FOOD HABITS, REPRODUCTIVE BIOLOGY, AND LAMPREY SCARRING OF PLANTED LAKE TROUT (SALVELINUS NAMAYCUSH) IN THE INSHORE WATERS OF LAKE MICHIGAN AT LUDINGTON, MICHIGAN

Thesis for the Degree of M. S.

MICHIGAN STATE UNIVERSITY

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1973

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ABSTRACT

FOOD HABITS, REPRODUCTIVE BIOLOGY, AND LAMPREY SCARRING OF PLANTED LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN THE INSHORE WATERS OF LAKE MICHIGAN AT LUDINGTON, MICHIGAN

By

Thomas L. Chiotti

The lake trout population of the inshore waters of Lake Michigan near Ludington, Michigan, was sampled 28 times from April 10, 1972, through November 16, 1972. The three major objectives were to study changes in food habits with time of year and size of lake trout in a specific area, reproductive biology of mature planted fish, and lamprey scarring rate.

Fish made up nearly 100 percent of the diet and occurred in 99.7 percent of the stomachs which contained food. The alewife, smelt, and sculpin accounted for 90.8 percent of the total food volume. Food habits varied by size and month.

The equations $Y=39.03 + 0.17X$, $Y=18.60 + 0.16X$, and $Y=64.34 + 0.01X$ describe the relationship between total trout length and the standard length of the three most commonly consumed forage fish, the smelt, alewife, and sculpin, respectively.

Females began maturing at age V and had an average weight of 2640 grams. Most spawning occurred from November 1 to 15. Males made up 71.9 percent of the catch of the spawning population. Ovaries showed greatest development from July to October, and comprised 12.43 percent of the total body weight at spawning. Fecundity increased with age and weight. Equations for the relationship between fecundity and weight, length, and age were developed. Mean interim K_{TL} for all fish was 0.99.

Abundance and size distribution varied seasonally and with water temperature in that a relatively high density of large fish were present in both the spring and the fall. Smaller fish were present mostly during the summer season. Toward the end of the summer when the water temperatures were highest, the least numbers of fish were collected.

Lamprey scarring increased in both number of scars per fish and percent fish scarred as the age of the fish increased.

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1973

ACKNOWLEDGMENTS

I wish to sincerely thank my colleagues, Dr. Charles Liston, Dan Brazo, John Armstrong, and Greg Olson, for their help in collecting data for this study.

I would also like to thank Dr. Peter I. Tack, my committee chairman, for his guidance during the course of my study, and also the other members of my committee, Dr. Eugene W. Roelofs and Dr. Gordon E. Guyer.

Sincere appreciation is also extended to Consumers Power Company of Michigan for their financial assistance in my study from the period of June, 1971, to June, 1973, through a research grant to Michigan State University.

Special thanks also to Susan Pichette for her time-consuming efforts in preparation of the original manuscript.

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INTRODUCTION

With the decline of large predatory fish species, primarily the lake trout, there was a void in the predator-prey relationship of fish species in the Great Lakes. This decline was believed to be caused primarily by the destruction of the lake trout by the sea lamprey (Eschmeyer, 1957; Loftus, 1957; and Budd and Fry, 1960).

The void caused by the absence of predatory species encouraged the rapid population increase of the forage fish, the alewife. The alewife, in turn, displaced all major planktivorous species of fish as a result of direct competition (Smith, 1960). Other species of fish were also depressed as a result of competition from the alewife. The result was a drastic change in the fish fauna of the Great Lakes and severe biological instability.

When the sea lamprey was brought under control, by the use of lampricide, it was again feasible to fill the predator void in an attempt to achieve a better-balanced forage base and reduce the population of alewives in the Great Lakes. Alewife die-offs had become a pressing problem to lake shore property owners and on beaches, especially on Lake Michigan.

The lake trout was reintroduced into Lake Michigan in 1965. Since then, yearly plantings of lake trout have been made. In addition, two species of Pacific salmon, the coho (Oncorhynchus kisutch) and chinook (Oncorhynchus tschawytscha) which are mid-water feeders that prey upon the alewife in open waters, are being stocked annually. The steelehead (Salmo gairdneri) is also being stocked annually in the lake.

It was the purpose of this study to investigate the biology of the lake trout in a specific area of Lake Michigan. Two food studies have been done on Lake Michigan lake trout but only on smaller immature fish, which were taken from very large areas of the lake (Van Oosten and Deason, 1938; Wright, 1968). No study has been done on mature fish with repeated sampling of a small area of Lake Michigan so that monthly variation in food habits of fish in a particular area may be determined.

Now that reintroduced lake trout are becoming mature, it was felt that fecundity and aspects of the reproductive biology of these planted fish, such as age and weight at maturity, sex ratio at spawning time, and time of spawning, should be studied to determine if these parameters differ from those of native fish of the past.

Each year more lake trout are becoming old enough and large enough to become targets for sea lamprey attack. Therefore, a study of the lamprey scarring rate was included as part of this study to investigate the effectiveness of the sea lamprey eradication program.

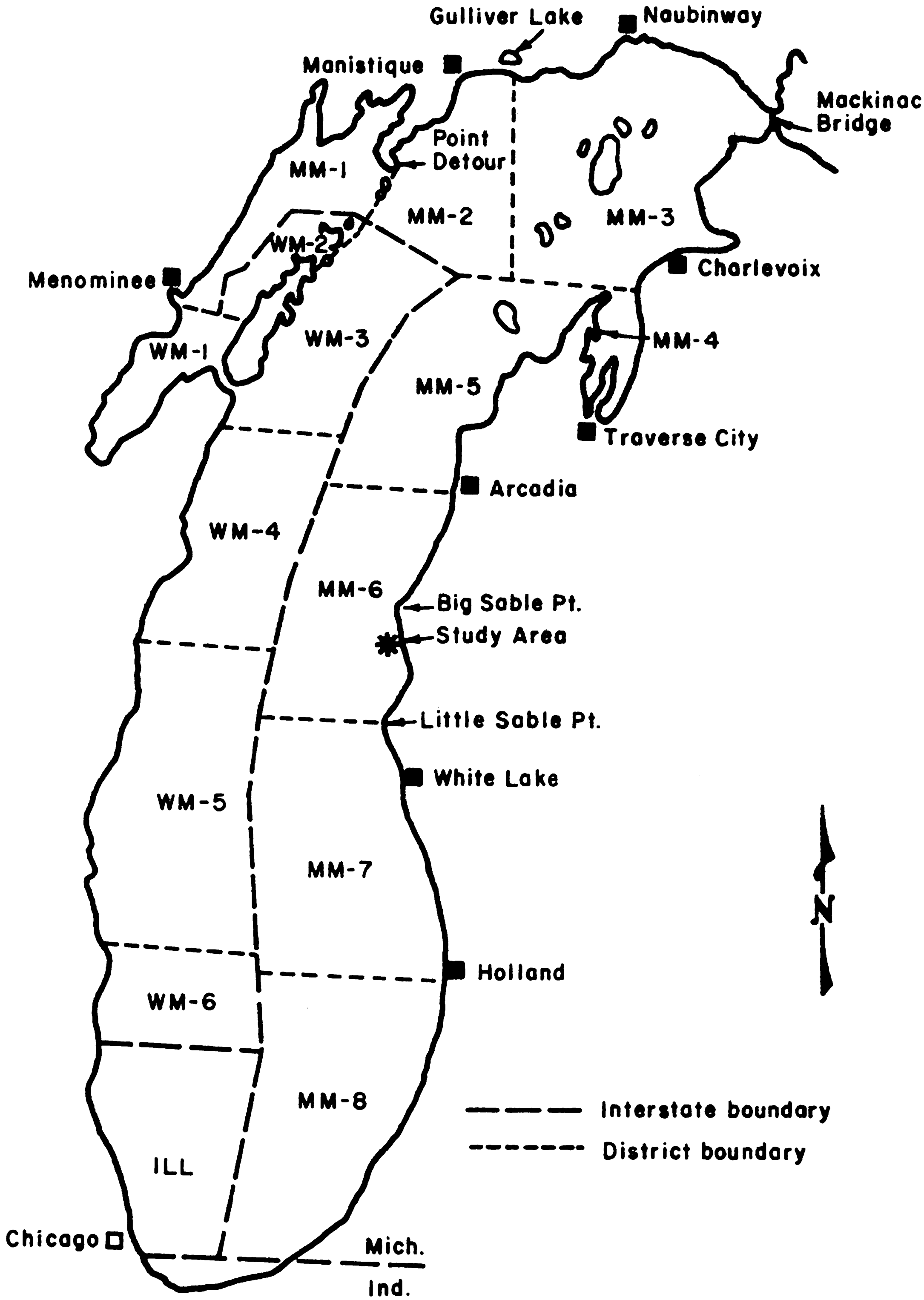
DESCRIPTION OF AREA OF STUDY

This study was made on a small sector of Lake Michigan's statistical district MM-6 (Smith, Buettner, and Hile, 1961) (Figure 1). Specifically it was made on an area which is located seven kilometers south of Ludington, Michigan at the site of a large pumped storage electric generating project, which was being installed there by Consumers Power Company of Michigan. This study was part of a broad ecological base-line study of the possible effects of the installation of this large pumped storage reservoir on the study area.

