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SEA LAMPREY INVESTIGATIONS

2. Egg development, maturity, egg production and percentage of unspawned eggs of sea lampreys, *Petromyzon marinus*, captured in several Lake Huron tributaries[1]

by

Vernon C. Applegate

Introduction

This study constitutes the second of a series of reports which embody the findings and results of investigations begun early in 1947 by the Michigan Institute for Fisheries Research on the life history and habits of the predatory sea lamprey. These investigations were initiated and are being carried on in an effort to provide a sound biological basis for any proposed method of reducing or controlling the numbers of this dangerous fish parasite in the upper Great Lakes. The first report of this series deals with the distribution

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[1] Contribution from the Institute for Fisheries Research of the Michigan Department of Conservation. Some financial assistance in this project was contributed by the Associated Fishing Tackle Manufacturers' Trust Fund for Fisheries Research in the University of Michigan.

of sea lamprey spawning populations in Michigan streams.[1] The present account is concerned primarily with the biotic potential of this fish. Subsequent studies will delineate other phases of the life history.

All field observations upon which this study is based were made between April 9 and July 10, 1947, on the Ocqueoc River and Carp Creek, Presque Isle County, Michigan. The foregoing dates are each within several days of the extreme time limits of the sea lamprey spawning migration into these streams. The peak of the migration occurred during the second week in June. In Carp Creek, a weir and trap were operated and the entire sea lamprey run, 1617 individuals, was captured. All of these specimens were examined at capture by the writer. In the Ocqueoc River the spawning migration was unimpeded, but large samples of the migrants were obtained and examined. The entire ovaries were removed from 70 migrant females and preserved in F-A-A (a solution of formalin, acetic acid and alcohol). Fifty-eight of these specimens were taken in Carp Creek, eight in the Ocqueoc River, one in Ocqueoc Lake (taken in a gill net, presumably while migrating through the lake to the spawning grounds in the river upstream from the lake), and three were captured in the Cheboygan River, Cheboygan County, below the power dam in Cheboygan, Michigan. Pertinent mensural data were collected on all specimens at the time of capture. The specimens utilized were deliberately selected for length so that all size-groups in the migrant population would be adequately represented in the data. To obtain a

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[1] Applegate, Vernon C. (MS) An inventory of sea lamprey spawning streams in Michigan.

better measure of the variability in egg production at any given size, additional specimens were collected in the 17.0 - 18.0-inch (432 - 457 mm.) size group. This group embraces the mean length (17.4 inches, 442 mm.)[1] of the 603 females which entered Carp Creek in 1947.

The earliest specimens represented in my series of 70 migrant females (Nos. 1, 2 and 3) were speared just before midnight on April 15 and on April 16 in Hammond Bay, about 100 feet offshore from the mouth of Carp Creek. These undoubtedly represent the earliest migrants arriving from deeper waters of Lake Huron as determined by repeated observations during the period April 9 through April 15. Those observed were making no effort to enter the creek at that time. They arrived on the gravel fan off the mouth of the creek about two hours after dark and dropped back into deeper water with the beginning of dawn. Upstream migration began on or about April 19. After April 15-16, specimens for this study were collected at five- to ten-day intervals throughout the migratory period.

In addition to the gravid females, 40 spent and dead or dying specimens were collected in the Ocqueoc River, the Little Ocqueoc River (a tributary of the former) and in the Manistique River, Schoolcraft County (one specimen). The remnants of the ovaries and all eggs remaining in the body cavity were removed and preserved in F-A-A.

Egg development and maturity in spawning migrants

Female sea lampreys when sexually mature and ripe have a single, elongate ovary extending nearly the entire length of the body cavity

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[1] The data from which certain averages mentioned in this report are derived will be discussed in detail in a subsequent report.

(Plate 1). The anterior tip of the ovary begins just behind the last pair of gill pouches and extends posteriorly to the anus. The ovary, when the eggs are ripe, or nearly so, constitutes a large percentage of the total weight of the female. In 18 ripe or nearly ripe females collected between June 12 and June 26, the ovaries averaged 22.4 percent of the total weights of the females and ranged from 13.6 to 29.5 percent. On the other hand, in eight less mature females collected between April 15 and April 30, at the beginning of the run, the ovaries averaged only 11.3 percent of the total weights of the females and ranged from 8.2 to 15.8 percent.

When the eggs are fully ripe, they are shed into the coelom (body cavity) and are forced to the exterior during the spawning act through a pair of genital pores. One of these pores enters each side of the urogenital sinus which is provided with a median pore to the outside on a papilla situated behind the anus. No Müllerian ducts (nor vasa efferentia in the male) are present, unless the paired pores represent these. The ripe eggs are spherical to pear-shaped in form and sandy to light tan in color. At the time of extrusion, they are non-buoyant and somewhat adhesive; sand grains stick to them readily.

In order to determine the nature of the ova present throughout a given ovary, and the degree of egg development (i.e. stage of maturity) in females at different times during the spawning run, diameter measurements of ova were made from eight specimens. Measurements were made by means of an ocular micrometer in a compound binocular microscope; calibration of the ocular micrometer with a stage micrometer indicated a value of 0.05 mm. for each micrometer unit; diameters were therefore determined to the nearest 0.05 mm.

Plate 1.--Dissection of a ripe female sea lamprey showing size, extent and position of ovary. Note atrophied remains of digestive tract lying on and within the ovary. (Photo by George Skadding).

Due to the effects of preservation and the natural shape of many of the eggs, very few were perfectly symmetrical. In order to avoid any selection of the longest or shortest diameter, the micrometer was fixed in a vertical position upon the field of vision and the diameter parallel to the graduations on the micrometer measured. This gave the longest diameter of some eggs, the shortest of others, or intermediate measurements between the two. Clark (1925) tested this method and found it to be reliable. It was used again by the same author (Clark, 1934) and by Carbine (1944) with excellent results. Although the eggs appeared equally turgid and well-formed after preservation as when examined fresh, I do not know if any small shrinkage occurred due to preservation. If any did occur, it could hardly have been a appreciable amount. In any event, the relative values obtained would retain their identity.

The first ovary analyzed was from a 12.6-inch (320 mm.) female taken in the Carp Creek weir on June 16, 1947. The weight of this female was 70 grams and the ovary weighed 13.50 grams or 19.2 percent of the weight of the specimen. `Sections were removed from the anterior, middle, and posterior thirds of the ovary. The eggs were teased out of the sections, a random sample of 500 eggs was obtained, and these eggs were measured. A frequency diagram of these ova measurements appears in Figure 1. For each section, the average diameter and range were as follows:

Anterior section - average: 0.87 mm., range: 0.35 - 1.10 mm.

Midsection - average: 0.90 mm., range: 0.50 - 1.15 mm.

Posterior section - average: 0.82 mm., range: 0.35 - 1.15 mm.

