A POLYMORPHIC POPULATION OF *ONCORHYNCHUS NERKA* AT BABINE LAKE, B.C. INVOLVING ANADROMOUS (SOCKEYE) AND NON-ANADROMOUS (KOKANEE) FORMS.

by

PETER JAMES McCART

B.A., University of Oregon, 1958

M.Sc., University of British Columbia, 1963

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J. D. McPhail

James D Berger

THE UNIVERSITY OF BRITISH COLUMBIA

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Chairman: Dr. J. D. McPhail

ABSTRACT

The sockeye and kokanee are, respectively, the anadromous and non-anadromous forms of the Pacific salmon species, Oncorhynchus nerka. Both life history types inhabit Babine Lake, British Columbia, a tributary of the Skeena River system. The purpose of this study was to examine the ecology, morphology and behaviour of sockeye and kokanee in the hope that an understanding of these would provide clues to the genetic relationship of the two forms in Babine Lake.

A comparison of the life histories of sockeye and kokanee at Babine Lake revealed a number of differences. At the time they undertake their seaward migration (usually during the spring of their second summer) sockeye smolts have a mean length greater than that of same-age kokanee. Smolts have an approximately equal sex ratio while, among kokanee, males usually exceed females in abundance. As a result of better growth conditions in the ocean, sockeye, at maturity, are much larger than kokanee. Related to this basic difference in size are differences in fecundity, egg size and testis weight in each of which sockeye exceed kokanee. Laboratory experiments revealed that, regardless of the male parent, progeny of the larger sockeye eggs had an initial size advantage over the progeny of kokanee eggs which they maintained through July of their first year. There was no conclusive evidence of differential mortality to hybrid embryos.

There are differences between sockeye and kokanee in two meristic characters: number of lateral line scales and number of vertebrae. In both instances, mean values for sockeye exceed those for kokanee. It is suggested that this difference may not be genetic in origin but rather the result of differences in the amount of yolk incorporated in eggs. The two forms did not differ in gill-raker count.

Electrophoretic examination of haemoglobins and muscle myogens revealed no differences between Babine Lake sockeye and kokanee.

A detailed examination of the reproductive behaviour of sockeye and kokanee revealed that they spawn sympatrically in a group of streams known as the "early streams." These are small streams which experience considerable fluctuation in water levels and spawning suitability from year to year. Sockeye and kokanee in the early streams overlap almost completely in their spawning season and in their distribution on the spawning grounds. Evidence is presented that hybridization does occur under natural conditions.

A study of the homing performance of mature sockeye and kokanee displaced from early streams indicates that they are less likely to home than are sockeye displaced from Pinkut Creek, a large, stable stream in the same area. It is suggested that a reduced homing tendency might be an adaptation to the unstable nature of the early streams. Fish homing to an early stream to which access is blocked, either by low water or by an obstruction, have the alternative of entering other, nearby streams of similar type.

The hypothesis which most readily encompasses the available information is that the sockeye and kokanee in the early streams at Babine Lake are part of the same polymorphic population. This polymorphism is presumably maintained by a balance of contending advantages and disadvantages. Kokanee suffer the major disadvantage of smaller size resulting in reduced fecundity, smaller egg size and, probably, reduced spawning success. However, it would appear that they persist in the early streams because they are able to utilize spawning grounds which are unavailable to sockeye under low water conditions. The existence of such a sockeye/kokanee polymorphism and the reduced tendency to home are both thought to be genetically regulated adaptations which enable the early stream populations of O. nerka to maximize their utilization of the available spawning grounds in the face of extreme fluctuations in the suitability of spawning streams.

The hereditary mechanism which would regulate such a sockeye/kokanee polymorphism is not known. Possibly a super-gene is involved. Whatever the mechanism, it would appear that factors other than genotype can influence the tendency to smolt: females are more likely to smolt than males; larger and/or faster growing fish are more likely to smolt than smaller, slower growing fish; immature fish are more likely to smolt than those in which maturation processes have already begun.

The applicability of the polymorphism hypothesis to sockeye and kokanee populations in other areas is discussed.

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GENERAL INTRODUCTION

The sockeye and kokanee are, respectively, the anadromous and non-anadromous forms of the Pacific salmon species, Oncorhynchus nerka. Both life history types inhabit Babine Lake, British Columbia, a tributary of the Skeena River System.

After emerging from the spawning gravels, sockeye at Babine spend a year (occasionally more) in the freshwater of the lake before migrating seaward in the spring. In the ocean they grow rapidly. On their return as mature fish, usually in their fourth or fifth year, they are subject to a gillnet fishery at the mouth of the Skeena River. This fishery is an important part of the economy of the area. Approximately half the total run is taken in the fishery, the remainder (averaging about 470,000 fish in recent years) escape to continue the journey to the spawning grounds.

Kokanee, unlike sockeye, do not undertake a seaward migration and mature entirely in freshwater. Their growth rate is slower than that of sockeye and when mature they are much smaller. Their small size renders them commercially unutilizable and, though subject to a small sport fishery, they are of little economic significance. Most Babine Lake kokanee spawn in their fourth year, many of them in streams which, additionally, provide spawning grounds for populations of sockeye.

In some years kokanee are extremely abundant and the total number of spawners can exceed one million fish (Johnson, 1958). In such years they constitute a large proportion of the total population of O. nerka spawning at Babine Lake, particularly in the Main Lake area where kokanee are concentrated The presence of such large numbers of kokanee may have sizable effects on the production of the more economically important sockeye. Obviously, essential to a rational management of the Babine Lake sockeye populations, is some indication of the systematic relationship of the two forms. Do they constitute distinct, non-interbreeding populations or are they simply alternative life-history types arising within single populations? If the latter, what factors determine whether an individual fish will migrate seaward or remain in freshwater? The purpose of this study was to examine the ecology, morphology and behaviour of sockeye and kokanee at Babine Lake in the hope that an understanding of these would provide clues to the genetic relationship of the two forms. The emphasis has been on field observation and experimentation rather than laboratory work: first, because, with its long life history, *O. nerka* is a difficult experimental animal and second, because meaningful laboratory experimentation should be based on a thorough understanding of the animal in its natur setting. Hopefully, a study of this kind will result in an hypothesis which can serve as the basis for subsequent experimentation under controlled, laboratory conditions.

SECTION I

COMPARISON OF THE LIFE HISTORIES OF SOCKEYE SALMON AND KOKANEE AT BABINE LAKE, B. C.

INTRODUCTION

A comparison was made of those aspects of the life history of sockeye and kokanee which appeared to be pertinent to the problem of their relationships at Babine Lake.

The data come from a variety of sources: some have been previously published; some are the unpublished work of personnel of the Fisheries Research Board of Canada and the Resource Development Branch of the Department of Fisheries of Canada; some are the original work of the author.

Because of the diverse nature of the material, I have not included a separate Materials and Methods section. Most of the techniques are standard and have been the subject of previous publication to which reference is made. Where the methods are unusual, they are described along with the results.

RESULTS

Distribution of sockeye and kokanee resident in Babine Lake

Underyearling sockeye

Johnson (1958) found that the densest populations of underyearling sockeye salmon occur in the North Arm - Nilkitkwa Lake region of Babine Lake, adjacent to the large Babine River spawning grounds. During the eight-year period (brood years 1955 to 1962) August fingerling densities in this area of the lake averaged 2,750 fish per acre (Table I). Fingerling densities

TABLE I. Comparison of the density, weight and survival to smolt stage of sock eye progeny from the North Arm-Nilkitkwa (N.N.) and Main Lake (M.L.) regions of Babine Lake, 1955-1962.
Data supplied by W. E. Johnson (personal communication).

		August Fingerlings		October Fingerlings	Smolts Produced		
Class	Region	Est. No. (Mill)	Density (No./acre)	Mean Weight (g)	Est. No. (Mill)	Per cent Survival (From Aug.)	Mean Weigh (g)
1955	N.N.	1.9	132	4.0	-	-	-
	M.L.	10.9	105	4.0	5.2	47.7	6.0
1956	N.N.	29.7	2063	3.4	14.4	48.5	4.9
	M.L.	70.1	674	4.0	8.4	12.0	5.7
1957	N.N.	42.2	2931	2.3	9.0	21.3	4.1
	M.L.	67.4	648	3.7	24.9	36.9	5.1
1958	N.N.	83.3	5785	2.6	26.0	31.2	4.5
	M.L.	105.6	1015	3.5	31.1	29.5	5.9
1959	N.N.	37.2	2583	2.9	7.5	20.2	4.0
	M.L.	57.9	557	3.6	13.3	23.0	5.1
1960	N.N.	22.8	1583	2.8	4.7	20.6	5.6
	M.L.	38.8	373	3.4	12.4	32.0	5.7
1961	N.N.	51.5	4576	2.3	7.5	14.6	4.3
	M.L.	37.4	360	3.7	6.8	18.2	5.4
1962	N.N.	47.5	3299	2.6	-	-	-
	M.L.	52.1	501	2.8	-	-	-
Means	N.N.	39.6	2750	2.9	11.5	25.9	4.6
	M.L.	57.1	549	3.6	14.6	26.4	5.6

in the Main Lake area were much lower, averaging 549 per acre during the same period, only 20 per cent of those in the North Arm - Nilkitkwa region. However, because it encompasses a much larger area (88 per cent of the total lake surface area of 120,000 acres) the absolute number of sockeye fingerlings and resultant smolts in the Main Lake region usually exceeds that in the North Arm - Nilkitkwa region (the 1961 year class was an exception).

TABLE II . Catches of kokanee in standard gillnet sets in the North Arm - Nilkitkwa and Main Lake regions of Babine Lake. Data for 1946 from F. C. Withler (personal communication). Data for 1958 courtesy of W. E. Johnson (personal communication).

	1946		1958	
	No. of Sets	Catch/ Set	No. of Sets	Catch/ Set
North Arm - Nilkitkwa	155	0.06	6	4.0
Main Lake	365	0.52	14	40.5

Kokanee

Standardized gillnet sets made during 1946 and 1958 suggest that the distribution of kokanee is the reverse of that of underyearling sockeye (Table II). Comparisons between the two years are not possible because of differences in nets and in techniques but within years, the differences in catch between the two major regions of the lake are of the same order of magnitude. Main Lake catches exceed North Arm - Nilkitkwa catches by 8.7 times in 1946 and 10.1 times in 1958. The ages of these kokanee are not known but the mesh sizes used (minimum 3.8 cm stretch mesh) suggest that most would have been age II or older. The distribution of underyearling kokanee is not known.

There is some indication that, prior to spawning, large numbers of kokanee leave the North Arm and move into the Main Lake (C. Groot, personal communication). These presumably spawn in streams flowing into the Main Lake.

Distribution of sockeye and kokanee in spawning streams

Sockeye

The Babine Lake drainage, exclusive of the Morrison system, has an average annual spawning escapement of 469,000 sockeye salmon. Approximately 19 per cent of these are thought to spawn in the lake itself, the remainder spawn in various streams. There are four large and about fifteen smaller spawning streams in the North Arm - Nilkitkwa and Main Lake areas of Babine Lake (Table III and Fig. 1). Their physical characteristics are given by Brett (1952).

The smaller streams are termed the "early streams" because the sockeye entering them spawn earlier in the season than those utilizing the four larger streams. They have a number of characteristics in common. Along with small size, they have limited drainage basins and, as a result, water flows and spawning suitability are highly variable.

Three types of early streams can be distinguished.

Type 1: Streams in which there is almost always sufficient water for fish to enter although there are occasional partial mortalities to spawning fish due to low water levels resulting in high water temperatures and low oxygen levels. Streams in this category include Pierre, Twain, Four Mile, and Shass Creeks.

Type 2: Streams which are normally accessible to spawning salmon but are dry during years of low rainfall (e.g., 1952, 1956, 1961). This category

TABLE III. Numbers of sockeye and kokanee spawning in streams at Babine Lake, 1964 to 1967. Dash indicates no estimates available but numbers small.

Stream	1964		1965		1966		1967		4 Year Average	
	Sockeye	Kokanee	Sockeye	Kokanee	Sockeye	Kokanee	Sockeye	Kokanee	Sockeye	Kokanee
L. Babine	46,000	200	176,000	a few	113,900	0	54,000	--	97,475	< 100
U. Babine	222,000	--	120,000	--	69,000	--	133,000	--	136,000	< 100
Five Mile	50	0	150	0	150	15	100	200	112	54
Nine Mile	1,500	2	500	0	600	100	1,000	500	800	150
Fulton	120,500	--	141,300	--	90,000	200	136,500	--	122,075	<500
Tachek	3,000	7,000	700	3,000	150	2,000	900	17,000	1,187	7,250
Sockeye	2,000	2,000	50	0	900	7,000	600	1,000	887	2,500
Kew	0	100	dry		2	350	0	150	<1	150
Pierre	22,000	5,000	10,000	5,000	8,000	10,000	32,000	30,000	18,000	12,500
Twain	9,000	12,000	3,000	5,000	3,500	16,000	9,000	10,000	6,125	10,750
Cross	1,350	1,300	dry		dry		dry		337	325
Donalds	800	1,000	dry		dry		dry		200	250
Pinkut	146,000	--	34,000	a few	30,000	250	33,400	--	60,850	<200
Gullwing	1,500	800	100	70	200	400	1,000	100	700	342
Four Mile	2,500	1,900	1,400	4,400	1,600	3,400	3,600	2,800	2,275	3,125
Shass	8,000	3,000	5,000	30	3,500	5,000	2,600	2,000	4,775	2,507
TOTAL	586,200	34,302	492,200	17,500	321,502	44,715	407,700	63,750	451,799	40,800

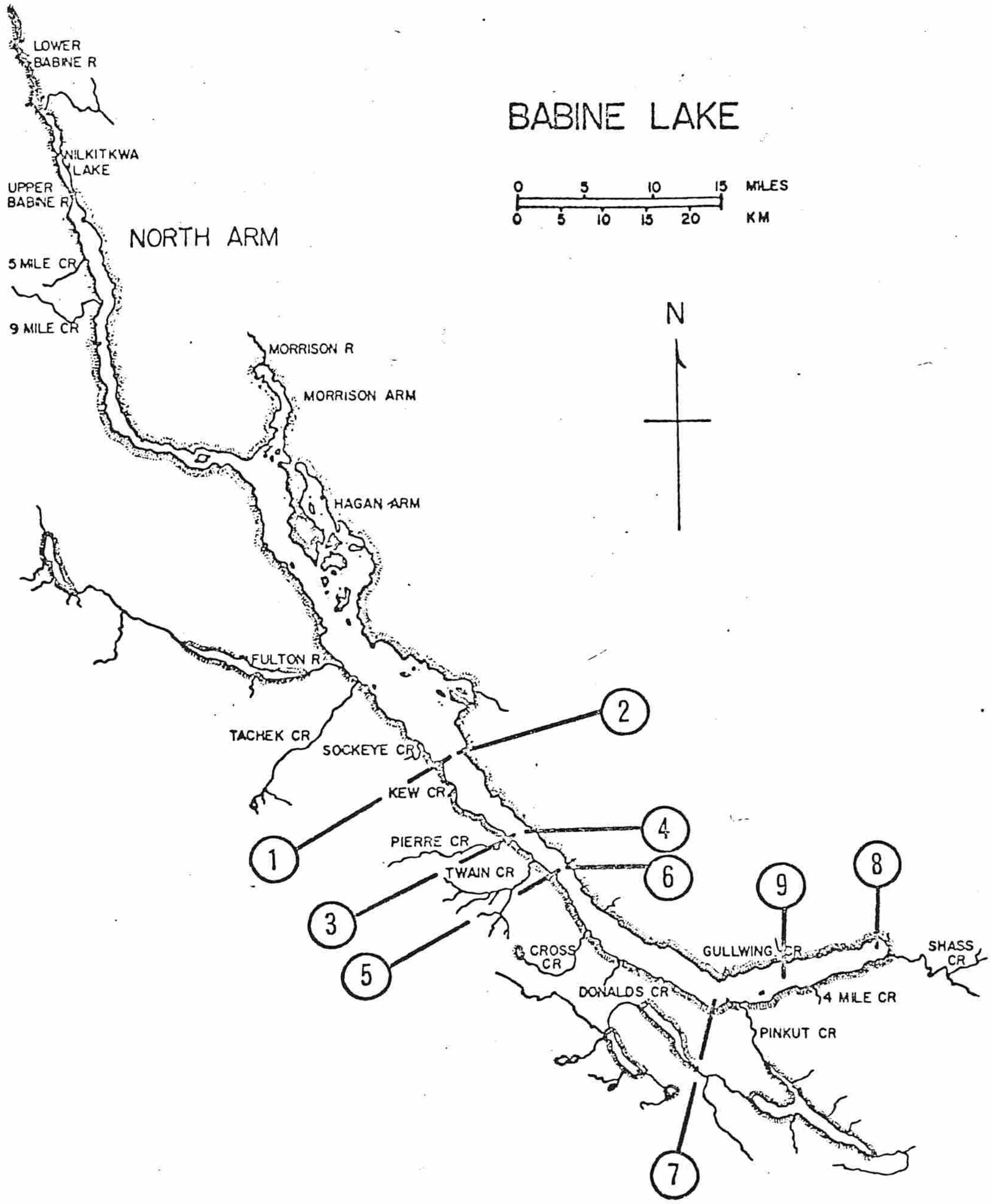

Figure 1. Map of Babine Lake showing locations of sockeye and kokanee spawning streams. Circled numbers indicate position of homing experiment release sites.

includes Five Mile, Nine Mile, Tachek, Sockeye and Gullwing Creeks.

Type 3: Streams which are normally dry during the spawning season but which are utilized by sockeye during years of high rainfall (e.g., 1953, 1954, 1959, 1964). Included are Kew, Forks, Pendleton and Donald's Creeks.

Table IV summarizes the success of sockeye spawning in Main Lake streams over 20 recent years (1948 to 1967).

The early streams are heavily shaded and have little or no drainage from lakes, marshes, beaver dams or other sources of warm water. As a result, when flows are normal, water temperatures seldom exceed 15° C, even during the warmest months of the year. Each of the early streams was visited a number of times during August 1 to September 25, 1966. Water temperatures recorded during these visits ranged from 5.2 to 15.0° C. During August, when spawning was at its height, temperatures were usually between 10.0 and 13.0° C. Miscellaneous observations made over a number of years, during the course of spawning ground surveys, suggest that these temperatures are typical of the spawning period.

Sockeye salmon bound for the early streams pass through the counting fence (weir) on the Lower Babine River during late July and early August (Fig. 2). They are already in an advanced state of maturity and many of them have assumed the red and olive-green colouration of spawning fish. These fish move rapidly uplake and enter the spawning streams with little delay. Some may enter streams as much as 160 km away within five days. Spawning normally peaks during the second or third week of August and is complete by the first week in September. There is some variation in this general pattern, however. In some early streams, notably Pierre and Four Mile Creeks, numbers of fish may enter during the first half of September when the earlier, larger population has nearly completed spawning. The sig-

TABLE IV . Summary of spawning success of sockeye salmon in early streams at Babine Lake (1948-1967). Data from Smith and Lucop (1966) and the author's field notes. For further explanation, see text.

Stream	NUMBER OF YEARS				Stream Type
	Stream Dry	Partial Mortality	Normal Spawning	Total	
Five Mile	6	2	12	20	2
Nine Mile	2	1	17	20	2
Tachek	3	1	16	20	2
Wright	19	0	1	20	3
Sockeye	3	1	16	20	2
Kew	7	0	4	11*	3
Pierre	0	1	19	20	1
Twain	0	1	19	20	1
Cross	10	0	10	20	3
Donald's	17	0	3	20	3
Gullwing	3	1	16	20	2
Four Mile	0	2	18	20	1
Telzato	18	0	2	20	3
Shass	0	1	19	20	1

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* No data for Kew Creek for 9 of the 20 years.

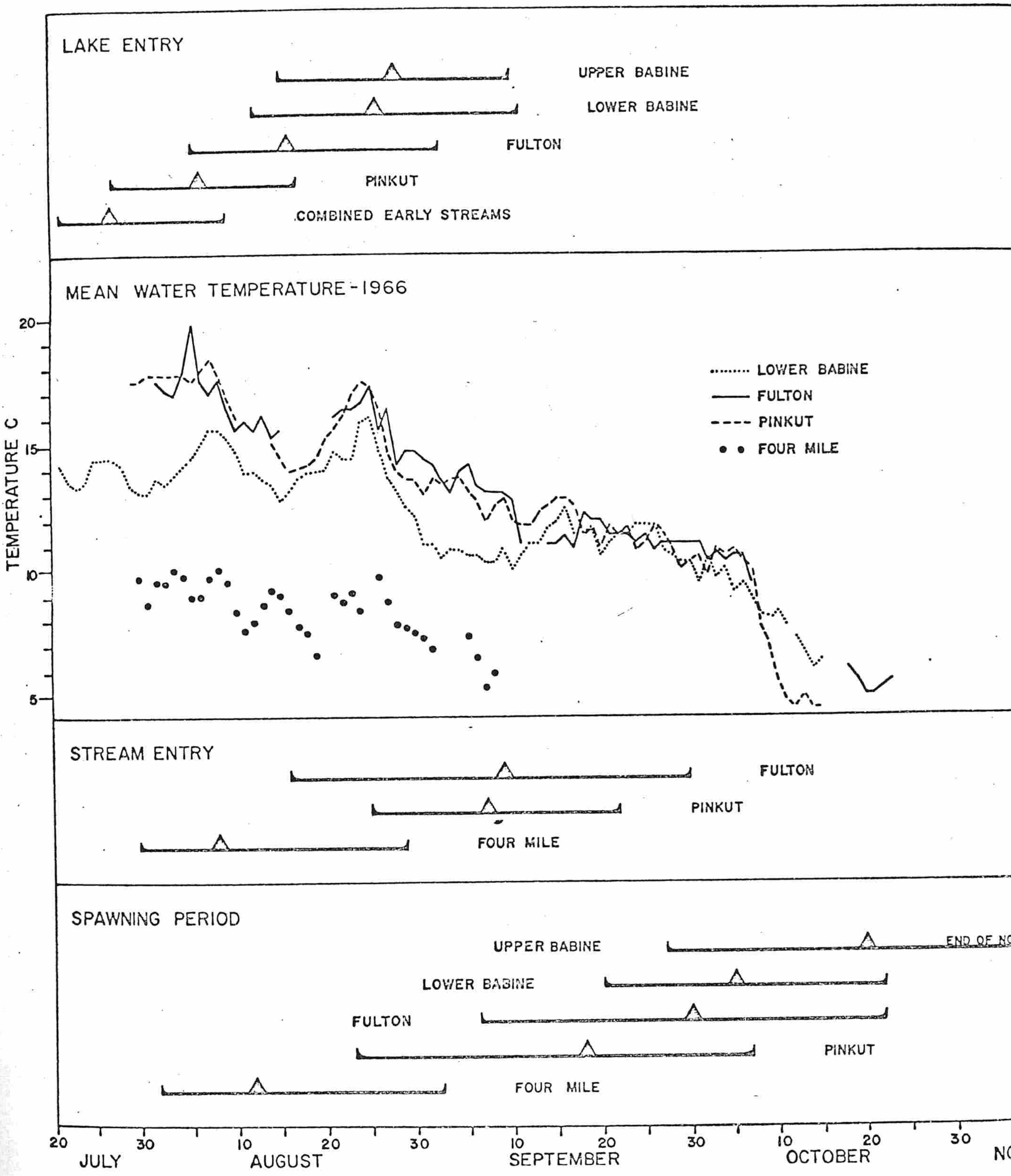


Figure 2. Seasonal periodicity of lake entry, spawning stream entry and spawning for various Babine Lake sockeye populations. Also shown is mean water temperat of various spawning streams in 1966.

nificance of these subsidiary runs is not yet clear but some of the fish may be strays from the larger streams in which the fish spawn later.

From 1949 to 1966, sockeye spawning in early streams constituted between 11 and 12 per cent of the total run (Table III). Pierre Creek had the largest spawning population, nearly half of all the sockeye spawning in early streams.