Data were taken during the 1972 calendar year at five predetermined sampling sites around the periphery of the installation. A sixth sampling site five kilometers south of the installation served as a control. Depth of water at the sampling sites ranged from 6 to 24 meters; two sites were located in 6-8 m of water; three in 12-14 m of water; and one in 24 m of water.

The lake bottom graded from coarse gravel on the beach, to finer gravel as depth increased. Clay outcrops and large stones were also interspersed at depths of 12 m or more. A preliminary fall sampling period the year before the data were collected,

Figure 1.--Statistical Districts of Lake Michigan.



Gulliver Lake
Naubinway
Manistique
Mackinac Bridge
Point Detour
MM-1
MM-2
MM-3
WM-2
Charlevoix
Menominee
MM-4
WM-1
WM-3
MM-5
Traverse City
Arcadia
WM-4
MM-6
Big Sable Pt.
Study Area
Little Sable Pt.
White Lake
WM-5
MM-7
N
Holland
WM-6
MM-8
Interstate boundary
District boundary
ILL
Chicago
Mich.
Ind.

showed that lake trout (*Salvelinus namaycush*) and two species of coregonids spawned in this area.

Experimental gill nets were the sole means of sampling the area. Trawling with both an otter trawl and a steel framed Helgoland trawl proved fruitless because of the clay outcrops and rocky bottom.

METHODS AND MATERIALS

Experimental gill net samples were taken at weekly intervals if weather conditions permitted. All but two sampling periods were 24 hours in length. The nets were set in the same position, which was marked by a bouy, each time. The direction of set was also maintained as nearly as possible to due east and west. Fifty-foot panels of 2, 2.5, 3.0, 4.0, 4.5, and 6-inch stretch-measure net were fished. In addition, a smaller, one-inch stretch-measure size was added midway through the sampling period, but no lake trout were ever taken in this net size. These nets were constructed to fish an area from the bottom to six feet above the bottom, and were an effective method of collecting lake trout which is primarily a bottom dwelling fish.

After the fish were removed from the nets, they were packed in ice to retard digestion of stomach contents. When sampling was completed, the fish were taken to a field laboratory, where they were measured in millimeters, weighed in grams, and sexed. Scale samples and fin-clips were both recorded for age determinations. Questionable fish were later then checked by making scale impressions on acetate (Smith, 1954). Data were also taken on the number, relative age, and location of lamprey scars on the fish.

The stomachs of the fish, the area between the esophagus and the pyloric valve, were then removed. Food remains in the intestinal tract were not identified or included in the study. After removal, the stomachs were individually wrapped in cheese cloth and tied, and an identification tag was attached to each. Stomachs were fixed in 10-percent formalin and later preserved in five-percent formalin. Before analysis, they were allowed to soak overnight in tap water to remove some of the formalin from the stomach contents.

Contents of the stomachs were analyzed by volumetric displacement of water. Percentage total volume of specific food items was determined by dividing the volume of that category by the total volume of stomach contents.

Frequency of occurrence of food items was also determined. This was done by dividing the number of trout containing a specific food item by the number of trout containing food and recording these data as a percentage.

A combination of these methods was used because each method when used alone has a tendency to bias the data to some extent. Percentage of total volume tends to empasize large bulky food items, but does not take into account the relative occurrence of items. Percentage frequency of occurrence, however, tends to over emphasize the occurrence of items with small volume. When both methods are used and the data shown together, the bias of a single method is reduced.

The fecundity of the lake trout was estimated in the following manner. Maturing ovaries were removed from the fish, fixed in 10-percent formalin, and later transferred to five-percent formalin for preservation. Only ovaries which were intact, were utilized in the fecundity study. Those ovaries with loose egg masses or which may have been partly spent were not included.

Three aliquots of eggs were randomly selected from each pair of ovaries. Ovarian tissue was included in the aliquots, since separation of this tissue from the ova was not possible in the preserved ovaries. Preliminary examination showed that there was little variation in the number of ova in each of the three aliquots, meaning that ovum size and the amount of ovarian tissue, which surrounded the ova, was quite consistent. This permitted the extrapolation of the number of eggs in the ovaries to be made from an average of the three samples. The aliquots were made exactly five ml each by placing exactly 10 ml of water in a 50-ml graduated centrifuge tube from an automatic buret. Ova were added until a volume of 15 ml was attained. The water was then decanted and the ova placed on wet paper toweling and counted using a probe to separate the individual ova. No attempt was made to measure the average diameter of the ova.

In conjunction with fecundity, the ovaries of all mature female fish were removed from April to spawning time and preserved as above. These preserved ovaries were then weighed and expressed as a percentage of total body weight.

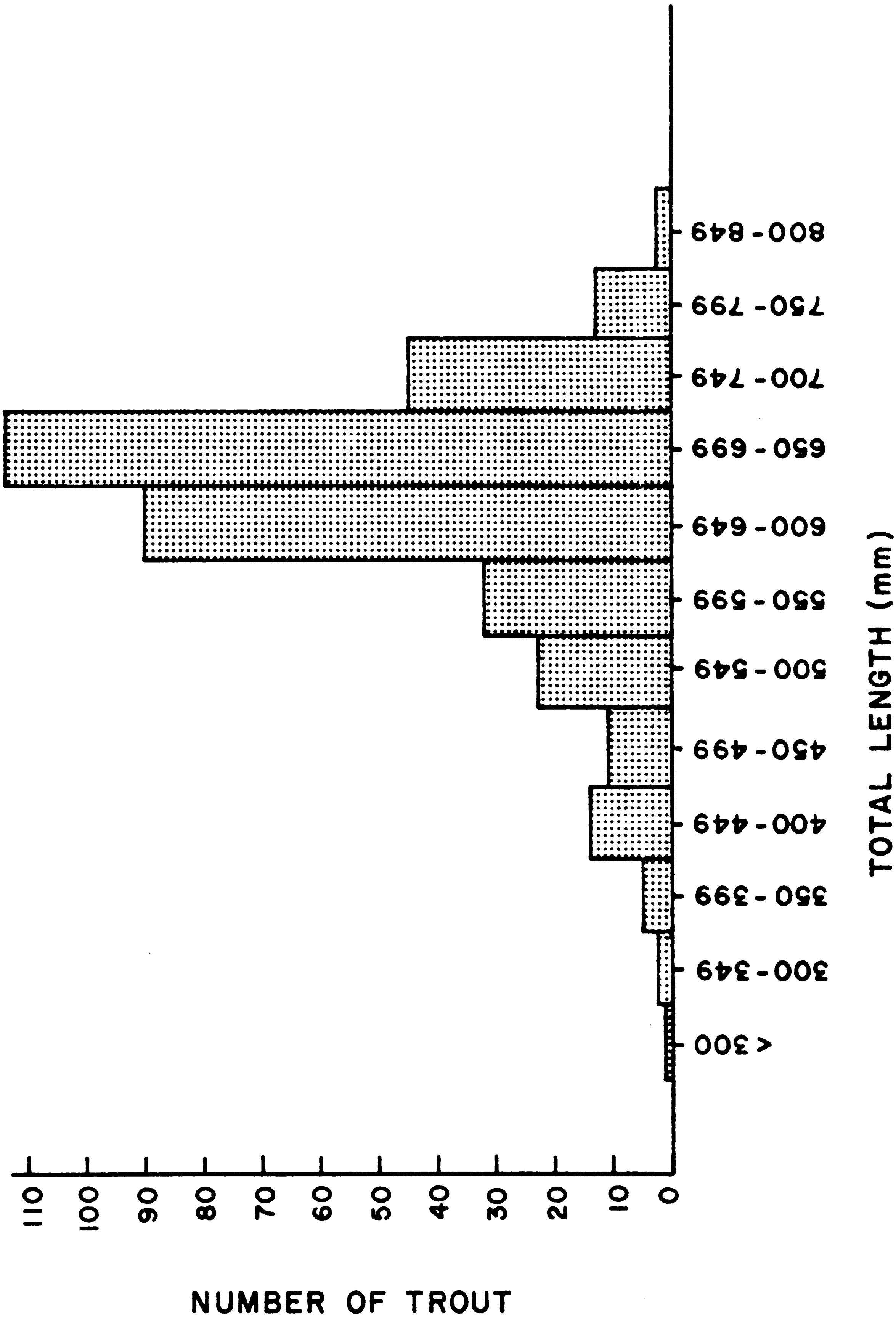
FOOD STUDY

General Food Habits

In this study, the stomachs of 352 lake trout were examined for food contents. Food items were found in 209 (58.8%) of the stomachs, while 148 (41.5%) were empty. These values differ greatly from those obtained by Wright (1968), who found that 93.4 percent of 1581 lake trout stomachs examined from Lake Michigan contained food. They do agree quite closely, however, with those of Van Oosten and Deason (1938) who found that only 55.7 percent of 4979 stomachs collected from Lake Michigan contained food.