It is apparent from these data that the ova in the midportion of the ovary are slightly larger than those developing in the front

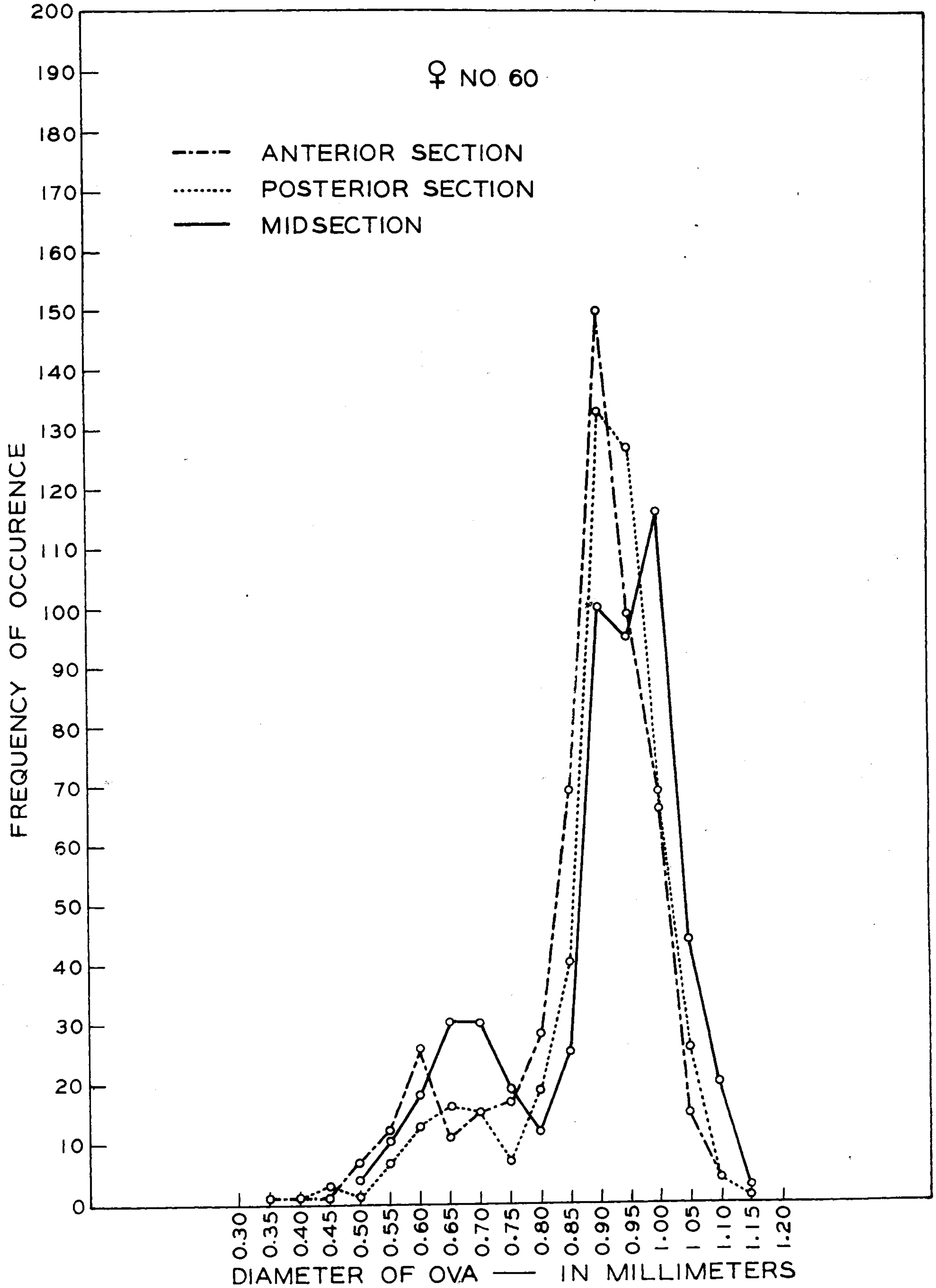

Figure 1.--Frequency distributions of ova diameter measurements made from samples taken from the anterior, mid, and posterior sections of the same ovary.

and back portions. The difference is so small, however, 0.03 mm. and 0.08 mm., that no appreciable error is involved in the other measurements and calculations made from midsections only.

Jordan (1905) reported that "A. Mueller, in 1865, showed that all of the ova in the lamprey were of the same size, and that after spawning, no small reproductive bodies remained to be developed later." It is not quite clear to which species he has reference. In the light of the examination of this and subsequent specimens of the sea lamprey, this statement is in need of qualification. Three categories of ova were present in the material examined. First, there are the developing ova (represented by the highest modes in Figure 1). These are by far the most numerous in the ovary and are the eggs which are destined to be spawned very shortly. Second, there are ova of apparently retarded development which I term "partially developed ova" (these are represented in Figure 1 by each low mode to the left of the high ones representing the developing ova). The partially developed ova are scattered throughout the ovary and differ from the larger ones only in size and amount of contained yolk; the form appears similar. Such eggs are present in variable numbers in all females but are more commonly found in the smallest specimens and are quite infrequent in the larger ones. The individual represented in Figure 1 is believed to have contained the largest number of partially developed ova in the entire series studied. It probably represents the greatest proportion of this kind of eggs present in an average spawning run of females. In examining females in which the eggs had burst into the coelom, I find that some of these retarded ova are extruded with the fully developed ones. The majority, however, remain trapped in the remnants of the ovary. Whether or not those that are extruded with the mature ova can become fertilized is not now known. Ova in the third category are microscopic in size, generally between 0.20 and 0.30 mm. in diameter. They are variable in number in different females, but as a rule they are quite numerous. These ova, unlike those of the other two categories, are transluscent, contain little or no yolk, and are still firmly attached to pedicels in the gonad. Since they could only be found readily in the frayed ovarian tissue of spent females, they do not enter into any of the measurements or counts that were made. They were too small to be seen with the magnification used in making the counts and measurements of the other two kinds of eggs. It seems logical to conclude for the sea lamprey that mature ova develop at the expense of the retarded and undeveloped ones and/or that some mechanical impediment aborts the development of the latter. I do not believe that either of the latter categories could be construed to represent a potential reserve stock that would enable the female to spawn again in the following year.

Jordan (1905) further states "......the most careful microscopical examination of ovaries or testes has failed to reveal any evidence of new gonads or reproductive bodies." My preliminary examinations seem to confirm this. Even if it should be demonstrated that the ovaries or testes of some spent sea lampreys contain spermatogonia (and spermatocytes) or oögonia (and oöcytes), the presence of such germ-cell stages need not necessarily indicate that these specimens would have lived to spawn in another season. Weisel (1947) has shown the presence of these germ cells in spent, land-locked sockeye salmon (Oncorhynchus nerka) of both sexes. Individuals of this species become sexually mature and spawn only once, dying very shortly thereafter. Weisel concluded that some factor, other than a potential supply of germ-cells, limits the spawning of this Pacific salmon to a single season.

In general, the developmental stages of the ova found in the sea lamprey are similar to those found in other fishes that spawn during a single brief period, i.e., the maturing eggs constitute a single size group more or less discreet from the immature ova. However, the sea lamprey differs fundamentally from such fishes in one respect. In females of those species that spawn in several or many seasons, the immature eggs greatly outnumber the maturing eggs at the time of spawning (Carbine, 1944). It is herein demonstrated that in the sea lampreys studied, the maturing eggs outnumbered the undeveloped ones present. This fact, the absence of any germ-cell stages, and the nature of other physiological changes at spawning I consider very strong evidence that the sea lamprey spawns but once and then dies.

