EGG SIZE AND EGG NUMBER IN SOME FRESHWATER FISH OF BRITISH COLUMBIA

by

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ABSTRACT

Fecundity data were obtained for twelve species of British Columbia freshwater fishes by use of a displacement method. Data for an additional fourteen species were obtained from the literature. Fecundity relative to a unit body weight was considered superior to absolute fecundity for use in racial studies. Egg diameter was significantly larger in anterior than in posterior regions of ovaries from five species tested. Egg diameter was positively correlated with fork length within and between species. Amongst twenty-six freshwater species considered, egg diameter was found significantly correlated with reproductive characteristics. Fish with eggs of large mean diameter generally have amber to salmon colored eggs, non-adhesive eggs, long incubation periods, redd construction, stream spawning and variable spawning season. Fish with eggs of small mean diameter have white to yellow eggs, adhesive eggs, short incubation period, lack of redd construction, variable spawning location and spring or summer spawning season.

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INTRODUCTION

In all types of fisheries work a knowledge of the reproductive potential of fish species under study is fundamental to any understanding of population relationships or densities.

A considerable amount of work has been done in the past, primarily by fish-cultural organizations, in attempts to use egg number as a means of racial separation. Some of these attempts apparently had a limited success, but the majority were of little value because of wide variability between samples taken at different times from a single area.

In the present study an attempt was made to determine the degree of variability in egg number and egg diameter of some common fish of British Columbia. Egg number and egg diameter were compared with fork length of several species. Egg diameter was also compared with fish age in rainbow trout from Paul Lake, British Columbia. A study was made of relationships between egg diameter and characteristics of the reproductive life history of a number of species. All fish examined by the author were from collections of the Institute of Fisheries at the University of British Columbia. Additional data were obtained from a review of literature.

In this thesis "relative fecundity" refers to the number of eggs carried by a mature female, relative either to one unit fork length or to one unit body weight. "Absolute fecundity", or simply "fecundity" refers to the total number of eggs carried by a mature female immediately prior to spawning.

METHODS AND MATERIALS

Early methods of egg enumeration were extremely crude, consisting in general of such procedures as that of Page (1888) who refined earlier techniques by determining average numbers of ova per quart for each species, rather than for individual females. Von Bayer (1908) devised a more elaborate technique involving the principle that the volume of a sphere varies as a cube of its diameter. After the early 1900's little change took place in methods of egg enumeration until Burrows (1951) attempted a review of several methods. Burrows examined the Von Bayer method, in which egg numbers were determined from diameters by the use of prepared table; the Canaday weight method in which the weight of a known number of drained eggs taken at random from a large number is compared with the total sample weight; the improved weight method involving more careful water removal than the Canaday method; and the displacement method of Burrows in which water displaced by samples of known number is measured in accurately calibrated burettes and compared proportionately with water displaced by large numbers of eggs. The Von Bayer method was the only one producing a biased statistic. Calculated egg numbers were found to be consistantly higher than numbers obtained by direct counts. All three of the other techniques produced unbiased results. The Canaday weight method showed a wide variability which was reduced substantially in the improved weight method. The displacement technique was the most accurate.

Time involved in making the various measurements was an important consideration. In the tests made by Burrows, the Von Bayer technique required the greatest number of man-hours for evaluation of large numbers of eggs. The two weight methods were found extremely fast, and because of its greater accuracy, the improved weight technique is the more favorable. The displacement technique though requiring twice as many man-hours as the weight techniques, is still more accurate, and should therefore be used in detailed fecundity studies where accuracy is more important than time.

In the present investigation the improved weight method was compared with the displacement method. In each case samples of known egg number were measured, compared proportionately with measures of total ovary weight or volume, and total egg number calculated. Actual egg number in the ovaries was then determined by counting all eggs. Results of this comparison appear in Table I. The displacement method was found superior in that variability tetween samples appeared to be considerably lower than for the weight method. For this reason the displacement technique as described by Burrows (1951) was used in all fecundity determinations made by the author.

Measurements of egg diameter were made in a V-shaped aluminum trough, in the bottom of which was fixed a metric rule. Twenty eggs were taken from each of the anterior, middle and posterior regions of an ovary and placed in the trough. The average diameter for these twenty eggs was taken as representative of that particular region of the ovary.

The majority of specimens used in the present investigation were obtained from the fish museum of the Institute of Fisheries at the University of British Columbia. The remainder were collected by the author. Additional data were obtained by personal communication and

Table I. Comparison of displacement with weight methods of egg enumeration using two species of fish.

Species	Total Ovary Volume (cc)	Volume of 100 Egg Samples (cc)	Total Ovary Weight (gm)	Weight of 100 Egg Sample (gm)	Egg No. by Volume	Egg No. by Weight	Egg No. by Count	Percent Error by Volume (%)	Percent Error by Weight
Mylocheilus	34.60	0.27	37.2	0.27	12,815	13,777	12,970	-1.20	+7.15
caurinum	32.30	0.27	32.9	0.29	11,962	10,972	11,146	+7.32	-2.46
(Summit Lk.)	39.65	0.27	42.7	0.29	14,865	14,788	15,175	-2.04	-2.55
(Prince George)	35.80	0.26	37.2	0.28	13,769	13,286	14,417	-4.48	-7.84
Mylocheilus	4.0	0.25	—	—	1,952	—	2,025	-3.06	—
caurinum	5.5	0.28	—	—	1,964	—	1,863	+5.42	—
(White Lk.)	5.3	0.21	—	—	2,524	—	2,491	+1.32	—
(Salmon Arm)	5.1	0.21	—	—	2,429	—	2,561	-1.25	—
Oncorhynchus									
nerka	21.6	5.26	23.4	5.43	413	494	415	-0.48	+19.04
kennerlyi	20.0	5.66	28.0	5.94	353	358	360	-1.98	-0.55
	26.7	5.71	26.8	5.71	484	471	462	+4.76	+1.95
(Nicola Lk.)	28.7	4.78	30.3	5.00	589	591	597	-1.34	-1.01

from a review of literature.

All specimens were originally fixed in 5 to 10% solutions of formalin, and were subsequently transferred to 40% isopropyl alcohol for permanent storage in the museum. Shrinkage and weight loss due to preservation were thus considered comparable in all specimens.

A list of species used, and collection sites is provided in Table II. Geographic locations were obtained from the Gazetteer of Canada--British Columbia, 1953. In the text reference is generally made to common names only.

Table II. Scientific names, common names and collection sites of species used in this thesis.

Scientific Name	Common Name	Collection From	Location	Position
Prosopium williamsoni (Girard)	Mountain whitefish	Nicola Lk., B.C.	N.E. of Merritt	50° 120° SW.
Thymallus arcticus signifer (Richardson)	Arctic grayling	Lewis R. Yukon	N.W.T.	
		Swede-Johnson Lk.	N.W.T.	
Coregonus clupeaformis (Mitchill)	Lake whitefish	Swede-Johnson Lk.	N.W.T.	
Prosopium cylindraceum (Richardson)	Round whitefish	Dease Lk., B.C.	Cassiar Dist.	58° 130° SE.
Prosopium coulteri (Eigenmann & Eigenmann)	Pygmy whitefish	See Literature		
Oncorhynchus keta (Walbaum)	Chum salmon	See Literature		
Oncorhynchus tshawytscha (Walbaum)	Chinook salmon	See Literature		
Oncorhynchus nerka kennerlyi (Suckley)	Kokanee	Meadow Ck., B.C.	Kootenay Dist.	50° 116° SW.
		Nickola Lk., B.C.	N.E. of Merritt	50° 120° SW.
		Shawnigan Lk. B.C.	Vancouver Is.	48° 123° NW.
Salmo gairdneri (Richardson)	Rainbow trout	Paul Lk., B.C.	Kamloops Dist.	50° 120° NE.
		Peterhope Lk. B.C.	Kamloops Dist.	50° 120° SE.
		Knouff Lk., B.C.	Kamloops Dist.	50° 120° NE.
		Jacko Lk., B.C.	Kamloops Dist.	50° 120° NE.
Salmo clarki Richardson	Cutthroat trout	See Literature		

Table II. Cont'd. Scientific names, common names and collection sites of species used in this thesis.

Scientific Name	Common Name	Collection From	Location	Position
Salmo trutta Linnaeus	Brown trout	See Literature		
Salmo salar Linnaeus	Atlantic salmon	See Literature		
Salvelinus fontinalis (Mitchill)	Eastern brook trout	See Literature		
Salvelinus malma (Walbaum)	Dollyvarden	See Literature		
Salvelinus namaycush (Walbaum)	Lake trout	See Literature		
Catostomus catostomus (Forster)	Longnose sucker	Shelley Slough, B.C.	N.E. of Prince George	54° 122° SW.
		10-Mile Lk., B.C.	N. of Quesnel	53° 122° SE.
Catostomus commersoni (Lacépède)	White sucker	Baker Lk., B.C.	N.E. of Quesnel	52° 122° NW.
		Summit Lk., B.C.	Hart Highway	54° 122° SW.
Catostomus macrocheilus Girard	Largescale sucker	Wolfe Ck., B.C.	Similkameen Dist.	49° 120° SE.
		Little Bull R., B.C.	Kootenay Dist.	49° 115° SE.
Richardsonius balteatus (Richardson)	Redside shiner	Paul Lk., B.C.	Kamloops Dist.	50° 120° NE.
		Shelley Slough, B.C.	N.E. of Prince George	54° 122° SW.
		Trembleur Lk., B.C.	Coast District	54° 125° NE.

Table II. Cont'd. Scientific names, common names and collection sites of species used in this thesis.

Scientific Name	Common Name	Collection From	Location	Position
Rhinichthys cataractae (Cuvier & Valenciennes)	Longnose dace	Tulameen R., B.C.	Similkameen Dist.	49° 120° SW.
Mylocheilus caurinum (Richardson)	Peamouth chub	White Lk., B.C.	Shuswap Dist.	50° 119° NE.
		Hansard Lk., B.C.	Cariboo Dist.	54° 122° SE.
		Terrace, B.C.	Coast Dist.	54° 128° NW.
Lota lota (Linnaeus)	Burbot	Dutch Ck., B.C.	Kootenay Dist.	50° 115° SW.
Perca flavescens (Mitchill)	Yellow perch	See Literature		
Micropterus dolmieui Lacépède	Smallmouth black bass	See Literature		
Micropterus salmoides (Lacépède)	Largemouth black bass	See Literature		
Cottus asper Richardson	Prickly sculpin	Bella Coola R., B.C.	Coast Dist.	52° 126° SW.

RESULTS

EGG NUMBER

Variation in Absolute Egg Number

Many workers in the past have counted egg numbers in a few species of game fish, in attempts to estimate total fish production as a result of natural spawning in a lake or stream system. A few workers have done a considerable amount of work on variations in egg number with increasing parent size, variations between races of a single species, and so on. Ricker (1932) found a logarithmic relationship between total egg number and fork length of parent fish in eastern brook trout. Foerster and Pritchard (1941) described a positive correlation between egg number and parent length and weight in the genus Oncorhynchus. Rounsefell (1957), has demonstrated for the Salmonidae in general, given a wide range in fork length, that total egg number shows a curvilinear relation with length, although within the genus Oncorhynchus, in which the size range of mature adults is small, the relationship could be regarded as linear.

In addition Svärdson (1949) refers to enormous variation in egg number because of the correlation with parent size. Scott (1955) showed a positive correlation between fish length and egg number in rainbow trout. Donaldson's (1955) breeding experiments with rainbow trout do not show such a close relationship, but the same general trend is present.

In the present study, insufficient data were available from mature fish in the museum at the Institute of Fisheries to permit plotting of quantities of data for a species from any one locality. However, sufficient data were available to permit grouping into length classes, and calculation of mean egg numbers for each length class. These data were plotted in Figures 2 to 8, in which seven species for three families are represented. For each species, regardless of family, a positive correlation exists between egg number and fish length. As fork length increases, absolute fecundity increases at an accelerating rate. There is every indication, therefore, that the findings of earlier workers regarding a curvilinear relationship between total egg number and fish length for certain species of salmonid fishes can also be applied to other families of freshwater fish.

Variation in Egg Number Between Areas

In the preceding section the importance of parent size in determining total egg number has been pointed out. Therefore in any attempt to observe differences in fecundity within the geographical range of a species, fish of a comparable size-range must be used.

Many attempts have been made, frequently without recognition of the numerous variables involved, to use fecundity as a means of racial separation. This is particularly true of Pacific salmon of the genus Oncorhynchus. McGregor (1923) attempted, apparently with some success, to separate river races of chinook salmon in ocean-caught fish on the basis of egg counts. Ward (1952), however, attempted a similar type separation of races of Fraser River sockeye salmon, and found it impossible because of considerable overlap in ranges in egg number. Foerster and Pritchard (1941) strongly caution against use of egg number in such racial studies because of large, unaccountable fluctuations in fecundity among fish from one run, collected at the same location at different times.

Table III is a comparison of length, weight and range in egg number for five species of freshwater fish, each species represented from two or more localities. The same range in length has been used for each locality.

It is apparent from Table III, in spite of the small number of specimens available from each area, that considerable variation exists in range and mean egg numbers of fish from different localities. On this basis it might appear that mean egg number and range could be used in a limited way as a means of racial separation.

Scott (1955) stated that resorption of ova in rainbow trout was a process, continuous almost until complete maturity was reached. Variations in food abundance in different environments induced different amounts of resorption, resulting in variations in ultimate egg number. If this is true for other species of freshwater fish, then species having large numbers of small eggs might be expected to show even greater absolute variability in fecundity in different environments. Reference in Table III, to a single size range of mountain whitefish, redside shiner and peamouth chub from two or more localities within the province, indicates that this may be the case. The great variability in

Table III. Comparison of mean egg number, fork length and weight for six species of fish from different geographic locations.

Species	Number in Sample	Locality	Range in Length (cm)	Range in Weight (gm)	Range in Egg Number	Mean Egg Number
Kokanee	3	Nicola Lake	23.0-25.0	159.6- 164.5	360- 462	412
	2	Kootenay Lk.	23.0-25.0	124.1- 133.7	309- 345	327
Mountain whitefish	5	Nicola Lake	25.0-28.0	194.5- 302.5	1,555- 3,306	2,803
	6	Montana	25.0-28.0	170 - 227	1,426- 2,160	1,747
Largescale sucker	2	Wolf Creek	45.0-46.0	1,156 -1,349.5	21,117-22,662	21,890
	1	Little Bull River	45.0-46.0	1,648	20,000	20,000
Redside shiner	3	Paul Lake	10.0-12.0	15.3- 18.1	1,129- 1,372	1,363
	8	Shelley Slough	10.0-12.0	14.5- 22.7	1,071- 1,694	1,343
	4	Trembleur Lake	10.0-12.0	19.5- 23.1	1,508- 2,568	2,208
Peamouth chub	3	White Lake	24.0-25.0	218.5-226.7	10,974-12,381	11,777
	2	Terrace	24.0-25.0	194.7-219.3	13,261-13,376	13,318

Table III. Cont'd. Comparison of mean egg number, fork length and weight for six species of fish from different geographic locations.

Species	Number in Sample	Locality	Range in Length (cm)	Range in Weight (gm)	Range in Egg Number	Mean Egg Number
Rainbow trout	-	California	40			2,400
	-	California	50			3,900
	-	California	60			5,600
	-	California	70			7,600
	28	Paul Lake	38.5			2,121
	9	Knouff Lake	43.6			2,510
	6	Peterhope Lake	45.75			2,280
	8	Jacko Lake	63.4			7,041

fecundity shown within one length range of redside shiner (from Shelley Slough and Trembleur Lake, approximately 110 miles apart) is indicative of the magnitude of variation encountered.