There are several factors which contribute to these differences and similarities. Both of the previous studies were made on immature lake trout, whereas the present study was made on predominantly (67%) mature fish (Figure 2). Approximately one third of these fish (125) were taken during the spawning season, during which time only 10.4 percent of the fish contained food. Of 227 fish taken exclusive of the spawning season, 84.4% contained food. Spawning activity then can be seen to have a definite influence on the feeding activity of the fish.

Figure 2.--Length frequency distribution of 352 lake trout collected for food study analysis.


NUMBER OF TROUT
0
10
20
30
40
50
60
70
80
90
100
110
TOTAL LENGTH (mm)
< 300
300 - 349
350 - 399
400 - 449
450 - 499
500 - 549
550 - 599
600 - 649
650 - 699
700 - 749
750 - 799
800 - 849

The size of fish may also have an influence on the percentage of stomachs which contain food at any given time (Frantz and Cordone, 1970). Larger fish tend to consume greater amounts of food but tend to feed more sporadically than smaller fish. This is supported by the fact that exclusive of spawning time, 90.4% of the fish under 600 mm in total length contained food, whereas 79.4% of the fish 600 mm or more contained food.

The length of time which the nets were fished before the fish were removed is also a factor affecting the percentage of stomachs which contain food upon examination. The fish for this study were essentially all taken in short period (24 hour) sets. Wright (1968) took his data in a similar manner. Van Oosten and Deason (1938) collected data from nets set for five- to ten-day periods which was undoubtedly a factor in the low percentage of fish they found to contain food even though these fish were smaller, immature, non-spawning fish.

Fish made up nearly 100 percent of the diet of lake trout examined in this study and occurred in 99.7 percent of the stomachs containing food (Table 1). Insects made up only a trace amount (0.04%) of the diet, while occurring in 2.9 percent of the stomachs with food.

Table 1. Percent total volume and frequency of occurrence of food items in 209 lake trout stomachs containing food.

Item	Percent Total Volume	Frequency of Occurrence
Fish	100.0	99.7
Alewife (*Alosa pseudoharengus*)	35.0	49.3
Smelt (*Osmerus mordax*)	32.2	21.3
Sculpin (*Cottus* spp.)	23.6	37.4
Ninespine Stickleback (*Pungitius pungitius*)	0.4	3.3
Lake Trout (*Salvelinus namaycush*)	1.5	3.3
Burbot (*Lota lota*)	1.2	0.5
Unidentified fish	6.1	37.4
Insect	0.04	2.9
Diptera Chironomidae	Trace	0.9
Lepidoptera	Trace	1.9
Hymenoptera	Trace	0.5
Debris	Trace	0.9

Three forage fish species made up the great majority of the diet and accounted for 90.8 percent of the total food volume. These three species were the alewife (*Alosa pseudoharengus*), smelt (*Osmerus mordax*), and sculpin (*Cottus* spp.), which accounted for 35.0, 32.2, and 23.6 percent of the total food volume, respectively. The alewife also had the highest frequency of occurrence (49.3 percent). The alewife, even in the presence of the smelt and certain coregonids was also reported as the most important food fish in Lake Ontario in the late 1920's (Dymond, 1928).

Smelt occurred in 21.3 percent of the stomachs which contained food. Two species of sculpin, *Cottus bairdi* and *C. cognatus*, occurred in 37.4 percent of the stomachs with food. Smelt, although occurring only about half as frequently as sculpins, made up 8 percent more of the total food volume than did the sculpins. This is because smelt were eaten most in the spring of the year during their seasonal spawning runs and in large relative volumes. Sculpins were eaten generally throughout the year but in lesser volumes because of the size differential between the two. Alewives, eaten throughout the year, made up nearly the same volume as smelt and yet occurred twice as frequently.

Fish made up 99.2 percent of the volume and occurred in 95.2 percent of the stomachs of immature fish which contained food in the study by Van Oosten and

Deason (1938). Wright (1968) found that fish made up 97.4 percent of the volume and occurred in 80.4 percent of the lake trout stomachs which contained food. Of the trout he examined which were greater than 430 mm in total length, fish made up 99.97 percent of the total food volume. Ninety-six percent of the fish in this study were 430 mm or greater in total length which would undoubtedly influence the percentage of fish in their diet.

The three species of fish which made up the bulk of the diet of the lake trout in this study also made up the bulk of the diet of the lake trout examined by Wright (1968). Alewives were not found in the stomachs of lake trout examined by Van Oosten and Deason (1938). The fish examined in their study depended more heavily on sculpins and also consumed a high percentage of fish of the genus Coregonus. No fish from the genus Coregonus were found in the stomachs of fish examined in this study.

The alewife entered Lake Michigan in the late 1940's (Miller, 1956). It has been an important factor in the drastic change in the fish population of the lake (Smith, 1968). The abundance of fish in the genus Coregonus has decreased and the alewife along with the smelt has replaced them as lake trout food.

The consumption of smelt was found to increase proportionally with the size of the lake trout (Wright, 1968).

This may account for the relatively high proportion of smelt in the diet of fish examined in this study.

Other fish species were also found in the stomachs examined, but they made up only a small portion of the diet (Table 1).

Feeding Habits by Month

Food habits of the lake trout were calculated in monthly intervals in terms of percentage total volume and percentage frequency of occurrence (Table 2). Not enough fish were collected to warrant breakdown into size categories along with the monthly intervals.

During the month of April, sculpins made up the majority of the lake trout diet. Frantz and Cordone (1970) also found that the percentage contribution of sclupin to the diet of lake trout in Lake Tahoe was greatest in the spring. After April, the frequency of sculpins in the diet of the lake trout decreased, and became absent in August. Smelt made up 83.2 percent of the diet in May, and only 39.4 percent in April. After May, the importance of smelt in the diet shows a sharp decrease. The alewife became a very important food item in June after only minor importance in the previous months. The importance of the alewife increased throughout the remainder of the year until the lake trout spawning season in November.

TABLE 2.--Percent total volume of various lake trout food items by month. (Percent frequency of occurrence in parentheses.)

	April	May	June	July	August	September	October	November
Alewife	9.4 (13.5)	3.4 (11.4)	63.2 (68.5)	81.0 (72.2)	87.7 (69.2)	100 (100)	100 (100)	20.6 (38.4)
Smelt	25.0 (29.7)	72.6 (71.4)	4.6 (13.0)	0.4 (1.9)	8.8 (7.7)	- -	- -	- -
Sculpin	61.1 (81.1)	16.9 (57.2)	18.8 (48.2)	13.5 (31.5)	0 (0)	- -	- -	1.0 (0.8)
Unidentified fish	4.7 (35.1)	3.4 (37.2)	12.8 (48.2)	3.2 (27.8)	2.4 (30.8)	- -	- -	27.0 (61.5)
Lake trout	- -	3.7 (17.2)	0.7 (1.9)	- -	- -	- -	- -	- -
Stickleback	- -	- -	- -	1.9 (11.1)	1.2 (7.7)	- -	- -	- -
Burbot	- -	- -	- -	- -	- -	- -	- -	51.4 (0.8)
Insects	0.2 (11.4)	- -	Trace (7.7)	- -	- -	- -	- -	- -
Number examined	38	38	57	59	27	10	2	125
Number with food	37	35	51	54	13	4	1	13
Total volume (ml)	1458.0	2911.5	1673.5	1432.5	235	103.5	5.0	194.5
Percent empty	2.6	7.9	10.5	8.5	51.9	60.0	50.0	89.6
Average volume of contents of stomach with food (ml)	39.4	83.2	32.8	26.5	18.1	25.8	5.0	15.0
Average volume of contents of all stomachs examined (ml)	38.4	76.6	29.4	24.3	8.7	10.4	2.5	1.6

From these data it is apparent that there are seasonal changes in the feeding habits of lake trout found in the area studied. Sculpins serve as an important food base early in the year, but after this time are only supplemental in the diet. Their importance is displaced by the appearance of the smelt on its spring spawning run. According to Dr. Stanford H. Smith (pers. comm.), lake trout seem to prefer smelt over alewives when both are present. The data from this study support this statement. Both alewife and sculpin consumption during the month of May, the peak of smelt abundance in the area, decrease from the previous month while smelt show a sharp increase. It was during this month also that of the stomachs which contained food, the greatest average volume of food (83.2 ml) per stomach was found. This volume was more than twice that for any other month (Table 2). These data agree with the findings of Frantz and Cordone (1970) who concluded that lake trout of Lake Tahoe fed most avidly in the spring months and that the greatest amount of food was consumed during this time.

