinook salmon, brown trout, and splake (Table 2). Terrestrial insects occurred frequently (21%-78%) in the stomachs of all species except offshore lake trout and siscowet trout.

Diets of inshore lake trout, chinook salmon, and coho salmon were dominated by rainbow smelt during most months, but changes in diet composition occurred seasonally (Fig. 1). Rainbow smelt composed from 56%-99% of the diets by weight of inshore lake trout, chinook salmon, and coho salmon during April and May. During the summer months, diet diversity increased. Rainbow smelt made up less of the summer diet, and percentages increased for:

1) coregonines, other fish, and terrestrial insects for inshore lake trout;

2) coregonines, terrestrial insects, and opossum shrimp for chinook salmon; and

3) terrestrial insects and opossum shrimp for coho salmon.

The diets of inshore lake trout and chinook salmon contained more rainbow smelt and coregonines during fall and winter. Also, consumption of coregonines was highest during this period. The diet of coho salmon remained diverse in the fall and winter. Invertebrates, rainbow smelt, and other fish were all found in their diet.

Marked differences were observed in the diet compositions of inshore and offshore lake trout. Diets of inshore lake trout consisted of 71% rainbow smelt and 15% coregonines by weight. Offshore lake trout diets consisted of 75% coregonines and only 8% rainbow smelt (Table 2). Offshore lake trout ate more opossum shrimp and sculpins than inshore lake trout. Food of offshore lake trout in this study closely resembled the historical diet of lake trout in Lake Superior prior to the invasion of rainbow smelt (Dryer et al. 1965).

Inshore lake trout of similar size (450-600 mm total length) from Minnesota and Wisconsin waters exhibited major diet differences. For this comparison, only data from May to September 1985-86 were used because sample sixes for both areas were adequate only for these months and years. During that period, terrestrial insects composed 27% by weight of the diet of lake trout from Minnesota waters and only 3% from Wisconsin. Rainbow smelt use was higher among lake trout from Wisconsin waters (74%) than from Minnesota (54%). Coregonines contributed 14% of the food eaten by lake trout in both areas. A lakewide comparison among all geographic areas was not possible because few inshore lake trout samples were obtained from either Ontario or Michigan.

Table 2. Mean percent by weight and percent frequency of occurrence of the diet

	N	Percent empty	Length range (mm)
Lake trout-inshore	5,899	42	170-932
Lake trout-offshore	135	10	221-932
Chinook salmon	410	49	240-980
Coho salmon	854	15	210-737
Siscowet trout	858	33	312-726
Rainbow trout	126	17	254-737
Brown trout	70	44	246-673
Atlantic salmon	13	62	425-724
Pink salmon	6	33	340-440
Brook trout	21	33	270-490
Splake	40	73	330-610

of salmonines from Lake Superior waters, 1981-87.

Mean percent by weight (percent frequency of occurrence)

Rainbow smelt	Coregonines[a]	Sculpins[b]	Other fish[c]	Terrestrial insects	Aquatic insects	Opossum shrimp	Other invertebrates[d]
71(56)	15(7)	2(4)	6(9)	4(28)	<1(<1)	1(7)	<1(4)
8(7)	75(38)	4(9)	4(4)	<1(2)	<1(2)	7(44)	2(1)
64(37)	19(8)	<1(2)	2(11)	7(21)	1(1)	6(23)	1(7)
37(24)	2(2)	<1(1)	7(10)	19(74)	19(1)	6(30)	11(1)
10(2)	20(15)	67(59)	2(3)	1(9)	<1(1)	1(18)	<1(1)
20(12)	0(0)	0(0)	0(0)	53(78)	11(13)	7(7)	9(2)
46(38)	9(5)	8(5)	8(13)	13(36)	10(5)	<1(8)	7(8)
77(40)	1(20)	0(0)	0(0)	4(40)	0(0)	19(40)	0(0)
33(75)	0(0)	0(0)	0(0)	33(25)	0(0)	0(0)	33(25)
47(4)	0(0)	41(3)	1(14)	5(71)	6(71)	0(0)	<1(7)
59(55)	0(0)	1(1)	19(18)	7(36)	13(9)	0(0)	2(1)

