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MATERNAL INFLUENCES ON THE AGE AT MATURITY OF SKEENA RIVER SOCKEYE SALMON (*ONCORHYNCHUS NERKA*)

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INTRODUCTION

In North America, sockeye salmon (Oncorhynchus nerka) may mature in their third to eighth year of life (Mosher, 1963). They typically spend one or two years in lakes before migrating to sea. For most of the major British Columbia stocks, sockeye migrate to sea early in their second year and the age at which they mature varies widely from brood year to brood year. Fish approaching four and five years of age, which migrated to sea in their second year of life (age-1.2 and /-1.3 fish[1]) have made up most of the adult returns to the Skeena River and Rivers and Smith inlets. For example, the average proportions of age-1.2 and /-1.3 Skeena River sockeye which returned from each brood year for the past 50 years have been about equal (Bilton et al., 1967). However, some marked departures have occurred with 1.2s forming as few as 21% and as much as 81% of the total return. Such wide annual fluctuations in the age of maturity have a profound influence on the number of fish available to the fishery in any one year, and have also contributed to the difficulty of predicting the contributions of adult sockeye of specific brood years to the fishery in any one year. There is need to examine the factors that influence the age of maturity.

The purpose of these studies was to examine maternal influences on age at maturity of Skeena River sockeye salmon which, when considered along with several other correlated phenomena, lead to an hypothesis of alternation of generations, e.g., age-1.2 female sockeye tend to produce age-1.3 offspring, of which the females in turn tend to produce 1.2 offspring.

FEMALE LENGTH-EGG-WEIGHT RELATIONSHIP

1. Materials and methods

In September 1964, at Scully Creek, a tributary to Lakelse Lake in the Skeena River drainage, eggs were taken from 19 female sockeye salmon of known age and size, and fertilized with sperm of 15 males of known age and size. In January 1965, individual weights of 50 "eyed" eggs from each female were obtained; weights were determined after lightly blotting the moisture from the eggs.

In October 1965, from the Babine River, at the outlet of Nilkitkwa Lake, eggs were taken from 89 age-1.2 sockeye. Eggs were fertilized, allowed

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[1]In the present paper the European system of age designation is used. Here, the number of annual rings formed is indicated. For example, a 1.2 is a fish with one annual ring that was formed while it was in fresh water, and with two annual rings that were formed while it was in the ocean. A 1.2 is the same as a 4_2 in the Gilbert system, where age refers to the year of life dating from time of egg deposition.

to water harden (swell in water) for approximately 2 hours, and 50-egg lots were weighed from each female. In September 1966, eggs were taken from 43 age-1.3 sockeye. In this case, eggs were not fertilized, were allowed to water harden for 2 hours, and 100-egg lots were weighed from each female.

In 1966 a test was conducted comparing the weights of fertilized and unfertilized eggs. Samples of eggs from each of five Babine sockeye were divided into two groups. The eggs in one group were fertilized, and the eggs in the other group were not fertilized. Water was added, and the eggs in each group were weighed on eight occasions over a 13-hr period. Analyses of variance indicated that differences in weight of eggs with time were statistically significant ($F = 2.248$; d.f. 7, 56; $P > 0.05$), but that differences between the weights of the fertilized and unfertilized groups of eggs ($F = 0.150$; d.f. 1, 8; $P < 0.05$) were not. There was also no significant interaction between the groups of fertilized, or unfertilized, eggs with time, indicating that the time changes are essentially similar for the two groups. These results indicated that the different methods used in the two years introduced no differential bias on weights of the sockeye eggs in the samples.

2. Results

The Scully Creek data indicated the average weights of eggs from age-1.3 sockeye of the 1959 brood year were larger than the average weights of eggs from age-1.2 females from the 1960 brood year (Fig. 1, Table 1).