The larger spawning streams are lake-fed. Pinkut Creek and the Fulton River drain chains of lakes, the Upper and Lower Babine Rivers drain Babine and Nilkitkwa Lakes respectively. They are larger and more stable than the early streams and are always accessible to spawning salmon. Because of the lake drainage, water temperatures during the summer are higher than those in the early streams and do not fall to equivalent temperature levels until late September or early October (Fig. 2).

Most sockeye bound for the larger streams move through the Lower Babine River weir during August-September, after the runs to early streams have passed. At the fence, they are less mature than early run fish and most undergo a maturation period of several weeks before they enter streams and spawn. Spawning activity reaches a maximum during the latter half of September (Pinkut and Fulton) or during October (the Upper and Lower Babine Rivers). An interesting variation of the general pattern is that, in some years, small runs of up to 200 mature sockeye (and some kokanee) enter both Pinkut Creek and the Fulton River during early August when large runs are entering the neighbouring early streams. Some or all of these early fish may be strays from the latter.

The runs entering Pinkut Creek, the Fulton River and the Upper and Lower Babine Rivers are the largest in the Babine system (Table III). Together they constitute about 89 per cent of the total stream spawning population of the North Arm - Nilkitkwa and Main Lake areas.

Kokanee

Although kokanee have, on occasion, been observed spawning in all the streams utilized by sockeye (including the Lower Babine River, K. V. Aro, personal communication), it is only in the early streams flowing into the Main Lake area that kokanee constitute more than a small proportion of the spawning population of the species. All the important kokanee spawning localities listed by Johnson (1958) are Main Lake early streams. This author's estimates of the numbers of kokanee spawning in various streams between 1964 and 1967 (Table III) reveal a similar distribution. During these years, approximately 96 per cent of the kokanee enumerated spawned in only six streams (in order of decreasing population size, Pierre, Twain, Tachek, Four Mile, Shass and Sockeye Creeks) - all Main Lake early streams. About eleven per cent of the sockeye enumerated during these years spawned in the same six streams. Between 1949 and 1963, 24.5 per cent of Main Lake sockeye spawned in early streams.

Incidental observations by the author and others indicate that, regardless of location, kokanee spawn late in July or in August. Thus, the few kokanee that spawn in the four large Babine streams precede the main runs of sockeye by four to eight weeks. It may be, as suggested for the subsidiary early runs of sockeye into these streams, that such kokanee are strays from early streams.

Growth of sockeye and kokanee in Babine Lake

Growth during first year

Approximately 99 per cent of the sockeye smolts leaving Babine Lake are age I. They have spent one full summer in the lake and migrate to the ocean during May or June of their second year. Age II smolts and, very rarely, older individuals make up the remaining one per cent (Dombroski, 1954). Smolts leave the lake in two distinct surges, an early run composed almost entirely of fish from the North Arm - Nilkitkwa area (that nearest the outlet) and a later run of predominantly Main Lake fish (Groot,1967).

The mean length of age I late-run smolts sampled during 1966 and 1967 at the lake outlet exceeded that of same-age fish still resident in the Main Lake, by 8.9 mm in 1966 and 4.6 mm in 1967 (Table V). The latter were sampled by purse seine. In 1966 the purse seine samples were obtained during the latter half of June when the late smolt run was virtually over, ensuring that few if any smolts were included. In 1967, there was considerable overlap in the sampling dates for smolts and Main Lake residents. However, it is likely that few smolts of the year were included in the Main Lake purse seine samples. The smolt run begins almost simultaneously in all parts of Babine Lake (Groot, 1967). Thus, those areas farthest from the outlet will be cleared of smolts when large numbers are still passing through areas nearer the lake outlet. The 1967 samples were taken so that the areas farthest from the outlet were sampled first. In view of the distance from the outlet (approximately 90 km for the most distant sampling areas) and the known rate of travel of migrating smolts (approximately 7.4 km per day, Johnson and Groot, 1963) it is unlikely that many of the fish sampled by purse seine would have left the lake that year.

The non-migrant fish sampled in the Main Lake are probably a mixture of fish which will leave the lake the following year as age II smolts and fish which will eventually mature as kokanee. If, as seems likely, kokanee constitute a majority of these non-migrant yearlings, the data suggest that at the end of their first year of life, kokanee are smaller than sockeye. Evidence from scale studies supports this conclusion.

TABLE V. Comparison of the fork lengths of late run, yearling smolts sampled at traps near the Lower Babine River (data courtesy of H. Smith) and same-age fish purse seined in the Main Lake area (data courtesy J. MacDonald).

1966	Sampling Dates	N	Mean Length (mm)	Standard Deviation	t
Migrants	May 18 - June 12	500	76.2	6.5	18.1**
Non-Migrants	June 15 - June 30	379	67.3	8.1	
1967					
Migrants	June 1 - June 16	400	79.2	6.7	9.2**
Non-Migrants	June 5 - June 23	403	74.6	7.5	

** Means differ at 1% level of significance.

Detailed studies of the scales of sockeye salmon (e.g., Andrew and Geen, 1960) have shown that various scale characters can be used as an indirect measure of growth. There is a positive relationship between fish length and such characters as number of circuli and scale diameter. The age I non-migrants sampled in the Main Lake June 15 to June 30, 1966 had significantly fewer circuli on their scales than did smolts sampled previously during the late run (Table VI). It has already been shown that these non-migrants tended to be smaller than smolts (Table V).

Comparisons, within year classes, of sockeye and kokanee from the Main Lake area indicate that, during their first year of life (i.e., within the first annulus), kokanee tend to form fewer circuli than sockeye. In 1965, the scale characteristics of three age groups sockeye and kokanee spawning in Four Mile Creek were compared. In every instance, the kokanee scales were smaller, containing fewer circuli at the formation of the first annulus (Fig. 3). Further comparisons of the number of circuli in the first annulus of Main Lake sockeye and kokanee (Fig. 4), give comparable results. These data suggest that kokanee are distinctly smaller than sockeye at the time of annulus formation, the end of their first summer growth period. This conclusion rests on the assumption that sockeye and kokanee have similar circulus number--body length relationships. This assumption cannot, as yet, be satisfied for natural populations.

TABLE VI. Comparison of the total number of circuli on the scales of: (a) late-run, age I migrants captured at the lake outlet, May 16 to June 14, 1966, and (b) non-migratory fish of the same year-class seined in the Main Lake, June 15 to June 30, 1966. Migrant data weighted by daily abundance.

Group	N	Mean Number of Circuli	Range	Standard Deviation	t
Migrants	499	12.55	6-18	1.66	5.08**
Non-Migrants	56	10.64	6-15	2.48	

** Means differ at 1% level of significance.

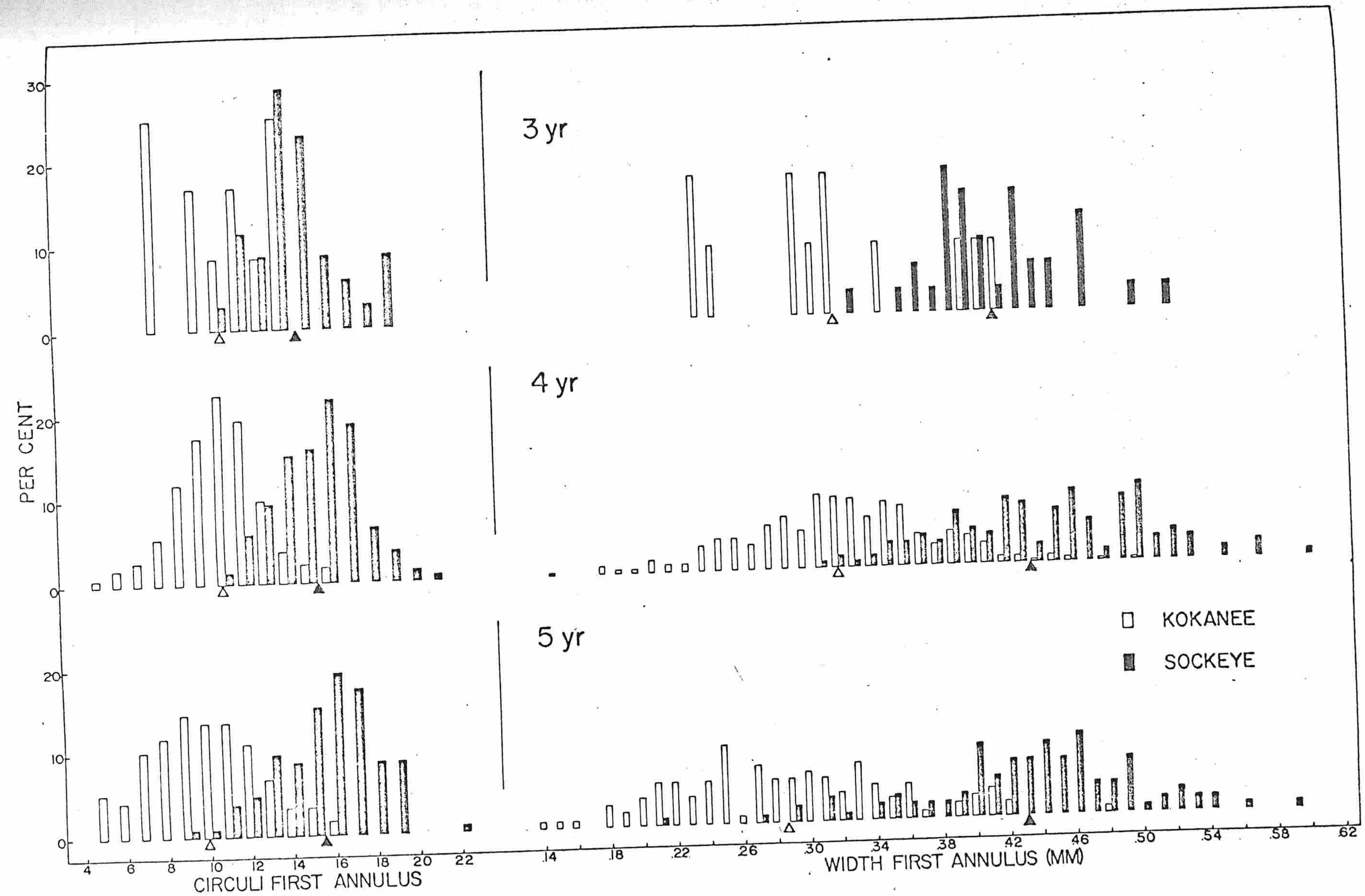


Figure 3. Comparison of a) the number of circuli within the first annulus, and b) the width of the first annulus, of samples of sockeye (black bar) and kokanee (open bar) taken from Four Mile Creek in 1965. Triangles indicate the mean counts for each group. Sample sizes are: age 3, 12 kokanee and 35 sockeye; age 4, 406 kokanee and 139 sockeye, and age 5, 117 kokanee and 103 sockeye.

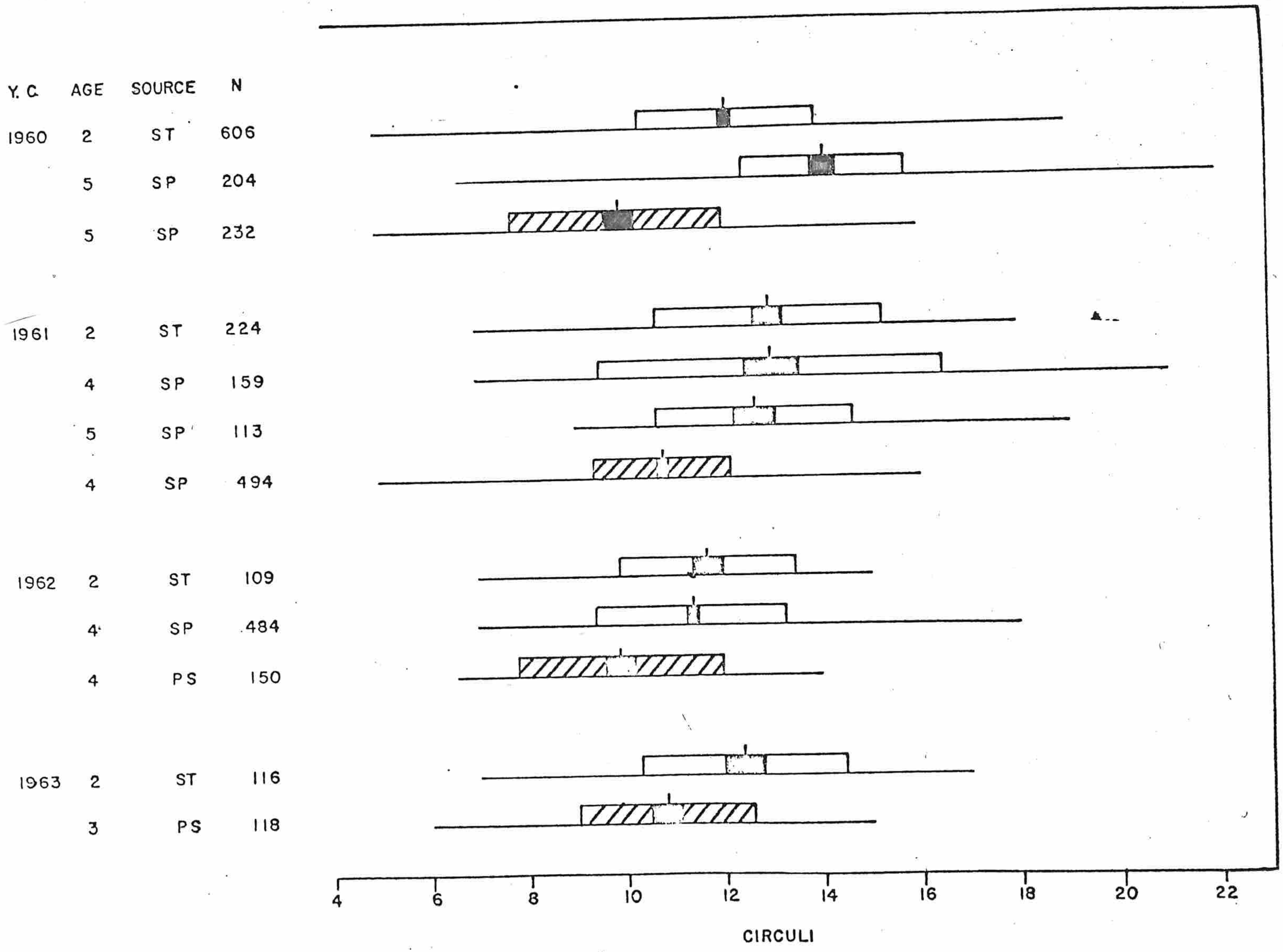


Figure 4. Comparison of the number of circuli within the first annulus of sockeye (open bar) and kokanee (cross-hatched bar) from Babine Lake. Includes year class (Y.C.), age at sampling, source (ST, Lower Babine River smolt trap; SP, spawning streams; PS, in open water by purse seine) and size of sample. Vertical stroke is the mean; black bar is four standard errors of the mean; black bar plus open or cross-hatched bar on either side of mean is one standard deviation; horizontal line is range.

Comparison of the early growth and survival of laboratory raised progeny of sockeye and kokanee

Several groups of sockeye and kokanee from Babine Lake have been raised simultaneously under laboratory conditions. These were of various types: Sockeye males were used to fertilize the eggs of both sockeye and kokanee females to produce, respectively S x S and S x K progeny (in each combination, the identity of the male parent precedes that of the female). Kokanee males were used to produce K x S and K x K progeny. In each case, several male and female parents were used to produce each group.

In 1964, S x S and K x K progeny were obtained from Pierre Creek. Immediately after being artificially spawned and fertilized the eggs were flown to the Lakelse Lake Hatchery near Terrace, B. C. They remained at the hatchery until eyed and then flown to the Biological Station at Nanaimo, B. C. The conditions under which they were raised have been previously described (McCart and Andersen, 1967).

In 1965, four kinds of progeny were produced at Four Mile Creek and flown to the Lakelse Hatchery. Some of the S x S and K x K were transferred to the Biological Station at the eyed stage. Some of each of the four types remained at Lakelse. In 1966, four kinds of progeny were again produced at Four Mile Creek. These were eyed at Lakelse and then transferred to the Biological Station.

There are indications of a difference in the rate of development of alevins developing from sockeye eggs and those developing from kokanee eggs. Comments on hatchery records suggest there was no apparent difference in the hatching dates of the S x S and K x K groups. However, it was noted that K x K alevins "buttoned-up" (absorbed the yolk-sac within the body wall) a week or more before S x S alevins. Hatching of the 1965 experimental groups took place between October 22 and November 1. By the latter date, 74% of the S x S, 79% of the K x S and over 99% of both the S x K and K x K groups were hatched. This suggests a slight difference in the hatching times of sockeye and kokanee eggs. As in 1964, there was a definite difference between kokanee and sockeye eggs in the time to buttoning-up. Fifty per cent of the former had buttoned-up by January 7, 1966 but 50% of the latter were not buttoned-up until January 10. The identity of the male parent seemed to have no effect on either hatching or buttoning-up times.

The difference in the size of eggs produced by sockeye and kokanee will be discussed below. The evidence suggests that the progeny of female sockeye maintain the size advantage originally conferred by large egg size through at least the first six months after buttoning-up. The 1964 and 1965 S x S groups maintained, through July, a length and weight advantage over K x K groups raised under similar conditions (Table VII).

Comparisons of the growth in length of four kinds of fry (Fig. 5) suggest that the identity of the male parent has little influence on early growth. Through July, there was no consistent difference between S x S and K x S progeny or between S x K and K x K progeny.

There is some preliminary information available describing the early mortality of the progeny of sockeye and kokanee and their reciprocal crosses (Table VIII). There was an initial mortality to each of the four groups which was primarily due to the presence of unfertilized eggs. Over 95% of samples of dead eggs examined between August 23 and October 22 were unfertilized (N = 78 S x S, 136 K x S, 96 S x K and 2900 K x K). The per cent mortality to crosses involving kokanee eggs was very high. This is thought to be due to difficulty in identifying the state of maturity of female kokanee, a diffi-

TABLE VII. Comparison of the mean standard lengths and weights of the progeny of sockeye (S x S) and kokanee (K x K) reared at the Nanaimo Biological Station (1964/65) and at the Lakelse Lake Hatchery (1965/66).

Date	N Sockeye	N Kokanee	Mean Length (mm) Sockeye	Mean Length (mm) Kokanee	t	Mean Weight (g) Sockeye	Mean Weight (g) Kokanee	t
1964/65								
Dec. 14	109	116	19.0	17.2	14.2**	.09	.06	27.0**
Apr. 16	50	50	23.3	21.3	10.1**	.11	.07	16.4**
May 30	96	138	22.4	20.8	12.5**	.09	.06	15.6**
June 7	101	102	22.8	21.2	10.2**	.09	.07	6.4**
June 14	97	100	23.8	22.1	7.2**	.11	.09	3.9**
June 21	101	100	24.4	23.6	2.3*	.13	.12	1.7
July 7	205	206	30.3	27.9	6.5**	.25	.21	3.6**
1965/66								
Nov. 3	74	75	19.2	17.9	9.9**	.11	.07	27.5**
Jan. 12	75	74	25.2	21.1	30.2**	.13	.09	21.1**
Jan. 24	25	23	25.3	22.3	13.2**	.13	.08	18.2**
Feb. 15	10	11	25.5	22.1	8.7**	.15	.09	8.3**
Feb. 24	25	25	26.4	22.8	13.9**	.16	.10	12.3**
Mar. 17	10	10	27.6	24.3	6.3**	.21	.13	5.7**
Mar. 28	25	25	28.1	24.8	6.9**	.23	.16	5.9**
Apr. 28	25	25	31.3	28.6	3.5**	.32	.25	2.3**
May 24	25	25	32.2	30.2	2.7**	.33	.27	1.6
July 14	100	100	48.6	41.0	5.9**	1.48	.90	5.8**

---

* means differ at 5% level of significance

** means differ at 1% level of significance

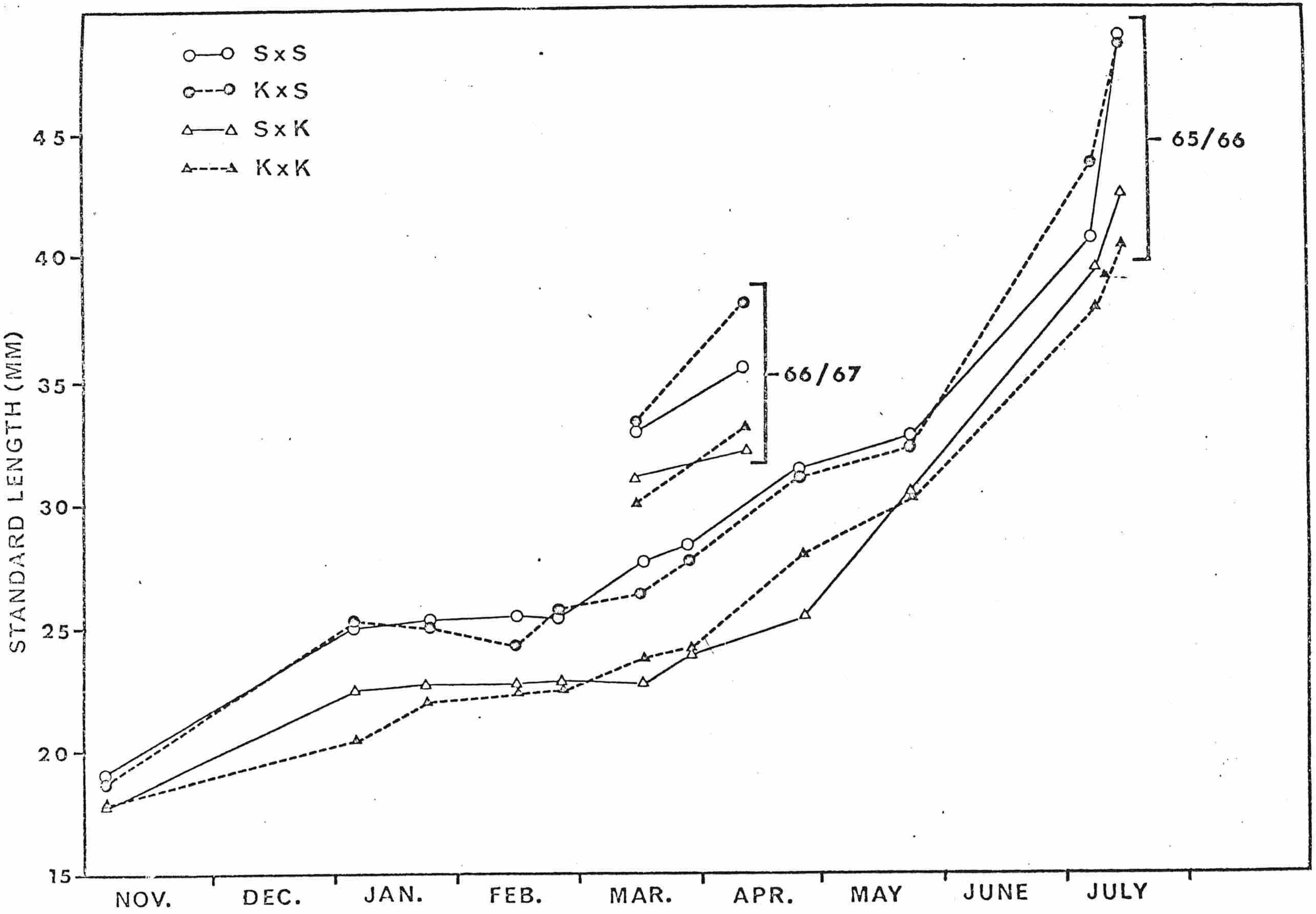


Figure 5. Growth in length of four groups of fry with sockeye (S) and kokanee (K) parents. Identity of male parent preceeds that of female. The 1965/66 groups were raised at the Lakelse Lake (B.C.) hatchery. The 1966/67 groups were eyed at Lakelse then raised at the Biological Station, Nanaimo.