[a] Mostly lake herring, with some deepwater ciscoes.
[b] Mostly slimy and deepwater sculpins.
[c] Alewife, burbot, ninespine stickleback, and white sucker.
[d] *Diporeia* spp., *Bythotrephes cederstroemi.*

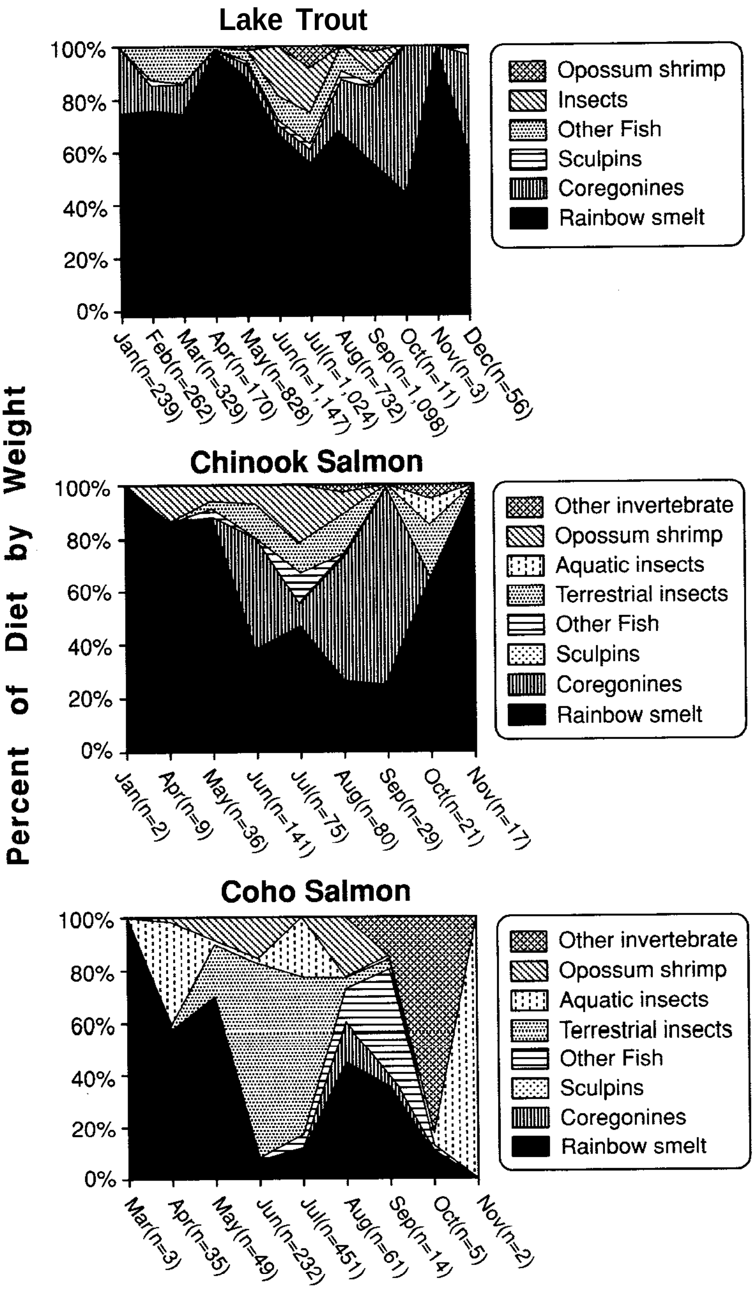

Fig. 1. Monthly mean percent composition by weight of the diet of inshore lake trout, chinook salmon, and who salmon from Lake Superior, 1981-87.