Analyses of covariance of data within each age-class indicated the relationship between egg weight and fish length was not significant (1.2s, $F = 1.17$; $P > 0.2$; d.f. 1, 8: 1.3s, $F = 1.46$; $P > 0.2$; d.f. 1, 7). This result was not unexpected due to the limited size range of samples from each age-class, and the large variance of egg weight within size groups. The egg-weight data for the two age-classes were combined on the assumption that the slopes and elevations of the possible (but not demonstrable) regression lines within age-classes were not significantly different from each other. Analysis of variance indicated a significant positive relationship between egg weight and fish length (probably age too, as the older fish are also demonstrably larger than the younger fish) ($F = 31$; $P < 0.005$; d.f. 1, 17). The regression formula was:

$$y = -2.1798 + 0.3537x,$$

where y = mean egg weight in grams × 100, and x = female parent hypural length in centimeters.

Eggs of age-1.2 and /-1.3 Babine River sockeye from the same brood year were compared to avoid brood-year differences. Eggs of age-1.3 females averaged larger than those from age-1.2 females (Fig. 2, Table 1). Analysis of variance of combined data for 1.2 and 1.3 fish indicated a significant relationship between egg weight and female length ($F = 96$; $P < 0.005$; d.f. 1, 131). Within each age group there was a significant positive relationship between egg weight and fish length (1.2s, $F = 22.69$; $P < 0.001$; d.f. 1, 88: and

1.3s, $F = 4.61$; $P < 0.05$; d.f. 1, 42). Covariance analysis indicated differences were not significant among either slopes ($F = 1.66$; $P > 0.2$) or elevations ($F = 0.054$; $P > 0.2$) of the two age-group regression lines. It may be inferred from these data that egg weight is a dependent function of fish length. This interpretation is represented by the combined data regression:

$$y = 0.0348 + 0.3242x,$$

where y = mean egg weight in grams × 100, and x = female parent hypural length in centimeters.

Covariance analyses on the Babine and Scully data (age-1.2 and /-1.3 fish combined in each case) indicated differences in the slopes of regression lines were not significant ($F = 1.599$; $P > 0.2$; d.f. 1, 149), but there were significant differences in the elevations of the lines ($F = 7.90$; $P < 0.01$). Thus at equivalent body lengths it appears that Scully Creek sockeye have smaller eggs than those of Babine River sockeye.

EGG WEIGHT-JUVENILE GROWTH RATE RELATIONSHIP

1. Materials and methods

In 1964 the eggs from 16 of the 19 Scully Creek females of known age and size that had been fertilized with sperm of males of known age and size (Table 2) were used in this study. After hatching, the progeny from these crosses were reared in separate tanks until October 1965. Five crosses were lost during the course of the experiment (one, 1.1 × 1.2; two, 1.2 × 1.2; and two, 1.3 × 1.3). During this period every attempt was made to keep the conditions in each tank the same. Temperatures were similar, the number of fish held in each tank was approximately the same, and all fish were fed an *ad libitum* diet. Fish were sampled 1, 2, 3, and 9 months after hatching. Each time 50 fish were removed from each tank, killed, and length and weight of each fish in each group recorded.

2. Results

Results of the 16 crosses of age-1.2 and /-1.3 sockeye indicated that the mean length and weight of fry at 3 months after hatching were positively, and significantly, correlated ($r = 0.601$-0.960) with egg weight and length of the female parent (Table 3, Fig. 3-5). Thus the larger females produced larger eggs which produced the larger fry. The results of comparison of the mean length and weight of fry at 3 months with the length of the male parent in each cross indicated they were not correlated ($r = 0.000$-0.033).

Comparison of mean lengths and weights of 9-month fingerlings of the surviving 11 crosses with length of female parent (Fig. 6-7) produced smaller correlation coefficients ($r = 0.585$-0.595) (Table 3, $P > 0.05$, < 0.10). The mean length and weight of 9-month fingerlings were not significantly correlated ($r = 0.473$-0.493) with mean egg weight ($P > 0.10$). The increase in variability in the size among the 9-month fingerlings may have been due in part to the *ad libitum* diet.

GROWTH RATE-AGE AT MATURITY RELATIONSHIP

1. Materials and methods

Scales of 13,780 age-1.2 and /-1.3 Skeena sockeye were sampled from the catch and/or the escapement for 10 brood years (1952-61) and were examined under a microprojector at a magnification of 100 diameters.