Ova diameters were obtained from seven additional specimens. Six of these were selected from the series available so that one of the earliest and one of the latest migrants and four migrants taken on scattered intervening dates were represented. For uniformity these were selected to fall within 17.0 and 17.5 inches (432 and 445 mm.) in total length. These factors only governed the selection of the specimens. A seventh specimen (No. S-41) of comparable length (16.4 inches, 417 mm.), taken on the spawning grounds, was chosen for examination since in this female the bulk of the eggs had burst into the coelom and presumably represented fully mature eggs. The data for six specimens is based on sample sections removed from the previously described midregion of each ovary. These samples were teased apart and a random sample of 500 ova from each was measured. For specimen No. S-41, a random sample of 500 ova was taken from the total number that were loose in the coelom. The data obtained for all seven specimens are presented in Table 1 and for six of the specimens (including No. S-41) are graphically portrayed in Figure 2.

Ova among the earliest spawning migrants entering a stream are about 3/4 of a millimeter in diameter (average: 0.75 mm., range: 0.40 - 0.85 mm.). Fully mature eggs average about 1.10 millimeters in diameter and range from 0.80 to 1.25 millimeters. Migrants entering the stream on progressively later dates demonstrate progressively advanced stages of egg development, as Table 1 will illustrate. However, it should be pointed out that the smooth progression of increasing average ova diameters with later dates of capture in Table 1 is most likely fortuitous. In examining nearly a thousand females, I found that many degrees of maturity were represented among the specimens taken on a single day, particularly in midseason. The mean values listed in Table 1 are considered to represent the average degree of egg development in females entering the stream on the dates indicated.

In migrants entering the stream in mid-April, 68.4 percent of the development of the ova had still to take place while the female was in the stream (computed on the basis of the relative volumetric proportions of individual ova with the assumption that they are perfectly spherical in shape). In females that entered the stream from mid-June until the end of the run, the eggs were very near fully developed, but not so far along as to have burst into the body cavity. In only a few of the late migrants, including the last ones taken in July, were any of the eggs found to be loose in the coelom.

Table 1.--Average Diameter and Range in Diameter of Developing Ova in Seven Female Sea Lampreys Collected at Intervals During the Period of the Spawning Migration.

Specimen number	Place of collection	Date of collection	Total length (inches)	Total length (millimeters)	Weight in grams	Condition of ovary	Ova diameters (in millimeters)[1] Average	Range
2	Hammond Bay - off mouth of Carp Creek	April 16, 1947	17.2	437	222	Green	0.75	0.40 - 0.85
4	Carp Creek weir	April 25, 1947	17.2	437	134	Green	0.76	0.50 - 0.95
14	Carp Creek weir	May 12, 1947	17.2	437	165	Green	0.83	0.40 - 1.00
23	Carp Creek weir	May 25, 1947	17.5	445	168	Green	0.91	0.45 - 1.10
36	Carp Creek weir	June 10, 1947	17.2	437	246	Green	0.98	0.45 - 1.20
73	Carp Creek weir	July 2, 1947	17.0	432	178	Ripe	1.03	0.60 - 1.25
S-41	Ocqueoc River	June 28, 1947	16.4	417	203	Eggs loose in coelom	1.10	0.80 - 1.25

[1] Range and averages for each specimen based on random sample of 500 Ova taken from the midsection of the ovary.

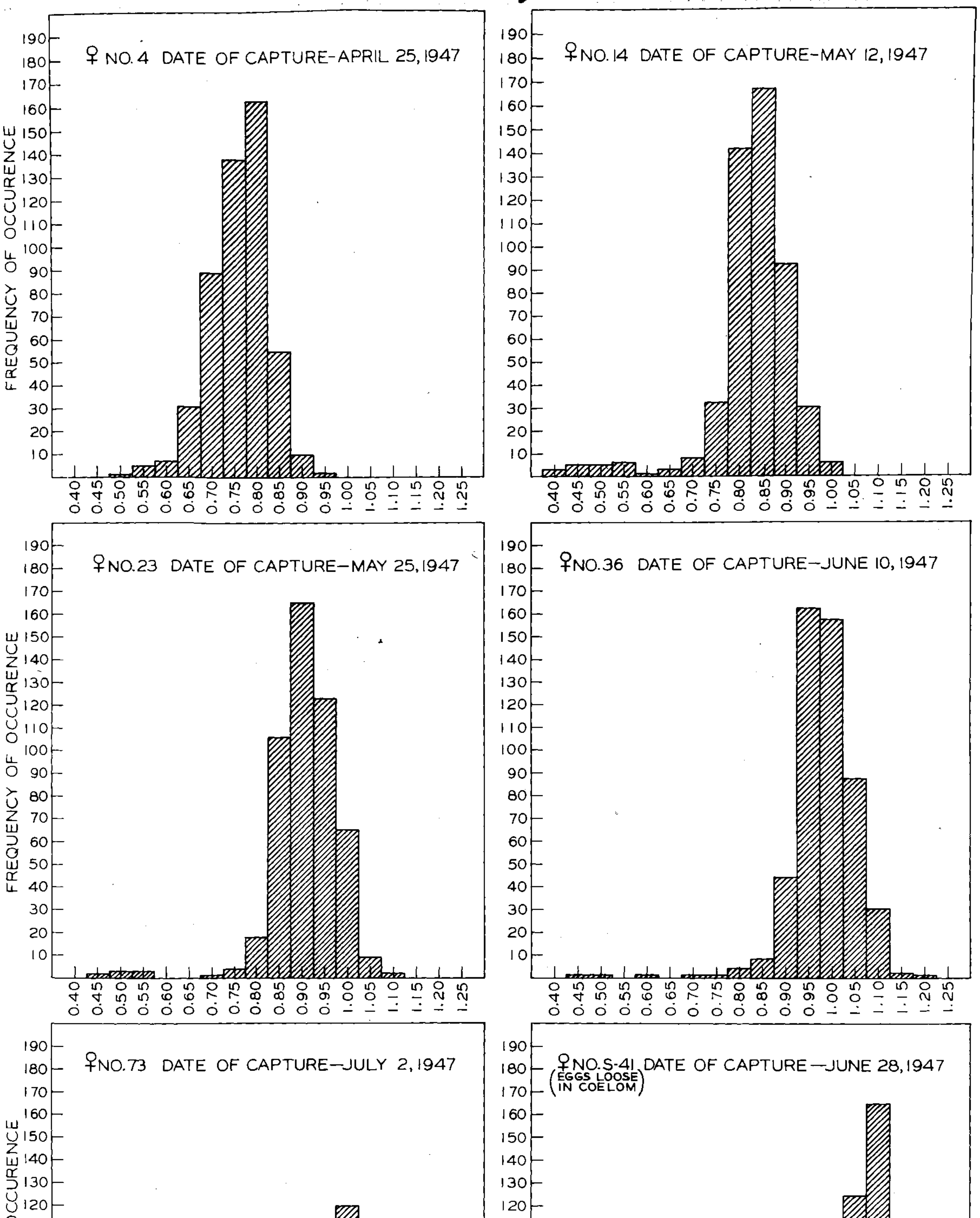

Figure 2.--Frequency distributions of ova diameter measurements from sea lampreys taken on successive dates. The upper left specimen was a very early spawning migrant; the upper right and two central specimens were captured prior to, and during, the peak of the run; the lower left specimen was taken after the peak of the run and that in the lower right was a female in which the fully ripe eggs had burst into the coelom.