Yearly comparisons of lake trout diets from selected years and locations indicated some changes in the diet of lake trout over time. Data from Minnesota waters from 198446 and the Apostle Islands from 1985-87 were selected because these data subsets allowed unbiased comparisons of diet composition across years. The percentage by weight of rainbow smelt in the diets of inshore lake trout in Minnesota increased from 59% by weight in 1984 to 87% in 1986. At the same time, the percentage of terrestrial insects decreased from 15% to 8% (Table 3). In the Apostle Islands, the percentage of rainbow smelt in the diet decreased from 78% in 1985 to 66% in 1987. Concurrently, the percentage of the diet weight composed of coregonines increased from only 8% in 1985 to 23% in 1987.

Table 3. Mean percent composition by weight of the diet of inshore lake trout from Minnesota and Wisconsin waters of Lake Superior, 1984-87.

		Mean percent by weight						
Year	N	Percent empty	Rainbow smelt	Coregonines	Sculpins	Other fish	Terrestrial insects	Opossum shrimp
				Minnesota				
1984	1,161	39	59	5	1	11	15	8
1985	838	34	84	3	<1	2	10	1
1986	587	27	87	2	<1	2	8	3
				Wisconsin (Apostle Islands)				
1985	836	53	78	8	4	8	2	0
1986	657	50	75	20	1	3	2	0
1987	695	50	66	23	2	9	<1	<1

Lake trout, chinook salmon, and coho salmon of the same size range (450-600 mm) ate rainbow smelt of different sizes. Length-frequency distributions of rainbow smelt in predator stomachs indicated that coho salmon ate mostly juvenile fish of total length 20-60 mm (Fig. 2). Lake trout ate mostly adult rainbow smelt of total length 110-160 mm. Chinook salmon ate equal numbers of juveniles and adults. A Kruskal-Wallis test revealed highly significant differences (H = 711.716, $P<0.001$) among the sixes of rainbow smelt eaten by all three predators. The maximum size of rainbow smelt observed in predator stomachs equalled the maximum size available in Lake Superior. Extensive spring bottom-trawl surveys conducted by the USFWS to index forage stocks document that few rainbow smelt are larger than 180 mm in Lake Superior (Fig. 2).

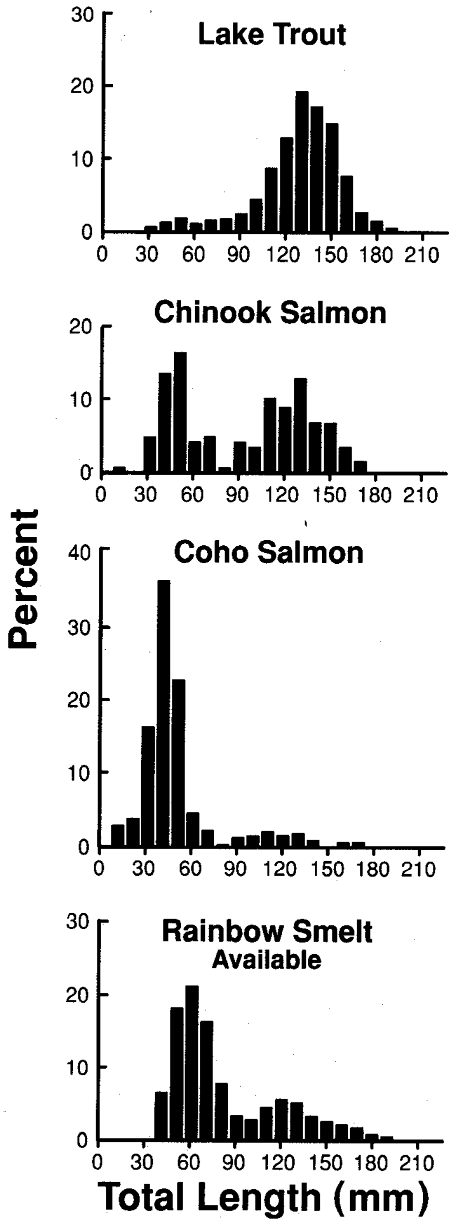

Fig. 2. Length-frequency distribution of rainbow smelt taken from stomachs of inshore lake trout, coho salmon, and chinook salmon, and from spring forage-stock assessments, Lake Superior, 1981-87. Rainbow smelt less than 40 mm long are absent from the assessment data because young-of-the-year are not present until late spring.