For the brood years 1952-55, only the number of circuli formed in fresh water was recorded. Counts were made along the longest anterior axis of the scale from the centre of the scale focus to the last freshwater circulus. In almost every instance the last freshwater circulus was the annulus. On only approximately 3% of all the Skeena River sockeye scales examined was there any definite indication of "new growth" freshwater circuli that had formed after the annulus.[a] The number of age-1.2 and /-1.3 sockeye in the samples from the catch and the escapement (samples of the escapement were obtained from test fishing catches made in the estuary just above the fishing boundary) in each freshwater circulus category were weighted to the estimated numbers of fish in each age-class in the weekly catch and the escapement. These data provided circulus-count frequencies, by age-class, in estimated absolute numbers of returning adults (catch + escapement) for each brood year (Table 4).

Scales from 3,008 migrant yearling Babine Lake (the main nursery area for sockeye in the Skeena system) sockeye for the years 1955, 1956, 1959 and 1960 were examined under a projector at a magnification of 100 diameters. Circulus counts were made along the longest anterior axis of the scale from the centre of the scale focus to the last freshwater circulus.

For the brood years 1956-61, the widths of the year-bands (a year-band includes both what is considered to be summer and winter growth to the last circulus in the annulus) in fresh water and the first two ocean year-bands were recorded for age-1.2 and /-1.3 sockeye sampled from the catch. Measurements were made along the longest anterior axis of the scale from the centre of the scale focus to the first annulus and then from the first annulus to the second annulus, and so on. The year-band widths were not weighted to the abundance of the sockeye in the catch.

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[a]Sometimes yearling sockeye scales exhibit a number of more widely-spaced circuli after the annulus. Clutter and Whitesel (1956) referred to this growth as "spring growth." On the average, over a 7-year period, 20% of the Babine yearling sockeye scales exhibited spring growth with an average of 1.0 circuli (Bilton, unpubl. data). Because the numbers of new growth circuli in Babine sockeye scales are small, identification of these circuli on the adult scales is extremely difficult. Therefore the percentage of Skeena River adult scales on which new growth circuli were identified may have been lower than the actual occurrence.

2. Results

For each of the 1952-55 brood years of Skeena River sockeye, the 1.2s had a significantly higher number of freshwater circuli than the 1.3s (Table 5). The difference varied from 0.30 to 2.10 circuli. Figure 8 shows the frequency distributions; an arbitrary division between 11 and 12 circuli indicates the difference graphically. The percentage of fish having less than 12 circuli ranged from 10.9 to 17.6 for age-1.2 fish, and 23.8 to 56.1 for age-1.3 fish (Table 5).

Circulus counts on scales from migrant yearling Babine Lake sockeye had a close, direct relation to fish length, with smaller yearlings having fewer circuli than larger ones (Fig. 9). Thus for the 1952-55 broods, the fact that a larger proportion of 1.3 adults had freshwater circulus counts less than 12, indicates that a larger proportion of this life-history type originated from smaller yearlings than did the 1.2s.

Mean freshwater year-band width was significantly greater for age-1.2 sockeye than age-1.3 sockeye for five of the six 1956-61 broods (Table 6). The mean width of the second year-band (first ocean year) of 1.2s was significantly greater for three of the brood years, the same in one brood year, and significantly smaller in two brood years. The mean width of the third year-band (second ocean year) of 1.2s was significantly greater than the 1.3s in all years. Furthermore the mean total scale width up to the end of the third year was significantly larger for age-1.2 sockeye than for age-1.3 sockeye. If the positive relationship between scale width and fish length for adult sockeye at Karluk Lake (Barnaby, 1932) also applies to Skeena River sockeye, then it is evident that age-1.2 sockeye grow more rapidly than age-1.3 sockeye.