Variation in Egg Number With Latitude

Certain morphological characters of fish have been observed to form clines throughout the range of a species. Egg number has been thought to form a somewhat similar cline in a north-south direction. Unfortunately, much of this work has dealt with family or generic groups of fishes rather than with any single species. Svärdson (1949), postulated lower fecundity and larger eggs in northern latitudes, as did Marshall (1953) for seven families of deep-sea fishes.

Rounsefell (1957) attempted to determine whether there was any relation between fecundity and latitude for five species of Oncorhynchus. Plotting mean egg number against fork length, Rounsefell was able to show that for four species egg number in the most southern locality was higher than expected for the average length of the fish. However he used only samples containing twenty fish or more in his figure illustrating latitudinal differences, and appears to have overlooked smaller samples from other areas. Table IV contains data for chinook salmon, taken from Appendix Table I of Rounsefell (1957). It is evident from figures presented in Table IV, that mean fork length at maturity tends to increase in a northerly direction. In addition, considering the small increase in size involved between California and British Columbia collections (with the exception of Namu), the fluctuations in mean egg number are strongly suggestive of, and quite within the range of, environmentally induced variations. In O. nerka (sockeye), on the other hand, in view of the increasing mean size at maturity, there does appear to be a valid trend toward lower fecundity in more northerly regions.

Much of this previous work with regard to clinal variation was carried out solely with Salmonid species.

Data from Table II have been plotted in Figure 1 for two cyprinid and one coregonid species, comparing relative fecundity against fork length of fish from different latitudes. Solid symbols indicate the southernmost samples of each species. A statistical analysis was made on mean relative fecundity from samples in more northerly areas in comparison with the means of the southernmost samples, and each difference was significant ($P < 0.10$).

The southernmost mountain whitefish have a lower mean relative fecumdity (P .05-.10) than would be expected if a cline was present toward larger eggs and lower fecundity in more northerly latitudes. Likewise the southernmost peamouth chub have a lower mean relative fecundity (P .02) than expected. The redside shiner on the other hand has one group with higher and another with lower mean relative fecundity ($P < .01$) than would be expected if clearly defined clines existed. The influence of environment on fecundity is strongly indicated by these results which, in general, apparently do not support findings of some workers for certain salmonid species.

Table IV. Mean egg number and fork length of chinook salmon from Appendix Table I, of Rounsefell (1957).

Locality	Average Egg Number	Average Fork Length (cm)	Number in Sample	Fecundity Relative to /Unit Length (cm)
Sacramento R. Calif.	4670	80.2	108	58.2
Fort Bragg, Calif.	5034	80.8	53	62.3
Klamath R., Calif.	3708	81.2	199	45.7
Fraser R., B.C.	4944	87.1	12	56.8
Cowichan R., B.C.	3885	86.4	25	45.0
Namu, B. C.	8426	103.4	11	81.5

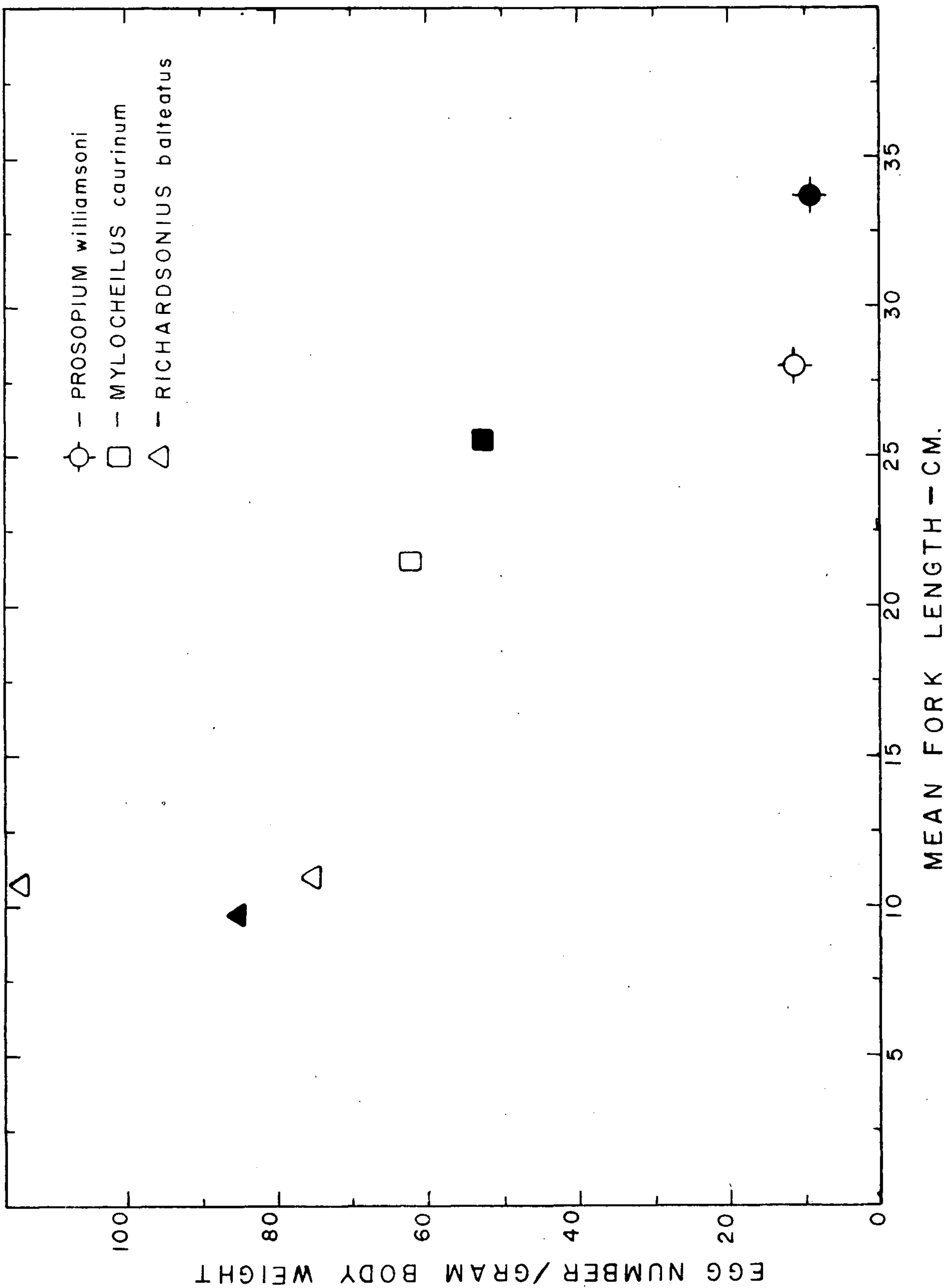

Figure 1. Relationship of relative fecundity to fork length of three species of fish from different latitudes. Solid symbols indicate data from southernmost locations.

EGG DIAMETER

Variation in Egg Diameter Within Individual Fish

Egg diameter was measured from anterior and posterior regions of each ovary for several species of fish. Actual measurements are presented in Appendix i. Sufficient data were available for five species, the longnose sucker, coarsescale sucker, peamouth chub, redside shiner, and mountain whitefish, to permit statistical analysis. Accordingly, the statistical sign test described by Dixon and Mood (1946) was applied to egg measurement data for these species. Results of these tests are shown in Table V.

No significant difference was found in egg diameter between right and left ovaries, or between dorsal and ventral regions of ovaries. Data for these measurements are therefore not presented.

A very significant difference was observed between egg diameter from anterior and posterior regions of both right and left ovaries. Egg diameter for each of the five species was found to be almost invariably greater in the anterior than in the posterior region of an ovary.

It was at first thought that this difference might be the result of differing rates of maturation of ova from the anterior and posterior regions of ovaries. Eggs from anterior parts of ovaries might mature prior to those in the posterior parts and would thus appear the larger if fish sampled were not completely mature. However, suckers and

Table V. Results of statistical sign test applied to egg measurement data of five species.

Species	Number of pairs of Observations	Number with Larger Anterior Eggs	Number without Larger Anterior Eggs	Level of Significance
Longnose sucker	20	18	2	<.01
Largescale sucker	16	14	2	<.01
Peamouth chub	36	36	0	<.01
Redside shiner	30	29	1	<.01
Mountain whitefish	12	10	2	.05

cyprinids, unlike salmonids, have a closed "oviduct" extending from the posterior portion of the ovaries (which fuse together) to the genital aperature. In both suckers and the cyprinids examined, eggs were completely free of ovarian tissue in the fused posterior portions of the ovaries, and in some cases free eggs were actually present in the duct. These fish were obviously fully mature and ready to spawn. Eggs of these fish were found to be consistently larger in the anterior than in the posterior portions of the ovaries.

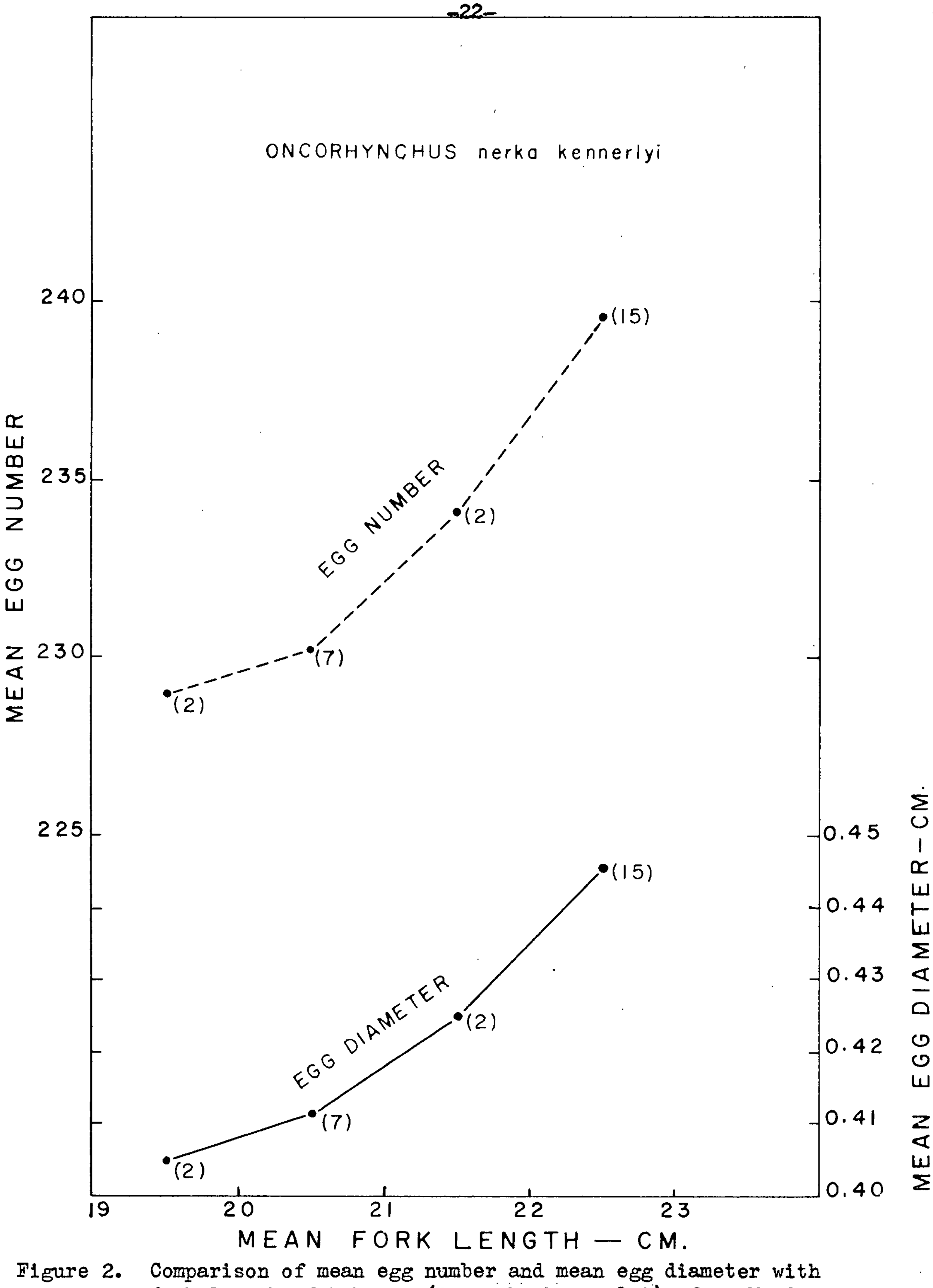

Figure 2. Comparison of mean egg number and mean egg diameter with fork length of kokanee (O. nerka kennerlyi), from Meadow Creek, B. C.

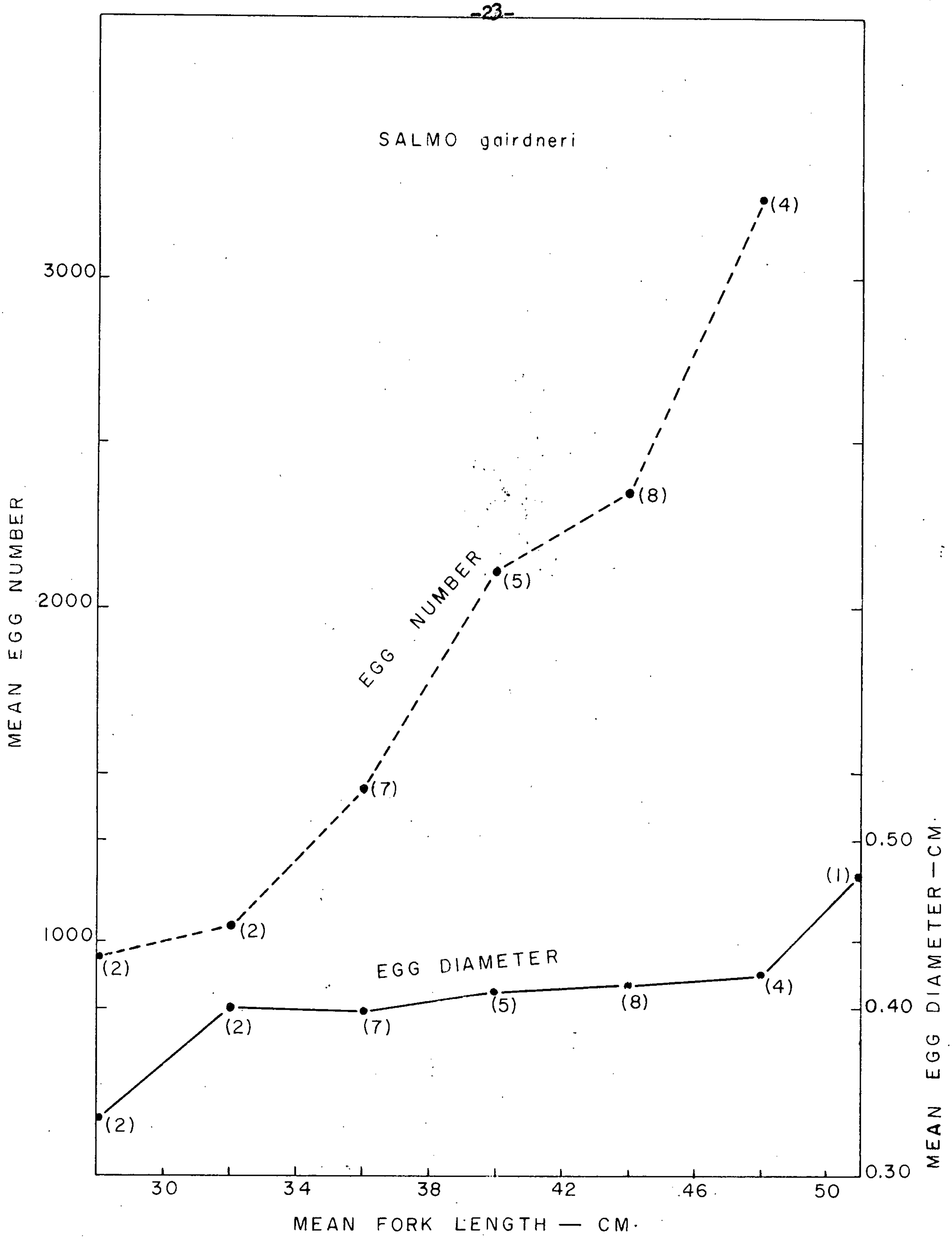

Figure 3. Comparison of mean egg number and mean egg diameter with fork length of rainbow trout (S. gairdneri) from Paul Lake, B. C.