In the frequency polygons presented in Figure 2, the preceding data are pictorially presented. Since a uniform horizontal scale was used for all six projections, the relative degrees of maturity of the specimens examined is apparent in the progressive shifting of the frequency distributions from left to right. Of particular interest, is the great scarcity of partially developed eggs found in most of the samples represented.

Egg Production

Of the seventy specimens utilized to determine egg production, actual numerical counts were made of the ova in ten specimens. These ten specimens include the largest (21.1 inches, 536 mm.) and the smallest (12.6 inches, 320 mm.) females in the series and eight of intermediate sizes. Prior to making each of these counts, the total volume and the total weight of the ovary were obtained. A sample section was removed from the middle of the length of the ovary and the volume and weight of the sample were likewise determined. Volumes were secured by a system of displacement of water into a cylinder bearing 0.2 cc. graduations and were read to the nearest 0.1 cc. Weights were obtained to the nearest 0.01 gram on a chemical balance. Excess moisture was removed as consistently as possible from all ovaries and sections before any determinations were made. Eggs in the sample section were counted first and the total production was computed by direct proportion for both the volumetric and gravimetric data. When the balance of the ova had been counted, the calculated totals by both techniques could be compared for accuracy. This procedure was followed for all ten specimens and the results were incorporated in Table 2 for evaluation.

Table 2.--Egg production of ten female sea lampreys as determined by numerical counts, compared with values as determined volumetrically and gravimetrically from sample sections of the ovaries.

Specimen data										
(1) Specimen number	#60	#58	#57	#70	#44	#73	#56	#23	#66	#63
(2) Place of capture	Ocqueoc River	Carp Creek	Carp Creek	Carp Creek	Carp Creek	Carp Creek	Carp Creek	Carp Creek	Cheboygan River	Ocqueoc River
(3) Date	6/16/47	6/15/47	6/15/47	6/26/47	6/11/47	7/2/47	6/15/47	5/25/47	6/26/47	6/20/47
(4) Total length in inches	12.6	14.2	14.9	15.0	16.3	17.0	17.1	17.5	18.0	21.1
(5) Total length in millimeters	320	361	378	381	414	432	434	445	457	536
(6) Weight in grams	70	100	137	128	182	178	165	168	236	316
(7) Total eggs by numerical count	23,986	21,000	48,694	66,537	53,012	67,604	59,185	55,486	69,736	107,138
(8) Total eggs in sample section by actual count	1,343	1,962	9,372	8,594	8,929	6,951	3,470	3,684	6,686	5,703
(9) Total volume of ovary (cc.)	12.5	13.6	34.8	37.6	37.9	55.5	46.7	28.2	66.3	76.9
(10) Volume of sample section (cc.)	0.7	1.3	6.6	4.4	6.0	5.2	2.7	2.0	6.0	3.9
(11) Calculated number of eggs	23,982	20,526	49,416	73,440	56,402	74,189	60,018	51,944	73,880	112,451
(12) Percentage error	0.0	-2.3	+1.5	+10.4	+6.4	+9.7	+1.4	-6.4	+5.9	+5.0
(13) Total weight of ovary (grams)	13.50	13.93	32.49	34.86	36.30	51.55	45.97	28.81	65.18	73.44
(14) Weight of sample section (grams)	0.68	1.30	5.70	4.56	5.93	5.15	2.72	1.97	6.11	3.86
(15) Calculated number of eggs	26,662	21,024	53,420	65,699	54,658	69,577	58,646	53,876	71,325	108,505
(16) Percentage error	+11.1	0.0	+9.7	-1.3	+3.1	+2.9	-0.9	-2.9	+2.3	+1.3
(17) Egg production of specimen[1]	24,021	21,000	48,694	66,552	53,026	67,617	59,198	55,491	69,806	107,138

[1] Where these figures differ slightly from actual numerical counts listed on Line 7 it is due to addition of a small number of eggs not preserved, but counted, at time of collection.

There was really very little difference in the accuracy of the two techniques (Table 2). By the volumetric technique, the calculated totals differed from the actual totals (numerical counts) by amounts varying from 0.0 to 10.4 percent. The mean percentage error was +3.2 percent. By the gravimetric technique, deviations from actual totals varied from 0.0 to 9.7 percent with a mean percentage error of +2.5 percent. The mean percentage errors of the two techniques are based on an algebraic average of the individual percentage errors. Although in most cases this statistic might produce an inaccurate result, it is felt that in this instance its application is justified. A mean error based on the algebraic sum of deviations expressed in numbers of eggs allows individual specimens (such as a small one of low egg count) to influence the results unduly, i.e., a female containing only 25,000 eggs and for which there is a $\pm$ 1,000 egg deviation between calculated and actual totals has a large percentage error. This latter statistic is a very real measure of the efficiency of the calculating technique in that particular case. However, an equal numerical deviation in a larger and more productive specimen results in a much lower percentage error. It follows, then, that if errors expressed in numbers of eggs tend to remain more or less constant (as they may if there is some small bias in the technique), too many small test specimens or too many large test specimens in a series will undoubtedly render too high or too low a mean error.

The preponderance of positive errors in calculating total egg production suggests some small bias in the techniques or procedures used. It is felt that the mean percentage error, as computed, provides the best measure of any bias, if it exists, resulting from some defect in the procedure. The mean percentage errors in this study are so small, however, that they may very well fall within the limits of chance occurrence. Consequently, the application of any small correction factor to the calculated data on egg production is not suggested.

The gravimetric method was utilized in calculating total egg production for the remaining 60 specimens as the smallest error was apparently involved in this technique and because the laboratory procedure is more rapid by this method. Data on collection, size, weight and egg production have been tabulated in order of increasing total length of specimens in Table 3. Where data are available for more than one specimen of a given length, these are listed in order of increasing egg production. In addition, weights of ovaries and data used in calculating numbers of eggs produced are presented. These data have been plotted upon two graphs to illustrate the relationship between egg production and total length (Figure 3) and between egg production and weight (Figure 4).

The first property evident in these figures is that the number of eggs produced by the sea lamprey varies greatly at any particular length or weight. Mean egg production was computed by one-inch size groups and by 50-gram weight groups and these values plotted upon the respective graphs. The curves appearing in Figures 3 and 4 have been fitted by inspection to these mean values. The number of eggs produced increases quite rapidly with increase in total length; however egg production with increasing weight is more directly proportional. The lowest egg production recorded, 24,021 eggs, was found in a 12.6-inch (320 mm.) female weighing 70 grams. The greatest recorded, 107,138 eggs, was found in a 21.1-inch (536 mm.) female weighing

Table 3.--Data on collection, size, weight and egg production for seventy sea lampreys with weights of ovaries and data used in calculating number of eggs produced.