CONCLUSIONS

The results of this study indicated that: (1) egg weight of Skeena River sockeye is positively correlated with length (and usually age) of the female parent; (2) egg weight is positively correlated with initial size and subsequent growth of juveniles, at least up to age 3 months; and (3) juvenile growth in the lake and ocean is inversely related to age at maturity. Hence, we may hypothesize that the larger, age-1.3 sockeye spawners tend to produce progeny which mature as smaller, age-1.2 fish, which in turn give rise to progeny which mature as larger, age-1.3 fish, and so on. Hence, an alternation of generations occurs.

Testing of the hypothesis has not yet been undertaken. Should the hypothesis be valid, its implications may well be significant to the management program for the Skeena River sockeye salmon resource.

ACKNOWLEDGMENTS

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Table 1. Mean egg weight for sockeye salmon, by length and age, from Scully Creek in 1964 and Lower Babine River in 1965 and 1966.

Hypural length of female (cm)	Scully Creek			Lower Babine River		
	Age	Mean egg weight (g)	No. of females sampled	Age	Mean egg weight (g)	No. of females sampled
39	1.2	.1252	2	-	-	-
40	1.2	.1045	1	1.2	.1246	1
41	1.2	.1152	3	-	-	-
42	1.2	.1408	2	1.2	.1317	11
43	1.2	.1265	2	1.2	.1349	12
44	-	-	-	1.2	.1492	15
45	1.3	.1447	1	1.2	.1477	24
	-	-	-	1.3	.1417	2
46	1.3	.1402	1	1.2	.1490	16
47	-	-	-	1.2	.1500	9
48	1.3	.1552	2	1.2	.1620	2
	-	-	-	1.3	.1552	3
49	1.3	.1505	2	1.3	.1546	4
50	1.3	.1383	1	1.3	.1704	6
51	1.3	.1615	2	1.3	.1655	12
52	-	-	-	1.3	.1737	5
53	-	-	-	1.3	.1591	6
54	-	-	-	1.3	.1754	4

Table 2. Numbers of age-class crosses completed on Scully Creek sockeye salmon, 1964

Female Age ↓ / Male Age →	1.1	1.2	1.3
1.2	2	3	3
1.3	3	0	5

Table 3. Correlations between female length, egg weight, and weight and length of resulting 3-month fry and 9-month fingerlings, for Scully Creek sockeye, 1964.

Correlation	Female length		Egg weight	
	r	P[a]	r	P[a]
Egg weight	+0.791	<0.01	..	..
Fry length (3 months)	+0.660	<0.01	+0.601	>0.01;<0.02
Fry weight (3 months)	+0.711	<0.01	+0.960	<0.001
Fingerling length (9 months)	+0.585	>0.05;<0.10	+0.492	>0.10
Fingerling weight (9 months)	+0.595	>0.05;<0.10	+0.473	>0.10

[a]P = probability of chance occurrence.

Table 4. Estimated numbers (thousands) of fish, by age-class, in each circulus category in the total resultant Skeena River sockeye stock (catch plus escapement) for the brood years 1952-55.

Brood Year	Age	Number of circuli																	Total	Total no. samples
		5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
1952	1.2	0.8	0.8	1.0	3.5	7.7	10.0	30.9	66.7	77.1	70.9	72.8	56.8	21.6	7.1	1.8	2.2	0.6	432.3	732
	1.3	0.2	3.2	9.6	9.8	15.1	29.1	34.3	31.5	30.3	19.7	11.9	4.8	2.2	..	..	..	..	201.7	872
	TOTAL																		634.0	
1953	1.2	..	0.5	1.2	3.8	10.4	24.1	46.2	127.9	135.8	87.4	29.6	16.3	2.4	3.3	..	..	..	488.9	1305
	1.3	0.9	1.2	3.3	46.7	82.6	152.4	172.6	132.6	125.8	67.4	24.1	6.5	2.6	0.4	..	..	..	819.1	1100
	TOTAL																		1308.0	
1954	1.2	..	..	2.4	1.5	6.8	17.4	32.6	91.1	181.8	151.0	46.1	18.8	3.4	2.3	..	..	..	555.2	948
	1.3	..	7.2	15.9	43.7	51.6	132.2	104.3	124.0	102.6	54.8	16.9	3.4	0.7	..	..	..	..	657.3	764
	TOTAL																		1212.5	
1955	1.2	0.4	2.5	5.2	3.4	6.5	11.1	6.9	37.4	63.2	74.8	22.5	6.9	1.5	0.6	..	..	..	242.9	405
	1.3	0.9	3.4	4.9	4.2	6.0	9.7	8.1	19.6	30.9	23.6	24.5	11.3	4.5	2.0	2.2	..	..	155.8	387
	TOTAL																		398.7	

Table 5. Weighted mean number of freshwater circuli on the scales of age-1.2 and /-1.3 Skeena River sockeye, brood years 1952-55.