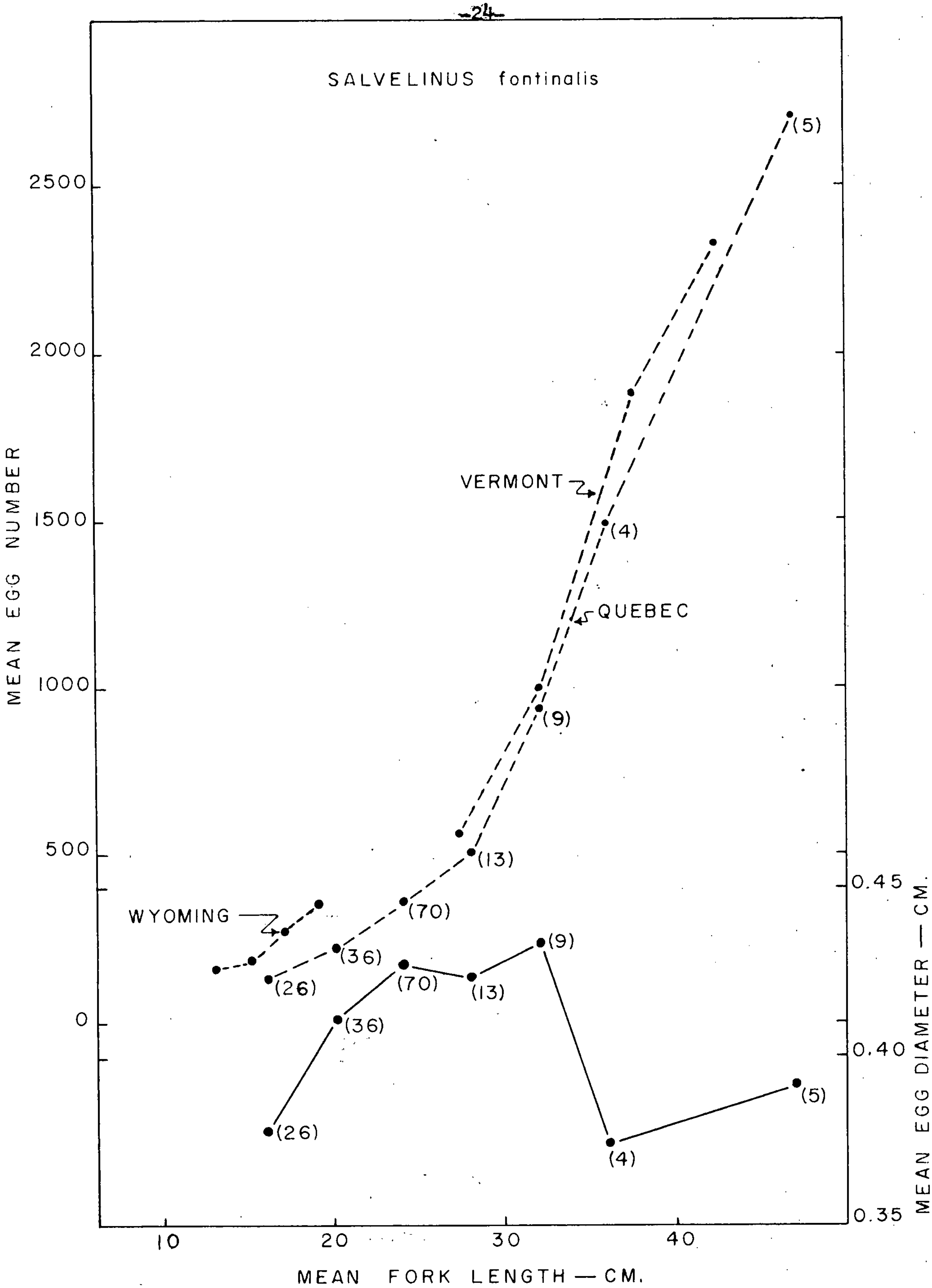

Figure 4. Comparison of mean egg number and mean egg diameter with fork length of eastern brook trout (S. fontinalis) from several localities.

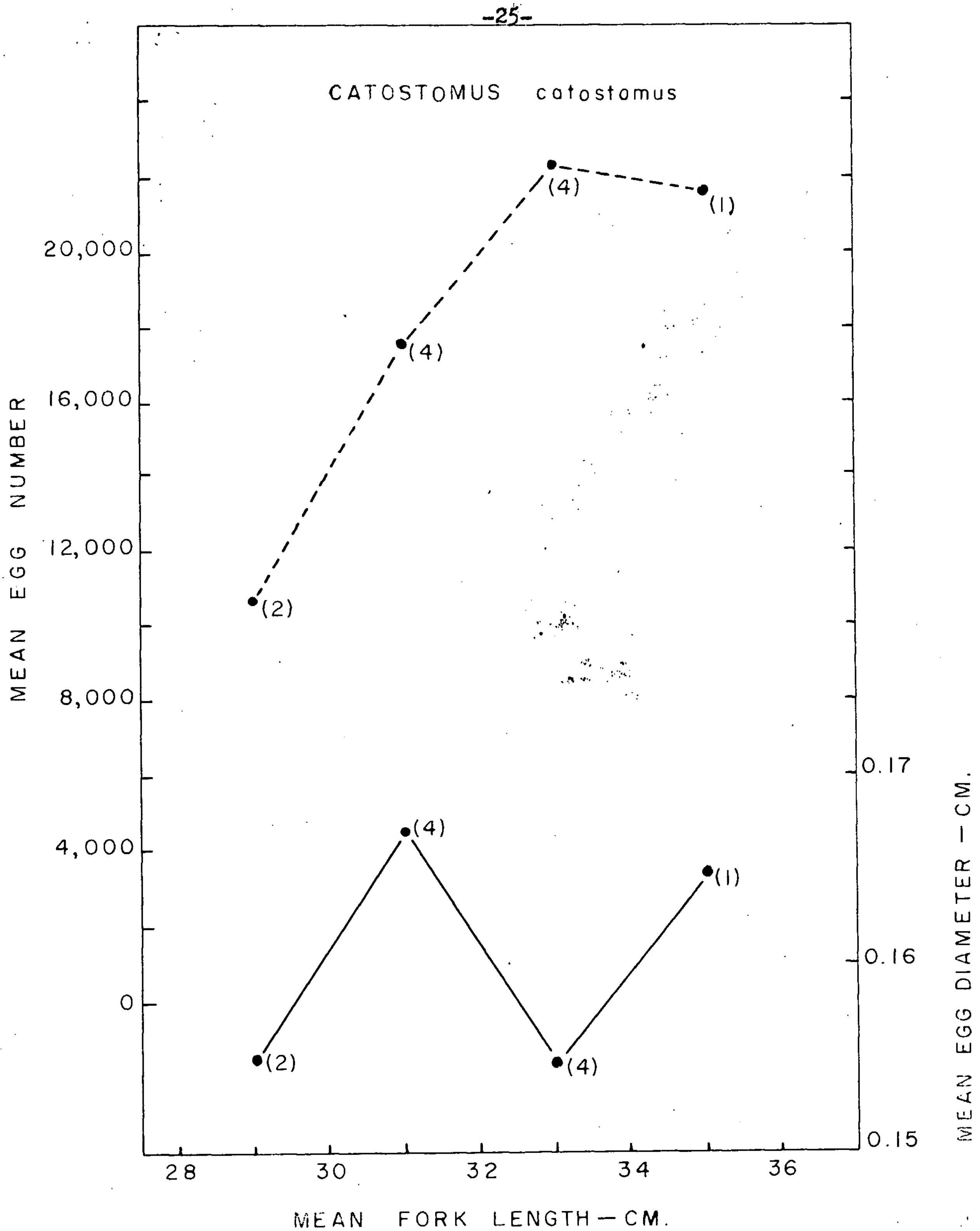

Figure 5. Comparison of mean egg number and mean egg diameter with fork length of longnose sucker (C. catostomus).

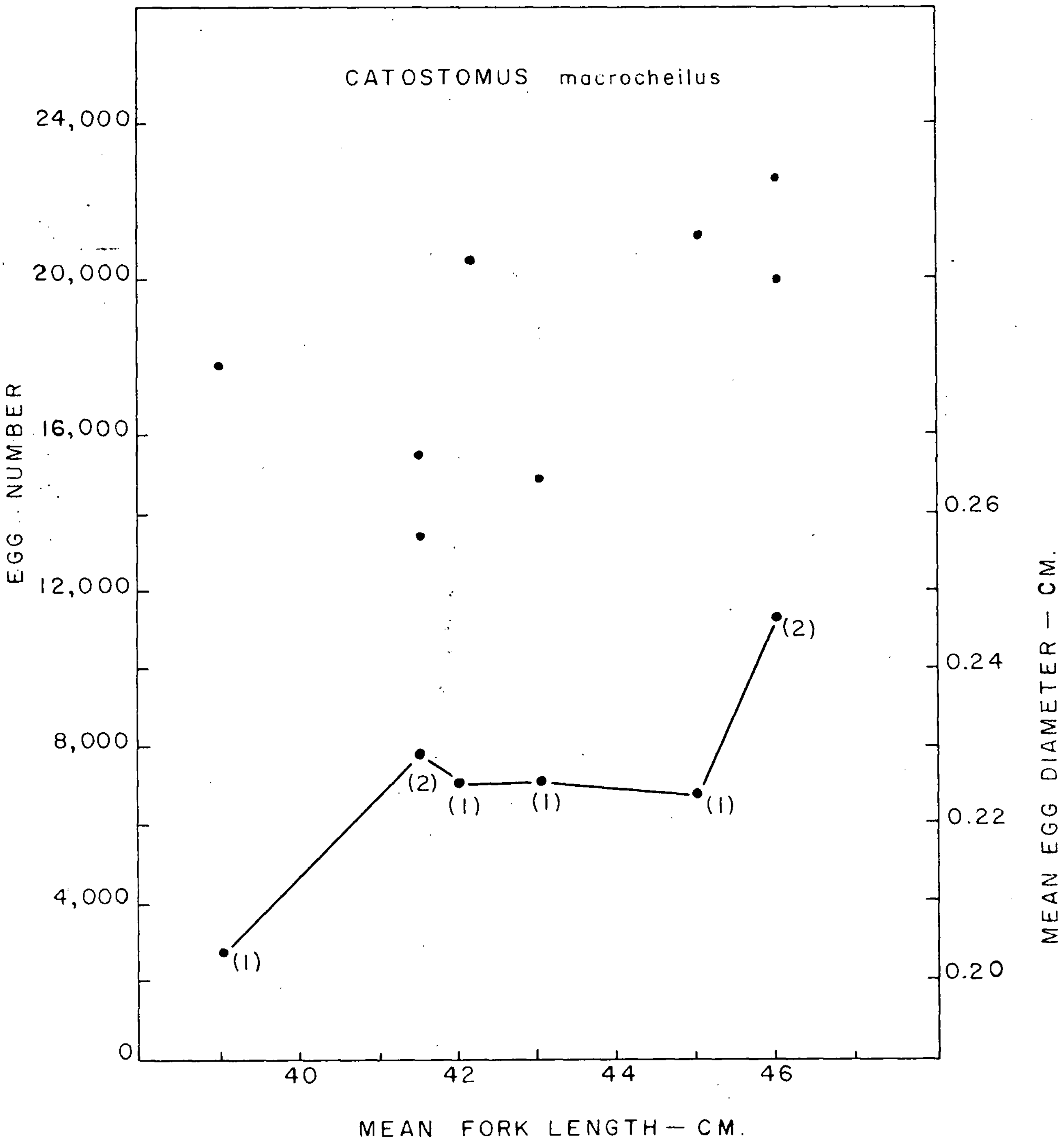

Figure 6. Comparison of mean egg number and mean egg diameter with fork length of largescale sucker (C. macrocheilus).

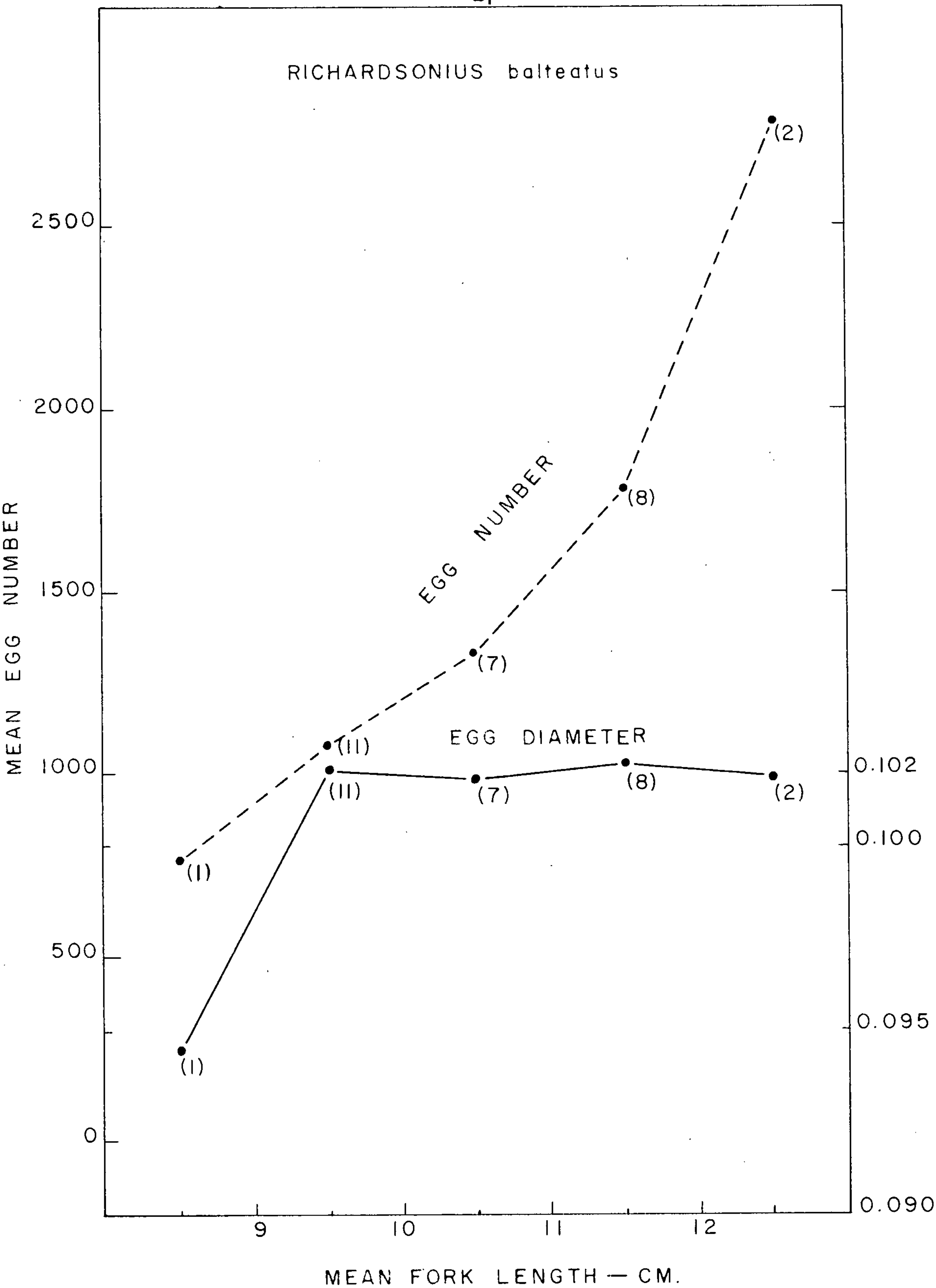

Figure 7. Comparison of mean egg number and mean egg diameter with fork length of redside shiner (R. balteatus).