In June, the smelt have dispersed, but rather than returning to sculpins for their major food source the lake trout rely on the alewife which has moved into the area to spawn (Wells, 1968). The larger relative size of the alewife, and its ready availability probably make it a more preferable food source than the sculpin. The lake trout tend to rely on the alewife as their major food source for the remainder of the year.

Predation on Small Hatchery-Planted Lake Trout

Evidence of predation on planted yearling lake trout was exhibited. Yearling lake trout, part of a plant of 75,000, planted at Ludington on May 4, 1972 were found in the stomachs of lake trout in this study. The sampling area where these fish were taken was located seven kilometers south of the Ludington planting site. However, significant numbers of small lake trout appeared in the stomachs collected on May 8, four days later. It is possible that there was an even greater consumption of yearling lake trout closer to the point of planting a day or two afterwards. Also if the smelt, a highly palatable food source, had not been available, a still higher rate of predation may have been witnessed.

Although studies have shown that fin-clipped young lake trout are not significantly more vulnerable to predation (Shetter, 1951), it is possible that hatchery-reared fish are for a period of time more vulnerable to predation than a native fish of similar size.

Feeding Habits by Size

Previous studies have shown that food habits of the lake trout vary with the size of the fish (Dryer, *et al.*, 1965; Van Oosten and Deason, 1938; Wright, 1968). The fish in this study ranged from 233 to 803 mm in total length. These were divided into 50-mm size classes (Table 3). As the size of the fish increased, the average volume of stomachs which contained food steadily increased except for data on two fish in the largest size class. The percentage of empty stomachs in each size class shows a general increase. In the fish greater than 600 mm the increase in the percentage of empty stomachs is because fish taken in these size categories at spawning time generally had empty stomachs. Practically all fish less than 600 mm in total length were immature, and yet this trend was also noticeable in fish of this size and smaller.

The average number of food items per stomach, and the average volume of each individual item in the stomachs were calculated for each of the twelve size classes (Table 3). The number of food items remains relatively constant, showing only a slight increase from small to large fish. The average volume of individual items in the stomachs shows a much greater increase than the number of items per stomach. Therefore, although the number of food items found in stomachs increases only slightly with size of the fish, the size of the food item itself increases greatly. Large fish obtain their energy source mainly by consuming larger food items and not by consuming more relatively small items.

TABLE 3.--Food of Lake Michigan lake trout near Ludington, Michigan, 1972 by fish size. (Percent frequency of occurrence in parentheses.)

	Size Interval (mm)											
	<300	300-349	350-399	400-449	450-499	500-549	550-599	600-649	650-699	700-749	750-799	800-849
Percent volume Alewife	-	55.2	49.4	36.4	59.9	41.3	46.9	33.8	34.3	27.6	20.3	23.1
	-	(50.0)	(60.0)	(61.5)	(62.5)	(52.6)	(64.3)	(41.5)	(50.9)	(43.8)	(50.0)	(50.0)
Percent volume Smelt	-	-	12.6	2.2	31.7	10.8	29.9	27.8	36.3	43.9	38.8	67.2
	-	-	(20.0)	(7.7)	(37.5)	(15.8)	(17.9)	(26.4)	(19.3)	(31.2)	(25.0)	(50.0)
Percent volume Sculpin	-	44.2	22.1	50.2	1.7	35.6	17.2	27.2	23.4	27.1	-	-
	-	(50.0)	(60.0)	(69.2)	(12.5)	(31.6)	(32.1)	(39.6)	(35.1)	(43.8)	-	-
Percent volume Unidentified Fish	100.0	-	5.2	6.2	2.5	11.0	2.7	9.3	4.7	1.4	5.8	-
	(100.0)	-	(40.0)	(30.8)	(25.0)	(31.6)	(28.6)	(47.2)	(38.6)	(18.8)	(25.0)	-
Percent volume Lake Trout	-	-	-	-	-	-	2.5	1.9	1.3	-	-	9.7
	-	-	-	-	-	-	(3.6)	(3.8)	(3.5)	-	-	(25.0)
Percent volume Stickleback	-	-	10.5	5.1	4.2	1.1	0.7	-	-	-	-	-
	-	-	(20.0)	(7.7)	(25.0)	(5.3)	(7.1)	-	-	-	-	-
Percent volume Burbot	-	-	-	-	-	-	-	-	-	-	35.1	-
	-	-	-	-	-	-	-	-	-	-	(25.0)	-
Percent volume Insects	-	-	0.2	-	-	0.2	-	0.1	Trace	-	-	-
	-	-	(20.0)	-	-	(5.6)	-	(3.8)	(1.8)	-	-	-

Number examined	1	2	5	14	11	23	32	90	114	45	13	2
Number with food*	1	2	5	13	8	19	28	53	57	16	4	2
Total food volume (ml)	2	9	47.5	137.5	118.5	452	1068	2194	2490	994	291	67
Percent empty*	0	0	0	7.1	27.3	17.4	12.5	41.1	49.6	64.6	69.2	0
Average volume of stomachs with food (ml)	2	4.5	9.6	10.6	14.8	23.8	38.1	41.4	43.7	62.1	72.8	33.5
Average volume of contents of all stomachs examined (ml)	2	4.5	9.6	9.8	10.8	19.6	33.4	24.4	21.7	22.1	22.4	33.5
Average number of food items per stomach*	5	3	3.5	3.2	3.8	3.8	4.4	4.9	4.8	6.2	6	4
Average volume of individual items in stomachs (ml)	0.4	1	3.4	3.4	4.0	6.6	8.6	8.9	10.6	12.0	15.6	16.8

*Calculations based on only those stomachs which contained food.

As the size of the lake trout increases, the alewife shows a slight decrease in relative importance as a food source, in both total volume and frequency of occurrence. This may mean that larger fish are more selective than smaller fish in terms of what they consume. This idea is supported by the fact that smelt increase in relative importance as size of the trout increases. Wright (1968) also found an increase in importance of the smelt in Lake Michigan lake trout as size of the trout increased. It is possible, however, that the time of the year at which these fish were taken may influence these data. (See Seasonal Abundance and Size Distribution.) The time of year that the relative proportion of each size class of fish was taken varied, and also food habits change considerably through the year.

Sculpins show a general decrease in relative importance as lake trout size increases, although this trend is slight. Van Oosten and Deason (1938) found a decrease in the consumption of sculpins as lake trout size increased. Larger fish tend to feed on larger forage fish. The small size of the sculpin then tends to make it less important as a food item for larger fish.

Another trend which is quite distinct is the decrease in relative importance of the stickleback as the size of the lake trout increases. The stickleback occurs most frequently in the diet of fish 350-399 mm long. It progressively decreases in importance and disappears completely in fish 600 mm and greater in length.

Yearling lake trout were found only in the stomachs of lake trout 550 mm and greater in length.