TABLE VIII. Early mortality of laboratory-raised progeny of sockeye and kokanee from Four Mile Creek, Babine Lake, 1965-1966. Chi-squares calculated from original data.

	IDENTITY OF GROUP			
	S x S	K x S	S x K	K x K
	Prehatching mortality - August 23 to October 22			
Original N	3211	3909	2947	4118
% mortality	27.2	11.7	63.3	70.7
Chi-square	225.8**		13.9**	
	Hatching to button-up - October 23 to January 13			
Original N	2246	3379	1128	1105
% mortality	0.4	0.5	1.2	3.0
Chi-square	0.9		8.0**	
	Aquarium - January 13 to April 30			
Original N	2131	2724	851	992
% mortality	4.7	3.8	34.9[1]	8.0
Chi-square	2.0		161.4**	
	Aquarium - May 1 to July 13			
Original N	915	515	295	376
% mortality	18.7	41.9[1]	24.0	15.7
Chi-square	66.5**		6.1*	

---

[1] mortality due primarily to disease.

* differ at 5% level of significance.

** differ at 1% level of significance.

culty experienced in several years. Females which appeared to be ripe produced a high proportion of unfertilized, green eggs. Possibly kokanee eggs ripen in groups within the ovary rather than nearly simultaneously as sockeye eggs appear to do.

The experiment was not replicated and no stringent conclusions about differential mortality to hybrid groups (K x S and S x K) can be drawn. However, mortalities to hybrid groups did not consistently exceed those of non-hybrids developing from similar eggs. Certainly hybrids did not suffer any catastrophic mortality.

Size at maturity

From the spring of their second year until they mature, sockeye and kokanee live very different lives. Sockeye spend one to three years in a rich marine environment and when they return to the lake to spawn they are considerably larger than the more slowly growing kokanee.

In 1965, a comparison was made of the age-length relationships of sockeye and kokanee at Four Mile Creek (Fig. 6). There was no overlap in the length-frequency distributions of the two forms. The largest four and five year old kokanee were 21 cm and the smallest three year old male (jack) sockeye, 24 cm in hypural length. Hypural length measurements (distance from posterior edge of eye socket to posterior edge of hypural plate) were used to obviate discrepancies due to sexual dimorphism and to the wearing of body tissues as a result of spawning activity.

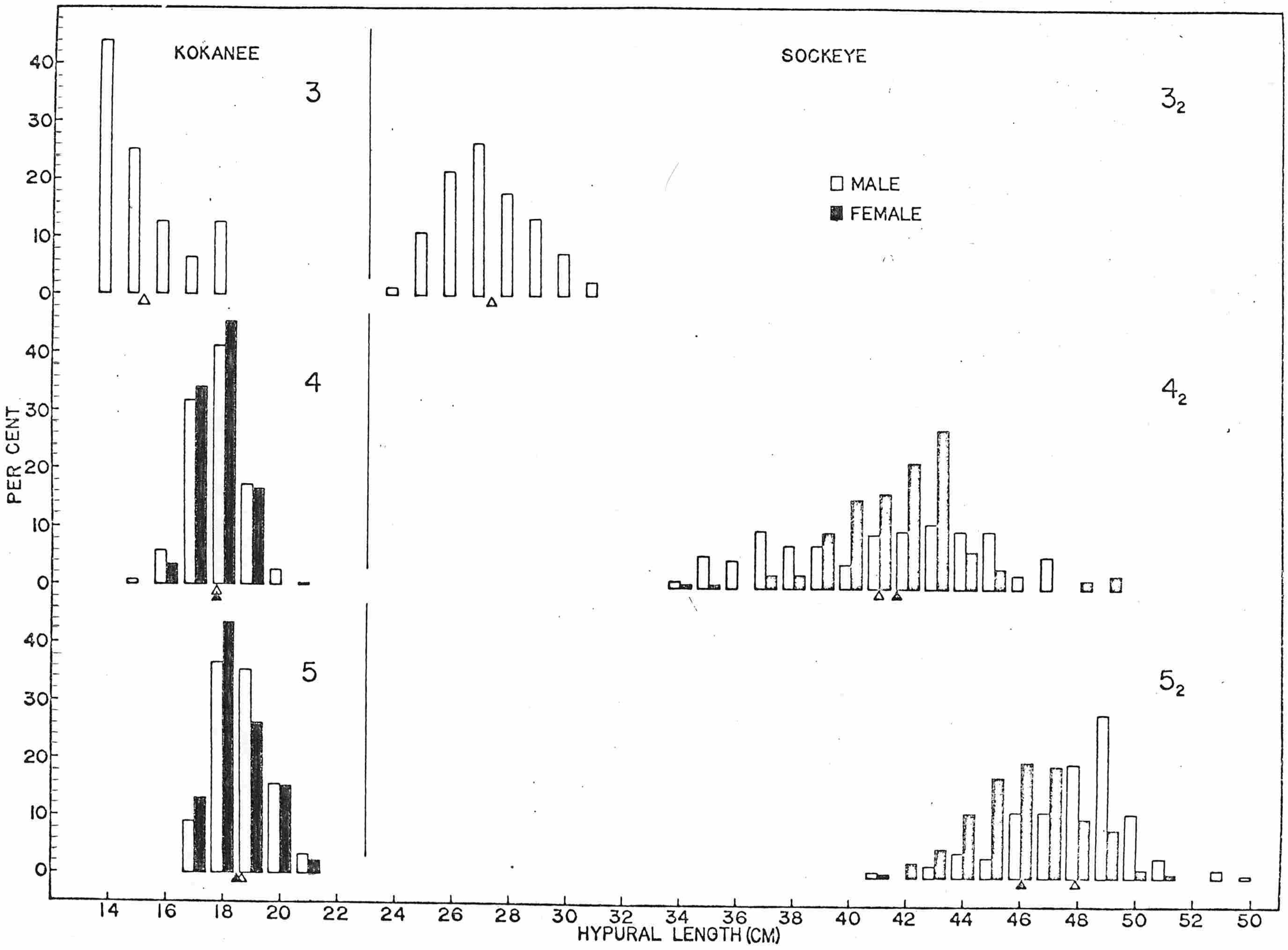
Age distribution of mature fish

Sockeye

A majority of the sockeye salmon spawning in the Babine system are in

Figure 6. Length frequencies of various age groups of sockeye and kokanee sampled at Four Mile Creek, 1965. Females, black bars and males, open bars. Triangles indicate mean lengths. Sample sizes were: Kokanee age 3 - 13 males
age 4 - 179 males, 149 females
age 5 - 52 males, 27 females

Sockeye age 3 - 84 males
age 4 - 160 males, 183 females
age 5 - 195 males, 327 females


KOKANEE
SOCKEYE
3
4
5
3₂
4₂
5₂
☐ MALE
■ FEMALE
PER CENT
0
10
20
30
40
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
50
52
50
HYPURAL LENGTH (CM)

their fourth or fifth year (Shepard and Withler, 1958). These age groups include over 95% of the female spawners and, in most years, a high proportion of the males. Occasionally, however, there is a large run of precocious three year old males (commonly called jacks). Six year old fish occur, but are never abundant.

The relative abundance of various age groups varies considerably from year to year both in the system as a whole and in individual spawning streams. This is illustrated by data on the age distribution of sockeye spawners in Four Mile Creek (Table IX).

In 1964, over 90% of both the male and female sockeye sampled at Four Mile Creek were in their fifth year. Only 7.2% of the males and 4.1% of the females were in their fourth year. Less than 1% of the males were jacks. In 1965, five year fish again predominated but the percentage of four year fish exceeded 30% for both males and females. The percentage of jacks increased to nearly 18% of the total males.

In 1966, only 100 male and 100 female sockeye were sampled to determine the age composition of the spawning run. No jacks, which can be readily distinguished from older fish by their size and appearance, were included among the former. However, it is known from counts made at the Four Mile trap that approximately 42.6% of the males entering the stream were jacks. This information was used in reconstructing the probable proportionate age distribution of the male spawners. Four year old males were second in importance (41.0%) only to jacks and were five times as abundant as five year olds (8.0%). Four year females (72.0%) were also more abundant than five year olds (26.0%); a four year old/five year old ratio of almost 2.8:1.

TABLE IX. Age distribution of sockeye salmon and kokanee spawning at Four Mile Creek 1964-1966.

		Number Examined	Number Aged	3 yr olds		4 yr olds		5 yr olds		6 yr olds		4/5
				No.	%	No.	%	No.	%	No.	%	
						Sockeye						
1964	M	824	824	8	0.9	59	7.2	749	90.8	8	0.9	0.08
	F	1209	1209	0	0.0	50	4.1	1148	95.0	11	0.9	0.04
	Total	2033	2033	8	0.5	109	5.7	1897	92.9	19	0.9	0.06
1965	M	471	471	84	17.8	150	31.8	233	49.5	4	0.8	0.64
	F	550	550	0	0.0	176	32.0	363	66.0	11	2.0	0.58
	Total	1021	1021	84	8.9	326	31.9	596	57.8	15	1.4	0.56
1966	M		100(4+)		42.6	82	47.1	16	9.2	2	1.1	5.12
	F		100		0.0	72	72.0	26	26.0	2	2.0	2.7
						Kokanee						
1964	M	674	330	26	7.9	288	87.3	16	4.8	0	0.0	18.00
	F	272	115	8	7.0	104	90.4	3	2.6	0	0.0	34.77
	Total	946	445	34	7.5	392	88.8	19	3.7	0	0.0	20.63
1965	M	668	244	13	5.3	179	73.4	52	15.3	0	0.0	3.44
	F	464	176	0	0.0	149	84.7	27	21.3	0	0.0	5.52
	Total	1132	420	13	2.7	328	79.1	79	18.3	0	0.0	4.15

Kokanee

Johnson (1958) stated that most of the kokanee spawning in streams at Babine Lake were in their fourth year, although three year old (predominantly males) and five year old fish do occur. In 1964 and 1965, the age distribution of kokanee in Four Mile Creek was examined (Table IX). Four year olds predominated in both years but fell from 88.8% overall in 1964 to 79.1% overall in 1965. This was due, primarily, to an increase in the proportion of five year olds (3.7% overall to 18.3%).

It is unlikely that the numbers of five year old spawners ever exceeds that of four year olds. The former did not occur in any abundance in lake-caught samples. In 1966, none of the kokanee purse-seined in the Main Lake area (N = 1257) were in their fifth year (J. McDonald, personal communication).

Reproductive parameters

Fecundity

Samples of female sockeye taken at Four Mile Creek in 1965 had a mean fecundity (3116 eggs) approximately 12 times that (260 eggs) of kokanee taken from the stream in the same year. A comparison of these counts with some made previously at Babine (Table X) shows that while the fecundity of the sockeye examined was close to average, that of the kokanee was low, even lower than that of samples with a smaller average length. This difference may have resulted from year-class differences in the length-frequency relationship of kokanee. The ratio of the overall mean fecundity of sockeye (3141 eggs) and kokanee (290 eggs) samples is close to 11:1, close to the 10:1 differential Johnson (1958) suggested for sockeye and kokanee at Babine Lake.

Female kokanee sampled at Four Mile Creek in 1965 tended to have more

TABLE X. Fecundity of female sockeye and kokanee sampled at Babine Lake.

Location	Date	N	Mean Fecundity	Mean Hypural Length (cm)
		Sockeye		
Babine Fence	1946	59	3281	49.9
	1947	73	3187	48.5
	1948	57	3353	48.9
	1965	136	3094	48.1
Fulton River	1962	41	3272	48.1
	1963	40	3013	45.4
	1964	30	3013	46.6
	1965	41	3024	44.9
	1966	30	3204	44.9
Pinkut Creek	1964	47	3035	44.1
	1965	30	3070	46.2
	1966	29	2872	43.3
Gullwing Creek	1950	22	2862	45.5
	1953	35	3452	49.8
Four Mile Creek	1965	24	3116	48.1
Grand Means			3141	47.3
		Kokanee		
Tachek Creek	1958	14	301	17.9
Pierre Creek	1964	12	287	17.9
Gullwing Creek	1953	7	411	20.7
Gullwing Creek Nets	1958	29	302	18.0
Four Mile Creek	1965	51	260	18.6
Sutherland River	1953	4	349	20.4
Grand Means			290	18.5

eggs in the right ovary than in the left (Fig. 7). Of 46 females examined, 36 had more eggs on the right side, a significantly greater ($p < .01$) proportion. In contrast, a majority of the sockeye examined had larger left (27 fish) than right (15 fish) ovaries. This difference, though suggestive, is not significant ($p > .05$).

In the kokanee examined, the mean deviation from equivalency in the egg counts of right and left ovaries was 37.1 eggs or 28.2% of the average content of single ovaries. For sockeye, the corresponding figures are 90.3 eggs and 5.9%. Thus, the discrepancy in the fecundity of right and left ovaries was proportionately greater in kokanee. In the most extreme case, the left ovary of a female kokanee contained 278 eggs, the right only 19, a deviation from equivalency of 129.5 eggs (87%).

Egg size

There is a positive linear relationship of egg size to female length in Babine sockeye (Bilton and Jenkinson, 1966). The female length-egg size relationship of Babine Lake kokanee has not been determined but their eggs are smaller than those of sockeye (Fig. 8). The weight distributions illustrated are those of eggs taken from females at Pierre Creek in 1964 and raised in a hatchery until eyed. The distributions of the samples did not overlap. The average kokanee egg (0.079 g) was approximately 2/3 the weight of the average sockeye egg (0.117 g). Sockeye and kokanee eggs from Four Mile Creek (1965) were similar in weight to those from Pierre Creek: 100 eyed sockeye eggs average 0.112 g and 60 eyed kokanee eggs 0.075 g. The largest kokanee egg and the smallest sockeye egg had identical weights, 0.095 g. Both samples were taken from hatchery trays and included eggs from a number of females.

Figure 7. Relationship of the number of eggs in the right and left ovaries of sockeye and kokanee from Babine Lake, 1965. Samples taken during the run of early stream fish through the counting fence on the Lower Babine River (Fence) and from the spawning run into Four Mile Creek (4 Mi).

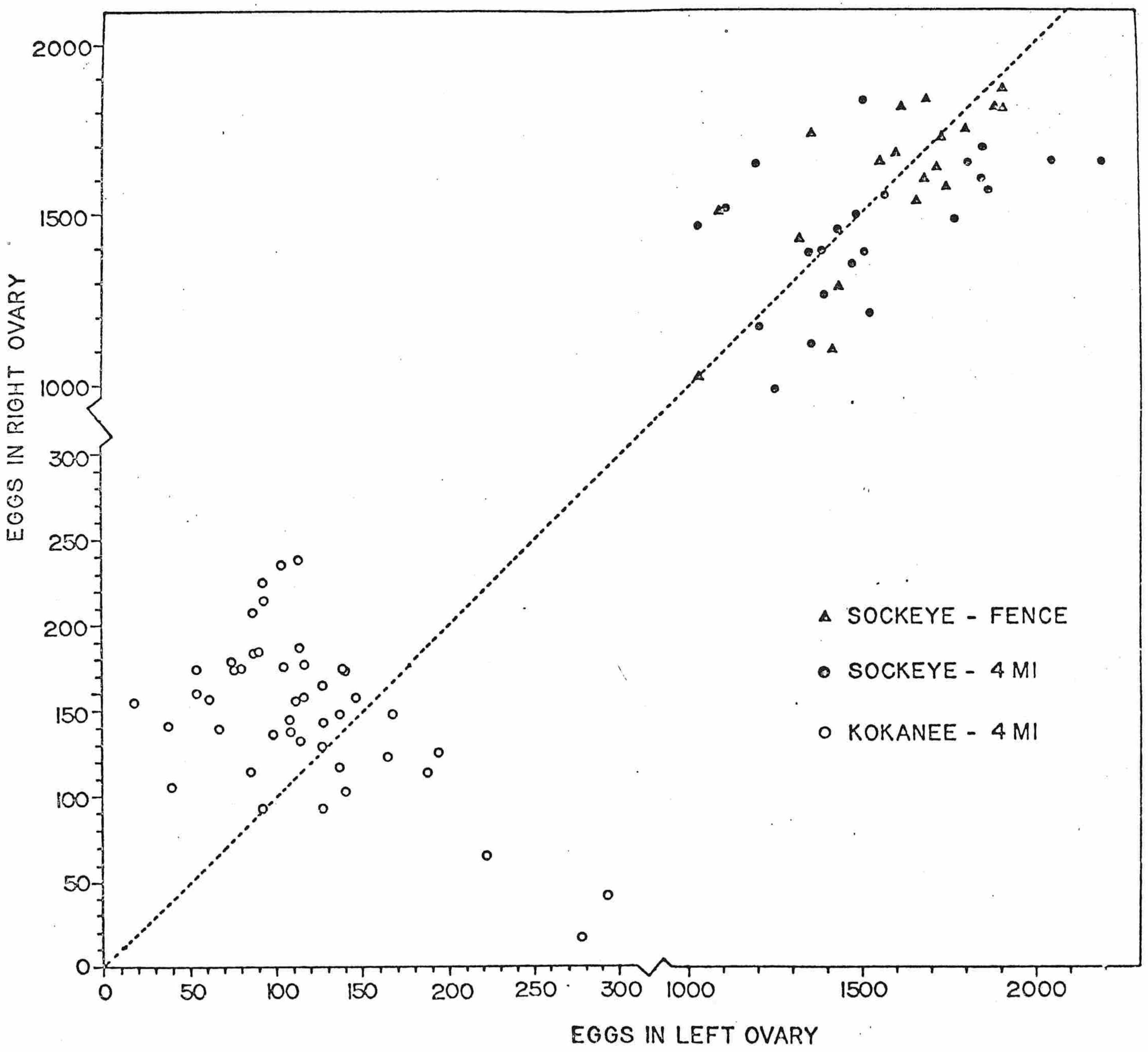
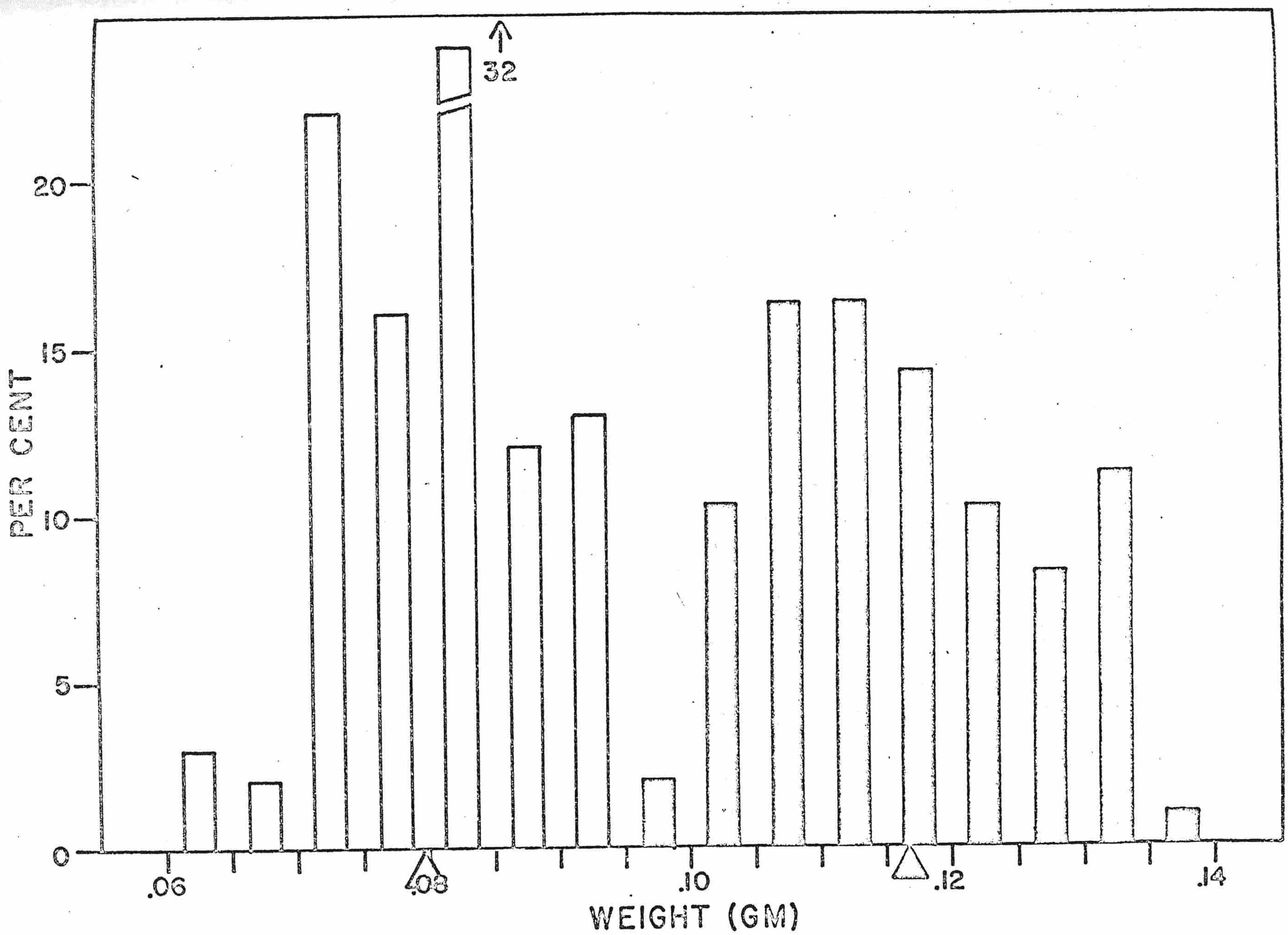

EGGS IN RIGHT OVARY
2000
1500
1000
300
250
200
150
100
50
0
0
50
100
150
200
250
300
1000
1500
2000
EGGS IN LEFT OVARY
▲ SOCKEYE - FENCE
● SOCKEYE - 4 MI
○ KOKANEE - 4 MI

Figure 8. Weight-frequency distributions of eyed eggs from Pierre Creek sockeye (black bars) and kokanee (open bars). Triangles indicate means. N = 100 for eggs of both types. Further explanation in text.


32
20
15
10
5
0
PER CENT
.06
.08
.10
.12
.14
WEIGHT (GM)

Weight of male gonads

In 1965, the testes of 41 kokanee and 23 sockeye (none of which were jacks) were removed and weighed. These were all fresh, unspawned fish taken from the Four Mile Creek trap. The kokanee ranged from 16.9 to 21.0 cm (mean 18.9 cm) hypural length, the sockeye from 38.3 to 53.1 cm (mean 48.5 cm).

Plots of the data indicated linearity and so the testis weight-hypural length relationships of the two samples were calculated by least squares regression. The calculated regression formulae were $Y = 0.16X + 3.9$ for kokanee and $Y = 2.65X - 65.0$ for sockeye, where Y equals the predicted average testis weight in g and X equals hypural length in cm. The mean lengths of the fish in the testis weight samples were somewhat greater than those of the much larger samples of fish measured during dead recovery in Four Mile Creek in the same year. The dead recovery samples averaged 46.0 cm for male sockeye four years and older and 17.8 cm for male kokanee. When these values, which probably better reflect the mean hypural length of the Four Mile Creek spawning populations are substituted in the regression equations, the expected mean values for testis weight are 6.8 g for kokanee and 56.9 g for sockeye. Thus, in 1965, male sockeye four years and older had testes about 8.4 times heavier than those of male kokanee.

Sex ratios of sockeye and kokanee

Sockeye

Samples of sockeye smolts taken in traps at the outlet of Babine Lake suggest a 1:1 ratio of males to females. Over a four year period, Dombroski (1954) sampled 8299 one year old and 57 two year old smolts. The percentage males was 50.3 for the former and 50.9 for the latter, in neither case significantly different from a 1:1 ratio. An additional sample of two year old smolts taken in 1966 and examined by the author yielded 33 (50.8%) males and 32 females; again, not significantly different from equality.

It is not yet possible to reconstruct the sex ratio of mature sockeye within individual year classes. First, because male sockeye tend to mature at an earlier age than female sockeye and second, because males are more subject to fishing mortality than females (Foerster, 1968: p. 117).