Brood Year		Age 1.2	Age 1.3
1952	$\bar{x}$	13.70	11.60
	S.D. ±	2.57	1.44
	N	732	872
	t	21.2	
	% <12 circuli	12.6	50.2
1953	$\bar{x}$	12.75	11.52
	S.D. ±	1.23	1.53
	N	1305	1100
	t	18.2	
	% <12 circuli	17.6	56.1
1954	$\bar{x}$	13.16	11.48
	S.D. ±	1.33	1.47
	N	948	764
	t	20.7	
	% <12 circuli	10.9	53.9
1955	$\bar{x}$	13.09	12.79
	S.D. ±	2.38	3.56
	N	405	387
	t	1.74	
	% <12 circuli	12.8	23.8

Note: Underlined value of t indicates significance at the 5% level. S.D. = Standard Deviation.

Table 6. t-tests of mean freshwater and ocean year-band widths of age-1.2 and /-1.3 Skeena River sockeye, for brood years 1956-61.

Brood Year		1st year		2nd year		3rd year		Total width to end of 3rd year	
		1.2	1.3	1.2	1.3	1.2	1.3	1.2	1.3
				(mm × 100)					
1956	$\bar{x}$	41.01	36.79	114.60	106.14	88.01	79.75	243.62	222.68
	N	68	77	68	77	68	77		
	t	6.78		9.74		9.52			
1957	$\bar{x}$	38.08	35.87	99.53	98.21	99.77	95.59	237.38	229.67
	N	281	1434	281	1434	281	1434		
	t	9.74		4.55		13.36			
1958	$\bar{x}$	38.96	39.63	107.22	109.02	92.06	89.16	238.24	237.81
	N	998	168	998	168	998	168		
	t	2.27		4.47		7.07			
1959	$\bar{x}$	39.95	39.05	107.15	108.16	86.79	80.57	233.89	227.78
	N	494	868	494	868	494	868		
	t	4.68		4.16		24.04			
1960	$\bar{x}$	40.35	37.85	105.19	105.52	83.20	75.60	228.74	218.97
	N	210	581	210	581	210	581		
	t	9.17		0.90		20.65			
1961	$\bar{x}$	38.19	36.54	106.08	103.62	92.35	87.39	236.62	227.52
	N	869	1219	869	1219	869	1219		
	t	10.48		11.35		23.37			

Note: Underlined value of t indicates significance at the 5% level.

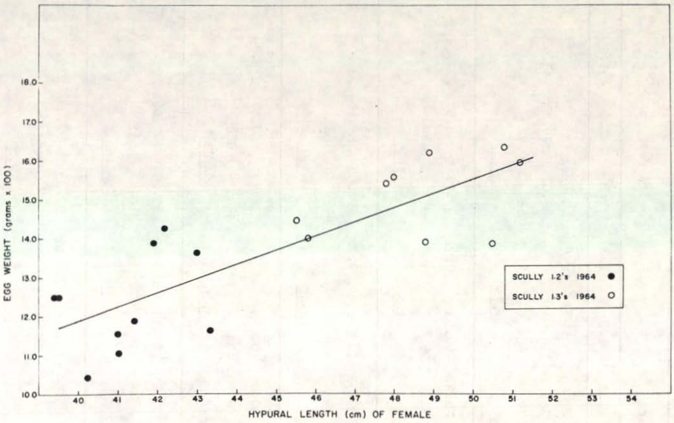

Fig. 1. Mean egg weight for age-1.2 and /-1.3 Scully Creek sockeye, by length of female parent, 1964.