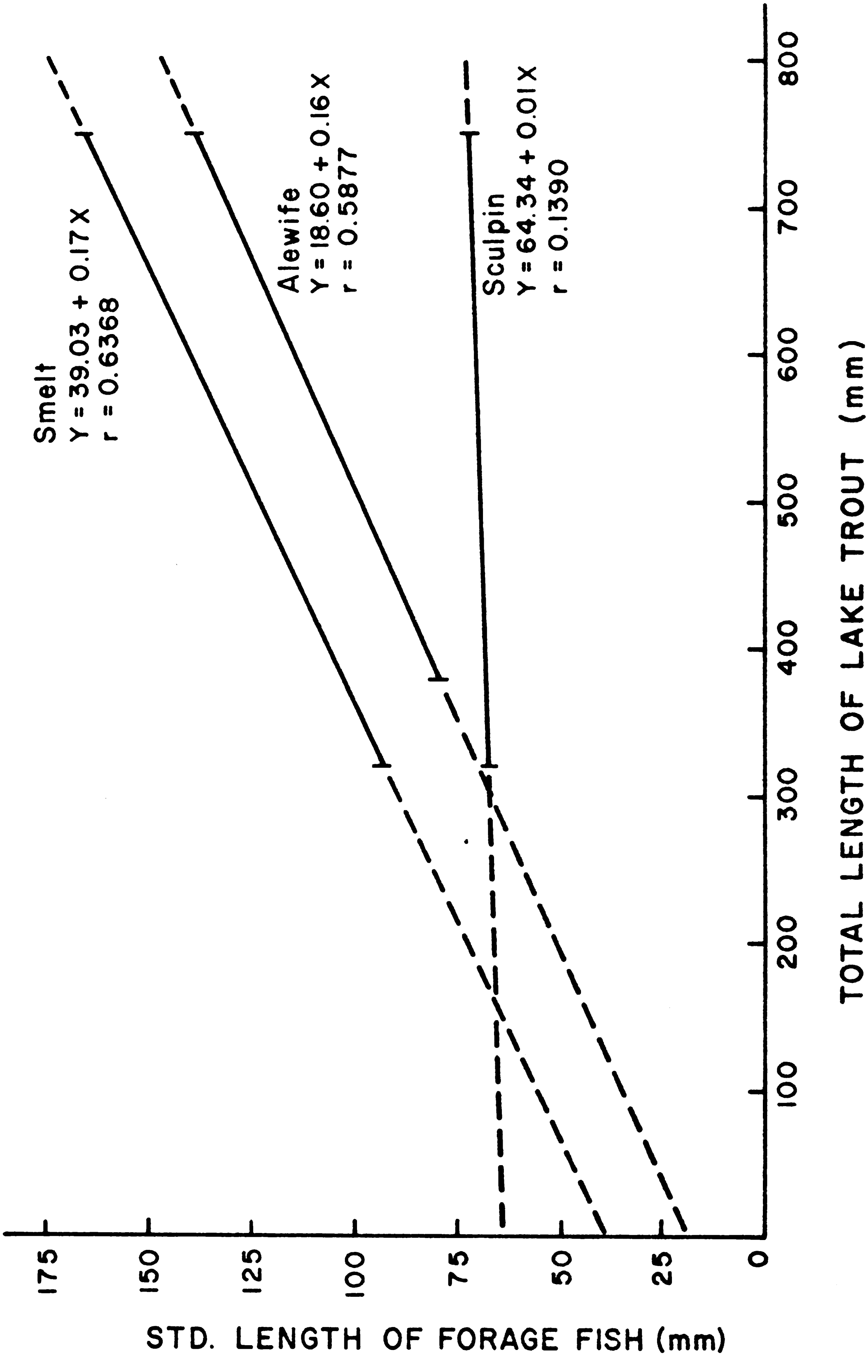
Relationship Between the Length of the Lake Trout and the Length of the Forage Fish Consumed

Linear regressions using the least squares method were calculated for the total length of the lake trout and the standard length of the three most frequently consumed forage fish, the alewife, smelt, and sculpin (Figure 3). Where more than one fish of a given species was present in a stomach, the average standard length was used in the computation.

The greatest correlation was found between the length of the lake trout and the average standard length of the smelt consumed (r=.6368). Within the range of the data, the standard length of the smelt consumed increased 17 mm for every 100-mm increase in the total length of the lake trout.

This relationship for alewives showed a slightly lower correlation coefficient (r=.5877). Within the range of the data, the length of the smelt consumed was about 20 mm greater than the length of the alewife consumed by lake trout of equal lengths. The average length of the alevife consumed increased 16 mm for every 100-mm increase

Figure 3.--Linear Regression: Length of lake trout versus length of the forage fish consumed. The solid line represents the interval for which actual data were available.


Smelt
Y = 39.03 + 0.17 X
r = 0.6368
Alewife
Y = 18.60 + 0.16 X
r = 0.5877
Sculpin
Y = 64.34 + 0.01 X
r = 0.1390
0
25
50
75
100
125
150
175
STD. LENGTH OF FORAGE FISH (mm)
100
200
300
400
500
600
700
800
TOTAL LENGTH OF LAKE TROUT (mm)

in lake trout length. This increase was approximately the same as that for smelt.

Sculpins showed very little correlation (r=.1390) between the total length of the lake trout and the standard length of these fish consumed. There is very little slope to the equation of this line. The average legnths of the sculpin consumed increased only one millimeter for every 100-mm increase in lake trout length. There is a high degree of variability associated with this relationship. This variability may be because that since sculpins of the genus *Cottus* are small, even when mature, they will therefore be consumed by small and large lake trout alike when available.

REPRODUCTIVE BIOLOGY

Age and Weight at Maturity

Lake trout mature at various ages depending on the growth rate of the fish (Alm, 1959). Male fish may mature at an earlier age than female fish (Loftus, 1957; Martin, 1970). Miller and Kennedy (1948) found that the slow growing lake trout of Great Bear Lake did not begin to mature until age XIII, and reached 100 percent maturity at age XVII. Native female lake trout began to mature in Lakes Superior (Loftus, 1957), Huron (Budd and Fry, 1960), and Michigan (Van Oosten, 1943) at seven years of age.

Lake trout planted in Lake Michigan appear to be maturing earlier than those of previous studies. Forty percent of the five-year-old female trout (n=40) taken prior to the spawning season were mature. This figure increased to 70 percent of those (n=16) taken during the spawning season. All female fish age VI and VII (n=57) that were collected were mature.

The early maturing of these lake trout may be the result of an exceptionally fast growth rate. The average weight of a sample of 832 five-year-old fish from South Bay, Lake Huron taken from 1947-50 by Fry (1953) was 1300 grams per fish. Van Oosten (1956) reported a mean weight of only 457 grams per fish from a sample of 53 age V fish taken from Lake Michigan during 1930-31. His data, however, may have been biased because, to collect his samples he used small mesh gill nets which may have been selective for smaller slow growing fish of a given age. The 151 age V lake trout collected in this study averaged 2640 grams per fish. Hesse (1969) also showed a rate of growth for the present population of lake trout that was greater than any previously reported for Lake Michigan.

Time of Spawning

Spawning activity for the lake trout in the area of study was initiated prior to November 1. Data were not collected from October 4 to November 1, however, because of inclement weather conditions. Three samples were collected during the month of November. Of 19 mature female fish collected on November 1, three (15.8%) were either spent or partly spent. On November 9, five of 10 (50%) mature female fish collected were spent or partly spent. This figure increased to 85.5 percent, 6 of 7 mature female fish, on the last sampling date, November 16. These data suggest that peak spawning activity occurred during the period of November 1 to 15 and was nearing completion by November 16. This is in agreement with Van Oosten (1935) who reported that the mean spawning period for lake trout in Lake Michigan was October 15 to November 15.

Sex Ratio at Spawning

Male fish made up 71.9 percent of a sample of 146 fish taken at spawning time. Similar proportions of male fish were reported in the spawning population of Lake Superior (Eschmeyer, 1955), Great Bear Lake (Kennedy, 1948), and in the lakes of Algonquin Park, Ontario (Martin, 1957).

The sex ratio of fish taken exclusive of spawning time was quite different than that at spawning time. Of 246 fish taken in this study prior to spawning time males made up 54.1 percent of the total. This value is in close agreement with that of Van Oosten (1956), who found that males made up 53.4 percent of a sample of several thousand young native lake trout taken during 1931-32 in Lake Michigan.

Two factors which may influence the sex ratio of fish collected during spawning time are that males may be more active than females, and males may spend more time on the spawning beds than do females. Eschmeyer (1955) suggests that the first of these two factors may be the cause. Martin (1949) offers the second possible reason why more males than females are taken at spawning time. He observed that during spawning periods males arrive first on the spawning beds, and were the last to leave, in their diurnal migration from deeper water. Recoveries of tagged lake trout on the spawning grounds (Eschmeyer,

1955) showed that some male fish remained on the spawning grounds for as long as three weeks whereas no tagged female fish were recovered from the area after spawning.