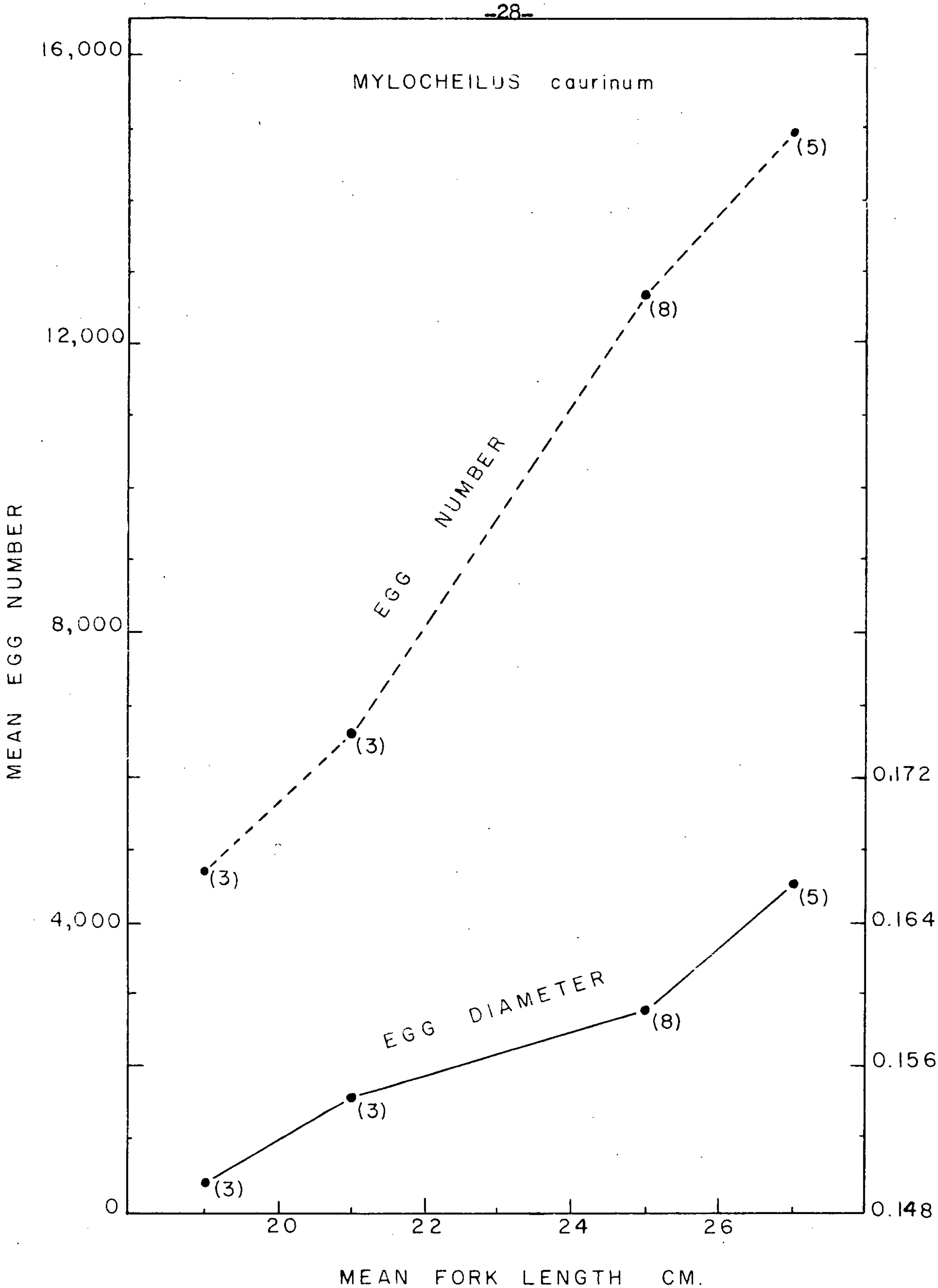

Figure 8. Comparison of mean egg number and mean egg diameter with fork length of peamouth chub (M. caurinum).

Variation in Egg Diameter with Parent Length

Very little work has been done on fish egg diameter except in a crude way for fish cultural purposes. A number of authors such as Titcomb (1897) and Belding (1934) refer to increasing egg diameter as parent size increases in brook trout and Atlantic salmon respectively. In neither case are data presented to substantiate the hypothesis. On the other hand Scott (1955) found no significant correlation between egg diameter and parent size for hatchery reared rainbow trout in the size range studied. Scott used both wild and hatchery reared trout, but considered only a small range in size.

In the present investigation, egg diameter data have been collected from seven species, representing six genera and three families of freshwater fish. Families represented are the Salmonidae, Cyprinidae and Catostomidae.

Figures 2 to 8 are plots of mean egg number and diameter against mean fork length for the seven species referred to above. Five of the seven indicate an increase in mean egg diameter as fork length increases. Brook trout display a comparable increase in diameter with the exception of the two largest size groups which show a decline in diameter. This decline may be the result of old age, or of specimens from different lakes.

Data available for the longnose sucker do not indicate any consistent tendency towards larger eggs in larger fish. This variability may be due to a lack of complete maturity in some of the few specimens available, or may indicate an absence of the trend in this species.

Age might be a major cause of larger eggs in larger fish, since Scott (1955) found in specimens from Penask Lake that second spawners had larger eggs than first-time spawners. However, mean fork length of the second-time spawners was greater than that of first spawners. Figure 9 is a plot of mean egg diameter against fork length for three age-classes of rainbow trout from Paul Lake. Data were collected by J. C. Lyons in 1950. The scale readings may be questionable for 2-year-old fish since mature 2-year-old female rainbow trout are rare (in nature). It is nevertheless apparent, considering only 3 and 4-year-old fish, that the trend towards larger eggs is more dependent on fish length than on age. Scott (1955) found no significant difference in egg size within the size range used in his study, however, he used only a very small range in size.

In many cases the number of specimens available was small; nevertheless, the persistence of the trend regardless of the number of specimens involved is in itself indicative that larger eggs in larger fish of a species is frequently a very real phenomenon.

Figure 10 presents mean egg diameter and mean fork length data for 21 species. A definite tendency is evident for larger fish to have larger eggs. The burbot is one noteable exception.

Therefore, on the basis of data presented above it appears that in general mean egg diameter increases with increasing fork length, not only within a single species, but also within a group of different species.

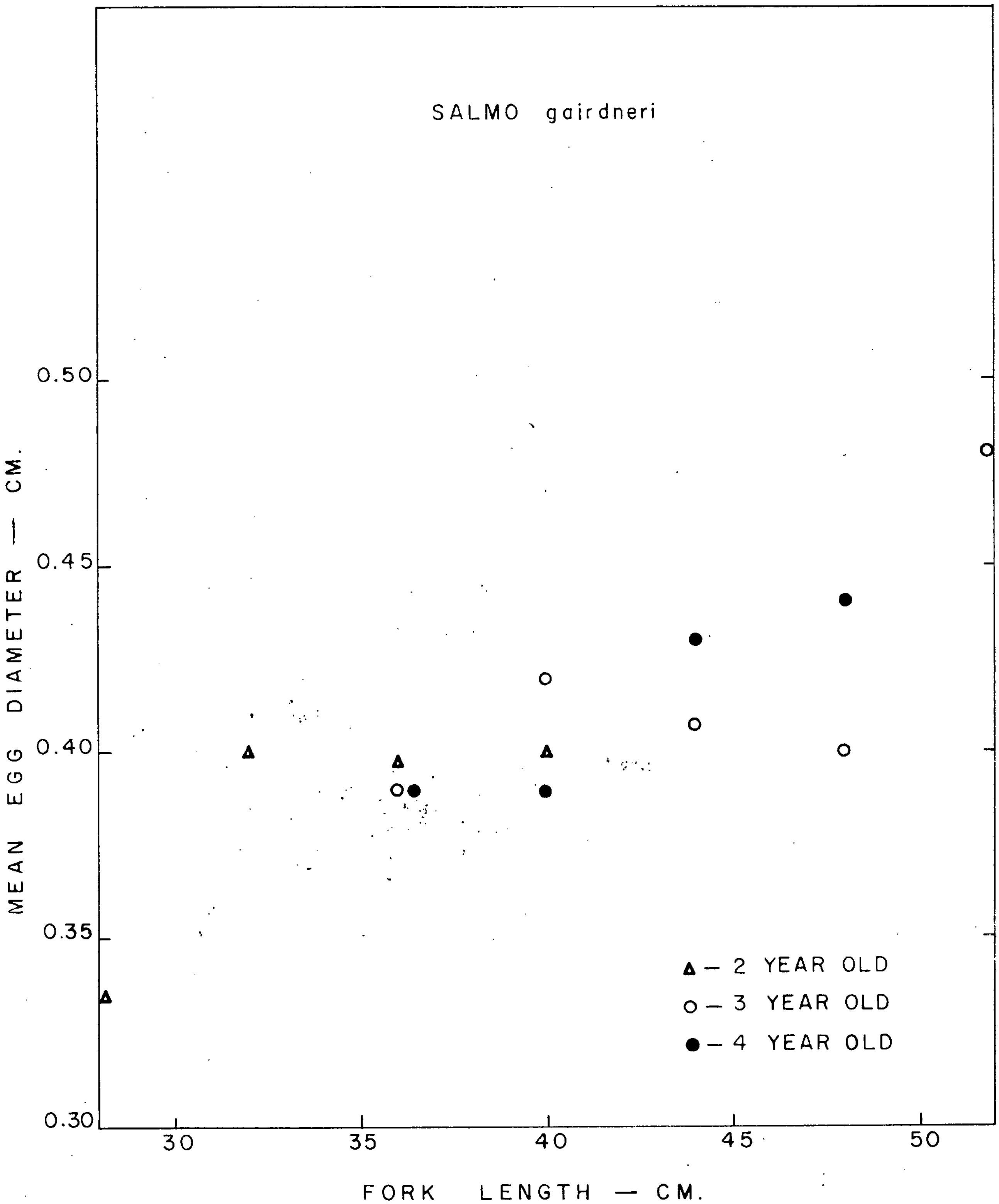

Figure 9. Mean egg diameter compared with fork length and age at maturity for 30 rainbow trout from Paul Lake.

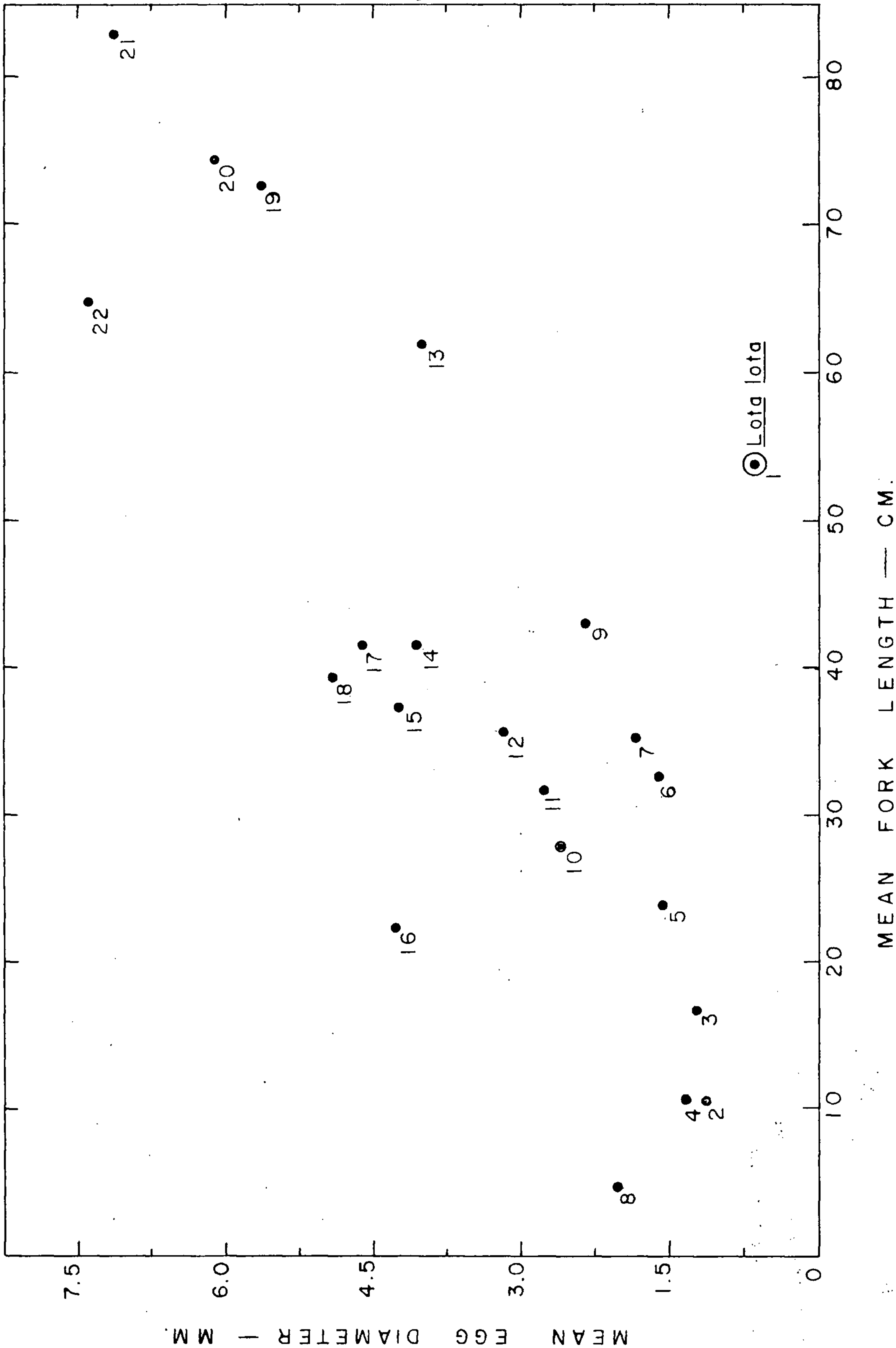

Figure 10. Comparison of mean egg diameter with mean fork length for 22 species of freshwater fish, representing 12 genera and 7 families. Numbers refer to species listed in Table VII.

RELATIVE FECUNDITY

Total egg number was shown in a previous section to be a poor method of comparing fecundities of several different species of fish, because of the close dependence of egg number on fish length. Egg number per unit body weight (in grams) or per unit body length (in centimeters) was considered less variable for fecundity comparisons in which different sized fish were involved. Theoretically this measure, which may be referred to as relative fecundity, would help to reduce large differences in fecundity as a result of fish length, and at the same time would not be seriously effected by differences in body shape.