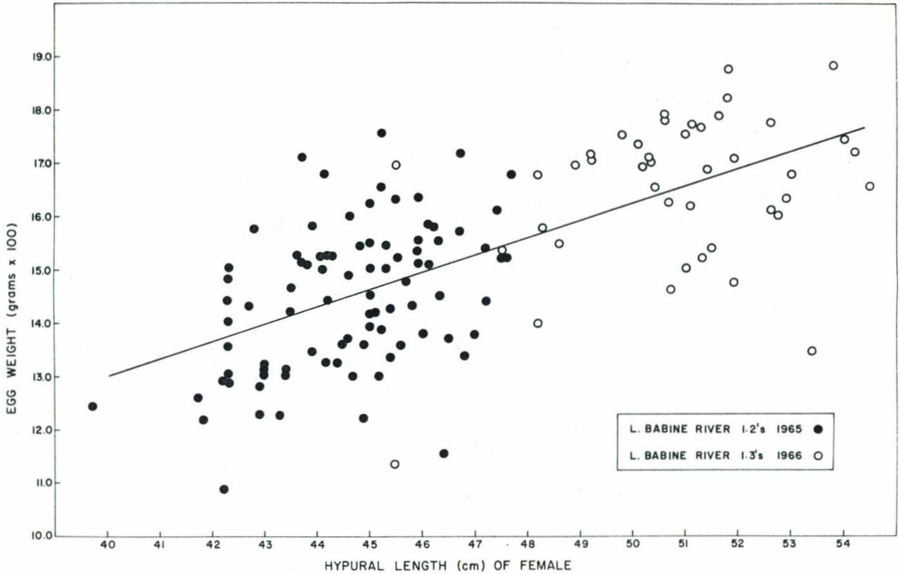

Fig. 2. Mean egg weight for age-1.2 and /-1.3 Lower Babine River sockeye, by length of female parent, 1961 brood.

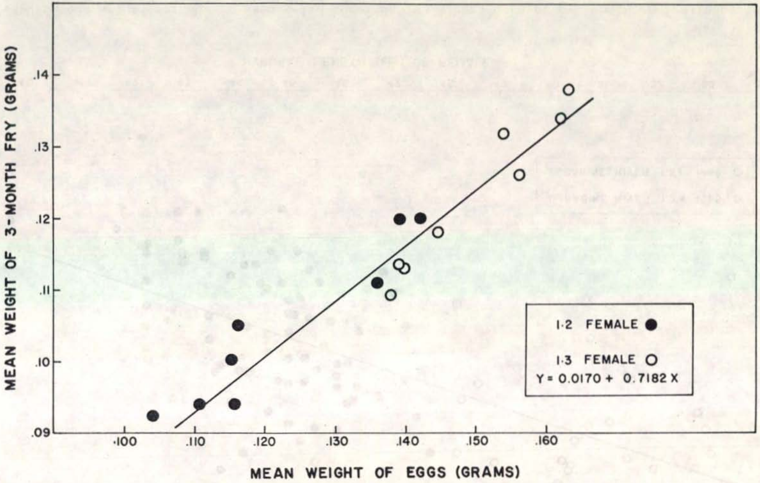

Fig. 3. Mean weight of age 3-month Scully Creek fry, by mean egg weight and age of female parent, 1964.