Kokanee

Males dominate nearly every year class of Babine Lake kokanee (Table XI). Except for age three kokanee purse-seined in 1966, the per cent males in samples exceeds that of females and, in most instances, the difference is significant. This is true of fish captured in the lake and in spawning streams, of mature and immature fish and of all age groups. The overall mean sex ratios of 57.9% males for fish captured in the lake and 65.8% for fish sampled in Four Mile Creek differ significantly ($\chi^2 = 25.7$, $p < .01$; calculations based on original numerical data) but this difference is almost entirely the result of the unusually high proportion of males (72.5%) in the 1966 spawning run. The per cent males in 1964 (57.5%) and 1965 (59.0%) spawning runs are similar to the overall average for lake-captured kokanee.

Laboratory-raised fish

Sex ratios were determined for four groups of Four Mile Creek sockeye and kokanee progeny raised at Lakelse Lake in 1965/66 (Table XII). These are the 1965 groups described above in the section on the growth and survival of laboratory-raised fish. The fish were killed and preserved July 14 to July 20, 1966, approximately 11 months after the eggs were fertilized.

TABLE XI. Sex ratios of kokanee captured in Babine Lake. Unpublished data from various sources: W. E. Johnson supplied the gillnet data, 1957 to 1960; J. McDonald supplied the purse seine data; the 1965 gillnet and the stream data are the author's. Figures in brackets are the per cent males in preceeding sample.

Year	Month	Method of Capture	Number Aged				Number Unaged	Total Sample
			2 yrs	3 yrs	4 yrs	5 yrs		
			Lake Captures					
1957	June-July	Gillnet					35(65.7)[a]	35(65.7)[a]
1958	May-Oct.	Gillnet	117(64.1)	297(56.6)	310(57.1)	3(66.7)	480(56.7)	1207(57.5)
1959	June-Sept.	Gillnet	12(91.7)	295(61.0)	244(56.1)	16(62.5)	448(61.2)	1015(60.9)
1960	Aug.-Oct.	Gillnet					751(59.0)	751(59.0)
1965	June	Gillnet					120(51.6)[a]	120(51.6)[a]
1965	July	Purse Seine					94(55.3)	94(55.3)
1966	June-July	Purse Seine	869(57.9)	296(46.6)[a]	92(61.9)			1257(55.6)
TOTAL			998(59.2)	888(54.7)	646(57.4)	19(63.1)	1928(58.7)	4479(57.9)
			Stream Samples - Four Mile Creek					
1964	August	Dead Recovery					1711(57.5)	1711(57.5)
1965	August	Dead Recovery		13(100.0)	328(54.6)	79(65.8)	712(59.7)	1132(59.0)
1966	July-Aug.	Weir Counts					3242(72.5)	3242(72.5)
TOTAL				13(100.0)	328(54.6)	79(65.8)	5665(66.4)	6085(65.8)

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[a] Number of males and females in sample not different at 5% level of significance.

TABLE XII. Sex ratios of laboratory-raised progeny of sockeye and kokanee from Four Mile Creek, Babine Lake. Crosses made August, 1965. Fry raised at Lakelse Lake Hatchery and sampled July 14 to 20, 1966.

Male x Female	N	% Males	χ^2
Sockeye x Sockeye	50	24	6.76*
Sockeye x Kokanee	100	52	0.09
Kokanee x Sockeye	125	44	1.57
Kokanee x Kokanee	100	51	0.01

*Differs at 5% level of significance.

Both groups of progeny of kokanee eggs, those fertilized by male kokanee and those fertilized by male sockeye, had sex ratios very close to 1:1. The kokanee-fertilized groups of sockeye eggs was 44% male, not significantly different from equality. However, the sample of the progeny of sockeye eggs fertilized by male sockeye was only 24% male, significantly fewer ($p < .01$) than expected.

DISCUSSION

Estimates of the numbers of fish spawning in streams at Babine Lake indicate that it is only in the early streams of the Main Lake area that sizeable populations of sockeye and kokanee occur sympatrically. Comparative studies in such areas of overlap can often provide clues to the systematic relationship of similar forms. Table XIII compares some important life history characteristics of sockeye and kokanee from the early streams.

Though the life histories of the two forms differ quite markedly in some respects, none of the differences is, in itself, indicative of the genetic

TABLE XIII. Summary of some important life histories between sockeye and kokanee spawning in early streams at Babine Lake.

Character	Kokanee	Sockeye
Length at end of first year	smaller	larger
Length at maturity	smaller	larger
Age at maturity	mostly 4	4 and 5
Fecundity	low	high
Egg size	small	large
Testis weight	small	large
Sex ratio	M > F	?

relationship between them. The significant difference in the size of yearling fish may only reflect the fact that, within populations, larger fish have a greater tendency to smolt than smaller ones. Size differences between same-age migrant and non-migrant fish have been reported for other localities where both sockeye and kokanee occur. At Lake Dalnee in the U.S.S.R., non-migrant fish have a greater average size than same-age smolts (Krokhin, 1967). At Cultus Lake (Ricker, 1938), one segment of the non-migrant population has a smaller average size than same-age smolts (as at Babine), another has a greater average size (as at Dalnee). Thus, size (or growth rate) would seem to have an important relationship to migration tendency. Foerster (1968, p. 305) examined the relationship of fish size and migration-tendency within sockeye populations and concluded that "For each year, in all sockeye areas examined, it has been found that those young sockeye that do not migrate in any one year but remain in the lake for a further season's residence are on the average always smaller...than those smolts that do migrate." However, he suggested (p. 306) that probably "...size alone is not the factor determining migration. Indeed, size as such is not likely to be involved at all, but rather some physiological condition positively, but far from perfectly, correlated with size."

A tendency for smaller fish to remain in the lake may have some selective value. Evidence is accumulating that, at Babine, smaller smolts have poor survival in comparison with larger (M. P. Shepard and T. Bilton, unpublished data). The fish remaining behind may smolt in subsequent years, when their internal state is more suitable due to an additional period of growth. Variable age of smolting can also occur in other salmonids. Johnston and Eales (1970) have shown that in laboratory populations, a greater percentage of large than of small Atlantic salmon parr develop the silvering characteristic of the smolting process.

The size difference between mature sockeye and kokanee is even greater than that distinguishing young of the two forms. The longer growing season and greater abundance of food in the marine environment probably accounts for most of the growth differential. Foerster (1947) released marked progeny of Kootenay Lake kokanee downstream of Cultus Lake, B. C. during the normal sockeye migration from the lake. Though the Kootenay Lake fish are normally non-migratory, the marked fish returned from the ocean, as mature fish, at a size little different from that of same-age sockeye. Foerster suggested that the size difference between natural populations of sockeye and kokanee is more likely due to environment than heredity.

Most of the other differences in life history listed in Table XIII are size related: fecundity (Foerster, 1968 ; Withler, 1950), egg size (Bilton and Jenkinson, 1966), testis weight (this study) and, very likely, age at maturity. A tendency for kokanee to mature somewhat earlier than their anadromous counterparts has been found at Cultus Lake (Ricker, 1938) and at Lake Dalnee (Krokhin, 1967) as well as at Babine Lake. Age at maturity is probably regulated by a complex of genetic and environmental factors among which size (and/or growth rate) would seem to be of major importance (see Foerster, 1968 : pp. 357-365, for a review of the available information).

Sex ratio data is equally inconclusive in indicating the genetic relationships of the two forms. At Cultus Lake and at Lake Dalnee, the kokanee populations are more than 90% male. In these lakes, kokanee are thought to be a segment of a larger population, most of which migrate to sea. At Lake Dalnee, when populations of kokanee are high, it has been possible to detect a complementary excess of females in the migratory part of the population (Krokhin, 1967). In one year (1935) a significant excess of females was detected among smolts leaving Cultus Lake (Ricker, 1938). The difference in the sex ratios of migratory and non-migratory fish is thought to result from a greater migratory impulse among female fish. Thus far, samples of smolts taken at Babine Lake do not indicate any significant departure from a 50:50 sex ratio. An excess of females would presumably occur among early stream smolts if the relationship of sockeye and kokanee spawning in these streams is similar to that hypothesized for Dalnee and Cultus Lakes. However, such a disproportion might be difficult to detect. First, the imbalance between males and females among Babine Lake kokanee is much less than that found in the other localities. Second, kokanee populations seem to vary considerably from year to year and during years when the kokanee populations are small, the excess of females among early stream smolts would also be small. Third, smolts originating from early streams are only a small proportion of those leaving Babine Lake. If the non-migratory yearling population were very large and if the proportion of males were high it might be possible to detect a complementary excess of females among smolts particularly if the samples were taken within the Main Lake.

An alternative explanation is that the excess of males among Babine Lake kokanee is genetically controlled. Unfortunately, there seems to be no published account of the mechanisms of sex determination in salmonid fishes. Foerster (1968 , p. 284 ff) summarizes data which suggest that at smolt-age the sex ratios of most sockeye populations are approximately 1:1. Among the laboratory-raised groups of Babine Lake fish (Table XII), the progeny of female kokanee had an approximately equal sex distribution regardless of the male parent while progeny of female sockeye tended to be more male than female. The equal sex ratio of the kokanee progeny was expected but there is no explanation for the preponderance of males among the sockeye progeny. A detailed investigation of the mechanisms of sex determination among salmonid fishes is long overdue.

Finally, one other approach which might have yielded some indication of major genetic differences, the laboratory experiments with hybrid crosses, was also inconclusive. Cross-fertilization is easily accomplished, hybrid zygotes appear to survive as well as the pure types and hybrids have approximately the same growth-form as pure types developing from similar-sized eggs. The experimental designs were admittedly crude and further experimentation along these lines might establish that there are, in fact, subtle differences in the survival and growth of the hybrids compared with the pure types.

SECTION II

COMPARISON OF SOME MERISTIC AND ELECTROPHORETIC CHARACTERS OF SOCKEYE AND KOKANEE FROM BABINE LAKE

INTRODUCTION

In a recent study of the systematics of threespine sticklebacks (*Gasterosteus aculeatus*) in British Columbia, Hagen (1967) used meristic and biochemical characters to distinguish the anadromous (*trachurus*) form and the freshwater resident (*leiurus*) form of this species from their hybrids. Such information is of great importance in determining the systematic status of sympatric forms. Consequently, a comparison was made of sockeye and kokanee from the early streams in the Main Lake area of Babine Lake to determine whether meristic and electrophoretic characters were of any value in distinguishing these two forms and their hybrids.

MATERIALS AND METHODS

A preliminary comparison was made of twelve meristic characters. Three of these, the numbers of lateral line scales, vertebrae and first arch gillrakers were selected for more detailed examination. These counts were easily made, highly reproducible and gave promise of differing between sockeye and kokanee.

The fish used for meristic analysis were of two kinds: mature adults captured on the spawning grounds in 1964 and 1965 and fish of known parentage raised under laboratory conditions. The latter were from matings of sockeye and kokanee made at Four Mile Creek in 1965 and 1966. The fertilized eggs were immediately transferred to Lakelse Lake Hatchery and raised there until after the vertebral column was ossified, at a size of between 30 and 50 mm fork length. They were then cleared and stained with potassium hydroxide and alizarin red (Hungar, 1969).

Counts were made as follows:

Vertebral counts were determined from X-rays of adult fish taken from streams and from cleared and stained specimens of laboratory-raised juveniles. All vertebrae, including the hypural vertebrae, were counted.

Lateral line scale counts included all scales along the lateral line from the most anterior scale to the hypural plate.

Gillraker counts included all gillrakers on the first arch on the left side of the body, rudimentary rakers included. Counts were made after the gill arch had been removed.

Electrophoresis of muscle myogens and blood haemoglobins was done by Dr. H. Tsuyuki of the Vancouver Station of the Fisheries Research Board of Canada. The techniques employed were those described by Tsuyuki and Roberts (1962). The fish examined were the progeny of sockeye x sockeye and kokanee x kokanee matings made at Pierre Creek, Babine Lake, in 1964. These were flown to the Lakelse Lake Hatchery where they remained until eyed. At the eyed stage they were transferred to the Biological Station at Nanaimo where they were raised. The fish used in the electrophoretic study were killed and examined early in their second year, just prior to smolting.

RESULTS

Meristic characters

Spawning ground samples

Preliminary examination of data for early stream spawners gave no indication of any consistent sex or year-class differences in the characters examined and these factors were not further considered.

In comparisons within streams and overall, the mean vertebral and lateral line scale counts of sockeye exceed those of kokanee by a small but significant amount (Fig. 9). Mean counts of samples of the same form (sockeye or kokanee) taken from different streams were more alike than were the means of samples of sockeye and kokanee taken from the same stream.

There were no significant differences between the two forms in the number of first arch gillrakers, within streams or overall.

Laboratory-raised progeny

Vertebral counts only were made for laboratory-raised fish. The mean vertebral counts of sockeye x sockeye progeny exceeded those of kokanee x kokanee progeny in both the 1965 and 1966 experiments. The Hubbs-Hubbs plot (Fig. 10) indicates that the differences in means (about 0.6 vertebrae in 1965/66 and 0.7 vertebrae in1966/67) were significant in both years. These differences were similar to the difference in the overall means of the sockeye and kokanee spawning ground samples, 0.7 vertebrae,though both groups of laboratory-raised progeny tended to have fewer vertebrae than the parental forms collected on the spawning grounds.

In the 1966 experiment, the mean counts for the reciprocal hybrids fell between, and were significantly different from, either of the parental types. In 1965, the sockeye x kokanee cross had an intermediate mean count but the kokanee x sockeye cross had a mean vertebral count almost identical to that of the kokanee x kokanee progeny and significantly lower than that of sockeye x sockeye progeny.

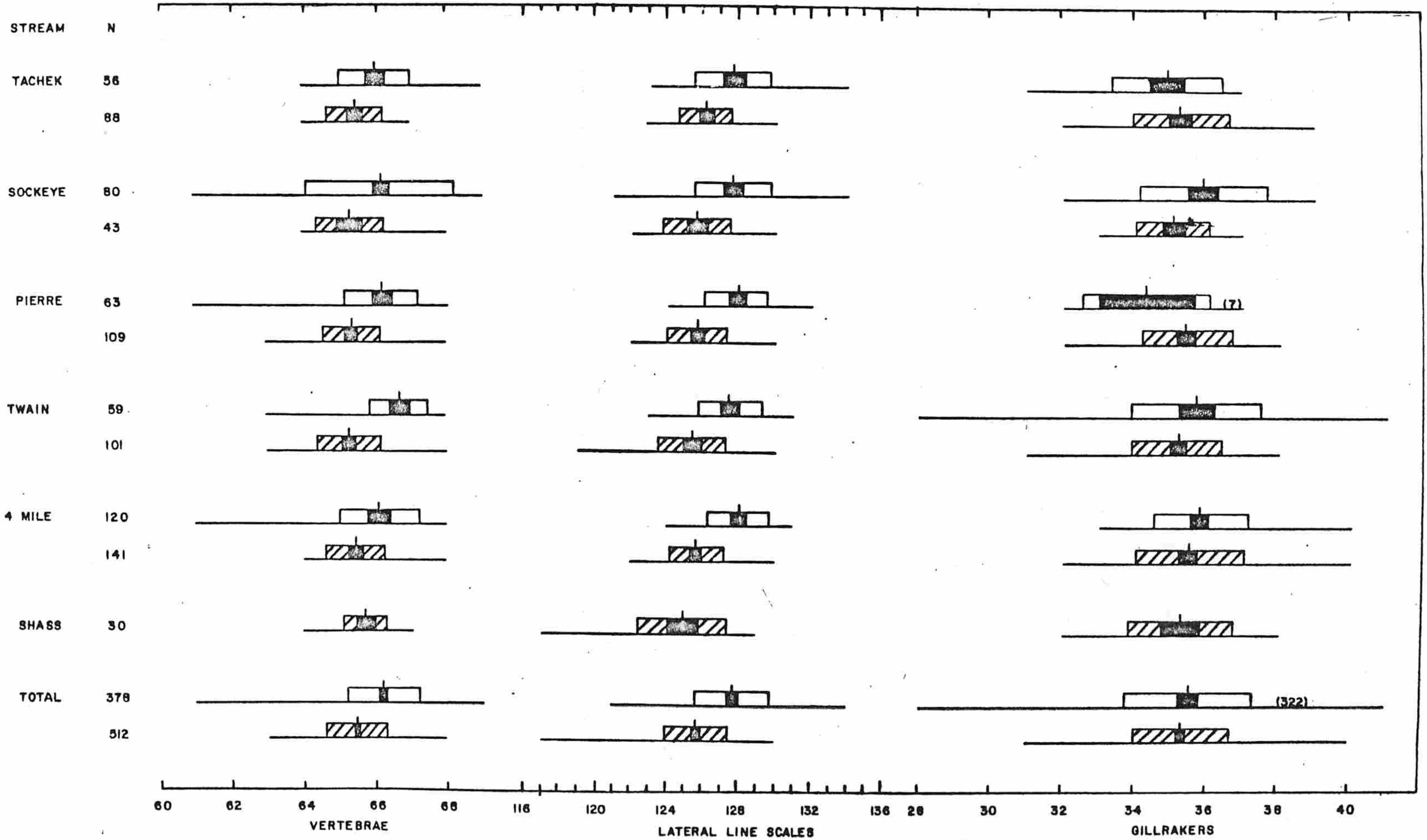


Figure 9. Counts of total vertebrae, lateral line scales and total first arch gillrakers for samples of sockeye (open bars) and kokanee (cross-hatched bars) taken from some Babine Lake early streams. Samples from 1964 and 1965 combined. Explanation of Hubbs-Hubbs plot as in Figure 4.

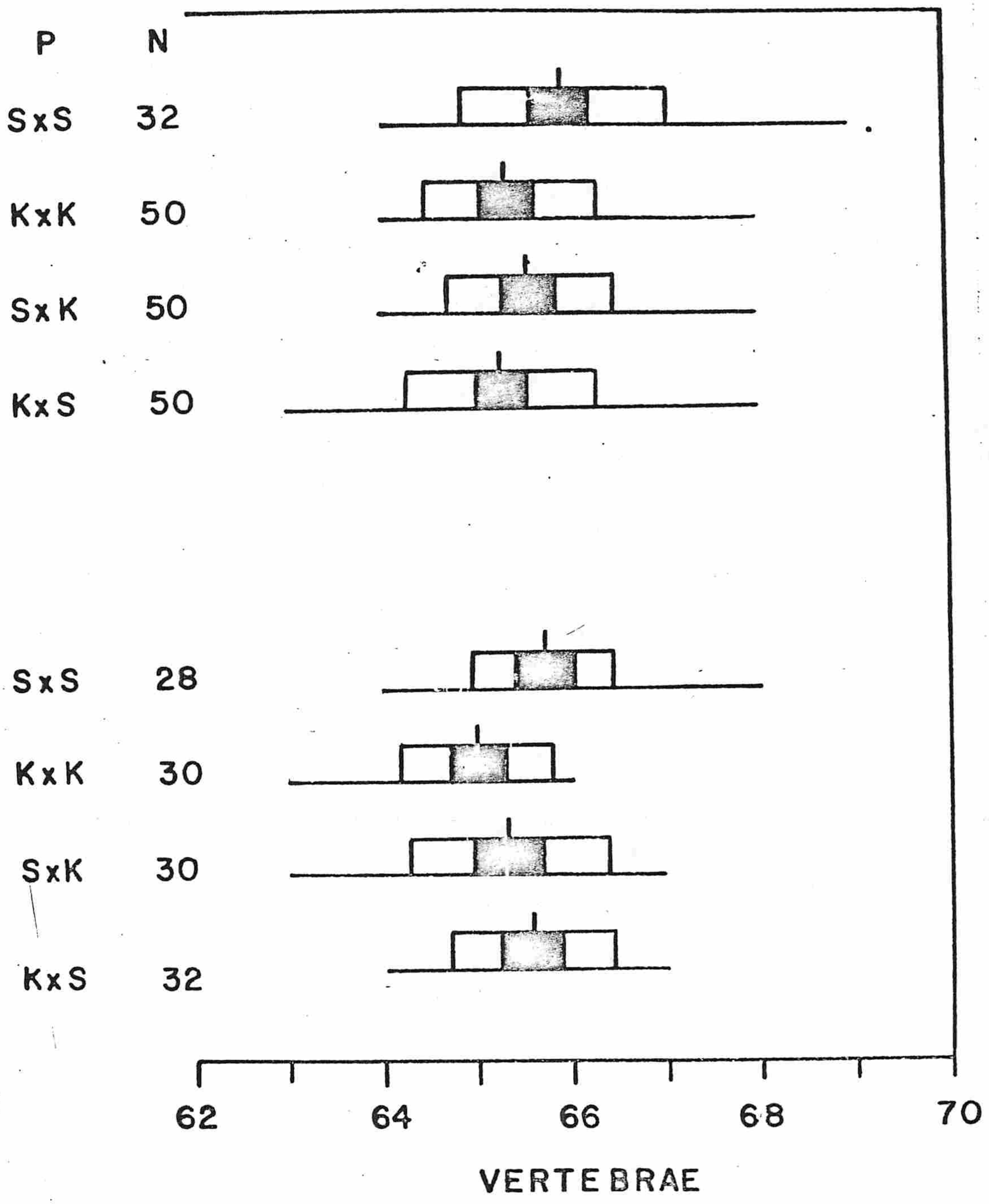


Figure 10. Vertebral counts of laboratory-raised progeny of sockeye and kokanee. Upper quartet, 1965/66 progeny; lower quartet, 1966/67 progeny. P indicates parentage, male parent preceeds female

Electrophoresis

Dr. H. Tsuyuki examined the muscle myogen and blood haemoglobin patterns of 24 sockeye x sockeye and 24 kokanee x kokanee progeny. He found (personal communication) that, with respect to these two biochemical characters, the two groups of sub-smolt yearlings were identical.

DISCUSSION

One of the three meristic characters examined, total first arch gill-rakers, did not differ between sockeye and kokanee taken from spawning grounds at Babine Lake though Nelson (1968b) has shown a distinct difference in this character between sympatric sockeye and kokanee from Takla Lake in the Fraser System. The two other characters, lateral line scales and total vertebrae, both longitudinal series, did differ significantly between the two forms.

Meristic characters in fish are known to be influenced by both environmental and hereditary factors (Blaxter, 1957). Environmental factors include a wide variety of variables (temperature, oxygen levels, light duration, etc.) which affect the rate of development of embryos. The hereditary component is probably polygenic, the patterns of inheritance being quantitative in character. Hybrids tend to be intermediate between the extremes represented by the parental types (e.g., the inheritance of meristic characters in *Gasterosteus aculeatus*; Hagen, 1967).

Garside and Fry (1959) have described differences in a meristic character (number of myomeres) in brook trout, *Salvelinus fontinalis*, which they ascribe to differences in the amount of yolk available to developing embryos. In comparison with embryos having a large yolk supply, those with less available yolk were smaller in size at a comparable stage of development and tended to develop fewer myomeres. Further, Blaxter (1957) has shown that in herring (Clupea harengus), the number of myomeres is positively correlated with the number of vertebrae that develop. This suggests the possibility that fish developing from small eggs, with a small yolk supply, will develop fewer vertebrae than those developing from larger eggs having a larger yolk supply available for growth. Other longitudinal series (e.g., lateral line scale counts) may be similarly affected.

Babine kokanee are known to produce much smaller eggs than sockeye. They also tend to have fewer vertebrae and lateral line scales. If the relationship of egg (i.e., yolk) size to vertebrae and lateral line scale counts is like that postulated above, the observed differences in these characters in fish from the early streams (Fig. 9) would be best considered as resulting from an environmental difference (food supply to the embryo) and not from genetic differences between the two forms.

The laboratory experiments were set up to determine whether genetic influences or egg size was most important in determining vertebral numbers. The fish were raised in similar situations to minimize differences in environmental influences. The presumption was that if quantitative genetic influences were paramount in determining number of vertebrae, then the reciprocal hybrids would tend to have counts intermediate between the two parental types. Alternatively, if egg size was of paramount importance, the vertebral counts of hybrids should be most like that of their female parent.