Regression analysis showed only a weak positive relationship between the total lengths of:

1) coho salmon (b = 0.17, r^2 = 0.05, $P<0.0001$),

2) chinook salmon (b = 0.06, r^2 = 0.03, $P<0.03$), and

3) lake trout (b = 0.02, r^2 = 0.001, $P<0.02$)

and the length of rainbow smelt in their stomachs. A stronger relationship was found between lake trout length and coregonine length (b = 0.33, r^2 = 0.23, $P<0.00001$), where the slope and coefficient of determination were both much higher than those obtained in the predator-to-rainbow smelt regressions. Coregonines consumed by lake trout ranged from a total length of 40-440 mm, and were significantly larger than rainbow smelt ($P<0.0001$) consumed by lake trout (Figs. 2 and 3). Because of small sample sizes, analysis of coregonine lengths from other predators was not possible.

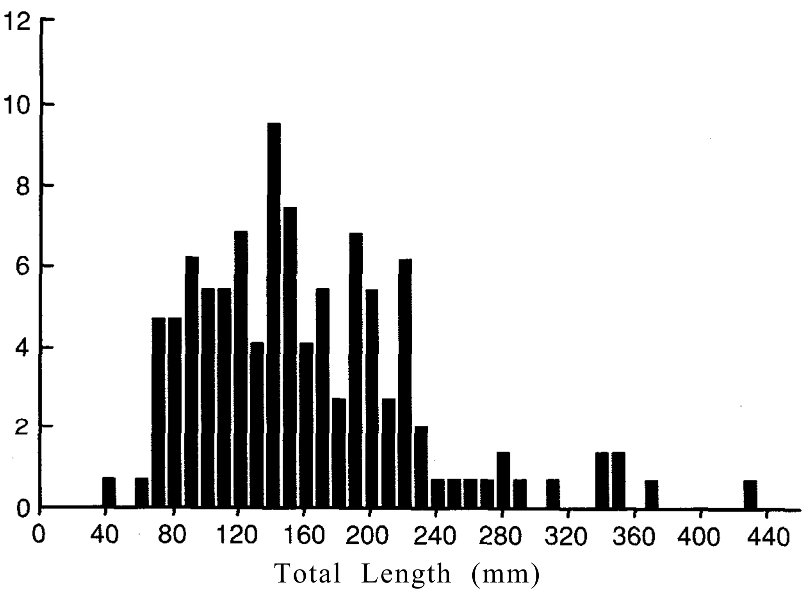

Fig. 3. Length-frequency distribution of coregonines from lake trout stomachs collected from Lake Superior, 1981-87.

Diet similarity indices revealed that inshore lake trout and chinook salmon exhibited the most diet overlap (Table 4), primarily because of similar proportions of rainbow smelt and coregonines in both diets. There was less diet overlap between inshore lake trout and coho salmon, and between chinook salmon and coho salmon. Diets of inshore and offshore lake trout were the least similar because of the predominant use of coregonines by offshore lake trout.

Table 4. Diet similarity indices among salmonine predators in Lake Superior.

Species pair	Similarity index
Inshore lake trout/chinook salmon	86
Inshore lake trout/coho salmon	52
Inshore lake trout/offshore lake trout	30
Chinook salmon/coho salmon	56

DISCUSSION

Diets of most Lake Superior salmonines were different than diets of salmonines from Lakes Michigan and Ontario, and more similar to Lake Huron salmonine diets. Rainbow smelt were the principal forage of most predators in Lakes Superior and Huron (Diana 1990). However, alewives dominated the diets of salmonines in Lakes Michigan and Ontario (Hagar 1984, Brandt 1986, Jude et al. 1987). Alewife density is much lower in Lake Superior (0.003 kg/ha) than in the other Great Lakes (Bronte et al. 1991), and alewives contributed little to salmonine diets in Lake Superior. Almost 40% of the diet of coho salmon in Lake Superior consisted of insects. This is in clear contrast to the predominantly alewife diet of coho salmon in Lakes Ontario and Michigan (Hagar 1984, Brandt 1986, Jude et al. 1987). Insects were also the primary food of rainbow trout in Lake Superior and in southwestern Lake Michigan (Hagar 1984). Insects were of secondary importance to rainbow trout in Lake Ontario (Brandt 1986).