Specimen number	Date of collection (1947)	Place of collection	Total length (inches)	Total length (millimeters)	Total weight (grams)	Weight o ovary (grams)	Weight of sample section (grams)	Number count of sample section	Calculate egg production	Correction[2]	Total egg productio
60	6/16	Ocqueoc River	12.6	320	70	13.50	0.68	1,343	...	...	24,021[1]
61	6/18	Carp Creek	12.6	320	61	11.88	0.91	2,387	31,162	44	31,206
28	6/4	Carp Creek	13.4	340	81	11.31	0.81	3,005	41,959	37	41,996
37	6/10	Carp Creek	13.7	348	101	13.90	0.96	2,512	36,372	16	36,388
59	6/16	Ocqueoc River	13.9	353	90	20.65	1.51	3,392	46,387	51	46,438
58	6/15	Carp Creek	14.2	361	100	13.93	1.30	1,962	...	...	21,000[1]
21	5/22	Carp Creek	14.4	366	104	6.62	0.60	3,816	42,103	19	42,122
16	5/12	Carp Creek	14.6	371	129	14.67	1.08	2,778	37,735	40	37,775
53	6/14	Carp Creek	14.6	371	100	21.85	1.58	3,648	50,449	22	50,471
31	6/5	Carp Creek	14.6	371	137	19.56	1.80	5,144	55,898	56	55,954
54	6/14	Carp Creek	14.7	373	92	16.32	1.25	2,868	37,445	24	37,469
49	6/12	Ocqueoc River	14.7	373	99	22.98	1.64	2,991	41,910	6	41,916
57	6/15	Carp Creek	14.9	378	137	32.49	5.70	9,372	...	...	48,694[1]
13	5/12	Carp Creek	15.0	381	122	15.75	1.33	3,937	46,622	8	46,630
70	6/26	Carp Creek	15.0	381	128	34.86	4.56	8,594	...	...	66,552[1]
7	4/30	Carp Creek	15.1	384	135	12.97	0.79	2,335	38,335	0	38,335
3	4/16	Hammond Bay[3]	15.3	389	110	10.37	0.56	2,472	45,776	0	45,776
55	6/14	Carp Creek	15.5	394	110	20.20	1.65	3,128	38,294	8	38,302
51	6/12	Ocqueoc River	15.5	394	136	38.97	3.13	3,716	46,266	15	46,281
38	6/10	Carp Creek	15.5	394	179	31.85	2.51	5,904	74,917	55	74,972
46	6/12	Carp Creek	15.9	404	132	26.46	2.25	4,156	48,875	5	48,880
47	6/13	Carp Creek	16.0	406	150	31.38	2.20	3,099	44,203	2	44,205
34	6/5	Carp Creek	16.1	409	137	18.90	1.61	3,954	46,417	10	46,427
48	6/12	Ocqueoc River	16.2	411	160	38.66	2.16	3,238	57,954	9	57,963
44	6/11	Carp Creek	16.3	414	182	36.30	5.93	8,929	...	...	53,026[1]
15	5/12	Carp Creek	16.4	417	142	16.98	1.13	4,061	61,023	0	61,023
1	4/15	Hammond Bay[3]	16.7	424	149	16.43	1.17	4,096	57,519	20	57,539
52	6/12	Ocqueoc River	16.8	427	158	43.65	3.18	5,044	69,236	1	69,237
22	5/25	Carp Creek	16.9	429	143	20.55	1.11	2,365	43,784	24	43,808
26	6/2	Carp Creek	17.0	432	170	19.65	1.08	2,417	43,976	34	44,010
19	5/18	Carp Creek	17.0	432	151	22.52	1.71	5,008	65,953	18	65,971
73	7/2	Carp Creek	17.0	432	178	51.55	5.15	6,951	...	...	67,617[1]
56	5/25	Carp Creek	17.1	434	165	45.97	2.72	3,470	...	...	59,198[1]
4	4/25	Carp Creek	17.2	437	134	13.40	0.71	2,553	48,183	17	48,200
36	6/10	Carp Creek	17.2	437	246	36.17	3.26	4,738	52,569	2	52,571
14	5/12	Carp Creek	17.2	437	165	23.10	1.28	3,306	59,663	11	59,674
18	5/17	Carp Creek	17.2	437	175	21.93	1.59	4,493	61,970	2	61,972
2	4/16	Hammond Bay[3]	17.2	437	222	22.97	1.02	3,572	80,440	0	80,440
9	5/1	Carp Creek	17.3	439	155	13.70	0.90	3,838	58,423	0	58,423
69	6/26	Carp Creek	17.3	439	176	33.82	1.71	3,522	69,657	51	69,708
27	6/2	Carp Creek	17.3	439	198	31.38	1.56	4,095	82,373	16	82,389
23	5/25	Carp Creek	17.5	445	168	28.81	1.97	3,684	...	...	55,491[1]
12	5/12	Carp Creek	17.8	452	182	14.55	1.14	4,372	55,801	12	55,813
66	6/26	Cheboygan River	18.0	457	236	65.18	6.11	6,686	...	...	69,806[1]
68	6/26	Carp Creek	18.0	457	216	40.51	2.79	5,075	73,688	0	73,688
35	6/10	Carp Creek	18.0	457	253	40.28	2.65	5,548	84,330	34	84,364
41	6/11	Carp Creek	18.0	457	228	49.52	3.52	6,495	91,373	21	91,394
40	6/11	Carp Creek	18.1	460	216	48.61	3.32	5,288	77,425	0	77,425
65	6/26	Cheboygan River	18.2	462	222	65.45	4.09	5,203	83,261	72	83,333
5	4/25	Carp Creek	18.4	467	179	14.72	0.91	2,947	47,670	48	47,718
50	6/12	Ocqueoc River	18.4	467	198	47.02	3.08	3,990	60,912	3	60,915
20	5/17	Carp Creek	18.5	470	236	45.54	3.47	6,106	80,135	8	80,143
11	5/12	Carp Creek	18.6	472	183	13.52	0.62	2,835	61,821	37	61,858
32	6/5	Carp Creek	18.6	472	251	40.32	2.50	4,830	77,898	9	77,907
6	4/25	Carp Creek	19.0	483	202	26.92	1.71	3,376	53,147	0	53,147
42	6/11	Carp Creek	19.0	483	186	30.04	2.22	4,484	60,675	25	60,700
8	4/30	Carp Creek	19.0	483	226	35.82	2.04	4,186	73,501	0	73,501
67	6/26	Cheboygan River	19.0	483	283	77.95	5.68	6,327	86,829	15	86,844
39	6/10	Carp Creek	19.2	488	277	54.45	3.09	4,397	77,481	5	77,486
30	6/4	Carp Creek	19.4	493	303	58.53	3.09	4,220	79,934	14	79,948
29	6/5	Carp Creek	19.6	498	285	49.02	4.00	5,965	73,101	10	73,111
45	6/12	Carp Creek	19.6	498	262	35.55	1.12	2,880	91,414	18	91,432
33	6/5	Carp Creek	19.7	500	231	32.78	2.44	6,126	82,299	21	82,320
24	6/1	Carp Creek	19.7	500	285	56.67	2.82	4,840	97,263	25	97,288
10	5/3	Carp Creek	19.8	503	240	26.31	1.04	3,037	76,830	6	76,836
17	5/15	Carp Creek	20.2	513	328	48.31	3.14	6,102	93,881	16	93,897
43	6/11	Carp Creek	20.3	516	296	56.72	3.84	5,898	87,118	12	87,130
25	6/2	Carp Creek	20.5	521	221	37.00	2.48	5,109	76,223	12	76,235
62	6/20	Ocqueoc Lake	20.5	521	270	59.55	3.27	5,190	94,515	11	94,526
63	6/20	Ocqueoc River	21.1	536	316	73.44	3.86	5,703	...	...	107,138[1]

[1] Total number of eggs determined by numerical count (see Table 1).