Because male trout appear to spend more time on the spawning beds, they would be more vulnerable to a stationary gill net than female fish that appear to leave the area after spawning, which may partially account for a greater percentage of male fish being taken at spawning time than during the rest of the year.

Development of Ovaries

Examination of mature lake trout from the month of April until the fish spawned in November showed that ovaries comprised a progressively greater percentage of the total body weight until the fish spawned (Table 4). Eschmeyer (1957) states that the major portion of development of the ovaries occurs during the five months preceding the spawning season. The period of most rapid development in terms of actual biomass added to the ovaries was from the end of June to the end of September. Eschmeyer (1955) found a greater proportion of the total body weight was composed of ovaries in lake trout which were about to spawn in Lake Superior than was found in this study. An average of five fish showed that 18.5 percent of the total body weight was composed of ovaries in his study, while an average of 21 fish in this study

Table 4. Percentage of total body weight of mature female lake trout composed of ovaries.

Date of Collection	Number of Fish	Percentage Wt. of Ovaries	
		Range	Mean
April 18-20	13	0.31- 1.85	0.73
May 8	11	0.46- 1.71	1.05
May 19-24	3	0.98- 1.51	1.30
June 3-6	5	0.73- 2.97	1.98
July 1-8	5	1.18- 4.23	2.42
July 17-29	6	3.28- 5.08	4.18
Aug. 13-28	5	5.71- 9.43	7.24
Sept. 27	4	8.64-12.58	10.32
Nov. 1-9*	21	7.20-19.38	12.43

*Includes only those fish which were not spent or partly spent at this time.

showed that the ovaries composed only 12.4 percent of the total body weight. Martin (1970) found that ovaries comprised approximately 14 percent of the total body weight from 1938-1946 and approximately 15 percent from 1955-1963, of lake trout in Lake Opeongo, Ontario. These values are in closer agreement, although still somewhat higher, than the value obtained in this study.

The number of eggs produced per kilogram of fish tends to be higher for larger fish (Eschmeyer, 1957). The size of the individual ovum, however, is independent of the size of the fish. Small fish will produce fewer but not smaller ova (Eschmeyer, 1957). It may be concluded then that the percentage of body weight comprised of ovaries is greater for large trout than for small trout, which is supported by the findings of Eschmeyer (1955). Many of the fish in the present study were spawning for their first time and were, on the average, younger and smaller than those of Eschmeyer (1955) and Martin (1970). It is believed that this is the reason why the ovaries comprised a smaller percentage of the total body weight than reported in the other two studies.

FECUNDITY

Relationship Between Fecundity and Weight

Lake trout were grouped in 500-gram increments for the fecundity study (Table 5). There is a progressive increase in the mean number of eggs produced as the weight of the fish increases.

There was not an increase in the mean number of eggs produced per kilogram of fish as the weight of the fish increased, as was observed by Eschmeyer (1955) for Lake Superior fish. The fish in this study, however, did not cover nearly the range of weight of those in Eschmeyer's study. Hanson and Wickwire (1967), however, showed no increase in the number of eggs produced per kilogram as the weight of Lake Tahoe lake trout increased.

Linear regression of weight versus fecundity for 33 fish produced the equation $Y=1065.1 + 1.4X$ (where Y is the fecundity of the fish and X is the weight in grams). Due to the extreme variability of the data the correlation coefficient (r) was low ($r=.45$). Hanson and Wickwire (1967) developed the equation $Y=17.7 + 1.4X$ for lake trout from Lake Tahoe. The slopes of the two equations are equal, meaning that for each one kilogram of increase in weight, there is an increase of 1,400 eggs produced.

Table 5. **Lake trout fecundity in 500-gram increments of weight.**

Weight Interval (kg)	Mean Wt. (kg)	Number of Fish	Number of Eggs per Fish			Number of Eggs per kg. of Fish		
			Range	Mean	Std. E.	Range	Mean	Std. E.
2.0-2.5	2.35	5	2867- 6691	4028	713	1251-2826	1714	296
2.5-3.0	2.73	11	2860- 7519	5207	407	1096-2460	1907	140
3.0-3.5	3.24	7	2800- 6870	5564	606	803-2286	1717	199
3.5-4.0	3.59	8	4006-11200	5993	825	1134-3135	1669	230
4.0-4.5	4.31	1	-	5868	-	-	1362	-
4.5-5.0	4.74	1	-	8806	-	-	1860	-

However, the intercepts of the equations are quite different. The fish in the present study produce approximately 1,000 more eggs than a fish of equal weight from the study by Hanson and Wickwire (1967).

The fish in this study produced an average of 1748 eggs per kilogram. This value is higher than values obtained in studies by Eschmeyer (1955) and Hanson and Wickwire (1967), who obtained values of 1422 and 1417 eggs per kilogram, respectively. The value for this study is in close agreement with a value of 1710 eggs per kilogram reported by Eschmeyer (1957) for native lake trout of Lake Michigan.

Relationship Between Fecundity and Total Length

The equation $Y=-6225.3 + 17.2X$ describes the relationship between the number of eggs produced and the total length of the 33 fish examined. The slope of the line shows an increase of 17.2 eggs per millimeter increase in fish length. This value is lower than a value of 22.9 obtained by Hanson and Wickwire (1967). This difference may be due to the variability of the data in this study and correspondingly low correlation coefficient ($r=.36$). It may also be an intrinsic characteristic of young fish with a fast rate of growth, that they produce fewer eggs per millimeter of length than slower growing fish of the same size and weight.

Relationship Between Fecundity and Age

The ages of the 33 trout collected for fecundity determination in this study ranged from five to seven years. Fecundity of fish of the same age also varied greatly as did fecundity of fish of the same weight and length (Table 6). There is, however, a progressive increase in the mean fecundity of the fish as age increases. The linear regression equation $Y=947.6 + 741.1X$ describes this relationship. There is a mean increase of 740 eggs with each year of increase in age, as shown by the slope of the line. The correlation coefficient for these data was also quite low ($r=.38$) due to large variability between fecundity and age of the fish.

Table 6.--Lake trout fecundity by age.

Age Class	Number of Fish	Number of Eggs per Fish		Standard Error
		Range	Mean	
V	14	2860- 6691	4636	398
VI	7	2800- 6870	5237	546
VII	12	4259-11200	6410	586

The fish in this study produced more eggs than fish of the same age from Lake Superior as reported by Eschmeyer (1958), who reported a mean production of 1007, 1890, and 2093 eggs for age V, VI, and VII fish, respectively. This increase is undoubtedly related to the much faster growth rate exhibited by fish in this study.

CONDITION FACTOR

The coefficient of condition (K) here defined:

$$K = \frac{W \times 10^5}{L^3}$$

where W=weight in grams and L= total length in millimeters was calculated for fish collected in this study (Carlander, 1969). Condition was calculated on a monthly basis for all fish and also for the fish grouped as mature and immature (Table 7).

These fish were, on the average, in better condition than any fish previously reported from the Great Lakes. Eschmeyer (1955) reported an average condition factor of K_{TL}=.91 for native fish of the same length from Lake Superior. Van Oosten (1956) reported a value of K_{TL}=.81 for smaller native fish from southern Lake Michigan.

The mean coefficient of condition for all fish was lower in April than for any month except November. As the fish began to feed more heavily in the spring, their condition factor increased to that of the remaining months. Low coefficient of condition of mature fish in November was due to loss of weight caused by not feeding during spawning time, and weight lost as eggs and sperm

Table 7. Monthly coefficient of condition for lake trout from Lake Michigan, 1972.

Month	Number of Fish	Mean K all Fish	Number of Fish	Mean K Mature Fish	Number of Fish	Mean K Immature Fish
April---	45	0.961	39	0.969	6	0.910
May---	43	1.048	41	1.042	2	1.166
June---	65	1.011	40	1.013	25	1.007
July---	60	1.011	28	1.106	32	0.928
August---	26	0.992	15	1.060	11	0.902
September---	3	1.015	3	1.015	-	-
October---	17	1.022	16	1.020	1	0.991
November---	147	0.952	140	0.955	7	0.921
Total fish---	406	-	322	-	84	-
Grand aver. weighted K	-	0.990	-	0.998	-	0.953

during actual spawning, although the apparent decrease in condition for immature fish is unexplainable.

Immature fish tended to show a lower coefficient of condition than larger mature fish. Coefficient of condition was found also to increase with increase in lake trout size in other studies (Hacker, 1957; Van Oosten, 1956).