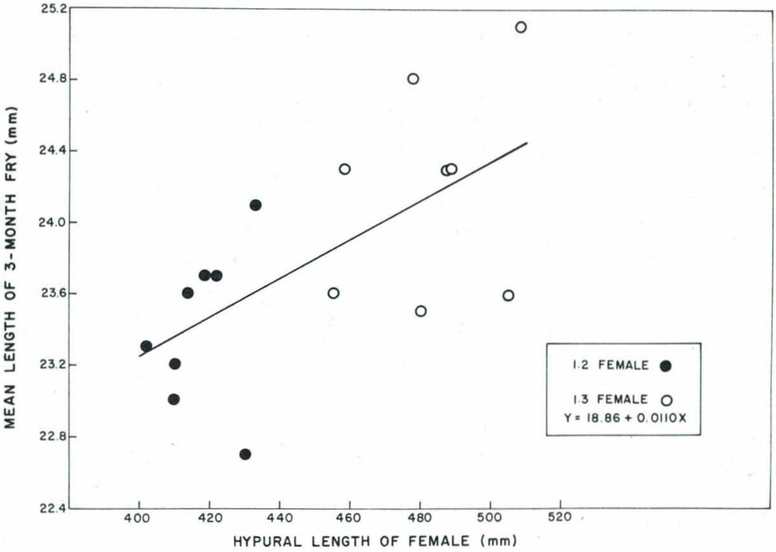

Fig. 4. Mean length of age 3-month Scully Creek fry, by length and age of female parent, 1964.

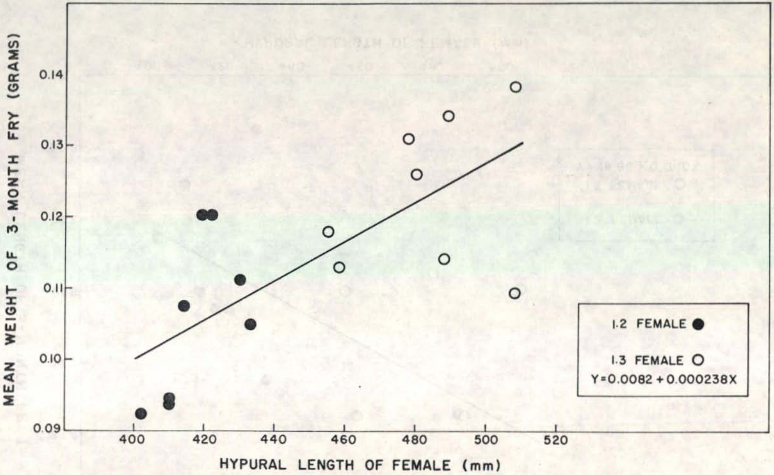

Fig. 5. Mean weight of age 3-month Scully Creek fry, by length and age of female parent, 1964.

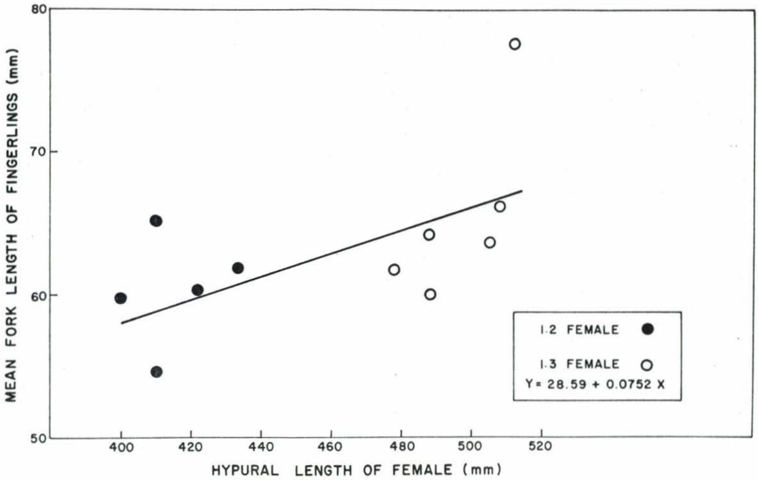

Fig. 6. Mean length of age 9-month Scully Creek fingerlings, by length and age of female parent, 1964.