Accordingly data were plotted on egg number per gram body weight vs. fork length for eight species of freshwater fish. In all species relative fecundity was found to vary, but no trend was observable as fish length increased. Relative fecundity varied within certain definite limits characteristic of each particular species, but these limits were not found to alter their range of variation with increasing fish length as did total fecundity. Relative fecundity therefore is considered a preferable measure to absolute fecundity when it is desired to make precise comparisons of fecundity within, or between, species.

Relationship to Egg Diameter

Total egg number in any fish is influenced considerably by egg diameter; similarly, relative fecundity will be influenced by egg diameter.

Vladykov (1956) compared relative fecundity of eastern brook trout with egg diameter, and found that when plotted, a curve resulted from which relative fecundity could be approximated for any given diameter of egg. Data presented in Appendix (iii), for 23 species, representing 12 genera and 8 families have been plotted on arithmetic axes in Figure 11, and on log-log axes in Figure 12. Figure 11 shows that for all species, regardless of body shape, decreasing egg diameter is accompanied by an accelerating rate of increase in relative fecundity. This is to be expected in view of the demonstrated (approximate) cubic relationship between egg diameter and egg volume. Considering the diverse phylogenetic relationships of species examined and the body shapes involved, remarkably little deviation is shown from the curve. In Figure 14 the same data have been plotted on log-log axes, transforming the curve of Figure 11 into a straight line described by the regression equation $\log 10X \doteq 5.866-2.670 \log 10Y$. This line has a high correlation coefficient ($r = -0.97$). Dotted lines indicate 99 percent confidence limits..

From Figure 12 it would be possible to calculate (within limits) the approximate total egg deposition of a population of spawning fish. For this calculation mean egg diameter and mean weight of mature females, as well as an estimate of numbers of mature females in a population must be known. Total approximate egg deposition can then be calculated. This method has the advantage of saving considerable time over displacement or weight methods of egg enumeration.

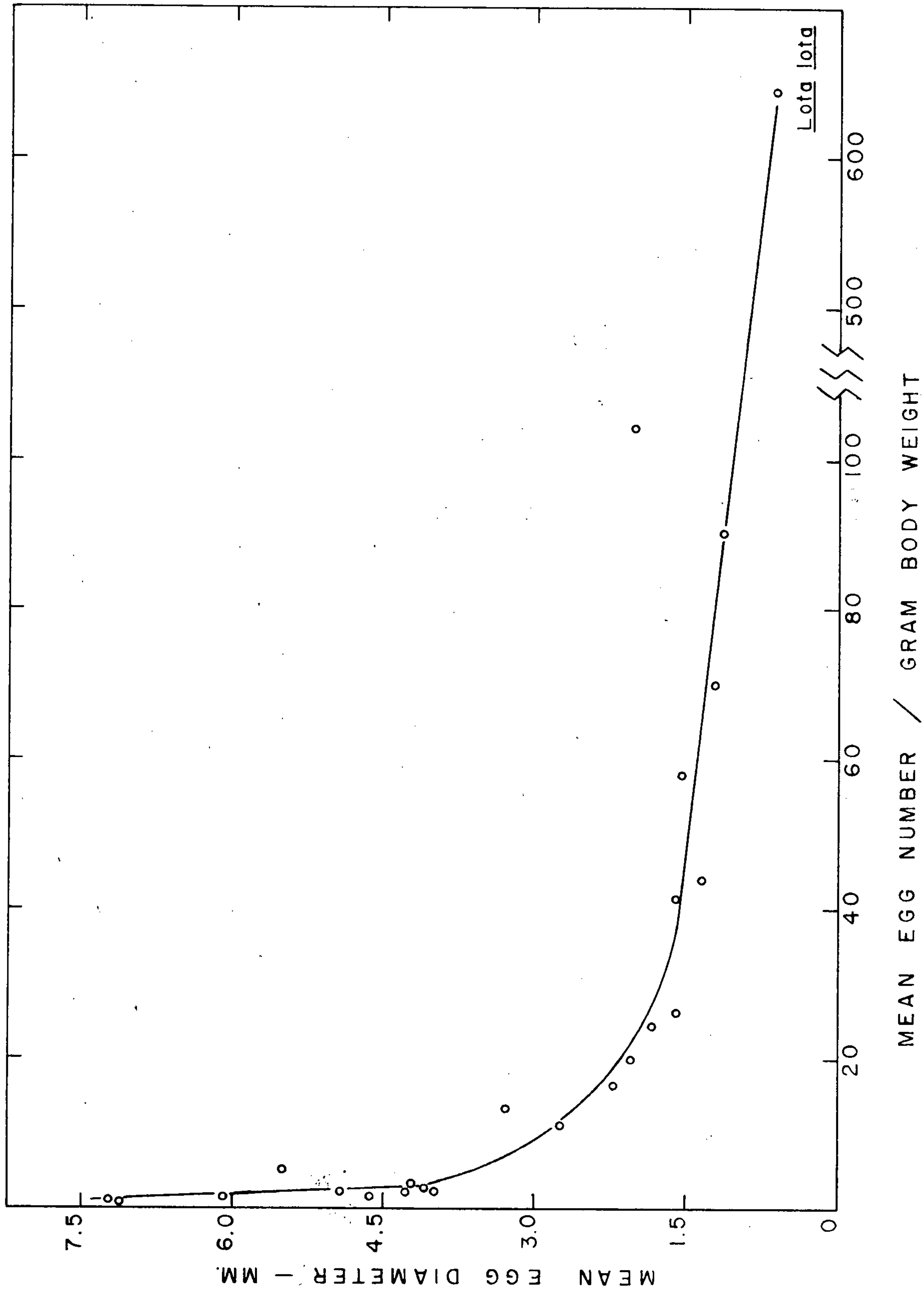

Figure 11. Relationship between egg diameter and relative fecundity for 23 species of freshwater fish.

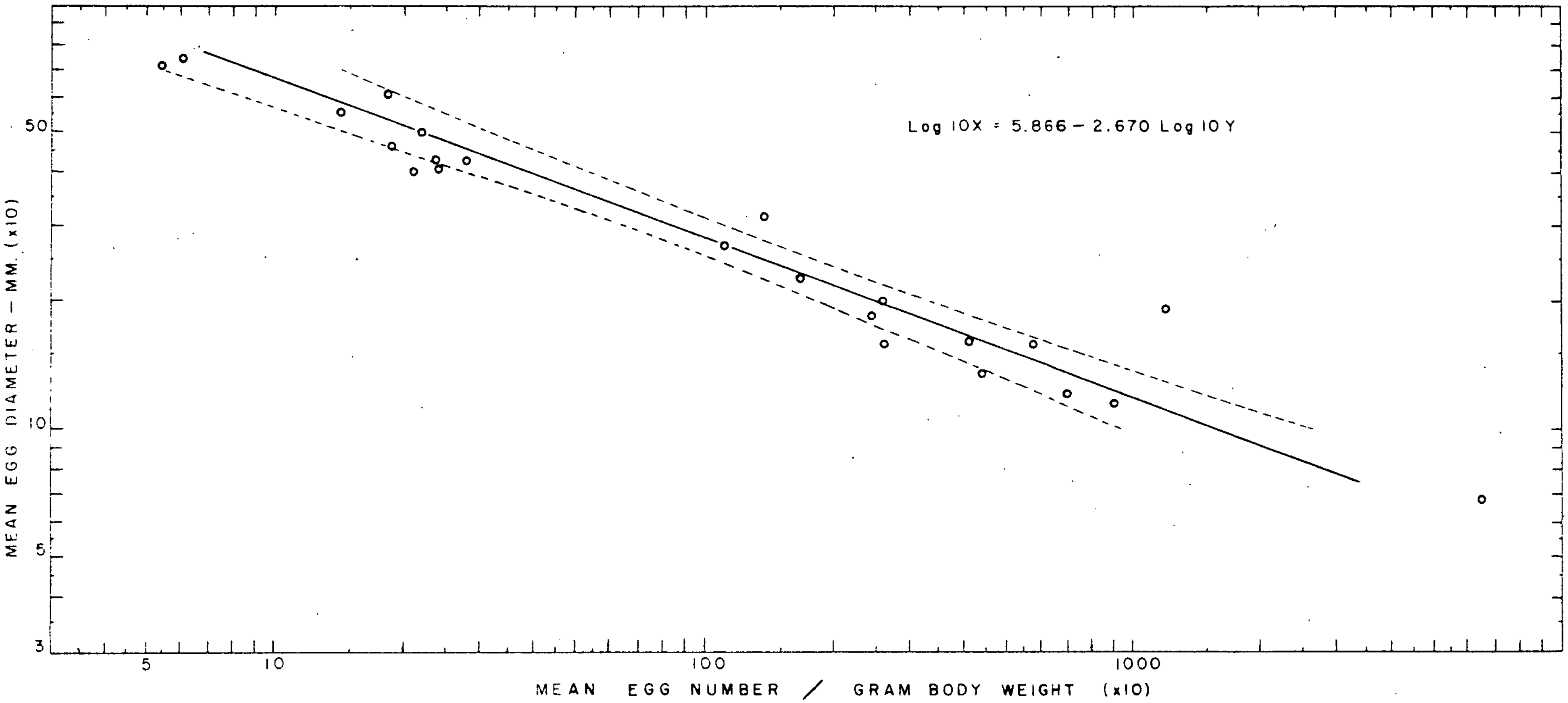

Figure 12. Regression of mean egg diameter (x10) on relative fecundity (x10) for 23 species of fish. Ninety-nine percent confidence intervals indicated (logarithmis axes).

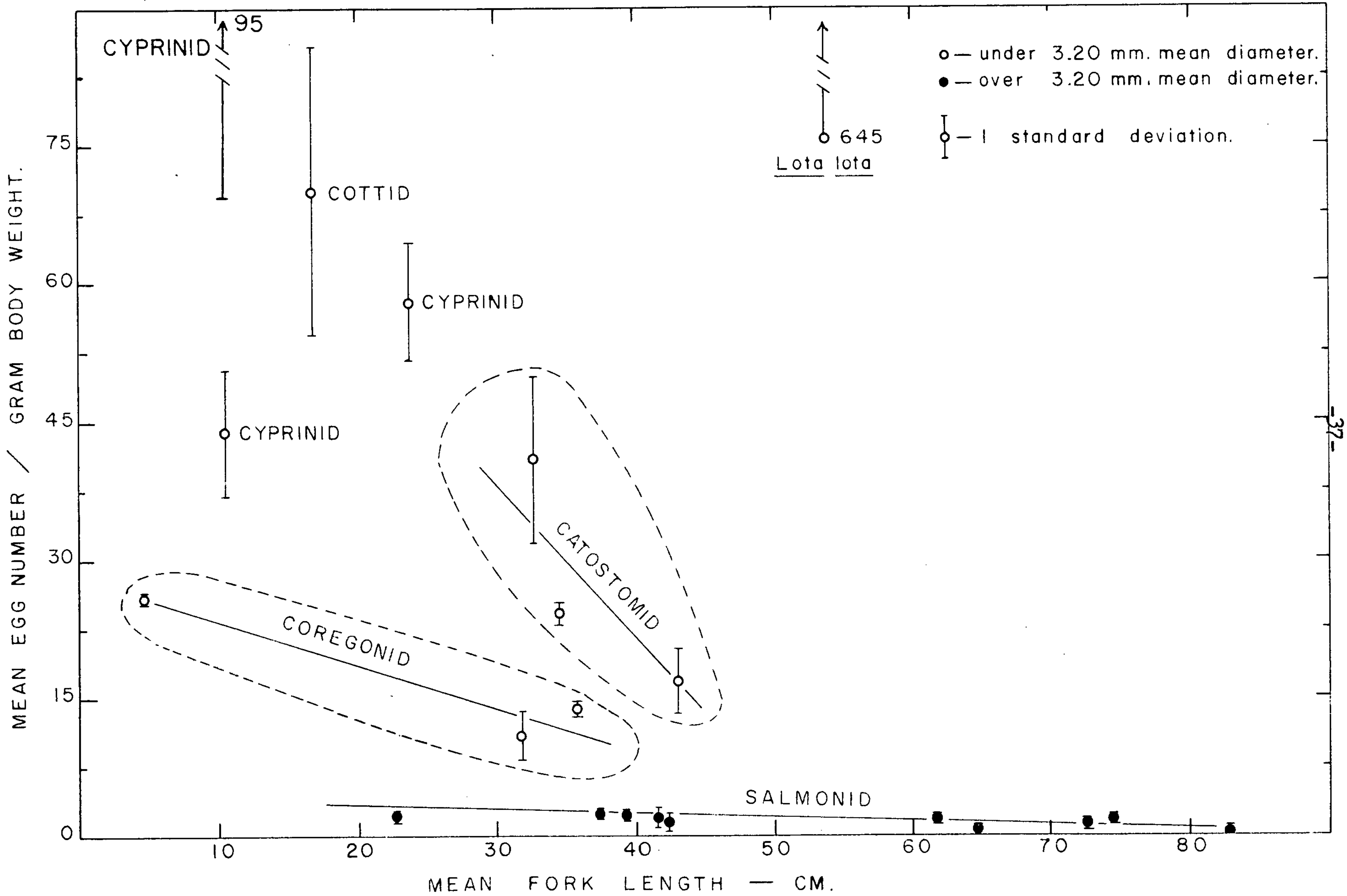

Figure 13. Comparison of relative fecundity with mean fork length for 20 species of fish.

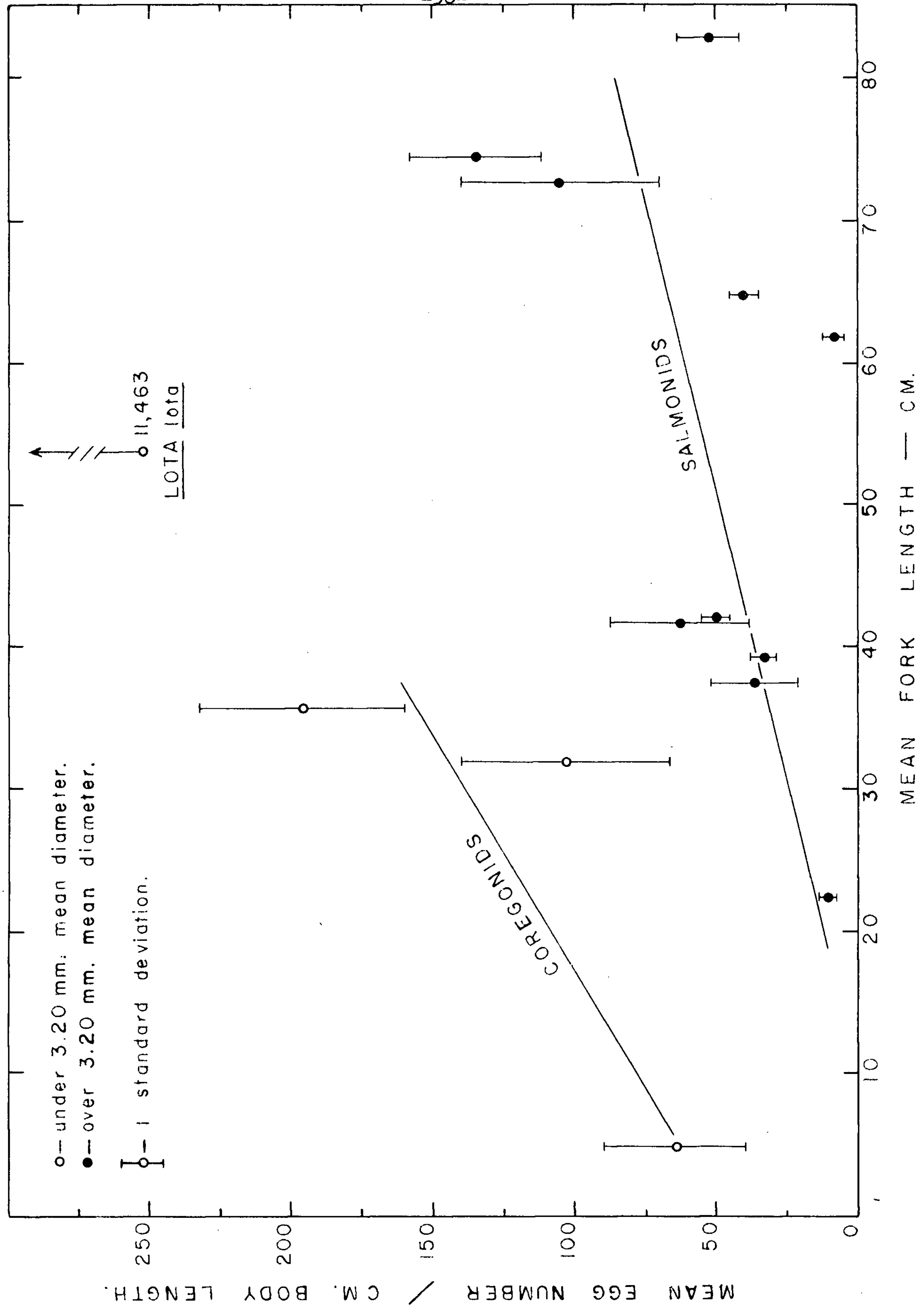

Figure 14. Comparison of relative fecundity with mean fork length for 14 species of fish.