The results are inconclusive. Data for the 1966 matings lend some support to either hypothesis. The means for the pure parental types are at either extreme and the means of both hybrid types are intermediate. At the same time, the hybrid developing from the larger sockeye eggs had a mean count higher (though not significantly) than that of the hybrid developing from the smaller kokanee eggs. In 1965 experiment, the means for the pure parental types were again at either extreme. One hybrid group (sockeye x kokanee) had an intermediate mean count but the other (kokanee x sockeye), a large egg mating, had a mean count lower than that of any of the mating groups. This result does not fit either hypothesis.

Much more elaborate experimentation is necessary before it will be possible to distinguish the relative contributions of heredity and egg size in determining the numbers of vertebrae and other meristic series. In any case, it was concluded that there was little hope, on the basis of the meristic of electrophoretic characters examined thus far, of being able to distinguish sockeye from kokanee and their hybrids in mixed natural populations.

SECTION III

ECOLOGICAL AND BEHAVIORAL RELATIONSHIPS OF SOCKEYE AND KOKANEE SPAWNING IN THE EARLY STREAMS AT BABINE LAKE

INTRODUCTION

It is not known whether the sockeye and kokanee of Babine Lake constitute genetically isolated populations or whether there is interchange of genetic material between fish of the two types. Factors which promote genetic isolation are termed "isolating mechanisms". Mayr (1963) lists two broad categories of these: first, those which prevent interspecific crosses (premating mechanisms) and second, those which reduce the success of hybrids, should they occur (postmating mechanisms). This study is an examination of the effectiveness of premating isolating mechanisms in preventing interbreeding of sockeye and kokanee in streams tributary to Babine Lake which support persistent spawning populations of both forms.

DESCRIPTION OF THE STUDY STREAMS

Observations were made at Four Mile Creek and Gullwing Creek, two small streams entering Babine Lake near its south end. Four Mile Creek is described by Hanson and Smith (1967). The stream had an average escapement of 2,206 sockeye spawners over the eighteen year period from 1949 to 1966 (H. Smith, unpublished data). Kokanee spawners were not counted prior to 1964, but Johnson (1958) records the creek as having, at most, a few hundred kokanee. Counts made during 1964, 1965, and 1966 when 1900, 4400 and 3400 kokanee entered the stream (in what were years of low kokanee abundance for the lake as a whole) suggest that this was probably an underestimate.

Gullwing Creek (Six Mile Creek) is smaller and less stable than Four Mile Creek. In some years (e.g., 1951, 1952, 1961) it is completely dry during the spawning season. At high water levels, as many as 3500 sockeye have entered the stream. The average sockeye escapement over the past eighteen years has been 978 spawners (H. Smith, unpublished data). In 1965 and 1966, when behavioural observations were made on this stream, water levels were low enough to restrict the movements of sockeye (though not kokanee) into the stream. In fact, in both years, it was not until several blockages had been removed by the author and others that any large sockeye were able to ascend more than a few hundred meters. When water conditions are favourable sockeye can ascend approximately 2000 m. The kokanee run into the stream is not large. Johnson (1958) suggests a spawning population of a few hundred at most. The largest count made during this study was 800 (1964).

MATERIALS AND METHODS

Most of the observations reported in this study were made at Four Mile Creek. In 1964, 1965 and 1966 a barrier and trap were placed across the stream about 10 m above its mouth. The barrier was holed on one occasion, August 3, 1964, when an estimated 409 sockeye and an undetermined number of kokanee escaped upstream. Normally, sockeye and kokanee were unable to move upstream without entering the trap. Fish were usually removed from the trap and counted between 0700 and 0800 hr (P.S.T.) and between 2200 and 2300 hr. When large numbers of fish were known to be entering the stream, the trap was emptied more frequently.

The fish were variously treated after removal from the trap. In 1964 and 1965, in conjunction with a second study being carried out at Four Mile Creek (Hanson and Smith, 1967), all sockeye taken in the trap were tagged with numbered Petersen disc tags before being released upstream. The tags varied in shape and size but averaged about 2.5 cm in diameter. Females were tagged immediately ahead of the dorsal fin; males, through the dorsal hump, 10 to 15 cm in advance of the dorsal fin. At the time of tagging, the sex, fork length and state of maturity of the fish were recorded. In 1966 sockeye were counted and sexed but not otherwise treated.

In 1964, kokanee were counted and passed upstream. In 1965, some kokanee were tagged with small (1.3 cm diameter) round Petersen tags, red for females and white for males. No attempt was made to tag all kokanee entering the stream. On some days the entire run was tagged; on others, when catches were large, a sample of 100 to 200 fish was tagged and released. Sex, fork length and state of maturity were recorded for each of the tagged kokanee. Fish remaining were simply counted and passed upstream. The sex ratio of the tagged sample was assumed to apply to the entire catch. In 1966, kokanee were counted, sexed and passed upstream untagged. Once again, when catches were large, sex ratios were determined from subsamples of 100 to 200 fish.

In 1965, there were daily collections of all sockeye and kokanee dead in the stream. The tag number (where present) and orbit-hypural length were recorded for each dead fish. The tag data was used to determine the length of stream life of fish entering each day.

Surveys of the distribution of spawners with Four Mile Creek were made by observers walking quietly along the stream banks. Separate counts were made of the fish in each of 56 m (100 ft) stream sections.

Behavioural observations were made on fish spawning, under natural conditions, in Four Mile and, to a lesser extent, Gullwing Creek. Spawning sockeye and kokanee are rather insensitive to disturbances and, when approached with care, return to their normal activities within a few minutes. Most observations were made at a distance of less than three meters, from the stream bank or from platforms (Four Mile Creek only) overlooking favourable observation areas. Observations were of two kinds:

1) Detailed observations during which all the classifiable activities of individual fish were recorded for known time periods, generally five min.

2) General observations during which only activities of special interest were recorded.

In 1966, six pens were placed in Four Mile Creek. Each enclosed an area 1.2 m by 1.8 m (4 ft by 6 ft) and was designed to prevent the occupants from viewing anything in the stream outside. The 1.2 m (4 ft) high walls were of plywood fringed along the bottom with a 0.6 m (2 ft) depth of 2.5 cm (1 inch) square mesh, hardware cloth. The hardware cloth, buried in the stream bottom, prevented fish from digging their way out. Water entered the pen at the upstream end and left at the downstream end through a system of vertical wooden baffles screened by hardware cloth. The fish were viewed from a catwalk placed alongside the pens.

In 1966, a comparison was made of the nests of kokanee and sockeye. Linear measurements of nest excavations were made with a meter stick; current measurements with a Gurley Pygmy current meter. After measurement, the nests were marked with a numbered stake which was used to relocate the site after spawning was complete. Gravel permeability readings were made in the completed nest with the apparatus described by Terhune (1958). A gravel sample was then removed with a shovel and stored in a burlap sack for later analysis. Gravel seive-analysis was done by Terra Engineering Laboratories, Victoria, B. C.

RESULTS

Seasonal periodicity of stream entry

There was broad overlap in the seasonal periodicities of stream entry of sockeye and kokanee (Fig.11). In each of the three years, fish of both forms began moving into Four Mile Creek in late July or early August and their numbers increased rapidly thereafter. Most of the large daily movements of sockeye and kokanee occurred between August 1 and August 15 and the midpoints of the runs were reached on or before August 10. Despite these broad similarities, there were sometimes marked differences in day-to-day fluctuations in the numbers of the two forms suggesting that their upstream movements were largely independent of one another.

Male sockeye (other than the three year olds known as jacks) and male kokanee tended to enter the stream earlier than females. In 1965 and 1966, the 50th percentile of the total run of male kokanee entered Four Mile Creek 2 to 3 days before the 50th percentile of the total female run (Fig. 11). The upstream movement of the 50th percentile of the run of large male sockeye preceeded that of females by a day in 1965 and 1966. The 1964 data for sockeye are less complete but they suggest a similar sexual difference in the time of stream entry. In contrast to the larger males, jack sockeye tended to move into the stream later than the females; two days separated the 50th percentiles of the jack and female sockeye runs in 1965 and seven days in 1966. Very few jacks were present in 1964.

During the latter part of August, the numbers of sockeye and kokanee entering the stream declined to low levels. In each of the three years, the kokanee run was over by September 1, though sockeye continued to enter in

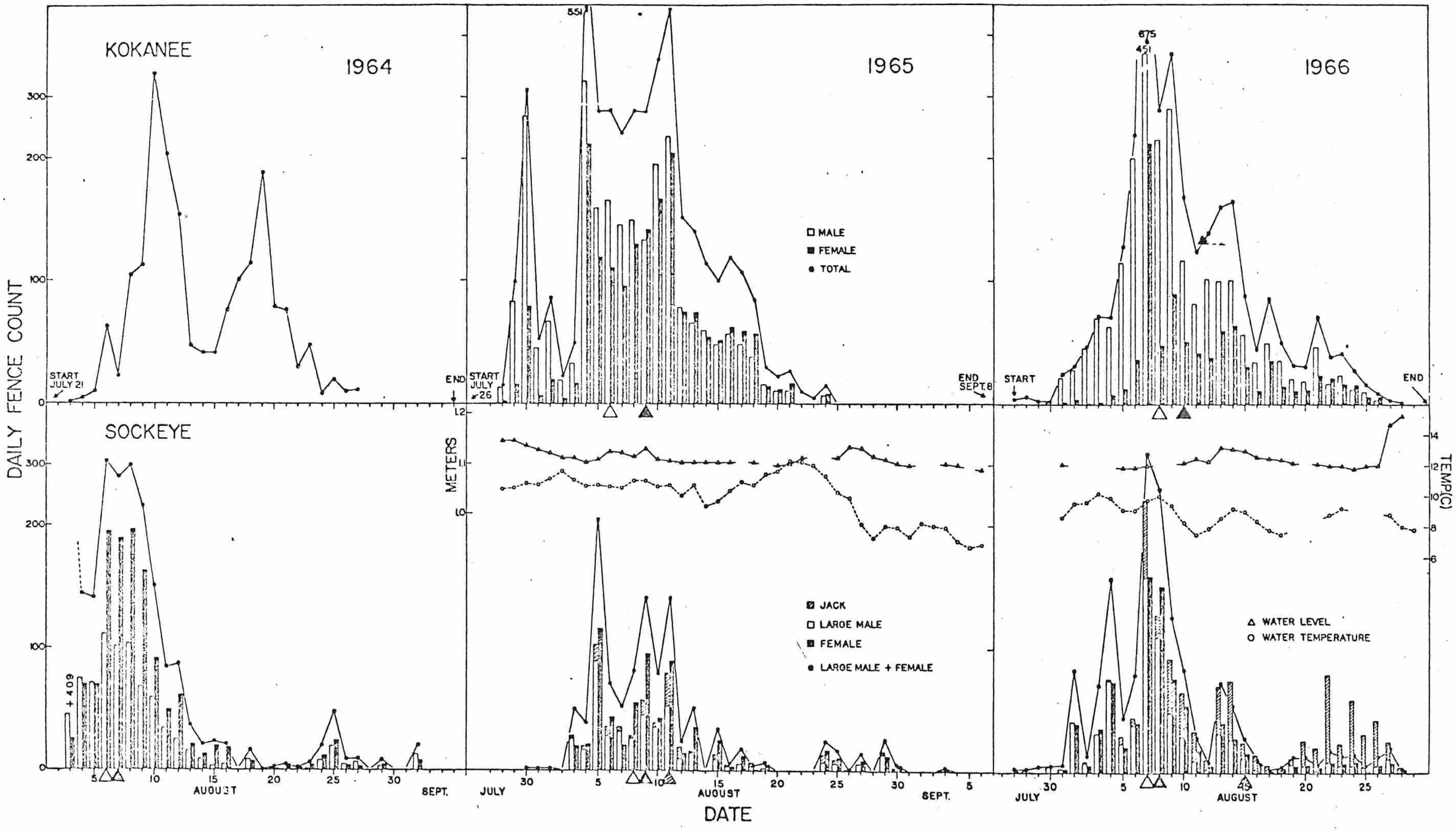


Figure 11. Seasonal periodicity of stream entry of sockeye and kokanee at Four Mile Creek, Babine, 1964-1965. The large triangles indicate the mid-point of stream entry of males (white triangles) and females (black triangles). For sockeye, the mid-point of the jack run (cross-hatched triangle) is shown separately from that of older males. Also shown (1965 and 1966 only) are seasonal fluctuations in water level and main daily water temperature.

small numbers. In 1964, 1965 and 1966 there were small, late runs of up to 200 sockeye which entered the stream early in September after the fence had been removed. These were not accompanied by kokanee and were not counted or included in this analysis.

Effect of low water on fish movements

There was evidence that kokanee were able to enter and utilize streams and areas of streams which were unavailable to sockeye due to shallow water or to obstructions. In 1965 and 1966 kokanee entered Gullwing Creek 7 to 10 days before sockeye. Though sockeye were present off the stream mouth and made repeated attempts to enter the stream, they were unable to do so because of a shallow-water obstruction near the mouth. It was not until the author and others rechannelled the stream that any sockeye were able to enter. There were similar obstructions further up the same stream which also blocked sockeye though not kokanee.

In 1967, a beaver dam across Twain Creek blocked all but a few sockeye from the upper third of the stream. Kokanee, in contrast, were common above the dam. Kokanee are able to wriggle through the interstices of beaver dams; sockeye, particularly males with their large, dorsal humps, experience great difficulty. Dead, unspawned sockeye are often found caught up in beaver dams. Dams are common on some early streams, particularly those lying on the west side of the lake between Pinkut Creek and the Fulton River, and must be repeatedly blasted to permit sockeye access to spawning areas lying upstream.

State of maturity of spawning fish at time of stream entry

In 1965, the state of maturity was recorded for each of the fish captured at the Four Mile Creek trap. Fish were judged ripe if sex products could be expressed by gentle pressure on the abdomen. There were three distinct trends (Fig. 12). First, for both sockeye and kokanee, a distinctly higher proportion of males than females were ripe at the time of stream entry. Second, for both males and females, proportionately more sockeye were ripe than kokanee. Third, except for male sockeye, most of which were ripe throughout the run, the proportion of ripe fish in each group tended to increase seasonally.

Length of stream life

In 1965, 83% of all tagged sockeye and 61% of all tagged kokanee were recovered as dead fish during the course of daily stream surveys. There was a marked seasonal decline in the average stream life of both sockeye and kokanee (Fig. 12). This decline was approximately linear in form. Covariance analysis revealed no significant difference between the sexes in either sockeye (sample, 290 males and 360 females) or kokanee (676 males and 470 females) in the mean stream life of males and females entering the stream on the same day and data for the sexes have been combined. However, the combined sample of kokanee had a significantly longer stream life than sockeye entering the stream on the same day. The overall average stream life of kokanee was 12.9 days; of sockeye, 10.8 days.

Distribution of spawning sites within streams

Both sockeye and kokanee ascended Four Mile Creek as far as the impassable falls and there were no important differences in their general distributions within the stream (Fig. 13). However, there were some differences

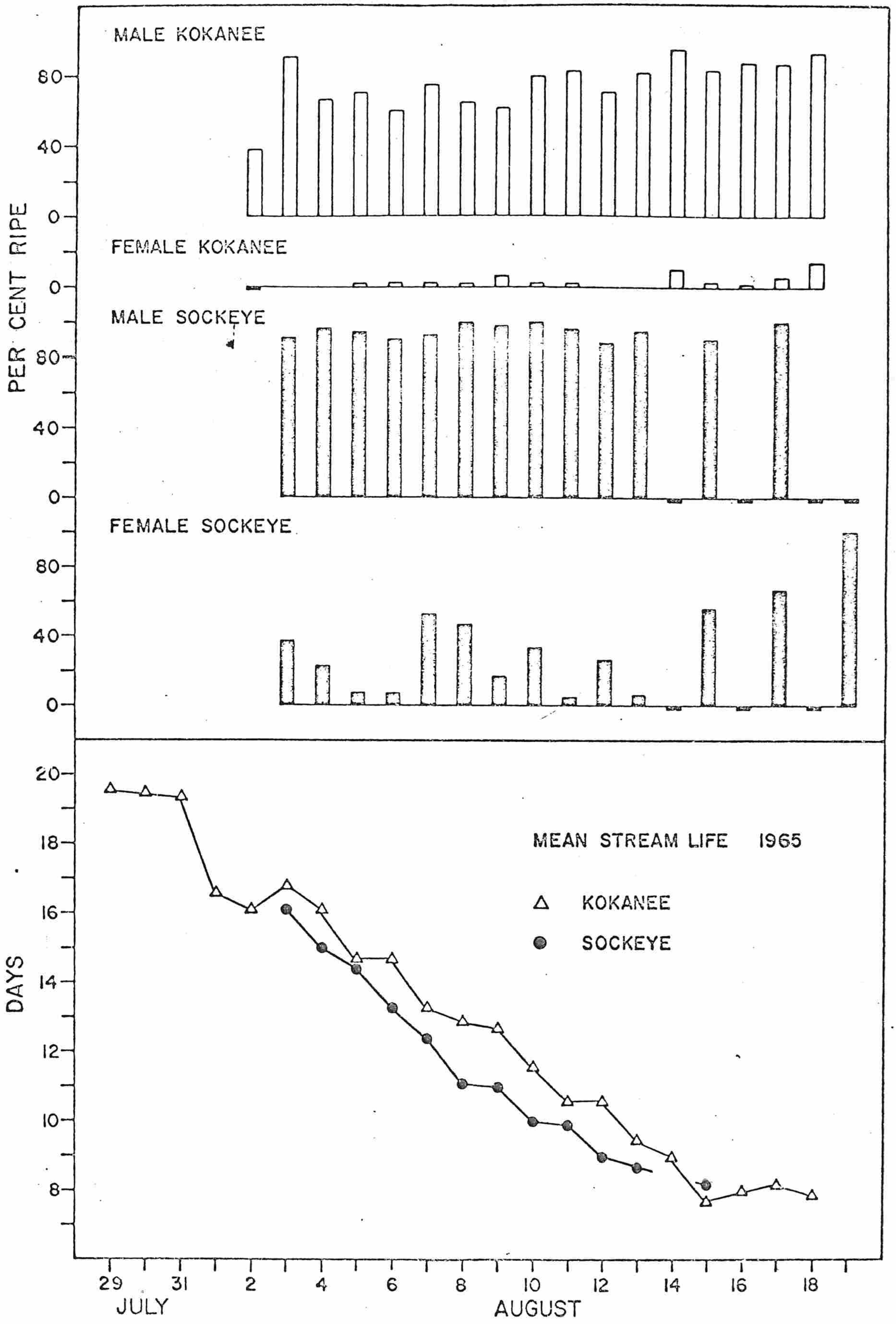


Figure 12. Seasonal changes in the proportion of ripe fish and mean stream life of fish entering Four Mile Creek during 1965. Data was included only for those days for which data for five or more fish were available. Horizontal bars indicate insufficient data available.

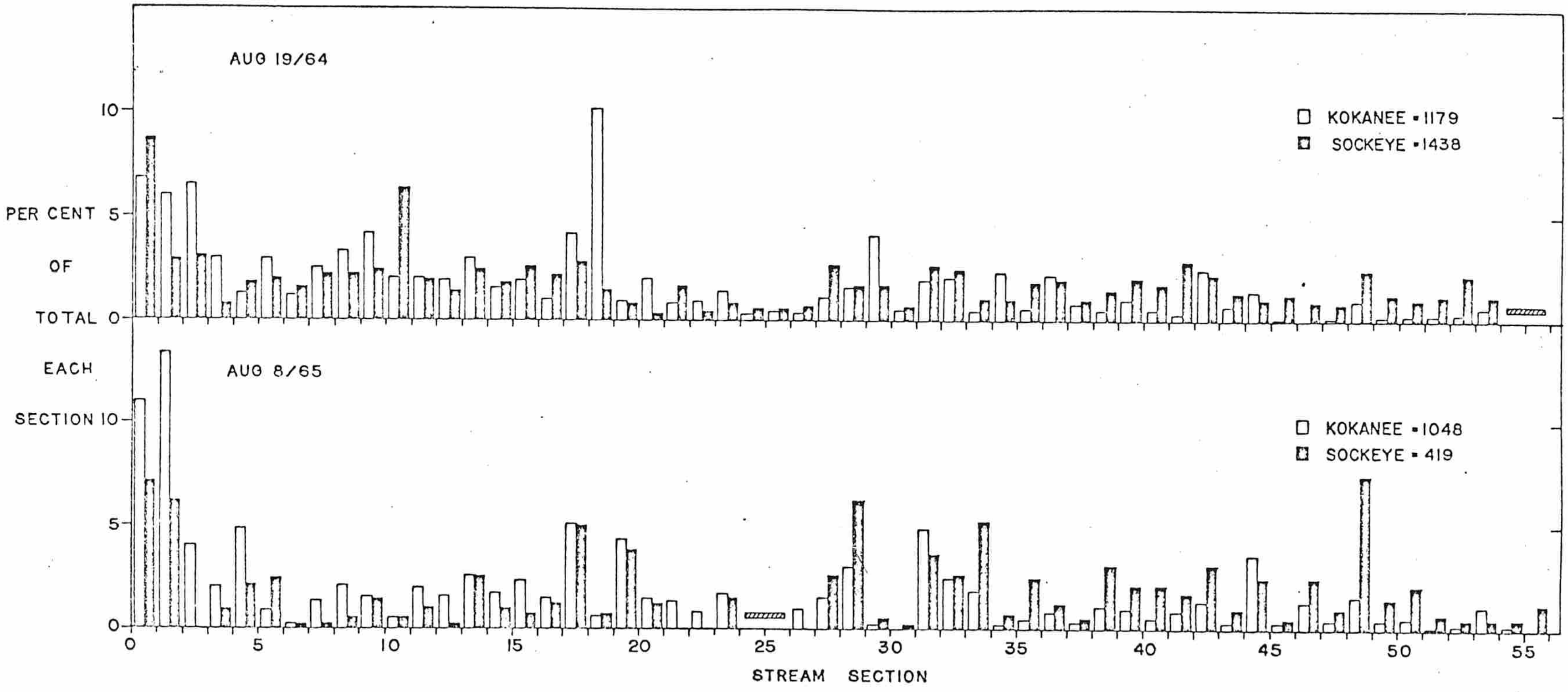


Figure 13. The distributions of sockeye and kokanee in Four Mile Creek on August 19, 1964 and August 8, 1965. The cross-hatched horizontal bars indicate no data available.

in the characteristics of their spawning sites (Table XIV). Female kokanee tended to spawn in areas of low water velocity - along the edges of the stream, in pools and behind large boulders. The mean water velocity over the sockeye nests examined (21.9 cm/sec) was almost twice that over the kokanee nests (11.3 cm/sec). There were other, associated differences. Typical kokanee nests contained a greater proportion of fine material (Fig. 14) and gravel permeabilities in kokanee nests were lower (Table XIV).

There was no indication that kokanee were influenced in their choice of spawning site by the presence of spawning sockeye. In 1965 and 1966, years of low water, kokanee entered Gullwing Creek 7 to 10 days before sockeye. Female kokanee in the early group spawned in situations similar to those selected by kokanee associated with sockeye.

TABLE XIV. Characteristics of sockeye and kokanee spawning nests measured at Four Mile Creek, 1966.