[2] Number of eggs not preserved at time of collection

[3] Specimens captured in open water of bay about 100 eet off the mouth of Carp Creek.

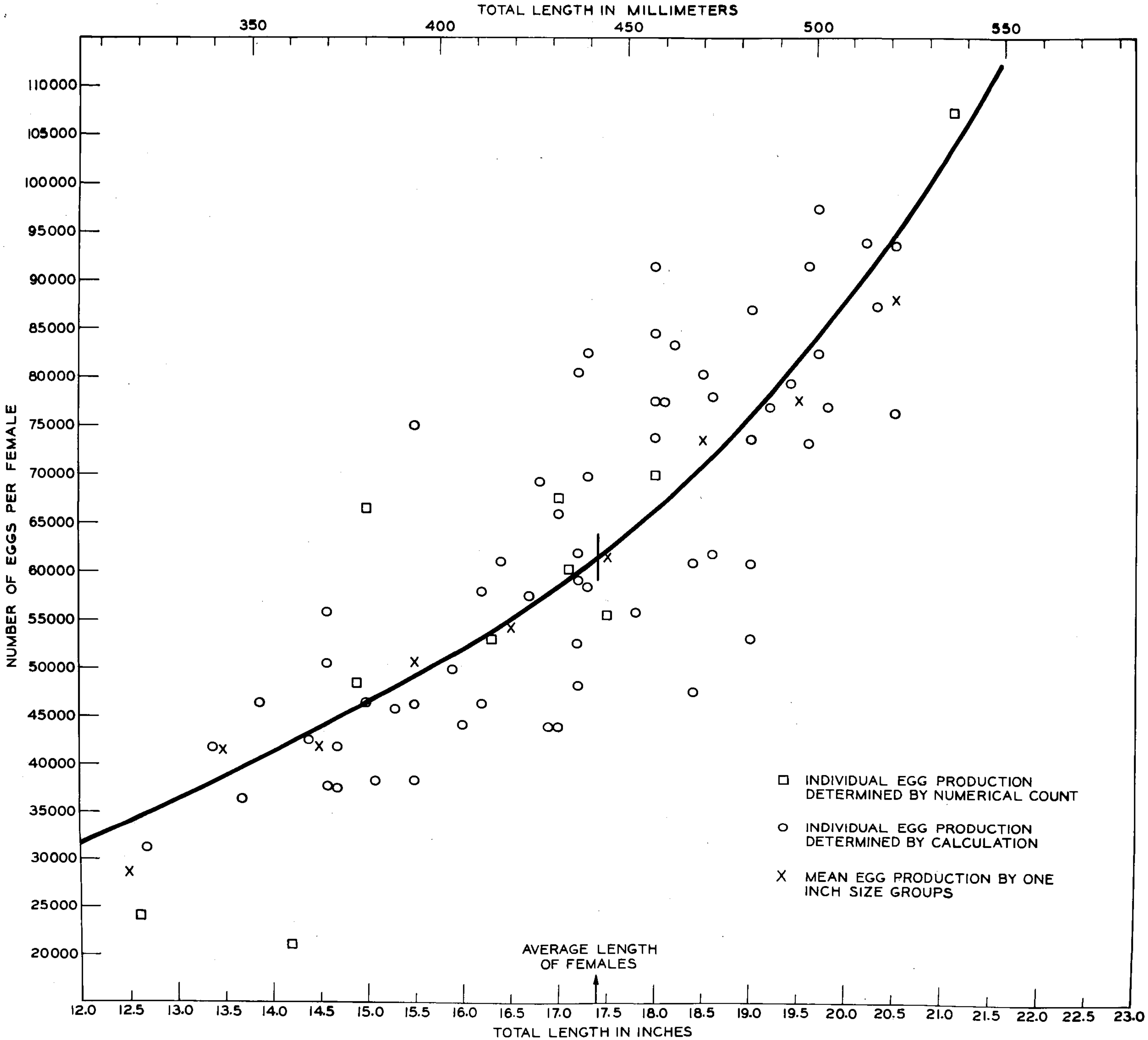

Figure 3.--Relationship between the number of eggs produced and the total length of the fish for 70 sea lampreys.