Rainbow smelt and coregonines were not consumed in proportion to their abundance in the lake. Although trawl surveys indicate that rainbow smelt averaged 27% and coregonines 68% of the spring forage biomass from 1981-87 (Hansen 1990), rainbow smelt composed 43% and coregonines only 15% of the food eaten by all salmonine predators. Although coregonine biomass was more that double that of rainbow smelt, salmonines consistently selected rainbow smelt.

Foraging patterns similar to those found in Lake Superior have recently been observed for salmonines in Lake Michigan. There, alewife populations decreased dramatically in the early 1980s, and native species such as yellow perch *(Perca flavescens)* and bloater *(Coregonus hoyi)* have increased greatly in some areas (Jude and Tesar 1985, Eck and Wells 1987). Despite these changes, through 1983 salmonines still consumed mostly alewives (Hagar 1984, Jude et al. 1987). In Lake Superior, some evidence of prey switching was observed from 198587 in the Apostle Islands where lake trout ate progressively more coregonines and fewer rainbow smelt. The distributions of rainbow smelt and lake herring (the major component of the coregonine group) overlap in the near-shore zone, making them both available to predators. Possible explanations for the continued inordinate use of rainbow smelt as food are:

1) predators may prefer familiar prey,

2) predators may fail to recognize edible prey that has only recently become abundant (Oaten and Murdoch 1975), and

3) rainbow smelt and lake herring may exhibit different predator-avoidance behavior.

Lake herring, unlike rainbow smelt, co-evolved with lake trout and may have developed more-effective predator-avoidance behavior that makes them more difficult to capture than rainbow smelt. For whatever reason, there appears to be a lag between the time that alternate prey (lake herring) becomes abundant and the redirection of predation away from less-abundant prey (rainbow smelt).

Large populations of salmonines may reduce prey abundance to a level where predator growth is affected. Stewart et al. (1981), using bioenergetics modelling, predicted that continued high stocking rates of salmonines could severely deplete alewife populations in Lake Michigan. If alternate prey was not used, salmonine growth could decline. Alewife abundance in Lake Michigan declined drastically (Eck and Wells 1987) from 1981-83, although environmental factors combined with predation may have been responsible. In Lake Superior, declines in lake trout growth have been noted lakewide since approximately 1980 following the sharp reduction in rainbow smelt biomass from 1978-81 (Busiahn 1985, Hansen 1990). Reduced growth of lake trout may be a result of lower rainbow smelt biomass. Declines in lake trout growth may delay rehabilitation by prolonging the time fish are exposed to fishing mortality before reaching sexual maturity. Among the compared species, lake trout and chinook salmon diets were the most similar. Competition for food between these two species may occur if rainbow smelt stocks continue to decline. Further changes in the rainbow smelt population may have additional effects on growth of lake trout and other salmonines.

Although significant predator-to-rainbow smelt-length relationships were identified, the slopes and coefficients of determination from these regressions were very low. Diana (1990) reported similar results for Lake Huron predators. As Lake Superior salmonines grow, they quickly reach a size where a positive predator-prey relationship may be impossible because rainbow smelt in Lake Superior now rarely exceed a total length of 180 mm. A positive predator-prey relationship can occur with lake herring as prey because of the broader size range of lake herring available to predators. Use of lake herring may lead to a more optimal diet if the cost of capture and handling does not differ with prey size. Lake Superior salmonines will probably use coregonines if rainbow smelt populations remain depressed or collapsed. This usage would be important in buffering salmonines from decreases in growth. If salmonines continue to switch to coregonines, a more stable predator-prey system may result because, based on fishery records (Baldwin et al. 1979), the lake's capacity to produce lake herring exceeds its capacity to produce rainbow smelt.

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