Variations Between Species

In the preceding section the close dependence of relative fecundity on egg diameter was demonstrated.

Data on fecundity relative to length and weight were available for twenty species. These data have been plotted graphically in Figure 13 and 14. Figure 13 is a plot of mean fork length against mean egg number per unit body weight, while Figure 14 is a similar plot using mean egg number per unit body length.

The following observations can be made from these data:

1. Each family of fishes appears to have a characteristic range of relative fecundity,
2. Standard deviations from mean relative fecundity appear to increase as relative fecundity increases, and hence as egg size decreases,
3. It is noteable, as in Figures 10, 11 and 12, that the burbot, only freshwater representative of the otherwise marine family Gadidae, does not conform to the pattern shown by freshwater families of fishes.

Variation in Gonad Weight as Fish Weight Increases.

Data have been presented in the preceding section suggestive of a decline in fecundity, relative to body weight, as fish length increases. In Figure 15 data are presented for two species, and are indicative of a slight decline in the ratio between gonad weight and total fish weight. This might account for the decline in relative fecundity observable in the previous section. However, percentage body weight attributable to gondas was calculated for sixteen species and arranged in Table VI in order of increasing fish size. No consistent trend toward a decline in maturity index can be observed as fish size increases. It would therefore appear that increasing egg diameter as fish length increases is at least partly responsible for the observed decline in relative fecundity.

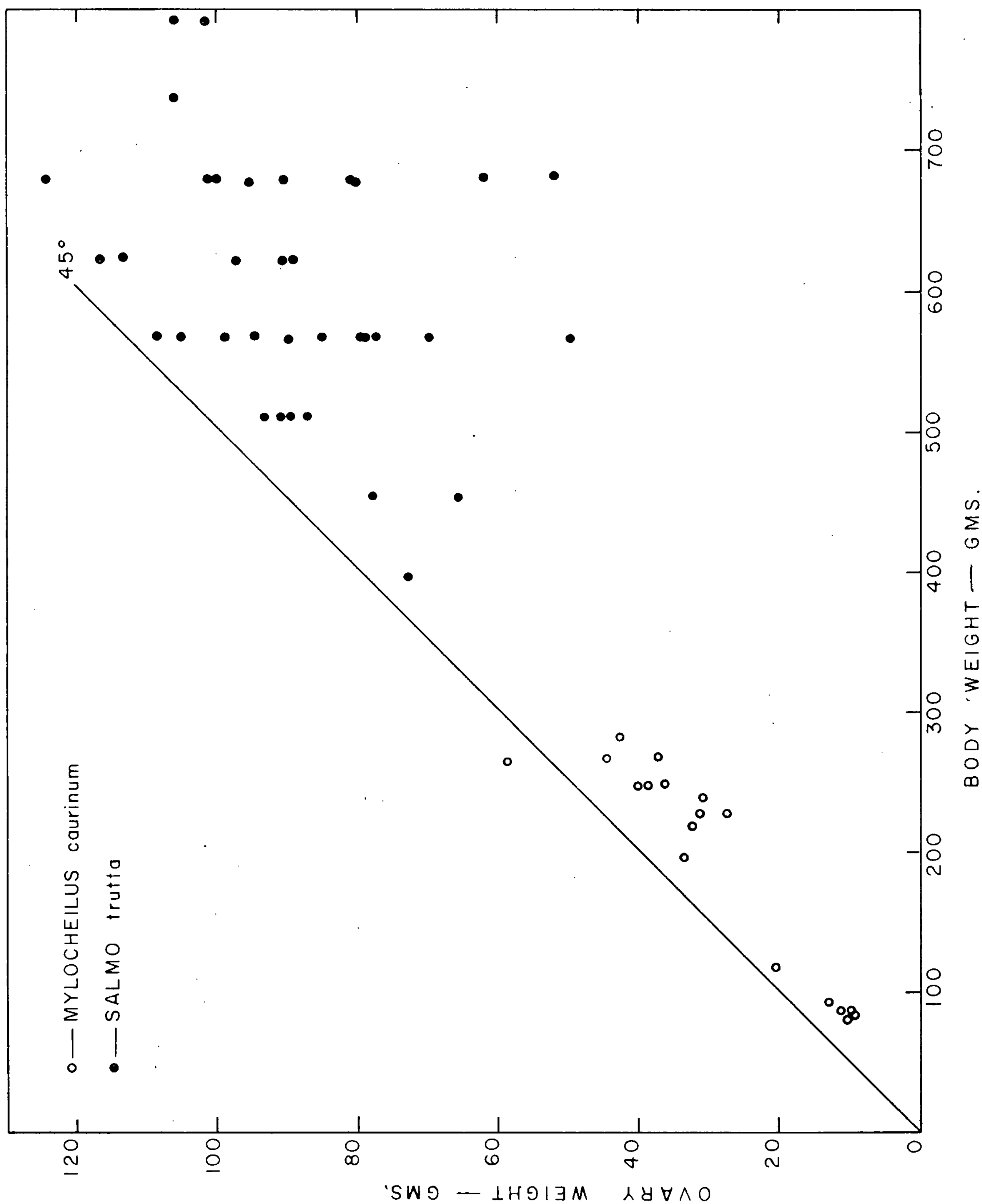

Figure 15. Relationship of ovary weight to body weight for two species.

Table VI. Percentage body weight attributable to gonads (maturity index) for sixteen species, arranged according to increasing body weight.

Species	Number in Sample	Total Body Weight	Gonad Weight (gm)	% Body Weight attributable to gonads	Authority
Pygmy whitefish	63	13.4	-	15.0%	Eschmeyer & Bailey, 1954
Redside shiner	29	16.0	2.4	14.8%	Cartwright
Longnose Dace	6	18.0	1.7	9.0%	Cartwright
Prickly sculpin	2	103.0	12.5	12.1%	Cartwright
Peamouth chub	19	170.0	25.4	14.9%	Cartwright
Kokanee	37	245.5	57.6	23.5%	Cartwright
Mountain whitefish	27	359.0	51.1	14.2%	Brown, 1952, Cartwright
Burbot	7	380.0	69.8	18.4%	Carlander, 1950, Cartwright
Longnose sucker	15	444.0	55.2	12.4%	Cartwright
Eastern brook trout	27	499.0	68.0	13.6%	Vladykov, 1956
White sucker	2	599.0	62.0	10.4%	Cartwright
Brown trout	37	600.0	90.5	15.1%	Rounsefell, 1957
Rainbow trout	42	934.0	126.5	13.5%	Cartwright
Largescale sucker	8	1124.0	142.4	12.7%	Cartwright
Lake trout	25	4819.0	699.0	14.5%	Dymond, 1928
Atlantic salmon	534	4999.0	1000.0	20%	Rounsefell, 1957

RELATIONSHIP OF EGG DIAMETER TO REPRODUCTIVE CHARACTERISTICS

Scott (1955) stated that egg diameter in rainbow trout was under strong genetic control. Results presented indicate that while this may be the case in Scott's experimental fish, diameter can and does vary within relatively wide limits in many species.

Correlations have been shown to exist between fecundity (hence in part egg diameter) and life history among some marine species. Hickling and Rutenberg (1936) showed for hake, haddock, herring and pilchard, that duration of spawning period could be approximated by graphically plotting egg diameter against frequency of occurrence in the ovaries. Neave (1948) stated that fecundity was closely linked with life history in Pacific salmon. Svärdson (1949) suggested that selection forces in an environment effected egg size and number.

On the basis of relationships between fecundity and life history or environment suggested above, an attempt was made to determine whether or not any relationships existed between a number of reproductive characteristics and egg diameter. An index system was set up, in which eggs of small or large mean diameter from twenty-six species, representing fourteen genera and eight families of fishes were compared with adhesive or non-adhesiveness of the eggs, coloration of the eggs, hatching time of the eggs, spawning season of the parents, spawning location of the parents, and degree of parental care(as exemplified by construction or non-construction of redds).

In a comparison of this type a boundary had to be selected to differentiate fish with eggs of large or small mean diameter. Species in Table VII are arranged in ascending order of egg diameter. A figure of 3.20 mm. was selected as a dividing point between small and large eggs not only because it occurs in a gap separating species with dissimilar reproductive characteristics, but also because it occurs near the mean diameter of the species. Selection of a division of this type has a number of disadvantages, however, in view of similarities in reproductive characters among species with small or large mean egg diameter, the author feels selection of the chosen boundary justified.

Chi-square tests were then made on each pair of characters in comparison with mean egg diameter above or below the selected boundary. Results of these tests, recorded in Table VIII, indicate that all six characters tested are significantly related to egg diameter.

In view of the relationships shown in Table VIII, it is desirable to know in precisely which way the characters tested are related to egg diameter as well as which species, if any, differ from the general trend. In this way, certain ecological relationships might be demonstrated. Table VII is an attempt to illustrate similarities and differences in reproductive characteristics for the twenty-six species tested in Table VIII. Plus signs indicate the presence of the characteristic, "o" indicates the absence of it.

In general, species having eggs in excess of 3.20 mm. appear to be much more consistent in the presence or absence of a character than do species having eggs smaller than this value. This is undoubtedly due in part to the fact that species with larger eggs are all of one family, Salmonidae, representing only 3 genera, while those with small eggs represent 11 genera of 8 families. Nevertheless, in view of the diverse number of families and genera possessing small eggs, it would be surprising to obtain Chi-square values or distributions like those observed in Tables VII and VIII if there were no relationship between egg diameter and the characteristic tested. The presence of the above relationship is made more evident by the fact that variability in the relationships of reproductive characters occurs only as egg diameter becomes larger, at which time more and more variability is observable. As egg diameter increases still further, an almost complete shift in the relationships of characteristics is evident.

Similarities can be seen to exist in Table VII between reproductive characteristics and groups of fishes which exhibit similar ranges in mean egg diameter. Chi-square tests were applied to the interrelations between each pair of characteristics with the result that a number of generalizations can be made.

With three exceptions, species of fish tested with a mean egg diameter less than 3.20 mm. had adhesive eggs. On the basis of Chi-square tests, the following reproductive characteristics also were found representative of this group of fishes:

1. Eggs were predominantly white to yellowish,
2. Incubation period was generally short (under four weeks),
3. Spawning occurred predominantly in spring and early summer,
4. No redd construction occurred.
5. Spawning occurred in either lakes or streams.

A group of seven species with an intermediate range in egg diameter, and possessing a mixture of reproductive characteristics is also evident. This group forms a "transition" zone between the two

Table VII. Reproductive characteristics of twenty-six species in relation to mean egg diameter. Plus indicates the presence of a characteristic, "o" the absence of it.

Egg Diameter		Species Number	SPECIES	Mean Egg Diameter	Adhesive	Non-adhesive	amber-salmon	white-yellow	Hatch under 4 wk.	Hatch over 4 wk.	Spawn Spring-summer	Spawn Fall	Spawn Lakes	Spawn Streams	Dig redds	Do not dig redds
UNDER 3.20 mm.	Small	1	Lota lota	0.68	+	0	0	+	+	0	+	0	+	+	0	+
		2	Richardsonius balteatus	1.15	+	0	0	+	+	0	+	0	+	+	0	+
		3	Cottus aspen	1.20	+	0	0	+	+	0	+	0	0	+	0	+
		4	Rhinichthys cataractae	1.35	+	0	0	+	+	0	+	0	0	+	0	+
		5	Mylocheilus caurinum	1.57	+	0	0	+	+	0	+	0	+	+	0	+
			Micropterus salmoides	1.58	+	0	0	+	+	0	+	0	+	+	0	+
		6	Catostomus catostomus	1.60	+	0	0	+	+	0	+	0	0	+	0	+
		7	Catostomus commersoni	1.85	+	0	0	+	+	0	+	0	0	+	0	+
			Perca flavescens	1.95	+	0	0	+	+	0	+	0	+	+	0	+
	Medium	8	Prosopium coulteri	2.00	0	+	0	+	0	+	0	+	0	+	0	+
		9	Catostomus macrocheilus	2.23	+	0	0	+	+	0	+	0	0	+	0	+
			Coregonus clupeaformis	2.35	0	+	+	0	0	+	0	+	+	0	0	+
		10	Thymallus arcticus signifer	2.50	+	0	+	0	+	0	+	0	0	+	0	+
			Micropterus dolomieui	2.54	+	0	0	+	+	0	+	0	0	+	0	+
		11	Prosopium williamsoni	2.78	0	+	+	0	0	+	0	+	0	+	0	+
		12	Prosopium cylindracium	3.18	+	0	+	0	0	+	0	+	+	+	0	+
Over 3.20 mm., large		13	Salvelinus malma	4.00	0	+	+	0	0	+	0	+	0	+	+	0

Table VII. Cont'd. Reproductive characteristics of twenty-six species in relation to mean egg diameter. Plus indicates the presence of a characteristic, "o" the absence of it.

Egg Diameter	Species Number	Species	Mean Egg Diameter	Adhesive	Non-adhesive	Amber-salmon	White-yellow	Hatch Under 4 wks.	Over 4 wks.	Spawn Spring-summer	Fall	Spawn Lakes	Streams	Dig redds	Do not dig redds
Large Over 3.20 mm.	14	Salmo gairdneri	4.06	o	+	+	o	o	+	+	o	o	+	+	o
	15	Salvelinus fontinalis	4.23	o	+	+	o	o	+	o	+	o	+	+	o
	16	Oncorhynchus nerka kennerlyi	4.28	o	+	+	o	o	+	o	+	+	+	+	o
	17	Salmo clarki	4.63	o	+	+	o	o	+	+	o	o	+	+	o
	18	Salmo trutta	4.94	o	+	+	o	o	+	o	+	o	+	+	o
	19	Salvelinus namaycush	5.51	o	+	+	o	o	+	o	+	+	+	+	o
	20	Salmo salar	6.10	o	+	+	o	o	+	o	+	o	+	+	o
	21	Oncorhynchus tschawytscha	7.14	o	+	+	o	o	+	o	+	o	+	+	o
	22	Oncorhynchus keta	7.40	o	+	+	o	o	+	o	+	o	+	+	o

Table VIII. Relationship of six pairs of reproductive characters to mean egg diameter (greater or less than 3.20 mm.)