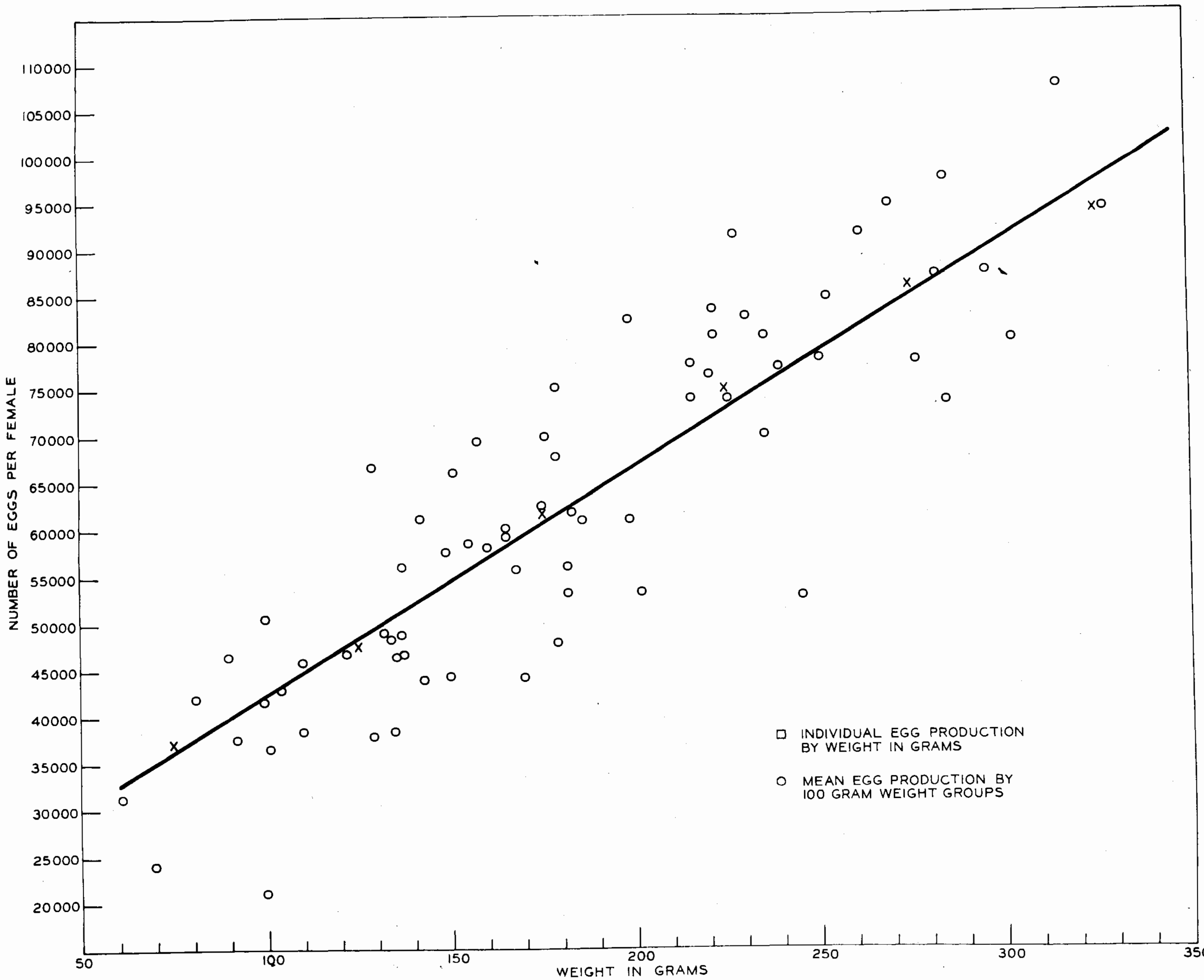

Figure 4.--Relationship between the number of eggs produced and the weight of the fish for 70 sea lampreys.

316 grams. Using values obtained from the curve projected in Figure 3, we find that the mean egg production for females of average length (17.4 inches, 442 mm.) is 61,500 eggs. Mean egg production data, as estimated from the curve in Figure 3, for successive one-inch size groups are listed in Table 4 with the mean deviation for each of the groups.

Percentage of unspawned eggs

The egg production determined for the sea lamprey in the preceding section represents the basic reproductive potential of the species in the region studied. This potential is obviously never realized in nature. Many factors inherent in the organism itself and in its environment tend to nullify the potential and the actual productivity of the species may be very low when these factors are considered. A preliminary experiment in the number of ammocoetes (larvae) produced per spawning female suggests that the larval hatch per number of eggs produced (and spawned) is quite small.

One of the inherent factors which may contribute to a low productivity is the percentage of ripe eggs remaining in the female after the spawning act is completed, i.e., the number of unspawned eggs. Forty spent females were collected to determine this percentage. In order to avoid any doubt as to whether they had completed as much of their spawning act as they were destined to, only dead (30) or obviously dying (10) specimens were collected. Most collections were made in the deeper pools below spawning riffles or in sloughs into which the dying sea lampreys had drifted. The females obtained varied from 11.8 inches (300 mm.) to 18.1 inches (460 mm.) in total length.

Table 4.--Estimated mean egg production by one-inch size groups as determined from the curve projected in Figure 3 and mean deviation for each of these groups.

Midpoint of size group (inches)	Mean egg production	Mean deviation
12.5	34,000	...[1]
13.5	38,700	4,449
14.5	43,800	7,805
15.5	48,300	8,960
16.5	55,200	7,287
17.5	62,200	8,541
18.5	70,600	10,560
19.5	81,900	9,896
20.5	94,800	6,853
21.5	110,300	...[1]

[1] Too few specimens to warrant computation.

For ten specimens, separate counts were made of the partially developed and fully developed eggs. For the balance, only the fully developed eggs were counted. These data are presented in Table 5 with appropriate data on collection, size and weight. The partially developed eggs were, as a rule, still trapped in the remnants of the ovary. Some fully developed eggs were found in like position (Plate 2) but where larger numbers of these were present, by far the bulk of them were loose in the coelom. The potential egg production of each female was determined from the curve projected in Figure 3. Using this figure and the number of developed eggs retained in females, the estimated percentage of unspawned eggs was computed (Table 5). The partially developed eggs were not considered in estimating this percentage since their occurrence is variable with length. They are present in nominal numbers only in all but the very smallest size groups.

As a general rule, only a very small percentage of developed (mature) eggs remain unspawned; the estimated average percentage was 5.00 percent. Among the specimens, however, there are several notable exceptions. For two individuals, the estimated percentage of unspawned eggs was 28.6 and 37.2 percent respectively. Two others were identical in having an estimated 19.4 percent of their eggs unspawned. All of the females displaying a relatively high percentage of unspawned eggs were late migrants, appearing at the very end of the spawning season. Observations made upon late migrants of both sexes indicate a very low vitality at that time. I suspect that these specimens examined which contained a large number of unspawned eggs were unable to complete their spawning act before approaching death made them incapable of doing so. In view of this, the average percentage of 5.00 unspawned eggs is believed to

Table 5.--Number of unspawned eggs (developed and partially developed) in forty spent and dead or dying sea lampreys and estimated percentage of potential egg production unspawned for each individual.

Specimen number	Date of collection (1947)	Place of collection	Total length (inches)	Total length (millimeters)	Weight (grams)	Unspawned eggs		Potential egg production[1]	Estimated percentage unspawned
						Partially developed	Developed		
1	July 2	Ocqueoc River	11.8	300	64	2,152	2,998	31,000	9.6
2	June 24	Ocqueoc River	12.0	305	88	224	121	31,700	0.4
18	July 3	Ocqueoc River	12.4	315	67	...	112	33,600	0.3
36	July 2	Little Ocqueoc River	12.6	320	92	...	9,880	34,500	28.6
10	July 3	Ocqueoc River	12.7	323	84	1,227	77	35,000	0.2
29	June 24	Ocqueoc River	12.8	325	101	...	13,215	35,500	37.2
38	June 28	Ocqueoc River	12.9	328	99	...	104	36,000	0.3
37	June 28	Ocqueoc River	13.1	333	82	...	1,809	36,900	4.9
21	June 24	Ocqueoc River	13.2	335	75	...	69	37,300	0.2
16	July 1	Ocqueoc River	13.3	338	104	...	4,980	37,800	13.2
27	June 23	Ocqueoc River	13.4	340	103	...	519	38,300	1.4
24	June 24	Ocqueoc River	13.4	340	103	...	225	38,300	0.6
3	June 22	Ocqueoc River	13.7	348	102	899	74	39,700	0.2
9	July 1	Ocqueoc River	13.8	351	79	470	3,879	40,200	9.6
5	July 1	Little Ocqueoc River	14.0	356	99	227	251	41,300	0.6
32	July 2	Little Ocqueoc River	14.3	363	102	...	647	42,800	1.5
8	July 2	Ocqueoc River	14.4	366	99	55	5	43,300	0.0
7	June 24	Ocqueoc River	14.4	366	78	134	1,518	43,300	3.5
15	July 7	Manistique River	14.5	368	108	...	453	43,800	1.0
23	June 28	Ocqueoc River	14.6	371	156	...	124	44,400	0.3
34	June 29	Ocqueoc River	14.7	373	131	...	6,392	45,000	14.2
33	June 24	Ocqueoc River	14.7	373	118	...	6,386	45,000	14.2
22	June 29	Ocqueoc River	14.8	376	119	...	222	45,500	0.5
19	July 2	Little Ocqueoc River	14.9	378	104	...	148	46,000	0.3
13	June 23	Ocqueoc River	15.0	381	117	...	470	46,500	1.0
4	July 3	Ocqueoc River	15.0	381	144	...	366	46,500	0.8
20	June 30	Ocqueoc River	15.0	381	145	...	271	46,500	0.6
40	June 29	Ocqueoc River	15.1	384	161	...	820	47,100	1.7
17	July 2	Ocqueoc River	15.6	396	166	...	322	49,800	0.6
39	June 28	Ocqueoc River	15.6	396	126	...	354	49,800	0.7
6	July 2	Ocqueoc River	15.7	399	112	33	48	50,400	0.0
31	June 29	Ocqueoc River	15.9	404	166	...	790	51,600	1.5
26	July 1	Little Ocqueoc River	15.9	404	153	...	92	51,600	0.1
28	July 3	Ocqueoc River	16.3	414	186	...	2,113	54,000	3.9
25	June 28	Ocqueoc River	16.4	417	203	...	10,584	54,500	19.4
12	June 26	Ocqueoc River	16.7	424	116	...	980	56,500	1.7
14	July 2	Ocqueoc River	16.8	427	123	...	1,397	57,100	2.4
35	June 28	Ocqueoc River	16.8	427	201	...	11,101	57,100	19.4
30	July 2	Ocqueoc River	17.0	432	192	...	1,806	58,400	3.1
11	June 20	Ocqueoc River	18.1	460	236	47	205	67,000	0.3