SEASONAL ABUNDANCE AND SIZE DISTRIBUTION

Seasonal Abundance

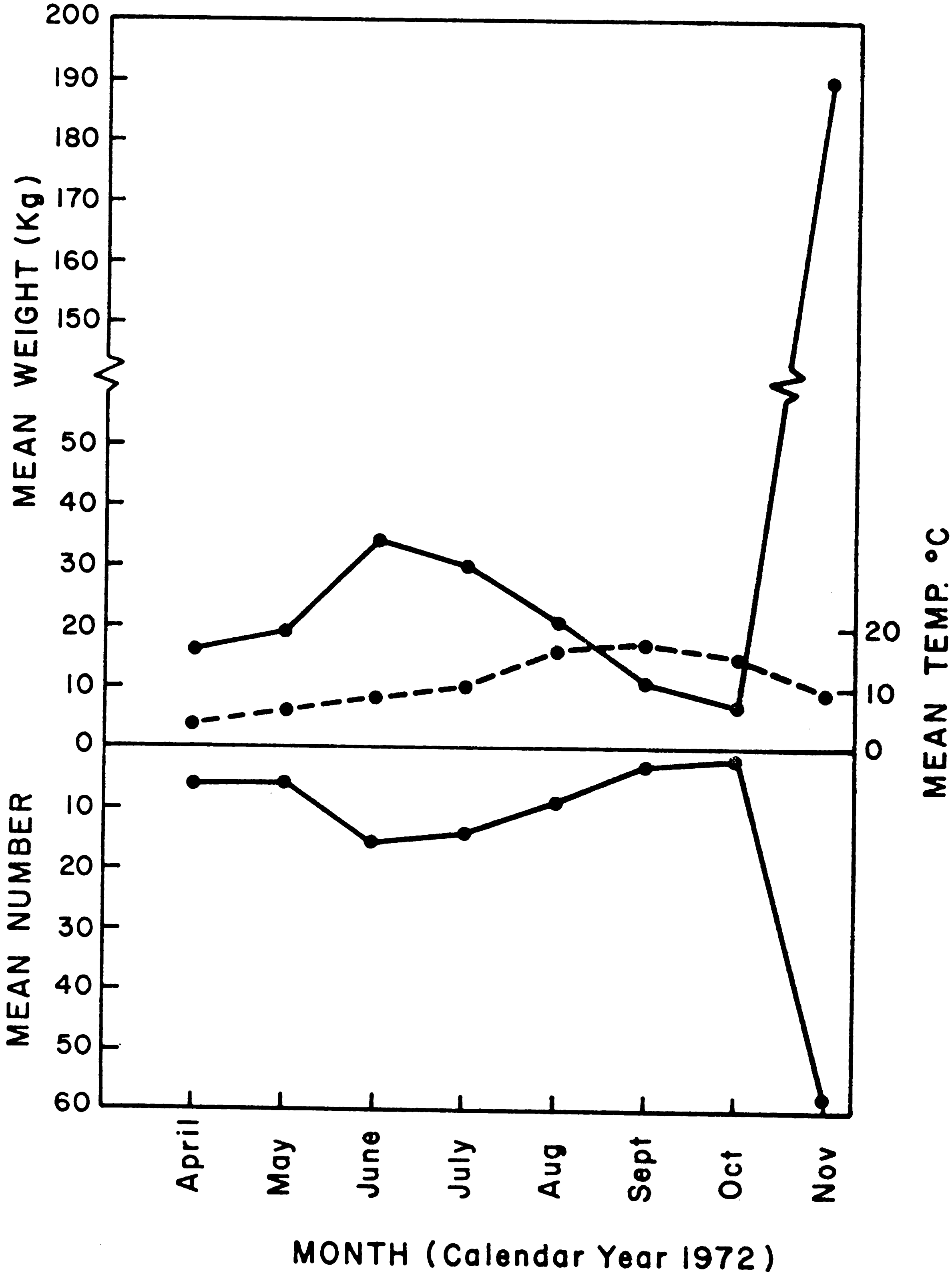
The mean monthly number and weight of lake trout caught per 24 hours of fishing effort was determined (Figure 4). Both the number and weight of fish collected in April were low and increased to a peak in June. The weight of fish taken then gradually decreased as water temperature increased. As water temperatures decreased in the fall and spawning activity was initiated, there was a very sharp increase in the number and weight of fish collected. The data for the month of October are undoubtedly too low, however, because only one collection was made which was on October 4 when the water temperature was quite high. Data points for October are therefore not believed to be representative for this time period.

The average number and weight of fish collected in November greatly exceeded that of any other month. This also indicates that the study area serves as an important spawning grounds for lake trout of the area.

Size Distribution

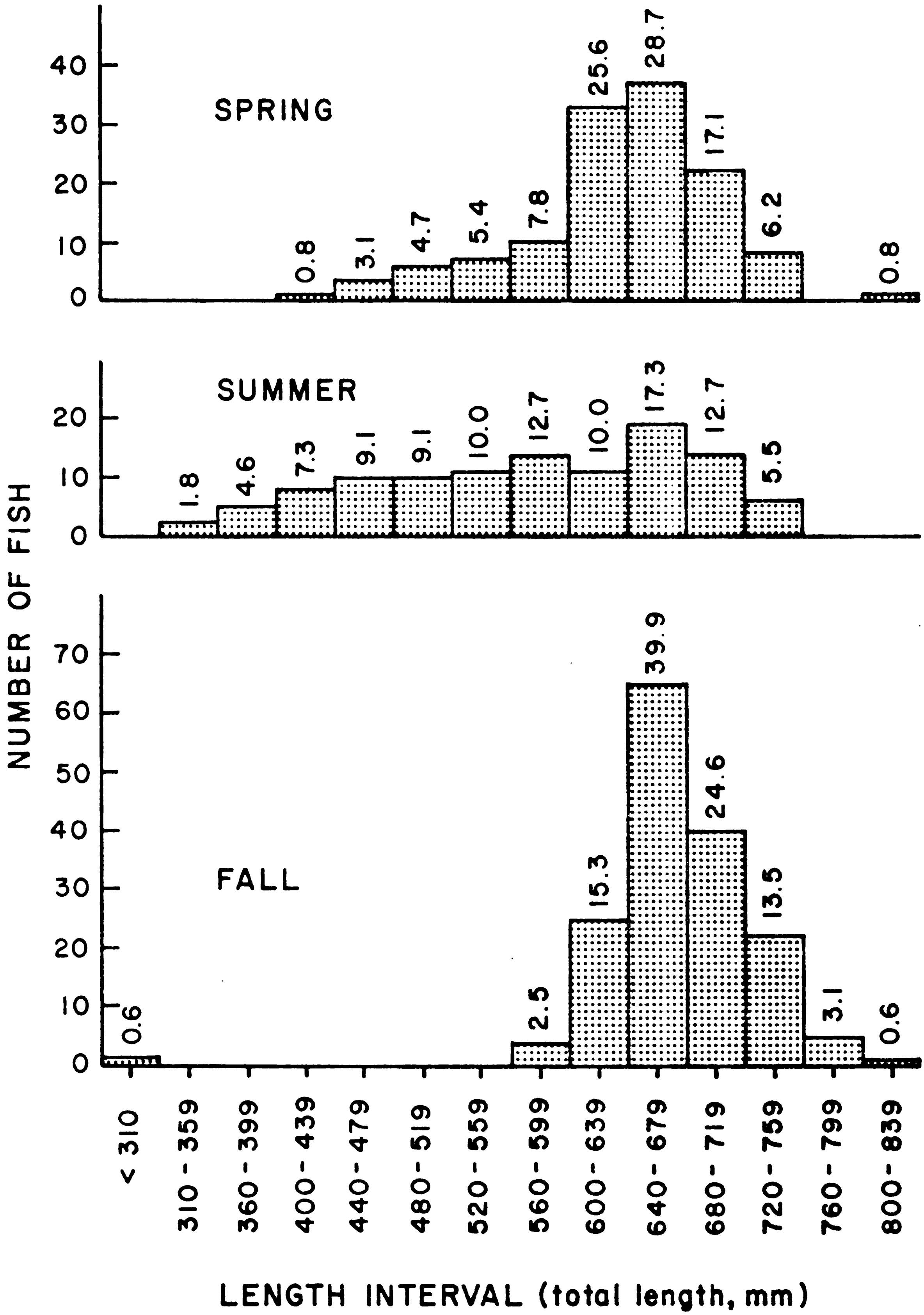
The size distribution of fish collected in the study area varied seasonally (Figure 5). In the spring

Figure 4.--Mean monthly weight and number of lake trout collected per 24 hours of fishing effort in all nets. The broken line indicates mean monthly water temperature at fishing depth.