Test No.	Characteristic of	Characters Tested	Calculated Chi-square values (X^2 at .01=6.635)
1	Egg	Adhesive	16.76
		Non-adhesive	
2	Egg colour	Amber-salmon	16.76
		White-yellow	
3	Incubation period	Under 4 weeks	13.99
		Over 4 weeks	
4	Spawning season	Spring&Summer	7.83
		Fall&Winter	
5	Spawning location	Lakes	6.20
		Streams	
6	Parental care	Dig redds	28.76
		Do not dig redds	

extremes, the only consistent characteristic of this group being that none of these species construct redds.

Species tested with a mean egg diameter in excess of 3.20mm. all had non-adhesive eggs. On the basis of Chi-square tests the following reproductive characteristics were found representative of this group of fishes:

1. Eggs were all amber to salmon coloured,
2. Incubation period was generally long (over four weeks),
3. Spawning may occur in spring, fall, or winter,
4. All species tested (possibly one exception) constructed redds,
5. Spawning occurred predominantly in streams.

DISCUSSION

Each individual fish of any species first approaches maturity with a fixed number of primary oöcytes in its ovaries, all of which represent potential ova. This initial number is almost certainly genetically controlled, and may to some extent be size dependent. However, egg number is essentially similar to other morphological characters, and as such, is subjected to numerous selective forces imposed by fluctuating environmental conditions which may alter egg number during subsequent development.

In the present investigation, as well as in previous literature, a positive correlation was found between fish length and egg number. As fish length increases, so does the size of the body cavity. Fish gonads continue growth just as do other parts of fish anatomy, and when mature occupy most of the available space in the body cavity. Egg diameter, however, determines the number of eggs that can be packed into any given space. Fecundity, therefore, although positively correlated with fish length (hence with size of body cavity), is also in part dependent on egg diameter. A similar type of relationship was observable between fecundity and fish weight, but since the variations were considerably greater than when length was compared with fecundity, this comparison has been omitted.

Environment has been demonstrated to have an influence on fecundity. For example, varying degrees of food abundance during the period of gonad maturation have been shown to alter fecundity in one size-range of rainbow trout. Rounsefell (1957) showed statistically that low sea temperatures were significantly correlated with greater egg number in pink salmon from Queen Charlotte Islands. Perhaps clinal variations in egg number with latitude or altitude, as suggested by some workers, are indirect reflections of the influence of environmental variables. Many fecundity variations almost certainly are.

Since existing knowledge of freshwater fish and their biology is limited, it is impractical to attempt to classify lakes according to their productivity for each species of fish present. Most fish species occupy diverse habitats, each of which is under the influence of a variable environment. It is therefore impractical, in view of the numerous unknown variables, to use fecundity alone as a racial or clinal separation.

Egg diameter as well as number has been shown, in the present study, to undergo considerable variation. The presence of larger eggs at the anterior than at the posterior of the ovaries of five species of mature freshwater fish is an illustration of variability in egg diameter within a single fish. This appearance of larger eggs in anterior regions of ovaries is an unusual phenomenon in view of the fact that eggs of most species are first deposited from the posterior end of the ovaries. Eggs in posterior regions of ovaries, if first to mature, should presumably be larger than immature eggs in more anterior regions. Such does not appear to be the case. In Salmonids, eggs from dorsal parts of ovaries mature first and are probably first to pass through the genital aperture. No significant difference was observed in egg diameter from these two regions. If the blood supply, innervation and physiology of developing ova are considered, one possible explanation becomes apparent. The richest blood supply is presumably located towards the anterior, where ovarian blood vessels first contact the ovary. Nutrient is absorbed into eggs by diffusion from the blood supply. Therefore, eggs in anterior regions of ovaries, if subjected to slightly higher concentrations of oxygen and nutrient than those in posterior regions might absorb slightly more nutrient, produce more yolk, and hence reach a slightly greater size.

The existence of the above phenomenon emphasizes the need for a standardized sampling procedure whenever egg diameters are to be measured.

Egg diameter has been demonstrated to increase with increasing fork length in most species studied. The possibility of a relationship between age and egg diameter was studied using rainbow trout. Age was found to have no consistent effect on egg diameter, except that occasionally the oldest fish were also the largest and hence had the largest eggs. This phenomenon may be the result of continuous growth throughout life as is common for most morphological structures of the majority of fishes.

In view of the variability in egg diameter mentioned above, the author must take exception to the hypothesis put forward by Scott (1955) that food availability during the period of maturation influences egg number, but not diameter, and that egg diameter was fixed within rather narrow genetic limits.

First, the question arises regarding the effect food availability has on egg size. If food is scarce and competition for it intense, sufficient nutrient may not be obtained to permit much growth. Maturation processes, however, continue. The result is that fish mature at a small size and have small eggs. On the other hand if food is abundant and easily obtainable, fish mature at a larger size and consequently have larger eggs. Therefore food availability during the period of maturation does influence egg diameter. Second, while little argument can be advanced regarding genetic control of egg diameter within upper and lower limits, the rigidity of this control between these limits is questionable. The magnitude of difference observed in egg diameter in the present study (as much as forty-five percent in rainbow trout from Paul Lake) indicates that egg size is quite variable, and is dependent on parent size, but indirectly on food availability, prior to maturity.

Much of the substance responsible for egg size is yolk. In order to produce yolk, nutrients must be transported in the blood of the parent to the tissues surrounding each individual ovum as it develops, and subsequently must be absorbed by the ova. These nutrient materials, once absorbed, are lost as nourishment to the parent fish except where resorption of ova occurs as was suggested by Scott (1955) and Vladykov (1956). Possibly, however, when ova undergo regression the follicles take on a hormone secretory function Brown (1957), in which case nutrients are still required by the follicles. Obviously a parent fish can provide only so much nutrient, dependent on feeding conditions, without endangering her own existence prior to spawning. On the basis of Scott's (1955) observations excessive resorption of developing ova occurred under conditions of low food abundance. Therefore, given conditions of great food abundance (and availability) more nutrient could theoretically be made available to ova over their whole period of development. This could result in the production of greater numbers of ova, as well as the absorption of larger quantities of nutrient by individual ova.

In Figure 10 data were presented on egg diameter for twenty-six different species in which a general trend toward larger eggs in larger fish is apparent. Therefore, considerable care should be exercised in selecting fish size if egg diameter is to be used in comparisons of groups of even closely related species, collected over wide ranges within the distribution of the species.

Furthermore, Marshall (1953) presents data in Table I of his paper, for four families of fishes which range from arctic to boreal regions. In two of these families the adult fish in arctic regions are substantially larger than in boreal regions. Data presented by Rounsefell (1957) also indicates that for many salmonids, spawners from the northern parts of their range are not only larger, but also frequently older than those from the southern parts of their range. They consequently would tend to have larger eggs. Perhaps this is one of the major reasons for the observation of larger eggs in polar regions, whether within or between species.

The relationship between total egg number and fish length has been shown to be too variable for use in any comparative studies. Fecundity relative to a single unit of body length or weight, however, might have possibilities. This system would in large part compensate for differences in length of parent fish, even when different species were involved.

Fish weight increases roughly as a cube of the increase in length. Egg number, because of its relationship with body cavity size and condition of the parent fish, does likewise. Examination of data has indicated that considerably less variability occurred in fecundity relative to a unit weight than to a unit length. Also, no consistent change was observed as fish length increased. For the above reasons, relative fecundity could be an extremely valuable tool in comparative fecundity studies, as fish of different species, in almost any size range, can be compared directly with one another.

Relative fecundity was shown in Figures 13 and 14 to be closely linked with egg diameter. Because of the correlation ($r = -0.97$) observed in Figure 14, it is possible to approximate relative fecundity for any given mean egg diameter. This method could prove a valuable tool, and time saver, in population studies as it obviates the necessity of counting large numbers of eggs when attempting to estimate total egg production of a spawning population of fish. If mean egg diameter, mean fish weight and approximate number of fish are known, approximate total egg number can easily be calculated.

Relative fecundity has seldom been used in the study of interspecific relationships. However, in view of the close relationship demonstrated between relative fecundity and egg diameter, the use of this measure might prove fruitful.

Within each family of fish a tendency can be seen to decrease fecundity relative to body weight, while at the same time an opposing tendency can be seen to increase it relative to body length, as fork length increases. This can be accounted for by the demonstrated increase in egg diameter as fish length increases. Egg number, assuming constant diameter, should increase in almost a direct proportion to increases in size of body cavity. Body cavity, in most fishes, increases in almost a direct proportion to increases in total fish weight which in turn increases in approximately a cubic ratio to each increment in fork length. It is therefore apparent that absolute fecundity will increase much more rapidly for each additional unit of length increment than it will for each unit of weight increment. For example, one centimeter increase in length would generally correspond with a greater fecundity rise than would one gram increase in weight. Relative fecundity behaves in a similar manner.

Egg diameter, however, has been shown to increase as fish length increases. This increase in diameter may be sufficiently large to cause the apparent decline in relative fecundity observable in Figure 13. The presence of larger eggs in larger fish might well be the major cause of a decline in fecundity of older fish as observed by Calhoun (1944) for yellowstone cutthroat (S. clarki lewisi).

The various points on Figures 13 and 14 have been separated into two groups, above and below 3.20 mm. mean egg diameter, in an attempt to illustrate the rather substantial differences in relative fecundity of the two groups. These differences may represent reflections of differences in life histories or in ecological relationships of the various species. An outstanding example is the burbot, only freshwater representative of the otherwise marine family Gadidae, whose life history and ecology differ from most other freshwater species of fish. Reference to Figures 10, 11, 13 and 15 abundantly demonstrates the magnitude of differences in relative fecundity and egg diameter of the burbot as compared with other species. It is suggested that these differences, certainly genetically controlled, are also directly related to certain phases of the life history and ecology of this animal. Data presented in Tables VII and VIII lend further support to this hypothesis.

If such environmental variables as food abundance (or quality), perhaps temperature, alter fecundity and egg diameter, ecological relationships could conceivably do likewise.

Tables VII and VIII present data which demonstrates the close relationship between certain "reproductive characteristics" and egg diameter in a number of species representing diverse phylogenetic and ecological groups. The presence or absence of most of the "reproductive characteristics" in these diverse groups, with eggs of either small or large mean diameter, is too consistent to be coincidental. They are in fact highly significant statistically.

Small eggs, among species examined, appear invariably associated with adhesiveness and a white to pale yellow coloration. Small eggs are more buoyant than larger ones because of a larger surface area-volume ratio. They hence are much more easily transported by water currents than are larger eggs. Most spawning occurs on either lake shores where wave action supplies water currents necessary for adequate gaseous exchange, or in streams where running water is present. Simple deposition of ova on the substrate in such places would almost certainly result in excessive mortality as a result of washing away in currents, stranding, or transportation of eggs by water currents, to predators. No species tested with small eggs showed any indication of redd construction. The development of adhesive eggs, however, would appear to have many advantages far outweighing the disadvantages. If adhesive, these small eggs could settle into narrow crevices between rocks, adhering to sides and bottoms of stones where they contacted them as a result of water currents. Many would, of course, adhere to exposed surfaces where they would be openly subjected to predation. However, their small size and pale color render them almost indistinguishable, at times, from sand grains. In many cases eggs become encased in a "shell" of sand grains (grayling), rendering them virtually invisible on any sandy substrate. It is thus possible to postulate processes of selection acting toward the development of neutral coloration and adhesiveness in fish with eggs of small diameter.

On the other hand large eggs, among species examined, appeared invariably associated with a lack of adhesiveness and an amber to salmon color: Because of the relatively large size of these eggs, fish must have fewer of them. The eggs are consequently very valuable to the species as a whole. Wolf and Wales (1953) demonstrated that rainbow trout had a definite preference for food pellets or corks dyed red, with orange as a second choice. No other colors attracted any attention. Similar preferences have been shown for other species of fish. They also showed rainbow trout to have a definite preference for bright red salmon eggs as compared with "pale" colored eggs. These large, amber-salmon colored eggs would appear to be exceedingly attractive to predators of many kinds. Brown (1957) suggested that the accumulation of carotenoid pigments in ova may be important in supplying chromatophore colors to the developing larvae, and as such, may be of considerable survival value. In addition, recent work indicates that carotenoid pigments of eggs may play an important part in fertilization by stimulating chemotaxis in spermatozoa. The presence of brilliant pigmentation in most large eggs would thus appear to be of some survival value to species which, because of large egg size, have considerably reduced egg numbers relative to fish with small eggs.

If eggs of these species were broadcast randomly over the surface of the substrate, predators would soon be attracted, resulting in excessive losses. Some type of parental care would be essential to survival of these large eggs. Construction of redds appears to be the direction in which forces of natural selection have swung, since all species studied with large eggs are known to construct redds of one form or another; none are known to build nests or guard the young after hatching. In addition, construction of a pit into which the eggs are deposited may permit more thorough mixing of sperm and eggs which, together with the suspected chemotactic effect of carotenoid pigments, may insure a higher successful rate of fertilization than would be possible if the eggs were merely broadcast on the substrate. Therefore, both redd construction and pigmentation may be of considerable survival value to species with large eggs and reduced egg numbers.

Eggs of large diameter, because of their relatively lower surface area to volume ratio require a greater flow of water for gaseous exchange than do eggs of small diameter. Hence this may represent a major reason for the prevalence of stream spawning in species with eggs of large mean diameter. Species with large eggs, and which spawn in lakes presumably do so in porous gravel through which springs flow. Perhaps this represents one reason why these species are selective as to spawning sites, for the gravel must be extremely porous, and virtually free of any fine particulate matter, which has been shown by Hobbs (1937) and Stewart (1953), to induce high mortality in eggs of rainbow and brown trout.

Adhesiveness appears to have been lost to eggs of large diameter. Adhesive eggs would cling to stones as they touched them, with the result that many could be crushed during the construction of redds. Non-adhesive eggs on the other hand would in all probability be moved aside by water currents from the moving stones, and subsequently come to rest in crevices between stones. Non-adhesiveness also prevents an excessive amount of "clumping" among larger eggs which otherwise could result in a curtailment of water flow around the eggs, or provide a favorable medium for growth of fungus around dead ova. Oxygen uptake would be a minor problem with small eggs because of their greater surface area-volume ratio, and greater ease of gaseous exchange. Fungus is a very real problem among small as well as large eggs, and is probably offset by increased numbers of the small eggs.

These processes of natural selection are almost certainly active at all times in all populations of fishes. Svärdson (1949) postulated selection pressures acting toward the development of larger eggs in all species. Brown (1957) states that larger eggs produce larger fry than smaller eggs reared under identical conditions. If it is true that fry from large eggs grow faster than those from small eggs, and may subsequently attain greater size, then there may be strong selection for fish to produce larger eggs. However, all fish do not have big, brightly colored eggs. It appears, therefore, that for many species, selection factors are acting very strongly towards development of small colorless eggs. Many factors could favor selection for small eggs. For example, considerably greater numbers of small eggs can be matured with much less drain on energy reserves of the parent fish than if large eggs were matured. Mature fish may then survive to spawn two, three or even more times, thus adding much to the reproductive potential of a population. Fry from small eggs, though frequently more numerous than those from large eggs may be more difficult for predators to find and hence in some cases may have greater chances for individual survival. The greater surface to volume ratio of small eggs may also be of considerable survival value in environments with restricted oxygen supplies, because of their greater ease of respiration.