	Sockeye (N=25)	Kokanee (N=14)
Depth of Water (cm)		
Min	9.7	5.2
Mean	16.9	13.9
Max	41.0	25.5
Velocity of Water (cm/sec)		
Min	0.0	4.3
Mean	21.9	11.3
Max	57.9	18.9
Permeability of Gravel (cm/hr)		
Min	100	0
Mean	23,000 (N=24)	9,000
Max	92,000	27,000

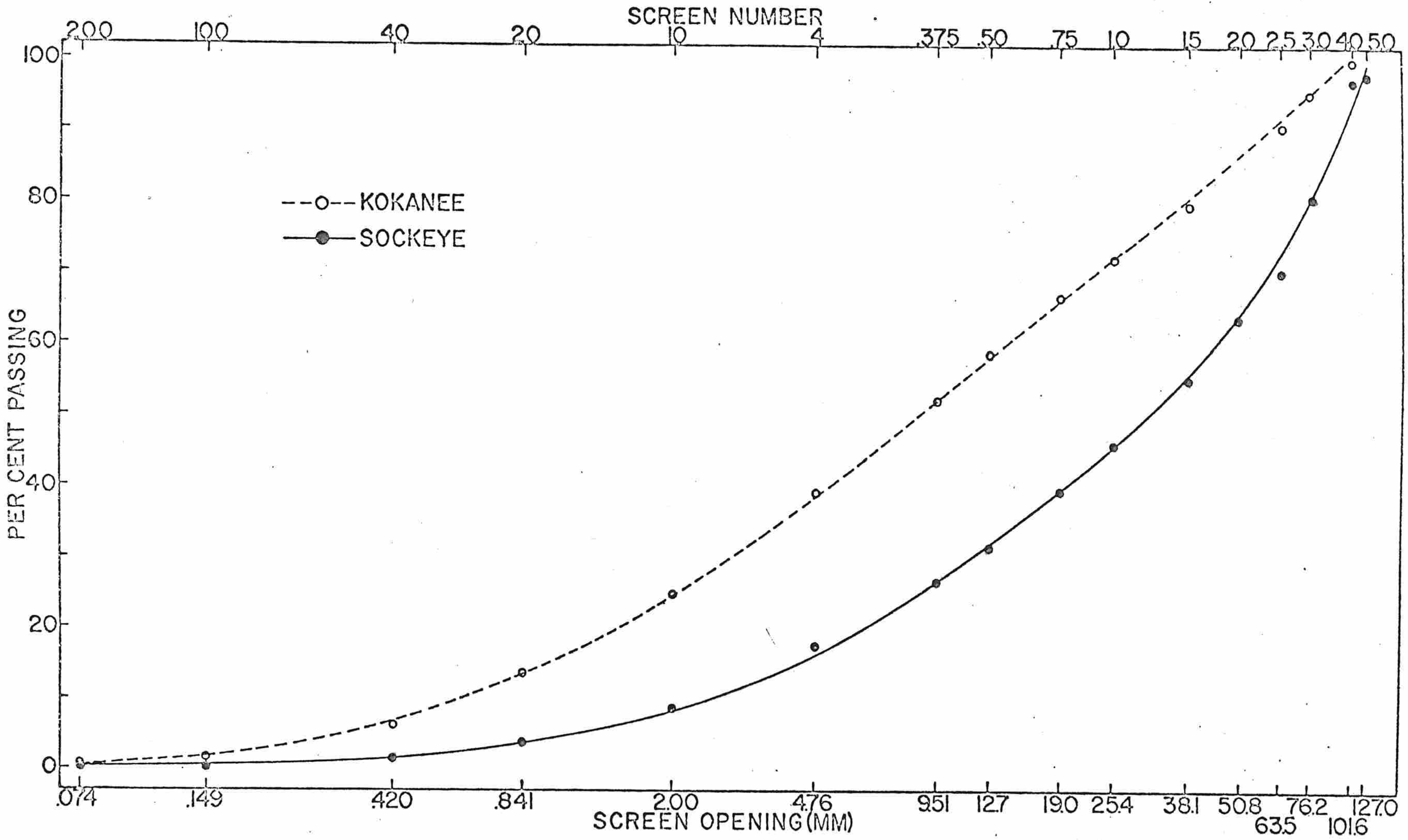


Figure 14. Grading curves of gravel taken from sockeye and kokanee spawning nests, Four Mile Creek, 1966. The points indicate the per cent of the total material passing through each screen. The curves were fitted by eye.

Prespawning behaviour

Composition of mating groups

Mating groups were sometimes complex. The nucleus of the group consisted of a female and a "dominant" male. The latter played the major role in prespawning courtship and in the actual spawning act. There were usually, in addition, a number of "accessory" males ranged in a semicircle about the principal pair. (The terms dominant and accessory are those used by Shapavalov and Taft, 1954.)

In 1966, the male attendants of 60 active female sockeye were recorded: 13 females observed on August 4, early in the run, and 48 on August 14 at mid-run (Table XV). Only one of these females was entirely unaccompanied by males. Fifty-eight of the dominant males were large, four- or five-year-old sockeye; one was a jack. All of the accessory males observed on August 4 were kokanee, an average 4.6 per female. By August 14 a large number of jacks had entered the stream and these, along with a few larger sockeye, were also found in accessory positions. At the same time, the average number of accessory kokanee males had fallen to 1.9. This probably reflects a declining surplus of male kokanee as more females, both sockeye and kokanee, entered the stream.

Female kokanee were most commonly accompanied by kokanee males, although the occasional pairing of female kokanee and jack sockeye was seen. Of 31 territory-holding, female kokanee observed in Four Mile Creek on August 18, 1966, 26 were attended by a dominant male kokanee and 2 by dominant jack sockeye. Three females were entirely unaccompanied. Seven of the 28 mated female kokanee had one additional accessory attendant, 3 had 2 accessory males and 1 female had 3. All the accessory males accompanying female kokanee on

TABLE XV. Numbers of accessory males observed attending actively digging female sockeye in Four Mile Creek, 1966.

Date	No. of females observed	Identity of males	Number of accessory males attending each female											Mean
			0	1	2	3	4	5	6	7	8	9	10	
August 4	13	kokanee	2		4		2		2	2	1		1	4.61
August 14	48	kokanee	7	18	9	7	4	2	1					1.95
		Jack sock.	36	12										0.25
		large sock.	44	4										0.08

this occasion were kokanee. During the entire study, only one instance was recorded of a jack sockeye accessory to a kokanee pair. The average number of accessory males per female kokanee, 0.5, was much lower than the number attending female sockeye four days previously. At Gullwing Creek, August 17, 1966, 24 of 38 active female kokanee were accompanied, all by male kokanee. The other fourteen females were mateless even though there was an abundance of male kokanee in the stream.

Behaviour of females

During the prespawning period, female sockeye and kokanee are almost entirely engaged in the preparation of the spawning nest and in aggressive activity associated with the defence of the area around the nest. The nest building behaviour of this species has been described by McCart (1969). Whe complete the typical nest is an oblong depression with its long axis parall to the current. There is a mound or tail-spill below the downstream end consisting of excavated material. Sockeye nests are larger, in every respect than those of kokanee.

The aggressive activities of females defending a nest take a variety o forms: threats, chases, bites, etc. These classifications grade into one an other and in this analysis they have been lumped as "aggressive acts".

Most aggressive acts end when the fish under attack swims off, before any contact is made. When contact is made, this usually takes the form of a butt with the snout rather than a bite. Sometimes, however, females do bite and hold. Opponents of a size similar to that of the attacking fish are us held by one of the fins or by the caudal peduncle. Smaller fish are often h sideways in the mouth. Female sockeye frequently held male kokanee and jac sockeye in this manner, sometimes shaking them for several seconds before release. No harm appears to result and the victims usually return to their normal activities almost immediately.

Female sockeye rarely attack dominant courting males. At Four Mile and Gullwing Creeks, such attacks were observed on only three occasions during 553 minutes of detailed observation, 0.9% of all attacks recorded (Fig. 15). Most attacks by female sockeye (73.8% of those recorded) were directed at males other than the dominant (Fig. 15), 54.8% against male kokanee, 7.5% against jack sockeye and 11.5% against larger male sockeye. A high proportion of the kokanee for which sex was unrecorded were probably also males. Most of the kokanee and jack sockeye attacked were accessory attendants of the attacking female, as were some of the large males. However, many of the latter were intruders passing upstream or swimming about, presumably in search of mates.

Females were most likely to attack accessory males either upstream or to one side of the nest. On one occasion, the direction of attack was recorded for a series of 108 attacks on male kokanee by a female sockeye. Fifty-two percent were made on fish alongside the nest, 37% on fish upstream, 9% on fish over the nest and only 2% on fish downstream of the nest when attacked.

Female sockeye often attacked other female sockeye (18.5% of all recorded attacks), particularly those holding territories in the same vicinity. It was against these that attacks of the highest intensity were launched, often while the victim was in the act of digging. Female kokanee were attacked occasionally (0.9% of all attacks) but were usually ignored. Attacks on female kokanee were not as vigorous as those on female sockeye. Female sockeye occasionally attacked trout (1.4% of all recorded attacks).

Figure 15. The figure illustrates: (a) The participants in the aggressive activities of various categories of spawning sockeye (S) and kokanee (K). The vertical columns indicate the per cent of aggressive attacks made on (white columns) or received from (black columns) each categories of secondary participants listed at the bottom of the figure. (b) The identity of participants in mutual lateral display. The vertical columns indicate the per cent of total mutual lateral displays which were performed with the categories of fish listed at the bottom of the figure.

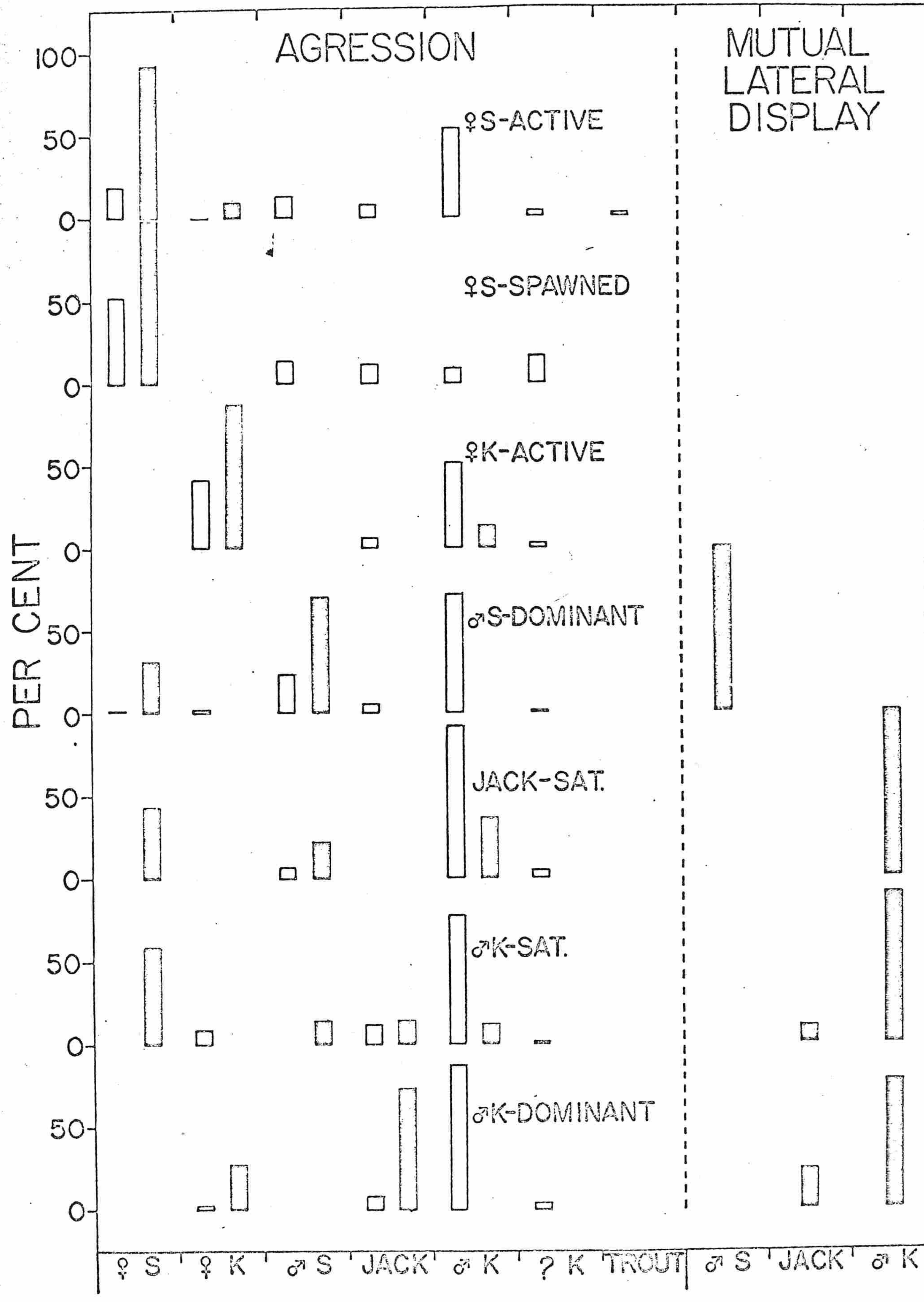

AGRESSION
MUTUAL LATERAL DISPLAY
PER CENT
100
50
0
♀S-ACTIVE
♀S-SPAWNED
♀K-ACTIVE
♂S-DOMINANT
JACK-SAT.
♂K-SAT.
♂K-DOMINANT
♀ S
♀ K
♂ S
JACK
♂ K
? K
TROUT

TABLE XVI. Frequency of various activities of sockeye and kokanee during the pre-spawning period. The frequencies are given as the average number of occurrences in each five-minute period.

	Total Observation Period (min)	Quivers	Dashes	Attacks Made	Attacks Received
Active Female Sockeye	533	0.0	-	3.1	0.2
Dominant Male Sockeye	463	2.4	-	1.9	0.2
Accessory Jack	214	0.2	1.1	1.0	1.0
Accessory Male Kokanee	212	0.4	1.1	2.5	1.0
Active Female Kokanee	337	0.0	-	2.5	0.2
Dominant Male Kokanee	164	0.3	-	1.6	0.3

Female sockeye guarding nests were not themselves attacked as often as they attacked other fish. They made 3.1 attacks per 5 min period but received only 0.2 (Table XVI). There is a general disparity in the rate at which attacks were made and received. This results primarily from the fact that the fish under observation were part of stable spawning groups while many of the fish attacked were transients. No data were recorded for the latter, but they were generally not aggressive. Dominant male sockeye occasionally attacked their female partner but accessory males were never seen to do so even though subject to continuous harassment. Almost all the attacks on female sockeye came from other territory-holding female sockeye in the immediate area: 90.9% of all recorded attacks received by female sockeye. Occasionally (9.1%), a female sockeye was attacked by a female kokanee.

Female kokanee rarely attacked sockeye larger than jacks. None of the female kokanee whose behaviour was recorded in detail attacked female sockeye, but, as indicated, such attacks were observed during the course of detailed observations of female sockeye. The most vigorous attacks were made on other female kokanee (40.7% of those recorded) but the most numerous attacks were made on male kokanee (51.5%). Attacks on jacks accounted for 5.4% Almost all the males attacked were accessories or intruders.

Behaviour of dominant males

At rest, the dominant male in any mating group was ordinarily positione closest to the female, downstream and slightly to one side, his snout at a level with her anal fin or caudal peduncle. Dominant males were the main participants in courtship behaviour. The most frequently observed courting activity was a quivering movement of low amplitude and high frequency. Typically, the male moved upstream alongside a female positioned over her nest until his snout was at a level with, or ahead of, her dorsal fin. At this point he stopped and quivered, his dorsal fin erect, its posterior edge usually twisted away from the female. Most quivers had a duration of about 1 sec. The dominant male sockeye observed (Table XVI) quivered more frequently (2.4 quivers per 5 min period) than did the dominant male kokanee (o.3 quivers per 5 min period). This may represent a real difference in the behaviour of the two forms or merely reflect differences in the spawning readiness of the individual fish selected for observation.

Dominant male sockeye and kokanee performed fewer aggressive acts tha their female counterparts (Table XVI). Of the recorded attacks by domina male sockeye, 98.1% were directed against other males: 70.6% against male kokanee, 22.5% against other large male sockeye and 5.0% against jacks.

On a few occasions (0.1%) dominant male sockeye attacked female soc eye (in each of the observed instances, their own mates). They also occasionally attacked neighbouring female kokanee (0.1%). Dominant male kokanee attacked other male kokanee 87.0% of the time and jacks 7.4% with a few attacks on female kokanee (1.8%). Attacks took the forms described for females.

Attacks on males of a size similar to that of the dominant male were often preceeded by a lateral display. (The lateral display of this species is described by Schultz and students, 1935, as the escorting act.) Only mutual lateral displays were recorded (Fig. 15). Dominant male sockeye only responded to lateral displays directed at them by sockeye of a size comparable to, or larger than their own. They either ignored the displays of smaller males or responded with a direct attack. Dominant male kokanee displayed with other male kokanee (77%) and with jacks (23%) but were not seen displaying with even the smallest, four-year-old sockeye.

Behaviour of accessory males

Detailed observations were made of the behaviour of jack sockeye and male kokanee accessory to female sockeye. No detailed records were kept of the behaviour of large male sockeye accessory to female sockeye or that of male kokanee accessory to female kokanee but there appeared to be no essential differences.

Accessory males were closely tied to their territories which seemed to be defined in relation to the position of the nest. They did not follow the female when she moved away from the nest for short periods of time but as the female moved upstream in building successive nests, they advanced with her. As a result, accessories often held the same relative positions over several days. They seldom left their territories except when chased or chasing or when dashing into the nest. Accessory males vigorously defended their territories against encroachment by other males. Though no quantitative data are available, it appeared that most vigorous and aggressive accessory males in any spawning group occupied preferred positions immediately downstream of the nest. They were thus close to the female and, at the same time, less subject to attack than accessories situated to one side or slightly upstream (see preceeding section on female behaviour).

The aggressive behaviour of accessory males took the same forms as that of dominant males. Male kokanee accessory to sockeye pairs attacked, in order of frequency, other male kokanee, jacks and female kokanee (Fig. 15). Jacks, less aggressive than male kokanee (Table XVI), attacked male kokanee most often with occasional attacks on the dominant male and other large sockeye males. No attacks on other jack sockeye were recorded during detailed observation but such attacks were observed incidentally on many occasions, especially late in the 1966 spawning season when jacks were very numerous.

Jack sockeye and kokanee accessory to female sockeye were more frequently attacked than any other group. Attacks came, in order of frequency, from the female herself, from other accessory males (jacks and kokanee) and from the dominant male sockeye and other large males (Fig. 15). Under natural conditions, accessory males usually avoided these attacks with ease and soon returned to their positions. In pens where the fish were narrowly confined and escape was more difficult, small males under attack by large spawning pairs assumed a distinctive submissive posture. They lay against the downstream end of the pen, head down and tail up at an angle of 30-40° to the bottom, quiescent except for slight movements of the operculum. In this posture, which they sometimes maintained for hours, they were rarely subject to attack. This submissive posture was observed only once in the stream, in an accessory male kokanee positioned alongside several large boulders preventing easy escape.

The frequency of mutual lateral displays (Table XVI) by accessory jacks (0.02/5 min) was much lower than that of accessory male kokanee (0.23/5 min). This probably resulted from the scarcity of other jacks in the spawning groups under observation and a disinclination on the part of the jacks to lateral display with kokanee males which were smaller.

A distinctive feature of the behaviour of accessory males, kokanee and jack, was their tendency to dash in under the bellies of the mating pair when either of these moved across the bottom of the nest. The mean number of dashes was the same for accessory kokanee and jacks, 1.1/5 min period. It seemed that the presence of a fish, regardless of sex, along the bottom of the nest was sufficient to excite the accessory males and they dashed in under the bellies of male and female indiscriminately. One accessory jack dashed under the female of a pair on 10 of 11 recorded occasions. Another jack dashed in under the male rather than the female on 10 of 14 occasions.

Often, one accessory male initiated the dash and was quickly followed b all the accessory males in the group. In the nest they tried to force themselves under the vent of the larger fish, as close to the bottom as possibl In constant danger of attack, they did not usually remain in the nest for m than a few seconds before returning to their territories. Field observation and an examination of cinefilm gave no indication that accessory males eith quivered or gaped while in the nest and no milt was observed in the water.

During periods when the dominant male was absent, an accessory male so times moved up alongside the female and assumed a dominant role. This was usually a large sockeye or jack but on one occasion a male kokanee repeatedly quivered beside a temporarily abandoned female sockeye. This was a very aggressive male which held a position directly downstream of the nest. Upon the return of the original dominant, temporary dominants invariably assumed their subordinate status.

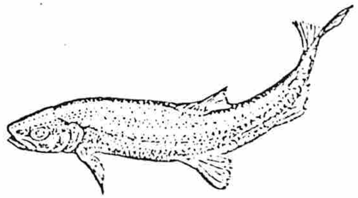
The spawning act

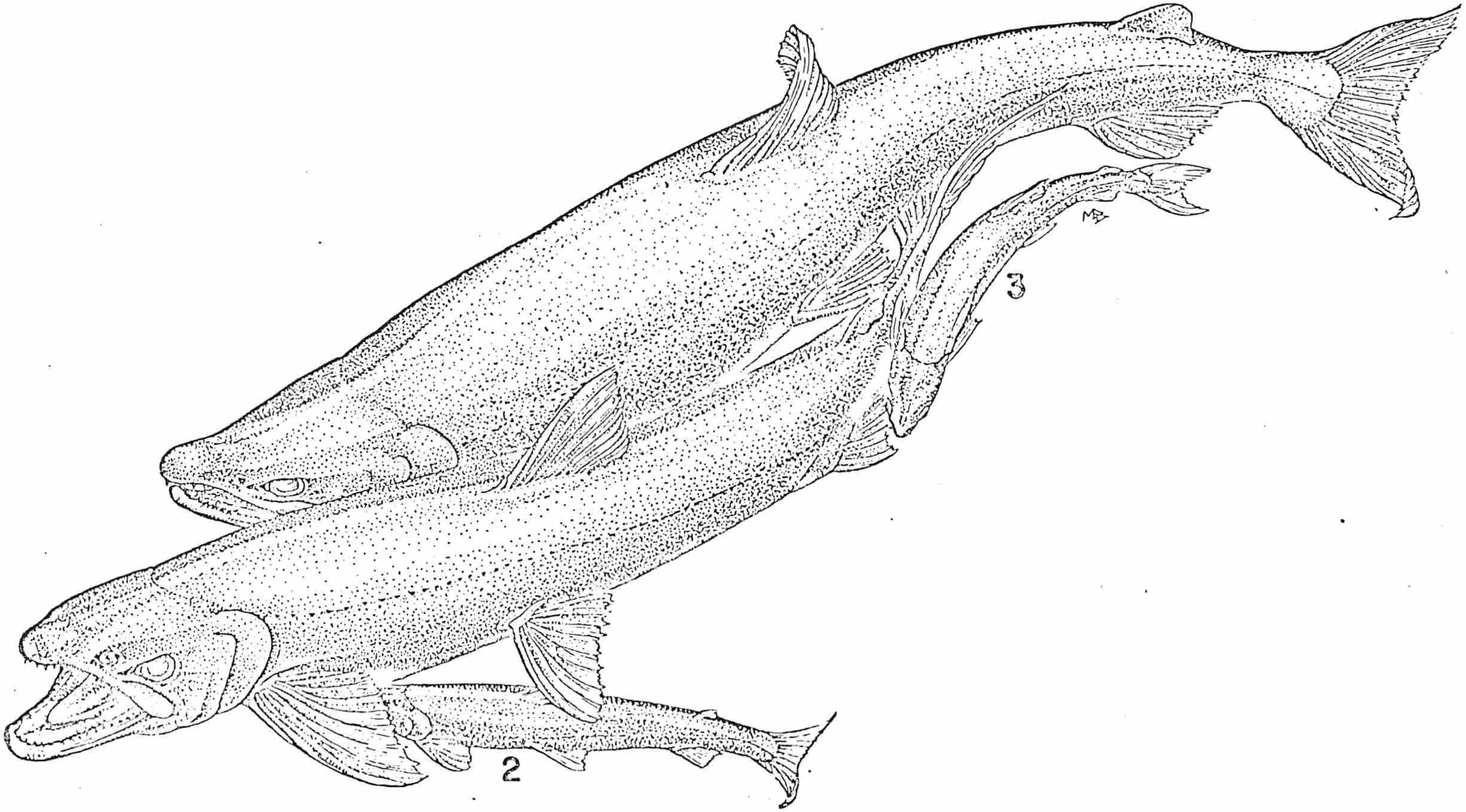
During this study, the spawning acts of five female kokanee and fourteen female sockeye (2 in pens, 12 under natural conditions) were observed. One spawning act, involving a male and female sockeye and six male kokanee was recorded on cinefilm.