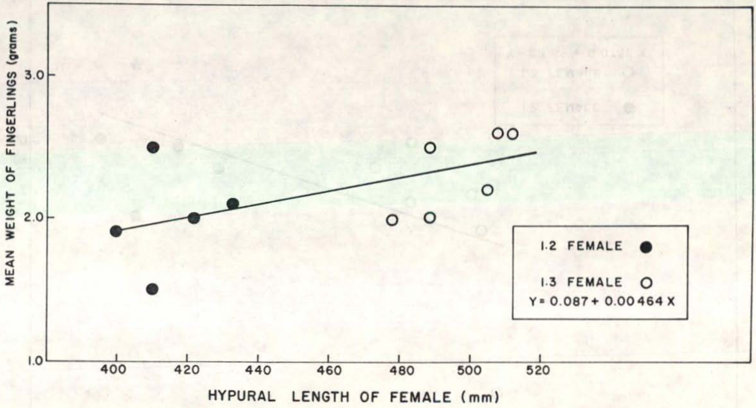

Fig. 7. Mean weight of age 9-month Scully Creek fingerlings, by length and age of female parent, 1964.

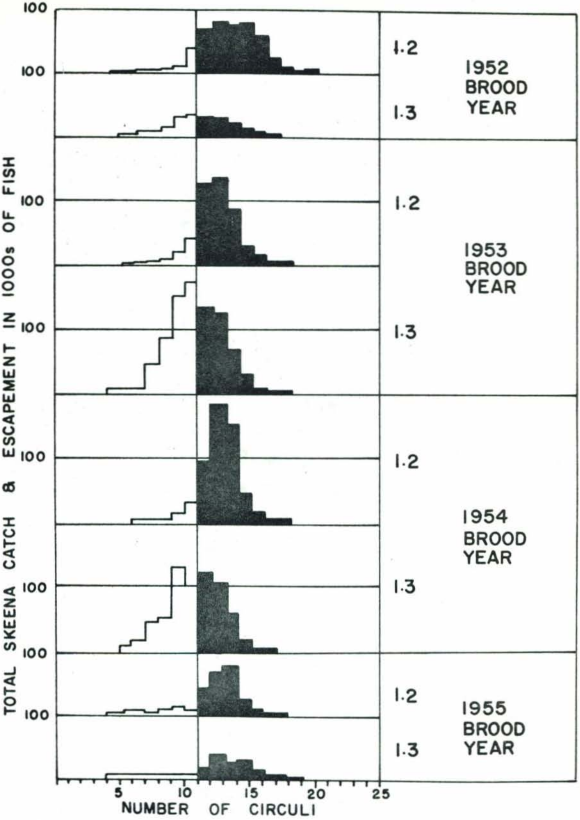

Fig. 8. Number of freshwater circuli on the scales of age-1.2 and /-1.3 sockeye (catch + escapement) from the Skeena River, by brood year, 1952-55. (Shaded areas indicate circuli counts of 11 or more.)

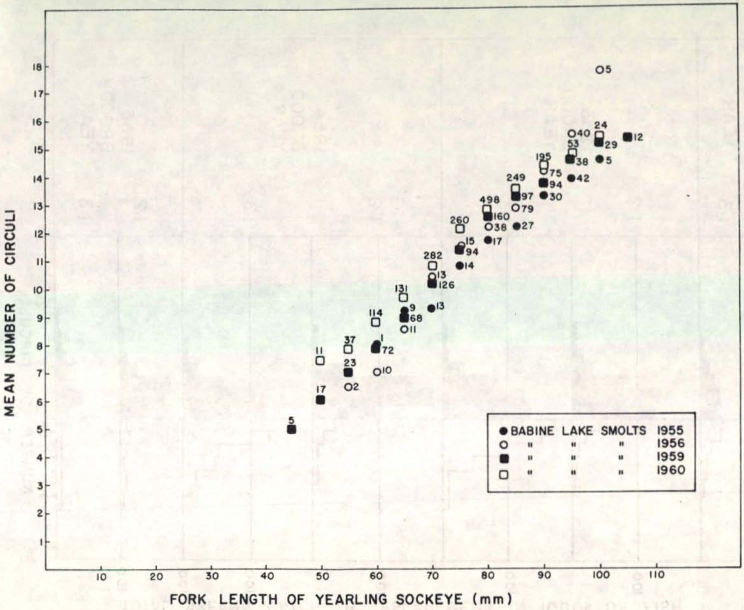

Fig. 9. Mean circuli counts on scales of Babine Lake sockeye smolts by length of fish, 1955-56 and 1959-60. (Numbers indicate sample size.)