In almost every set of environmental conditions, natural selection is probably constantly affecting egg size and number. Under each set of conditions selection for larger or smaller eggs probably attains a more or less stable level, the upper and lower limits of which are under genetic control, and may fluctuate with genetic changes. Therefore, as environment changes along with climatic or geographic fluctuations, fecundity can also be expected to change, but not necessarily toward lower fecundity and larger eggs. Selection may become equally intense for greater numbers of smaller eggs.

CONCLUSIONS

1. Results indicate that a positive correlation between fecundity and fork length exists for all species of fish examined as well as for salmonid species tested by earlier workers.

2. Fecundity, because of large, unpredicatable, environmentally induced variations, as well as variations caused by size and age of fish, cannot be considered practical for extensive use in racial or clinal studies.

3. It cannot be positively stated, with all existing evidence whether or not egg diameter or number form latitudinal clines in any or all species.

4. Egg diameter is variable within a single ovary of a fish. Of five species tested, all had significantly larger eggs (.05 - .01 levels) in anterior than in posterior regions of their ovaries.

5. Egg diameter apparently increases as parent size increases, both within a species and between species. This indicates the necessity of using comparable sized fish in all instances in which egg diameter is to be used for racial or clinal studies.

6. Age was found to have no apparent direct effect on egg diameter of rainbow trout from Paul Lake.

7. Range in fecundity relative to a unit of fish length or weight is superior to total egg number for use in racial or clinal studies because of reduced variability with increases in total fish length or weight.

8. Considering sixteen species tested, body shape appears to have little or no effect on relative fecundity.

9. Relative fecundity is closely dependent on egg diameter.

10. The burbot, the only freshwater representative of what is otherwise solely a marine family, differs substantially in many aspects of fecundity (and life history), from purely freshwater families.

11. In twenty-six species of freshwater fish, egg diameter was found significantly correlated with a number of reproductive characteristics.

12. Fish with eggs of small mean diameter generally have white to yellowish eggs, adhesive eggs, short incubation periods, no redd construction (parental care), variable spawning location and spring or summer spawning season.

13. Fish with eggs of intermediate mean diameter represent a group exhibiting variable reproductive characteristics.

14. Fish with eggs of large mean diameter generally have amber to salmon colored eggs, non-adhesive eggs, long incubation periods, redd construction (parental care), stream spawning and variable spawning season.

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Appendix i. Fecundity data of some British Columbia fish arranged in phylogenetic order.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No. Per cm.	Egg No. Per gm.
Prosopium	26.5	222.5	2.86	2874	108.5	12.9
williamsoni	27.0	275.5	2.82	3282	121.6	11.9
	27.0	255.5	2.77	3306	122.4	12.9
Nicola	27.5	302.5	2.66	2998	109.0	9.9
Lake	30.5	401.7	2.81	5128	168.1	12.8
	30.7	382.4	2.88	38.34	124.9	10.0
<u>Thymallus</u>	27.3	-	2.55	Partially		
<u>arcticus</u>	29.2	-	2.70			
<u>signifer</u>	26.0	-	2.50		spawned	
	27.9	-	2.40			
Yukon	29.9	-	2.42			out
<u>Oncorhynchus</u>	19.0	70.2	4.2	187	9.8	2.7
<u>nerka</u>	19.7	78.0	3.9	271	13.8	3.5
<u>kennerlyi</u>	20.3	80.0	4.1	208	10.3	2.6
	20.3	86.1	4.1	215	10.6	2.5
	20.3	74.8	3.8	242	11.9	3.2
J.C.Lyons	20.3	77.2	4.1	164	8.1	2.1
(1950)	20.6	85.1	4.6	184	8.9	2.2
	20.9	106.7	4.3	376	18.0	3.5
	20.9	76.8	3.9	225	10.8	2.9
Meadow Creek,	20.9	91.1	4.4	105	5.0	1.2
B.C.	21.6	97.2	4.3	228	10.6	2.4
	21.6	83.4	4.2	241	11.2	2.9
	22.1	110.6	4.4	316	14.3	2.9
	22.1	111.2	4.6	199	9.0	1.8
	22.1	105.3	4.5	252	11.4	2.4
	22.3	109.3	4.7	203	9.1	1.8
	22.3	105.8	4.2	189	8.5	1.8
	22.9	104.0	4.3	203	8.9	2.0
	22.9	116.3	4.2	277	12.1	2.4
	22.9	109.4	4.8	250	10.9	2.3
	22.9	105.5	4.1	309	13.49	2.9
	22.9	106.5	4.6	247	10.8	2.3
	22.9	119.6	4.3	230	10.0	1.9
	22.9	107.6	4.7	236	10.3	2.2

Appendix i. Cont'd. Fecundity data of some British Columbia fish arranged in phylogenetic order.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No. Per cm.	Egg No. Per gm.
Oncorhynchus	22.9	116.9	4.6	184	8.0	1.6
nerka	22.9	110.5	4.5	263	11.5	2.4
kennerlyi	22.9	114.3	4.5	236	10.3	2.1
J.C.Lyons,	24.1	133.7	3.8	309	12.8	2.8
(1950)	24.8	124.1	3.5	345	13.9	2.8
Meadow Creek,						
B.C.						
Nicola Lake,	23.3	159.6	4.5	462	19.8	2.9
B.C.	23.4	164.5	4.7	415	17.7	2.5
	23.8	160.8	4.4	360	15.1	2.2
	25.7	207.2	4.5	579	22.5	2.8
Shawnigan Lk.	28.0	296.2	4.9	1086	38.8	3.7
	28.8	347.5	4.9	1258	43.7	3.6
	29.0	340.7	5.1	963	33.2	2.8
	30.8	375.9	5.2	1077	34.9	2.9
Salmo	42.5	1127	4.7	1877	44.2	2.0
gairdneri	44.0	1264.7	4.3	2238	50.9	2.0
J.C.Lyons &	47.5	1357.3	4.4	2014	42.4	1.7
P.A.Larkin	47.5	1534.3	4.5	2744	57.8	2.0
(unpub)	48.0	1524.5	4.5	2527	52.7	1.9
Peterhope						
Lake						
Knouff Lake	28.0	286.4	3.6	750	26.8	2.9
	30.5	393.1	3.5	2064	67.7	5.9
	44.5	1036.5	4.3	2170	48.8	2.5
	47.5	1293.5	4.3	2067	43.5	1.8
	48.0	1449.0	4.3	3090	64.4	2.5
	50.0	1608.4	4.3	2330	46.6	1.7
	52.0	1783.0	4.2	3905	75.1	2.6
Jacko Lake	61.5	2849.5	4.0	6313	102.7	2.6
	63.0	3000.0	4.3	4831	76.7	1.8
	63.0	3700.0	4.3	6941	110.2	2.2
	70.0	3999.7	4.4	6991	99.9	2.0

Appendix i. Cont'd. Fecundity data of some British Columbia fish arranged in phylogenetic order.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No. Per cm.	Egg No. Per gm.
Salmo						
gairdneri	28.5	260.8	3.4	884	31.0	3.9
J.C.Lyons &	32.0	622.9	4.1	1121	35.0	2.0
P.A.Larkin	33.0	543.2	3.9	979	29.7	2.1
(unpub.)	35.0	393.2	3.9	838	23.9	2.4
Paul Lake	35.0	619.0	4.3	1306	37.3	2.5
	35.5	479.9	3.8	1621	45.7	4.0
	36.0	575.8	4.0	1326	36.8	2.7
	36.0	563.2	4.0	1556	43.2	3.3
	36.0	451.4	3.9	1451	40.3	3.9
	38.0	729.7	4.0	2111	55.6	3.5
	40.0	619.5	3.9	1204	30.1	2.2
	41.0	712.3	4.0	800	19.5	1.2
	41.0	887.6	4.3	1957	47.7	2.6
	41.5	962.5	4.3	2485	59.9	3.2
	42.5	820.8	4.6	1058	24.9	1.5
	43.0	723.3	3.6	1788	41.6	2.8
	43.0	936.5	3.8	2298	53.4	2.8
	44.0	999.8	4.2	2326	52.9	2.7
	44.0	842.3	4.2	1395	31.7	1.9
	44.0	1158.1	4.0	2919	66.3	2.9
	44.5	1159.8	4.4	2350	52.8	2.4
	45.0	1090.3	4.2	2423	53.8	2.7
	47.0	1260.0	4.4	2121	45.1	1.9
	47.0	1051.7	3.6	4970	105.7	5.9
	48.0	1275.5	4.7	1581	32.9	1.4
	49.0	1249.7	4.1	2623	53.5	2.4
Catostomus	28.6	297.4	1.60	8600	300.7	28.9
catostomus	29.0	304.5	1.50	12765	440.2	41.9
	30.7	371.2	1.70	15132	592.9	40.8
Shelley	31.5	399.3	1.64	18098	574.5	45.3
Slough	32.2	416.0	—	17603	546.7	42.3
	32.4	418.3	1.61	18544	572.3	44.3
	32.5	498.8	—	24978	768.6	50.1
	32.6	378.5	1.74	12033	369.1	31.8
	33.0	426.2	1.55	18544	572.3	44.3
	33.3	551.2	1.72	19593	588.4	35.5
	34.0	545.6	1.50	20300	1067.6	66.5

Appendix i. Cont'd. Fecundity data of some British Columbia fish arranged in phylogenetic order.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No. Per cm.	Egg No. Per gm.
Catostomus	34.5	544.7	1.61	18,000	521.7	33.0
catostomus	34.5	460.8	1.49	15,800	457.9	34.3
Shelley	35.0	528.8	1.66	22,833	652.4	43.2
Slough	35.0	510.5	--	20,787	593.9	40.7
Catostomus	39.0	741.2	2.01	17,963	460.5	24.2
macrocheilus	41.5	1,085.5	2.41	13,669	329.3	12.6
	41.5	930.0	2.20	15,463	372.6	16.6
	42.2	1,040.0	2.16	20,667	489.7	19.9
Wolf Creek	43.0	1,044.0	2.28	14,900	346.5	14.3
	45.0	1,156.0	2.23	21,117	469.2	18.3
	46.0	1,349.5	2.27	22,662	492.7	16.8
Little Bull R.	46.0	1,648	2.62	20,000	434.8	12.1
Catostomus	32.0	465.7	1.84	11,825	369.5	25.4
commersoni	38.5	733.2	1.89	17,405	452.1	23.7
Mylocheilus	24.0	218.5	1.59	10,974	457.2	50.2
caurinum	24.5	225.0	1.58	12,381	505.3	55.0
	24.7	226.7	1.66	11,972	484.9	52.8
White Lake	25.1	237.0	1.62	11,786	469.6	49.7
	25.2	247.5	1.59	14,170	562.3	57.3
	25.6	246.6	1.61	13,933	544.2	56.5
	26.1	264.7	1.68	17,261	661.3	65.2
	26.2	246.7	1.66	13,585	518.5	55.1
	26.2	266.4	1.68	13,796	526.5	51.8
	26.3	265.9	1.63	13,030	495.4	49.0
	26.8	282.7	1.62	17,268	644.3	61.1
Hansard Lake	19.6	81.3	1.48	5,222	266.4	64.2
	19.6	79.0	1.48	4,643	236.9	58.8
	19.9	80.5	1.53	4,335	217.8	53.9
	20.7	92.2	1.48	6,664	326.7	72.3
	21.2	86.1	1.59	5,256	247.9	61.0

Appendix i. Cont'd. Fecundity data of some British Columbia fish arranged in phylogenetic order.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No. Per cm.	Egg No. Per gm.
<u>Mylocheilus</u>	21.2	119.3	1.56	7,884	371.9	60.9
<u>caurinum</u>	24.7	194.7	1.55	13,376	541.5	68.7
Terrace	24.8	219.3	1.55	13,261	534.7	60.5
<u>Rhinichthys</u>	9.9	14.5	1.38	520	52.5	35.9
<u>cataractae</u>	9.9	14.0	1.53	775	78.3	55.4
	10.0	15.7	1.35	773	77.3	49.2
	10.9	21.3	1.51	890	81.7	41.8
Tulameen R.	11.3	20.0	1.38	756	66.9	37.8
	11.4	25.0	1.40	1,102	96.7	41.8
<u>Richardsonius</u>	9.9	13.9	1.26	1,198	121.0	86.2
<u>balteatus</u>	10.1	14.5	1.18	1,182	117.0	81.5
	10.2	15.9	1.21	1,071	105.0	67.4
Shelley	10.7	17.8	0.84	1,694	158.3	95.2
Slough	10.8	18.7	1.24	1,334	123.5	71.3
	10.9	18.6	1.21	1,243	114.0	66.8
	11.0	18.3	1.12	1,539	140.0	84.1
	11.5	22.7	1.34	1,404	122.1	61.9
	11.6	20.6	1.24	1,279	110.3	62.1
	12.4	30.7	1.20	2,205	177.8	71.8
Trembleur	9.2	10.9	1.22	1,404	153.6	128.8
Lake	9.2	9.7	1.24	1,688	183.4	174.0
	9.3	10.6	1.33	958	103.0	90.4
	11.1	20.0	1.10	2,327	209.6	66.4
	11.2	20.1	1.28	2,568	229.3	127.7
	11.5	19.5	1.23	2,472	214.9	126.8
	11.7	23.1	1.43	1,508	128.8	65.3
	12.7	24.6	1.20	3,384	266.5	137.6
Paul Lake	8.3	7.7	0.93	778	101.0	93.7
	9.3	11.9	1.04	827	88.9	69.5
	9.4	11.7	1.12	1,066	113.4	91.1
	9.4	12.8	1.17	1,129	120.1	88.2
	9.5	11.1	1.30	880	92.6	79.3
	9.7	13.2	1.29	1,166	120.2	88.3
	9.8	11.7	--	1,000	102.0	85.5

Appendix i. Cont'd. Fecundity data of some British Columbia fish arranged in phylogenetic order.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No Per cm.	Egg No. Per gm.
Richardsonius balteatus						
Paul Lake	10.2	15.4	1.12	1,372	134.5	89.1
	10.3	15.3	1.16	1,500	145.6	98.0
	11.5	18.1	0.99	1,216	105.7	67.2
Lota lota						
Dutch Creek	36.5	361	0.65	295,000	8,082	817.2
(Kootenay)	37.0	399.2	0.70	395,000	10,675	989.4
Cottus asper	12.4	27.1	1.23	1,571	404.5	69.9
Bella Coola	21.2	178.9	1.21	14,655	691.2	81.9

Appendix ii. Mean fecundity data of some British Columbia fish.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No. Per cm.	Egg No. Per gm.	Number in Sample
Prosopium williamsoni	28.2	306.6	2.80	3,570	125.8	11.7	6
Thymallus arcticus signifer	28.1	—	2.51	—	—	—	5
Oncorhynchus nerka kennerlyi	22.3	134	4.28	354	10.8	2.4	37
Salmo gairdneri	43.7	1,171.3	4.13	2,389	51.4	2.6	42
Catostomus catostomus	32.6	444	1.60	8,361	569.6	41.1	15
Catostomus macrocheilus	43.0	1124	2.23	18,305	424.4	16.9	8
Catostomus commersoni	35.2	599	1.85	14,615	410.8	24.5	2
Mylocheilus caurinum	23.8	194	1.57	11,095	453.3	58.1	19
Rhinichthys cataractae	10.5	18.4	1.35	802	75.6	44.0	6

Appendix ii. Cont'd. Mean fecundity data of some British Columbia fish.

Species	Fork Length (cm)	Weight (gm)	Egg Diameter (mm)	Egg Number	Egg No Per cm.	Egg No. Per gm.	Number in Sample
Richardsonius balteatus	10.5	16.2	1.15	1,453	137.0	90.1	29
Lota lota	36.8	380	0.68	345,000	9,378.5	903.3	2
Cottus asper	16.8	103	1.21	8,113	404.5	70.0	2