[1] Based on values obtained from curve projected in Figure 3.

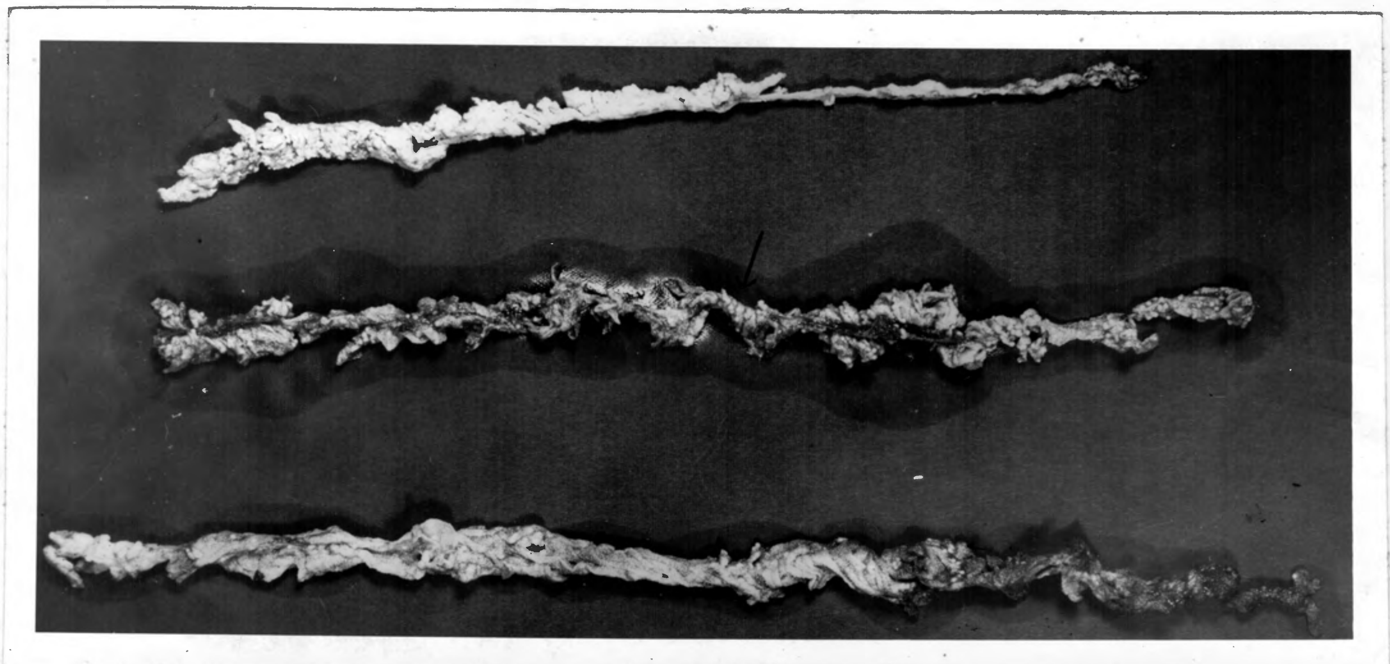

Plate 2.--Spent ovaries from three females. Upper: from a female 12.9 inches (328 mm.) in total length and weighing 99 grams. Middle: from a female 15.1 inches (384 mm.) in total length and weighing 161 grams. Lower: from a female 15.6 inches (396 mm.) in total length and weighing 126 grams. Note fully developed eggs still trapped in ovarian tissue.

represent the maximum average that occurs; indications are that this average would be lower if computed for specimens found spent nearer the beginning of the spawning season.

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Summary

1. The materials for this study consisted of 70 gravid and 40 spent sea lampreys. The spawning migrants were captured in a weir in Carp Creek, Presque Isle County, or captured in nets in the Ocqueoc River in the same county. Three specimens were obtained in the Cheboygan River, Cheboygan County. Spent females were collected near the spawning grounds in the Ocqueoc watershed.

2. Diameter measurements of ova made on sample sections from the anterior, mid, and posterior thirds of one ovary showed that the ova in the midsection of the ovary are slightly more developed than in the distal thirds of this organ. The difference is so small, however, that it would have no appreciable effect upon data obtained from the mid-sections of ovaries only.

3. Diameter measurements of ova made from seven additional specimens collected at different times during the spawning season show that the eggs average 0.75 mm. in diameter in the earliest migrants.

4. Mature eggs of the sea lamprey average 1.10 mm. in diameter and range from 0.80 - 1.25 mm.

5. Among late migrants the eggs are nearly fully mature upon the sea lampreys' entrance into the spawning stream. However, at the peak of the run, many degrees of maturity are represented in a single days' sample.

6. Three categories of eggs were present in most of the ovaries examined: (1) developing ova which are destined to be spawned shortly, and (2 and 3) partially developed and undeveloped ova which failed to mature. The latter categories seem to vary in number present with the size of the female, being more common among the smallest specimens. Those eggs which failed to mature were always surpassed in numbers by the ova approaching maturity. No indication was found of germ cells in the stroma of the ovaries although their presence may be demonstrated when more material is examined.

7. Actual numerical counts were made of the ova in ten specimens. Both volumetric and gravimetric methods of calculating egg production were tested.

8. The mean percentage error of calculation was +3.2 percent by the volumetric method and +2.5 percent by the gravimetric method. The latter technique was utilized in determining the total egg production of 60 specimens.

9. On the basis of ten actual counts and 60 calculated totals, the mean egg production for the average sized female (17.4 inches) was found to be 61,500 eggs. The range for all sizes was 24,021 to 107,138 eggs.

10. Egg production at any particular length or weight varies greatly. The number of eggs produced increases quite rapidly with greater length and is proportionate to increase in weight.

11. The estimated average percentage of unspawned eggs in 40 spent females was 5.00 percent. Individual percentages were nominal as a rule. Large percentages of unspawned eggs in several late migrants are attributed to low viability and the onset of death before completion of spawning.

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