MEAN WEIGHT (Kg)
200
190
180
170
160
150
50
40
30
20
10
0
MEAN NUMBER
10
20
30
40
50
60
MEAN TEMP. °C
20
10
0
April
May
June
July
Aug
Sept
Oct
Nov
MONTH (Calendar Year 1972)

Figure 5.--Seasonal size distribution of lake trout caught in terms of numbers and percentage of catch. (Percent of each seasons total catch shown at the top of each size interval.)



SPRING
0.8
3.1
4.7
5.4
7.8
25.6
28.7
17.1
6.2
0.8
SUMMER
1.8
4.6
7.3
9.1
9.1
10.0
12.7
10.0
17.3
12.7
5.5
FALL
0.6
2.5
15.3
39.9
24.6
13.5
3.1
0.6
NUMBER OF FISH
0
10
20
30
40
50
60
70
< 310
310 - 359
360 - 399
400 - 439
440 - 479
480 - 519
520 - 559
560 - 599
600 - 639
640 - 679
680 - 719
720 - 759
760 - 799
800 - 839
LENGTH INTERVAL (total length, mm)

(April 15-June 15), the size distribution was skewed toward larger fish with fish from 600 to 719 mm in total length dominating the catch. The size distribution during the summer season (June 15-September 15) is spread rather evenly over several size intervals with no single size category being predominant. Fish collected in the fall (September 15-November 16) were practically all larger fish, 97 percent of which were from 600 to 759 mm in total length. These fish represented the size of fish in the spawning population. Small immature fish had left the area, except for one very small 233-mm fish collected which was believed to be a stray.

Throughout the year, fish in the size interval 640-679 mm in total length were the dominant size group of fish collected. Fish in this size interval made up 28.7, 17.3, and 39.9 percent of the total number of fish collected in the spring, summer, and fall seasons respectively. Fish in the size interval on either side of this size interval also accounted for a high percentage of the catch except during the summer season.

LAMPREY SCARRING

Relationship Between Age of Fish and Scarring Rate

The sea lamprey is believed to be a major contributor to the past decline of the lake trout in the Great Lakes (Eschmeyer, 1957; Loftus, 1957; Budd and Fry, 1960). Of 363 lake trout examined in this study, 161 (44.4%) had one or more lamprey scars. The scarring rate showed a progressive increase with age of fish beginning with age IV (Table 8). No fish three years old or younger were found to have scars. The average number of scars per fish also showed a progressive increase with increase in age of the fish (Table 8). These data are in fairly close agreement with data obtained from Lake Huron in 1957 by Budd and Fry (1960), who found scarring rates of 4, 38, 66, and 63 percent for age III, IV, V, VI fish, respectively. These observations suggest that there may be a significant mortality of fish in the present lake trout population of Lake Michigan as a result of sea lamprey predation.

The increase in scarring rate with age may be attributed to several factors. The length of time the fish is subject to attack undoubtedly affects the scarring rate, since the percentage of fish with scars and also

Table 8. Lamprey scarring by lake trout age.

Age Class	Number of Fish	Number with Scars	Percent with Scars	Average No. of Scars per Fish
I	1	-	-	-
II	3	-	-	-
III	29	-	-	-
IV	44	7	15.9	0.18
V	142	52	36.9	0.51
VI	75	52	69.3	1.12
VII	69	50	72.5	1.55
Total	363	161	-	-
Weighted Mean	-	-	44.4	0.84

the average number of scars per fish increases with the age of the fish.

Hesse (1969) found an increase in the scarring rate of Lake Michigan lake trout with increase in the length of the fish. Hall (1954) also showed an increase in the scarring rate of the white sucker as the length of the fish increased. Coble (1967) concluded that the sea lamprey changed the size composition of the white sucker population in South Bay, Lake Huron, by removing the large fish from the population. These data suggest that there is a size selection factor involved which makes larger fish more susceptible to lamprey attack.

Still another explanation for increased scarring rate in larger older fish is one offered by Eschmeyer (1957), whose data suggested that the ability of lake trout to survive a lamprey attack increases with the size of the fish. Smaller fish would thus appear to have fewer scars because a higher percentage of them would be killed by a lamprey attack. This would result in the selective removal of small scarred fish from the population.

Location and Relative Age of Lamprey Scars

The location of lamprey attachment on a fish somewhat determines how lethal the attack may be. Of 184 scars recorded as to location, 164 (89.1%) were located on the abdominal region of the fish. This area was defined as the area below the lateral line and between the pectoral fin and the vent. Lennon (1954) reported that of 21 wounds on rainbow trout taken from Lake Huron, 75 percent were located in the above-defined abdominal region. His explanation was that wounds were not seen in other parts of the body as frequently because they were presumably more quickly fatal. This explanation may account for the high percentage of lamprey scars found on the abdominal portion of the lake trout body in this study.

Distinction was made between the relative age of lamprey scars also. A scar was termed fresh if it was still red and inflamed and not completely healed. Healed scars were those that were no longer irritated and were completely healed so that they could only be seen as a circular mark on the skin of the fish. Of a total of 273 scars recorded, 71 (26%) were termed fresh and 202 (74%) were termed healed. Therefore, three out of four scars had been on the fish for sufficient time to allow them to completely heal. These data differ greatly from those of Lennon (1954) for several species of fish from Lake Huron for which lamprey scars were recorded from 1950-1952. He found that 79.7 percent of the scars were new and only 20.3 percent were healing or healed. The data from this study suggest that although the scarring rate is high, lake trout are being attacked at a slower rate than were fish from Lake Huron from 1950-1952.

SUMMARY AND CONCLUSIONS

This study of the lake trout in the inshore waters of Lake Michigan has shown that:

1. Lake trout did not feed nearly as much during spawning as they did during the remainder of the year. Of 125 stomachs examined during spawning time, 84.4 percent were empty.

2. Except for a trace of insects, fish was the sole food of mature Lake Michigan lake trout.

3. Three types of fish (alewife, smelt, and sculpins) made up the bulk (90.8%) of the lake trout diet.

4. Sculpins were the most important item in the diet of the lake trout early in the spring, when the other fish species are not present.

5. Smelt were by far the most important single food item in the diet of the lake trout only during the month of May.

6. The alewife is the most important single food item in terms of food volume and frequency of occurrence. It becomes important in the diet of the lake trout in June and remains the most important food item until spawning time in November.

7. Predation upon yearling lake trout planted during the first week in May was evident until June, when these small planted fish dispersed.

8. Positive correlation was found between the length of the lake trout and the length of the forage fish which they consumed. The correlation coefficient, r, was greatest for smelt, intermediate for alewife, and lowest for sculpin.

9. Female lake trout taken from Lake Michigan matured at an earlier age than in the past and also weighed much more, at the same age, than those collected from the lake in previous studies.

10. The growth rate of the lake trout in Lake Michigan has greatly increased from that of the past.

11. Major spawning activity occurred during the period from November 1 to 15. These data agree with data reported for native Lake Michigan lake trout.

12. Approximately 70 percent of the fish taken at the time of spawning were males.

13. There was a progressive development of the ovaries of mature female fish in terms of percent body weight from April until fall spawning time. The period of greatest development occurred from July through September.

14. The relationship between fecundity and weight for the fish in this study was described by the equation $Y=1065.1 + 1.4X$.

15. The average number of eggs produced per kilogram of fish was 1748.

16. The relationship between fecundity and weight for these fish is described by the equation $Y=-6225.3 + 17.2X$.

17. The fish of this study produced more than twice the number of eggs produced by native fish of the same age from Lake Superior. The equation $Y=947.6 + 741.1X$ describes the relationship between fecundity and the age of the fish of this study.

18. The coefficient of condition of lake trout collected was higher for these fish than for any previously reported from the Great Lakes.

19. Seasonal abundance of the lake trout in the study area varied greatly. By far the greatest abundance was in the fall of the year at spawning time.

20. Size distribution of the lake trout varied with season. Smaller fish were more abundant in the summer than in the spring and fall. The fall size distribution was dominated primarily by large, mature, spawning fish, while in the spring, some smaller immature fish were present.

21. Lamprey scarring of lake trout increased with age. The scarring rate was nearly the same in this study as it was for fish of the same age in South Bay, Lake Huron, prior to the lamprey control program. It is felt that at

present rates of scarring, a significant mortality of lake trout may be occurring due to lamprey predation.

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