The filmed spawning act took place in Gullwing Creek, August 13, 1966 at 1449 hr. A series of drawings have been prepared from the film to illustrate the main features of the spawning act (Fig. 16 a to e). The general disposition of all participants was traced from a projection of the film. For the sockeye, the positions of the fins and mouth (other than the position of the tongue which could not be observed) are as they appear. The fins of the kokanee could not clearly be seen and are shown in neutral positions in the drawings. Details of the head and body were added using preserved fish as a guide.

The participants were the male and female sockeye and six male kokanee. The timing of the orgasm of the two sockeye and four of the kokanee was determined from the film strip and is illustrated in Fig. 17. Also shown is point in the spawning act represented by each of the five figures. In the figures, the four male kokanee have been assigned numbers according to the order in which they were observed in orgasm. Two others, hidden for a time

Figure 16 (a to e). The spawning act. Explanation in text.




MB
3
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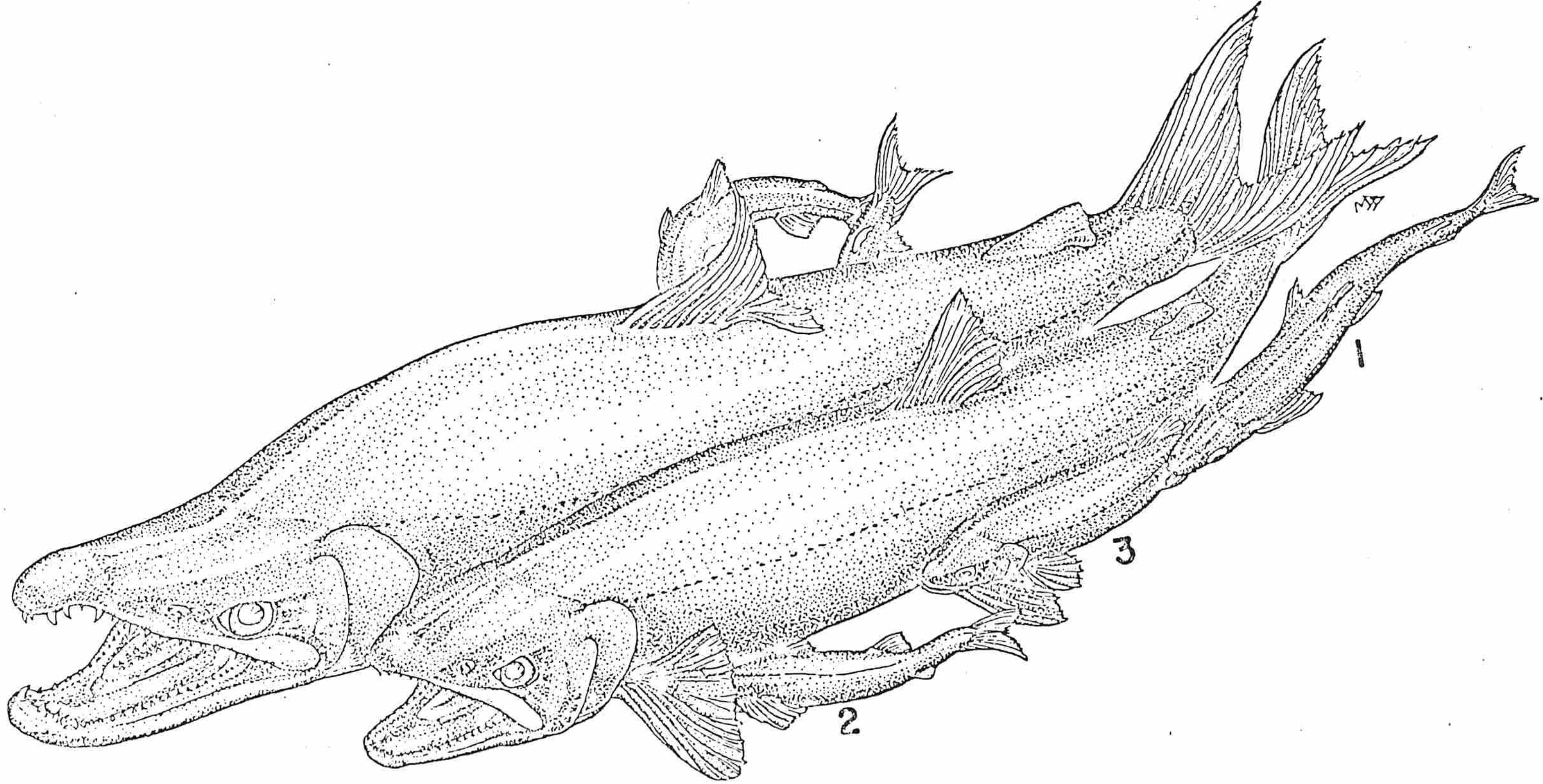


Figure 16b

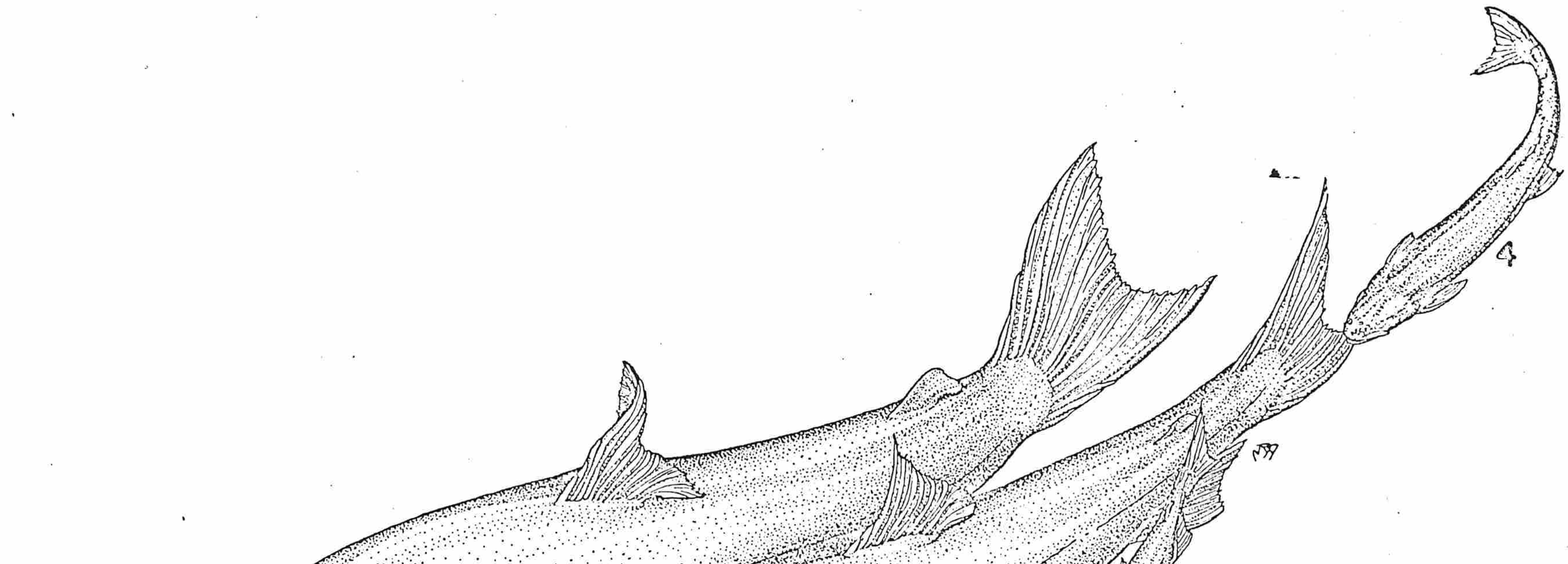


Figure 16

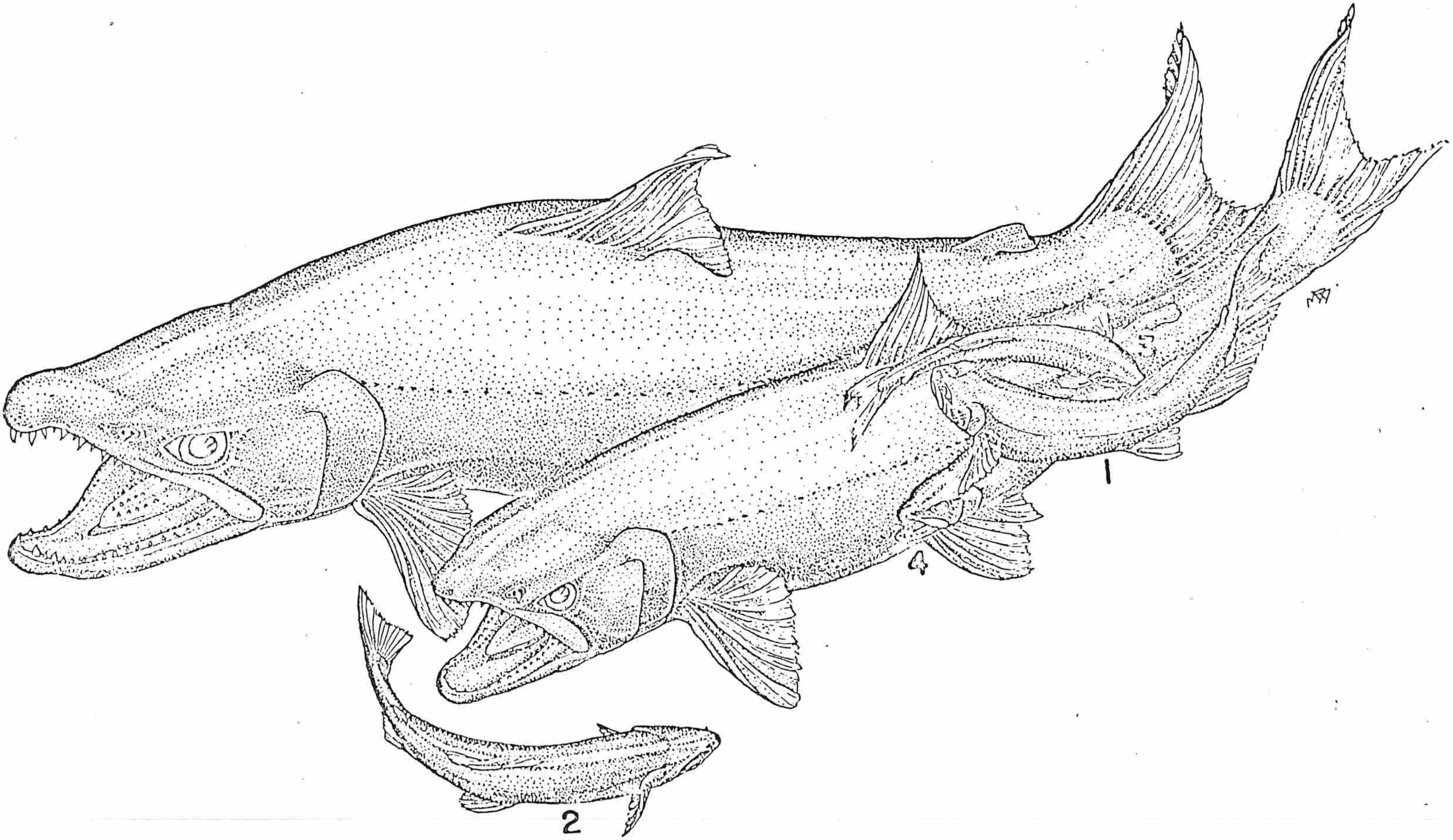
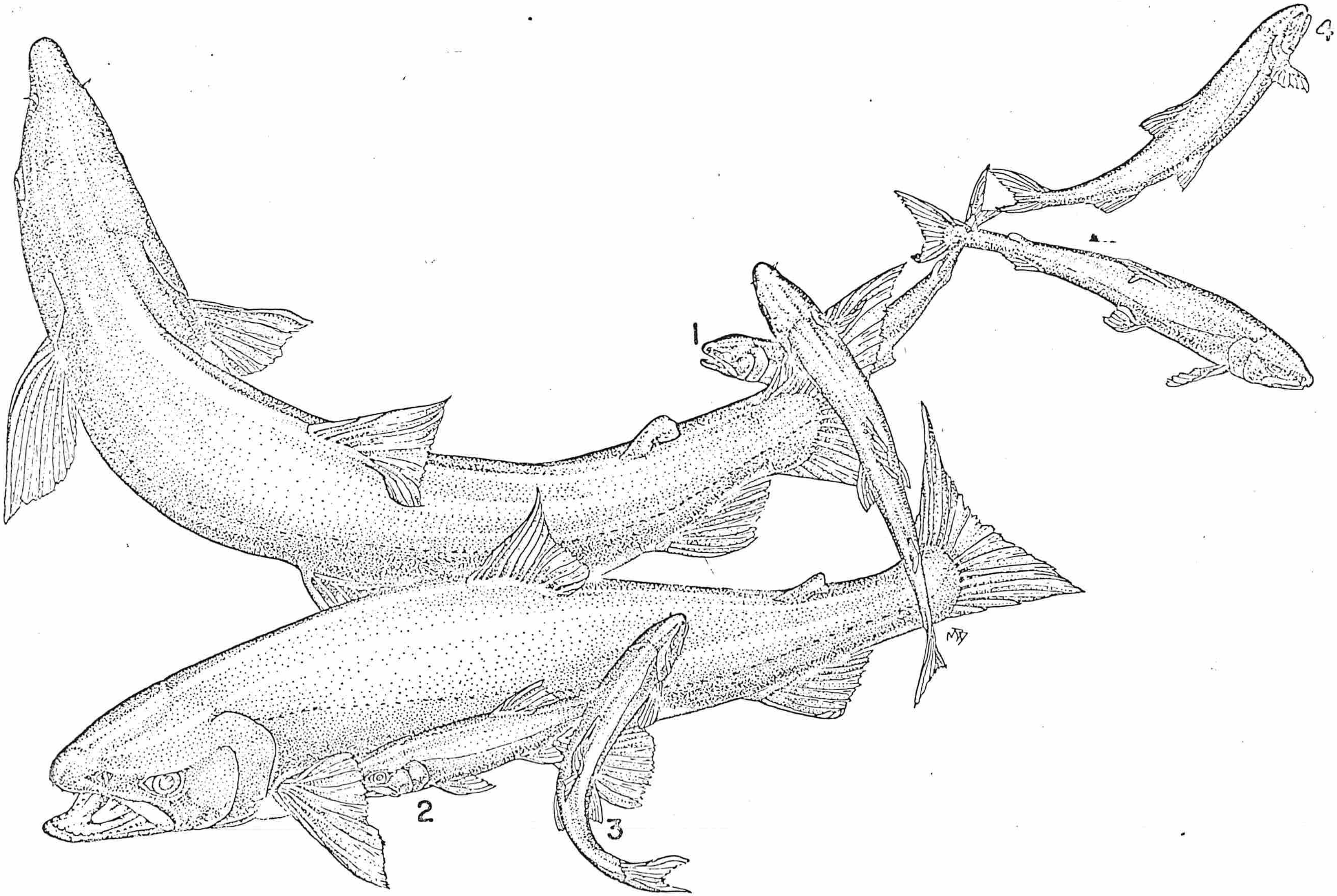


Figure 16d.


4
1
2
3

on the far side of the sockeye pair, were not observed gaping and are unnumbered.

Figure 16a. The female had taken up a stationary position in the bottom of the nest and was gaping widely as the male sockeye, mouth nearly closed, moved along her side. Three male kokanee were dashing in from their positions near the nest.

Figure 16b. The sockeye were side by side, both at full gape. Their bodies were vibrating vigorously causing their caudal fins to move laterally through an arc of 5 to 10 cm. The dorsal fin of the male, also vibrating, was twisted toward the female at its posterior edge. That of the female, though extended, did not appear to be either twisted or vibrating. The female's pectoral and pelvic fins were flexed, those of the male could not be seen in the film. One of the three male kokanee (number 2) on the near side had moved, on his side, under the pectoral region of the female. Two other kokanee could be seen disappearing under the male on the far side.

Figure 16c. The sockeye were as in the previous figure. The three kokanee on the near side (1, 2 and 3) were all gaping. It was not possible to determine whether their bodies were vibrating. A fourth kokanee (4) was dashing in toward the spawning group.

Figure 16d. The sockeye were still gaping but the vibration of their bodies had almost ceased. The male was now at a slight angle to the female, and his pectoral fin could be seen extended. One male kokanee (4) was still gaping. Kokanee males 1 and 2 were milling about with another unnumbered kokanee - one of those from the far side. Kokanee 3 could not be seen.

Figure 16e. The male sockeye was moving away from the female which was still gaping slightly. All six male kokanee were circling close to the female. At this point in the original film, a large cloud of milt hung over the nest.

The female remained stationary, mouth still partly open, for a short time after the male sockeye had left her side. She then moved back and forth over the bottom of the nest a few times. Such movements might serve to sweep eggs down into the gravel. It was not until almost ten seconds after closing her mouth that she made her first covering dig.

Other spawning acts were similar to the one just described except that in many instances, participating accessory males were closer to the vent of the female than those shown in Figures 16a to 16e. The female initiated the act by moving along the bottom to the center of the nest, stopping and opening her mouth. Males, dominant and accessory, reacted to females in this attitude by immediately moving along side.

All the dominant males observed spawning with female sockeye under natural conditions were medium- and large-size sockeye. No jack-female sockeye pairings were observed although these did occur in pens. Of the five female kokanee seen spawning, two were associated with dominant jack sockeye and three with dominant male kokanee. This proportion does not reflect conditions in the stream because considerable effort was expended in discovering jack-kokanee pairings.

Accessory males participated in almost all the spawning acts observed (Table XVII). Both sockeye (jacks and larger males) and kokanee participated as accessory males in the spawning acts of female sockeye. Only kokanee males were observed participating as accessories in those of female kokanee. However, Hanson and Smith (1967) report an instance, in Four Mile Creek, in shich a medium-sized, four-year-old male sockeye dashed in to participate in

TABLE XVII. Number of accessory males participating in spawning acts with female sockeye and kokanee.

	Number of accessory males										
	0	1	2	3	4	5	6	7	8	N	Mean
					With female sockeye						
Kokanee			1	6	1		2	1	1	12	4.2
Jack	7	5								12	0.4
Larger sockeye	9	3								12	0.2
TOTAL			1	3	1	2	2	2	1	12	4.9
					With female kokanee						
Kokanee	1		1	3						5	2.2

a spawning act involving a female kokanee, a dominant jack sockeye and three accessory male kokanee.

The gapes of the accessory male kokanee participating in the filmed spawning act were all quite short, the longest was less than 3 sec compared to about 6.5 sec for the dominant male (Fig. 17). No other accessory male were timed while gaping but the general impression was that they did tend to gape for a shorter time than dominant males. Male kokanee accessory to kokanee pairs and male sockeye accessory to sockeye pairs were observed releasing milt while gaping during the spawning act but no male kokanee accessory to a sockeye pair was actually seen to do so though gaping was often observe

Behaviour immediately after spawning acts

Immediately after a successful spawning act, females began to cover the nest. This process has been described by McCart (1969).

Dominant males generally lost interest in females immediately after spawning. Of 7 male sockeye for which data was recorded, 4 left the female within 5 min of spawning and 2 left 10-15 min after spawning. Only 1 remained with the female. Many wandering males eventually returned and began courting the same female preparatory to another spawning act. In contrast, accessory males did not usually abandon the female even temporarily after spawning. They hovered excitedly near the nest for 5 to 10 min after the spawning act, dashing in under the female whenever she moved across it. Whe the female began construction of a new nest, they assumed the same positio they had occupied relative to the old. Some individual male kokanee were observed occupying the same position with respect to a female sockeye for at least three days during which the female spawned several times.

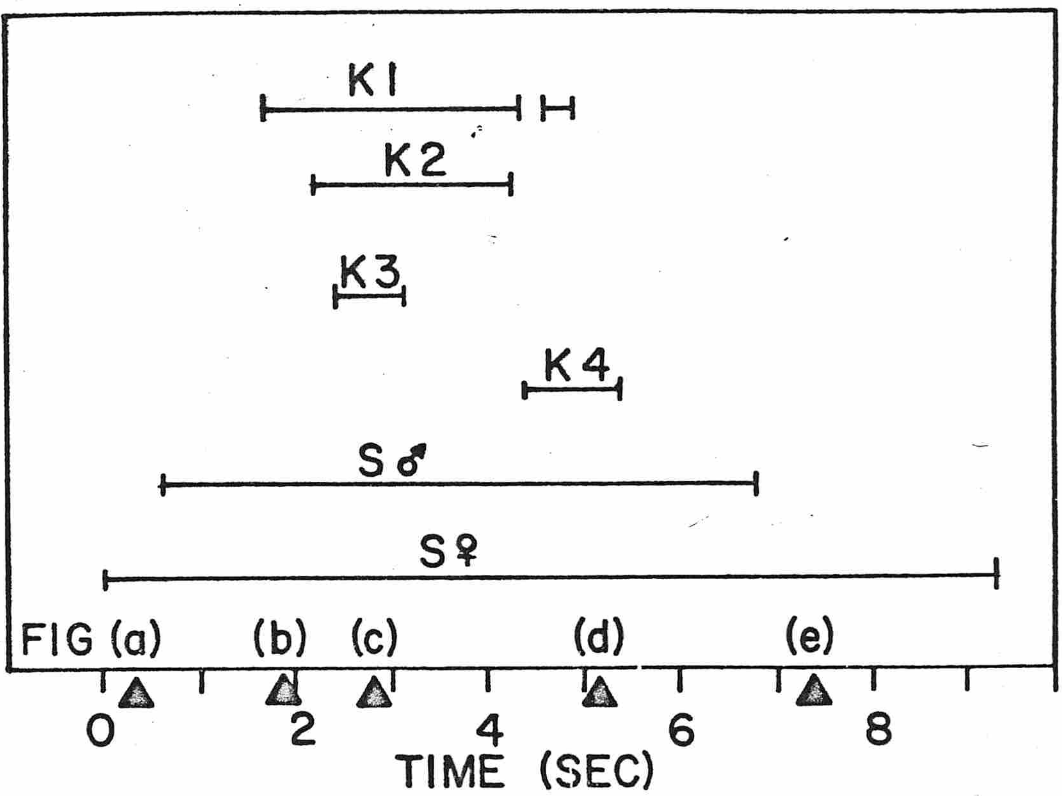


Figure 17. Duration of gape of various participants in the spawning act illustrated in Figure 16 (a to e). The triangles indicate the approximate point in the spawning act illustrated by sections a to e.

Behaviour of spawned-out fish

Females remained over the area in which they had deposited their eggs (the redd) for several days after they had completely spawned. The behaviour of spawned-out female sockeye was observed on a few occasions. Nest preparation ceased and they dug infrequently. They aggressively defended the redd from other fish, averaging 5.3 attacks in each five-minute period. Most of these attacks (51%) were directed at nearby females, the remainder at males, large and small, who ventured into the territory (Fig. 15).

Although dominant males soon abandoned spawned-out females, accessory males sometimes remained associated with them for several days before moving away. One female sockeye was still attended by four male kokanee and a jack a day after she had completed spawning.

Pen Experiments

In all the spawnings of female sockeye observed under natural conditions jack sockeye and male kokanee participated as accessory males. The primary purpose of the pen experiments was to determine whether, in the absence of large male sockeye, jack sockeye and male kokanee could assume a dominant role in relation to female sockeye and spawn normally.

The female sockeye used in these experiments were ripe but unspawned. When placed in the pens they began searching the bottom almost immediately and usually dug for the first time within a half hour. Six of seven females had completed a nest within 24 hr though one took nearly 72 hr. This behaviour was the same whether males were present or not.

Solitary females ceased almost all activity after the completion of the nest and lay quiescent near the nest, sometimes for days. However, when jacks or larger sockeye were introduced into the pen, the females soon resumed normal activity: digging, testing the substrate and, if these were present, attacking accessory males. On one occasion, a male sockeye and three male kokanee were introduced into a pen containing a quiescent female sockeye. The female resumed digging within the hour and, together with the large male, began attacking the kokanee. Unable to avoid attack, these soon assumed the submissive posture already described. The sockeye pair first spawned together approximately 10 hr after being brought together. A jack sockeye spawned with a previously quiescent female within 50 min of his introduction, another within 4½ hr. All three females were spawned out within 48 hr of the introduction of their mates.

The two jack-female sockeye spawnings were observed from a distance of 1 to 1.5 m. They appeared to be normal. In both instances, the jacks, which were 15 to 20 cm shorter than their mates, positioned themselves so that their vents were alongside those of the female. Three male kokanee were present in one of the pens. Only one of these participated in the spawning act, the others remained in the submissive posture.

The pen experiments clearly indicated that female sockeye could spawn normally with jacks. Experiments pairing female sockeye with male kokanee were less satisfactory but suggested that normal spawning acts, if they occurred at all, were achieved with difficulty.

When male kokanee were introduced into pens with quiescent female sockeye, the behaviour of the latter did not change: they continued to lie quietly near the nest, they almost never attacked the kokanee and they did not respond when the kokanee occasionally attempted courtship by quivering alongside. Normal male-female behaviour was not observed.

Two of three female sockeye penned with male kokanee eventually deposited their eggs but only after considerable delay. One did not deposit any eggs until the fifth day. On the ninth, when she was killed, she contained 20 eggs. The second female was unspawned on the eighth day but when examined on the ninth contained only 60 eggs. The third female, killed on the fifth day when she became badly fungused, was still unspawned. At the time they were placed in pens, these females appeared to be as mature as the three, mated to male sockeye, which spawned out within 48 hr.

Samples of eggs were removed from the pens of the two spawned females 15 days after the latter were killed. A total of 775 eggs were recovered from one pen, 373 from the other. In both instances, 75% of the eggs were still alive and fertile. Many of the deaths may have occurred subsequent to fertilization.

Apparently the kokanee had fertilized a large proportion of the eggs deposited by these females in spite of the almost complete absence of normal spawning behaviour and the long delay. Unfortunately, none of the spawnings was observed and it is not known how this came about.

DISCUSSION

Mayr's (1963) classification of pre-mating isolating mechanisms includes situations in which

a) Potential mates do not meet (seasonal and habitat isolation);
b) Potential mates meet but do not mate (ethological isolation);
c) Copulation attempted but no transfer of sperm takes place (mechanical isolation).

Mechanical isolation (c), as Mayr defines it, is not a factor in sockeye-kokanee spawning relationships.

Seasonal and habitat isolation

The Four Mile Creek data (Fig. 11) indicate that differences in the spawning season of sockeye and kokanee are not an important isolating mechanism. Though there are some differences in the seasonal periodicity of stream entry and the length of stream life, these are not great enough to bring about any more than minimal segregation. The greatest proportion of the spawning runs of sockeye and kokanee were in Four Mile Creek, in spawning conditions, at the same time. A similar situation prevailed at Gullwing Creek.

Briggs (1953) has suggested that size-influenced differences in choice of spawning site (habitat isolation) may have resulted in the genetic isolation of small, freshwater rainbow trout and large, anadromous steelhead. This has led to a high degree of spatial isolation between females of the two forms, i.e., the rainbow spawn in small tributaries, the steelhead spawn in larger streams. There are differences in the nest sites selected by sockeye and kokanee in Four Mile Creek (Table XIV) which are probably size-influenced. The most important consideration in nest site slection was probably gravel size.

Whatever the reasons for their choice, the average differences in the spawning habitats selected by female sockeye and kokanee did not result in distinct spatial segregation. Nests of the two forms were interspersed over the entire length of the stream and they regularly spawned in close proximity. This and the high mobility of the males suggest that, in the early streams at Babine Lake, habitat isolation is ineffective in preventing interbreeding between sockeye and kokanee.

In the absence of any effective seasonal and habitat isolation, potential mates can meet. We must next examine the behavioural relationships of sockeye and kokanee to determine if there are ethological barriers to mating. Mayr (1963) believes that these constitute the most important class of isolating mechanisms in animals.

Ethological isolation

At Four Mile and Gullwing Creeks, cross-fertilization of sockeye and kokanee might occur naturally in two situations: first, situations in which anadromous males, almost invariably jacks, mated with female kokanee; second, those in which accessory male kokanee participated in the spawning acts of anadromous fish. A third situation, in which male kokanee fertilized the eggs of female sockeye in the absence of male sockeye, was produced in the experimental pens but was not observed under natural conditions.

Matings of anadromous males and female kokanee were not common. In the survey conducted at Four Mile Creek, August 18, 1966, only 2 (6.4%) of the 31 active female kokanee observed were attended by jacks, both dominants. This is probably close to the maximum proportion of such matings that are likely to occur. Female kokanee were not particularly abundant in 1966 (approximately 890 entered Four Mile Creek) while the opposite was true of jacks. The 636 jacks constituted nearly 43% of all male sockeye entering Four Mile Creek. In years of low jack abundance, such as 1964 when only 8 jacks were observed, jack-kokanee matings must be very rare. Although jacks participated as dominant males in 2 of the 5 observed spawning acts involving female kokanee, this high proportion was the result of a diligent search for such unions. Probably few kokanee eggs are fertilized by anadromous males. As a result of the great disparity in the average fecundity of the two forms (Table X), the results of sockeye male-kokanee female crosses must constitute a very small percentage of the total egg deposition. They probably constitute an even smaller percentage of the young surviving to the emergent fry stage because of the likelihood that eggs deposited by female kokanee do not survive as well as those of female sockeye. The former are often deposited in shallow water areas (Table XIV), more subject to drying and freezing. Completed kokanee nests contain a higher proportion of fine material (Fig. 14) and gravel permeabilities are much lower (Table XIV). Such conditions have been found to contribute to increased pre-emergent mortality (Wickett, 1962).

Associations of male kokanee and female sockeye were very common. Two or more accessory kokanee participated in each of the twelve sockeye spawning observed under natural conditions (Table XVII) and almost every female sockeye in Four Mile Creek was attended by one or more male kokanee (Table XV).

The surplus of males in the kokanee population undoubtedly promoted such relationships. The behaviour of the accessory male kokanee (in common with that of accessory male sockeye) ensured that most of those associated with a particular female were present, and participated in the sexual act. During the spawning act itself, they dashed into the nest alongside and underneath the sockeye pair, gaped and presumably ejaculated.

At Four Mile Creek, accessory kokanee were repeatedly seen gaping alongside spawning sockeye although none was actually seen ejaculating sperm. However, male kokanee accessory to kokanee pairs were seen ejaculating sperm as were male sockeye accessory to sockeye pairs. The behaviour of these fish was in other respects similar to that of male kokanee accessory to sockeye pairs and it seems unlikely that the latter should gape and yet fail to release sperm like other accessory males. Jones and King (1952), investigating a comparable situation involving large anadromous Atlantic salmon and precocious parr, proved conclusively that the parr did, in fact, emit sperm. As participants in seven spawning acts involving anadromous females and large sterilized males, parr fertilized 97.7% of the eggs subsequently examined.

Males in an accessory role have been described for most of the nest-building salmonids that have been studied in the field (see Hanson and Smith, 1967, for a partial review). They are usually described as fish smaller than the dominant male, ranged below the spawning pair and darting in and out of the nest. There is little doubt that they fertilize some eggs. Successful fertilization by accessory males might have several advantages. Jones and King (1949) emphasize the importance of Atlantic salmon parr in situations, in which, for mechanical reasons, the dominant male fails to fertilize all the eggs. Accessory males might also serve fertilization should the dominant male prove sterile.

Jones and King (1952) point out that Atlantic salmon parr, which move right in under the female's vent, are actually in closer proximity to the unfertilized eggs than are large male salmon. This gives them an advantage in fertilization greater than their milt contribution would indicate, particularly when the large male fails to get deep into the nest or when the configuration of the nest is such that eddies do not facilitate the circulation of milt over the eggs. The behaviour of kokanee is similar in this respect and in some instances they might fertilize a disproportionately large number of eggs.

The failure of female sockeye to respond sexually to male kokanee does not necessarily indicate an incompatibility in their innate patterns of reproductive behaviour. At the same time, males and females of the two forms show obvious preferences in their spawning associations. Jack sockeye are much more likely to attend female sockeye as accessory males than to attend female kokanee as dominants. On August 14, 1966, 25% of the 48 female sockeye observed in a survey of Four Mile Creek were attended by an accessory jack and one was associated with a dominant jack (probably only temporarily). Four days later, when jacks were more abundant, only 6.4% of the 31 female kokanee observed were attended by jacks. Male kokanee also show a preference for associations with female sockeye. Female kokanee were accompanied by fewer accessory male kokanee (an average of 0.5 per female, August 18, 1966) than were female sockeye (1.9 per female, August 14, 1966). Fewer accessory male kokanee took part in spawning acts involving female kokanee (2.2 per act) than those involving female sockeye (4.2 per act). Also, nest-digging female kokanee were more likely to be entirely unattended by males (37% of those observed August 18) than were female sockeye (0% August 14) even though there was an apparent abundance of male kokanee in the stream. It appears that accessory males, sockeye and kokanee, are more likely to form associations with female sockeye rather than associations, even dominant ones, with female kokanee.

These data suggest that size selectivity plays an important role in the spawning relationships of sockeye and kokanee. It has already been demonstrated (Hanson and Smith, 1967) that at Four Mile Creek size is an important factor in the selection of mates by dominant male sockeye. Large dominant males are usually associated with large females. Smaller males tend to associate as dominants with smaller females or become accessory males ("satellite males" in Hanson and Smith's terminology). They found that small female sockeye are more likely to be unattended than were large females. Female kokanee are much smaller again than the smallest female sockeye so that one would expect them to attract fewer males.

An awareness of size differences would seem to be the obvious explanation for the observed pattern of mutual lateral displays (Fig. 15). Males rarely displayed with males smaller than themselves.

An awareness of size differences might also explain the behaviour of female sockeye toward certain classes of kokanee. They sometimes swam considerable distances to attack neighbouring female sockeye but seldom attacked nearby female kokanee (Fig. 15). Female sockeye did not ordinarily react to the courtship activities of male kokanee even when these were the only males present (pen experiments). They did, however, respond almost immediately to the courtship of jack sockeye. It is possible that the females in some way recognized jacks as males of their own kind. It is also possible that jacks exceeded some size threshold necessary to elicit normal spawning behaviour in female sockeye while male kokanee did not. The fact that the eggs of two female sockeye in pens were eventually fertilized by male kokanee suggests that female sockeye can mate with male kokanee if internal motivation is high enough. This is unlikely to occur under natural conditions because male sockeye are almost always present and the females seem able to delay spawning for many days until one becomes available.

Rate of hybridization

There is no direct method of determining the percentage of sockeye eggs fertilized by accessory male kokanee. Aside from the differences in growth resulting from differences in their life history, sockeye and kokanee at Babine Lake are very similar morphologically. Hybrids between them cannot, at present, be distinguished (Section II). However, if it is assumed that kokanee males participating in spawning acts are ejaculating sperm, the problem can be approached indirectly.

Kokanee testes weigh approximately 12% of those of sockeye (see Section I). The mean number of kokanee participating in the spawning acts observed under natural conditions was 4.2. This figure may be somewhat higher than the true average because of a tendency to select, for observation, those sockeye females which were well attended by kokanee. On the other hand, estimates of the average number of male kokanee attending female sockeye during nest preparation (4.6 on one occasion, 1.9 on another) probably underestimate the number of kokanee participating in spawning acts during that period. This is so because such estimates include poorly attended females, newly arrived on the spawning grounds, as well as those close to, or between spawning acts, which have accumulated a large retinue.

If 1.9 and 4.2 are reasonable limits for the mean number of kokanee participating in spawning acts with female sockeye then, in a spawning act in which only a single, large male sockeye participated, kokanee would contribute 18% to 33% of the total sperm to fertilize eggs. This assumes that sockeye and kokanee emit a comparable proportion of their total sex products at each orgasm.

In some spawnings more than one male sockeye participated. In such instances, the proportion of kokanee milt in the total quantity available would be less. On the other hand, in some years kokanee are far more abundant than they were in the three years of this study. In 1955, for instance, an estimated 1,000,000 kokanee, approximately 75% male, spawned in the early streams at Babine Lake (Johnson, 1958). In the same year there were only 7,600 sockeye in these streams. Under such extreme conditions, there were probably large numbers of male kokanee attending each female sockeye. Their combined milt contribution would be proportionately large. It is not known how many accessory males can attend a single female sockeye but one female observed in Shass Creek during 1966 was attended by at least 30 jack sockeye.

CONCLUSIONS

In conclusion, the evidence, though circumstantial, suggests that there is some interchange of genetic material between the sockeye and kokanee spawning in Four Mile and Gullwing Creeks. Jack-kokanee matings, though rare, were observed under circumstances which suggested that most of the kokanee eggs deposited would be fertilized by sockeye sperm. Male kokanee participated as accessories in almost all the observed spawnings of female sockeye and probably fertilized some of the deposited eggs. Spawning relationships of the latter sort were sufficiently common that, if even a small percentage of the sockeye eggs were fertilized by male kokanee, genetic differences between the two forms would be unlikely to persist in the absence of re-inforcement by a post-mating isolating mechanism such as hybrid inviability. Though there are differences in the spawning behaviour of sockeye and kokanee, these appear to be quantitative rather than qualitative in nature. There is no evidence of any fundamental incompatibility in the innate patterns of reproductive behaviour of the two forms. The demonstrated differences might as well result from environmentally induced differences in size.

SECTION IV

HOMING OF SOCKEYE AND KOKANEE DISPLACED FROM SPAWNING STREAMS IN THE MAIN LAKE REGION OF BABINE LAKE

INTRODUCTION

There is a large and growing body of evidence, most recently discussed by McCleave (1967), Hartman and Raleigh (1964) and Hasler (1966), that a high degree of reproductive homing is characteristic of salmonid fishes. However, Lindsey et al.(1959) and Frost (1963) have emphasized that some degree of straying has a long-term advantage in enabling a species to invade new areas, to repopulate old areas in the wake of local catastrophes and to respond immediately to abnormal spawning situations. A high degree of straying would seem to be advantageous to populations adapted to spawning in marginal areas subject to fluctuating environmental conditions and frequent catastrophe.

The situation in the early streams is one which might promote a high degree of flexibility in choice of spawning locality. In 1966 and 1967, a series of in-stream displacement experiments was performed to compare the homing of sockeye spawners from several early streams in the Main Lake Area of Babine Lake with that of sockeye from Pinkut Creek, a larger, more stable stream in the same area. In 1966, a number of similar experiments was performed with early stream kokanee.

MATERIALS AND METHODS

Fish used in the experiments were captured in two ways: in traps as they moved upstream or in a large beach seine set around groups of fish congregated off the mouths of spawning streams. Fish were tagged with numbered Peterson tags, approximately 2.5 cm (1 in.) in diameter for sockeye and 1.2 cm for kokanee. The tags were of various colours and shapes so that fish in each of the experimental groups could be identified on sight. At the time of tagging, fish were sexed and classified as either green or ripe. Ripe fish were those from which sex products could be expressed by firm pressure on the abdomen.

Control fish were released at the site of capture, immediately after tagging. Fish to be displaced were placed in a plywood tank approximately 120 cm wide, 240 cm long and 120 cm deep, half-filled with water. The tank was mounted on a barge. Water pumped from the lake was continuously sprayed into the tank and excess water drained through an overflow pipe. At the release site, displaced fish were dipnetted from the tank, a few at a time, and released in the lake. Fish displaced to the vicinity of streams were released as close to the mouth as possible.

During 1966, traps were operated at Pierre Creek and Four Mile Creek which prevented free access to these streams. Data was recorded for all tagged fish entering during the operation of the traps (July 21 to August 13 at Pierre Creek and July 21 to August 31 at Four Mile Creek). In addition, each of the other streams in the Main Lake Area was surveyed at regular intervals (every four or five days) throughout the spawning period. Pierre Creek and Four Mile Creek were also surveyed after the traps were removed. On each stream survey, as many tags as possible were recovered. Only data for tags whose description <u>and</u> number were recorded have been included in the results.

Tag recovery was easiest in the smaller streams surveyed (the early streams) and considerably more difficult in the two largest streams (Pinkut Creek and Fulton River). Tagged sockeye were more easily detected than tagged kokanee. The latter are much smaller than sockeye and, alive or dead, are more easily hidden under overhanging banks and under roots, rocks, etc.

Chi-square values were calculated from the original numerical data. In comparing the homing performance of displacement groups with that of their associated control group (Tables XVIII, XXIII), expected values for the homing of displacement groups were calculated by multiplying the per cent of recaptures of the associated control group taken in the stream of origin by the number of recaptures from the displacement group. In all other instances, expected values were calculated by multiplying the per cent characteristic of all groups included in the comparison by the total number of individuals in the particular groups being compared.

RESULTS

Sockeye Displacement Experiments

The results of the sockeye displacement experiments are summarized in Table XVIII.

Control Groups

The control groups (all those lettered "a") were released at the mouths of the streams at which they were originally captured. In 1966, the Pierre Creek (1a, 2a, 5a, 6a and 7a) and Four Mile Creek (4a) control groups consisted of fish taken in weir traps after they had voluntarily entered the stream. Overall, 266 (88.7%) of the 300 control fish released at Pierre Creek were recaptured in streams. Of the recaptured fish, 87.7% of the

TABLE XVIII Results of sockeye transfer experiments performed at Babine Lake in 1966 (Experiments 1 to 10) and in 1967 (Experiments 11 to 14). Method of calculating Chi-squares is described in the Materials and Methods section (p. 93). Blank in Chi-square column indicates no test made; dash indicates no significant difference in homing performance of control and displacement groups; single asterisk indicates a significant difference at p = 0.05; double asterisk indicates a significant difference at p = 0.01.

Sockeye Experiment	Group	Date	Stream of Origin	Site of Release	Distance (km)	Number Released	Recoveries in Streams											Chi-Square
							Fulton	Tachek	Sockeye	Forks	Pierre	Twain	Pinkut	4 Mile	Gullwing	Shass	Total	
1	1a	A4	Pierre	Pierre	0.0	50					36	7					43	
	1b	A4	Pierre	Fulton	22.2	50	3	4	6		15	1					29	**
	1c	A4	Pierre	Sockeye	15.4	50			35		8						43	**
	1d	A4	Pierre	Twain	3.8	50	1				14	22					37	**
2	2a	A5	Pierre	Pierre	0.0	50					47	1					48	
	2b	A5	Pierre	Pinkut	33.4	49			1		17	4	2	6		4	34	**
	2c	A5	Pierre	4 Mile	41.9	49					3	5	1	26			35	**
3	3a	A6	Gullwing	Gullwing	0.0	33	1					2		1	19	3	26	
	3b	A6	Gullwing	4 Mile	4.0	34						2	2	12	9	5	30	**
4	4a	A6	4 Mile	4 Mile	0.0	50					1		1	35	1	8	46	
	4b	A6	4 Mile	Pierre	41.9	50		1	3		17	8	1	9	1		40	**
	4c	A6	4 Mile	Pinkut	9.4	50							7	26			33	--
	4d	A6	4 Mile	Gullwing	4.0	50					1		1	30	6	1	39	--
5	5a	A8	Pierre	Pierre	0.0	50			1		43	3					47	
	5b	A8	Pierre	Fulton	27.2	50	13	2	7		6						28	**
	5c	A8	Pierre	Offshore 1	11.5	50			4		31	3					38	*
	5d	A8	Pierre	Offshore 1	11.5	50			22		16	1					39	**
	5e	A8	Pierre	Offshore 2	12.3	50			8		37	1					46	**
	5f	A9	Pierre	Twain	3.8	50			1		5	23					29	**
6	6a	A9	Pierre	Pierre	0.0	50			3		33	9					45	
	6b	A9	Pierre	Offshore 3	0.8	50	1				29	12					42	--
	6c	A9	Pierre	Offshore 4	1.6	50			1		27	11					39	--

TABLE XVIII (continued)

6	6d	A9	Pierre	Offshore 5	7.2	50					24	14		1			39	--
	6e	A9	Pierre	Offshore 6	8.0	50			1		19	10	2			1	33	*
7	7a	A11	Pierre	Pierre	0.0	50					34	3					37	
	7b	A11	Pierre	Offshore 5	7.2	50			1		21	10				1	33	**
	7c	A11	Pierre	Pinkut	33.4	50					9	5	9	2	2		27	**
8	8a	S2	Pinkut	Pinkut	0.0	50							28				28	
	8b	S2	Pinkut	Offshore 7	15.4	50							37				37	--
	8c	S2	Pinkut	Offshore 8	17.1	50							31				31	--
	8d	S2	Pinkut	4 Mile	9.4	50							24				24	--
9	9a	S3	Pinkut	Pinkut	0.0	50							30				30	
	9b	S3	Pinkut	Fulton	60.3	50	3				1		6				10	**
	9c	S3	Pinkut	Pierre	33.9	50					7		26				33	**
10	10a	S10	Pinkut	Pinkut	0.0	50							27				27	
	10b	S10	Pinkut	Fulton	60.3	50	2						3				5	
11	11a	J27	Pierre	Pierre	0.0	90			1		61	3		1			66	
	11b	J27	Pierre	Sockeye	15.4	91		1	5		37	9				1	53	**
	11c	J27	Pierre	Twain	3.8	90			3	1	40	12					56	**
12	12a	J28	Sockeye	Sockeye	0.0	75			39	1	12	3					55	
	12b	J28	Sockeye	Tachek	9.6	76		9	27		12	1		1			50	**
	12c	J28	Sockeye	Pierre	15.4	75			2		39	1					42	**
13	13a	J30	4 Mile	4 Mile	0.0	60		1						43	2	1	47	
	13b	J30	4 Mile	Gullwing	4.0	50	1				1	3		29	3	1	38	**
	13c	J30	4 Mile	Sutherland	8.8	50					1			28		7	36	**
14	14a	J31	Gullwing	Gullwing	0.0	40								2	26	3	31	
	14b	J31	Gullwing	4 Mile	4.0	40					2	2		5	15		24	**
	14c	J31	Gullwing	Offshore 9	0.8	41						1		6	26		33	--

Pierre Creek and 76.1% of the Four Mile Creek fish had repeated their initial choice (overall mean, 85.7%). Most of the control fish recaptured in streams other than the stream of origin had moved south, 23 (83.2%) of the 27 strays from Pierre Creek were recaptured in Twain Creek and 8 (72.7%) of the 11 strays from Four Mile Creek were recaptured in Shass Creek (81.6% overall).

All other displacement experiments involved sockeye seined off the mouths of streams before they entered to spawn. In 1966, there was only one experiment of this kind (Experiment 3), involving early stream fish. In 1967, all experiments were performed with fish seined off the mouths of early streams. In total, 298 control fish were seined and released. Of these, 225 (75.5%) were recaptured in streams, 83.6% in the stream of origin. There was no significant difference between trapped and seined early stream control fish in the proportion of recaptures made in the stream of origin ($\chi^2 = 0.0$, $p > .05$). Like those taken in traps; the seined control fish recaptured in streams other than the stream of origin had tended to move south, 27 (73.0%) of a total of 33.

The Pinkut Creek transfers also involved fish seined off the mouth of the stream. Two control groups were released (8a and 9a), a total of 100 fish. Of these, 58 (58.0%) were recaptured in streams, all in Pinkut Creek itself.

Table XIX summarizes the results of releases of control fish for early streams in 1966 and 1967 and for Pinkut Creek in 1966 irrespective of method of capture. Chi-square comparisons revealed no significant difference between the three groups in the proportion of stream recaptures recovered in the stream of origin.

The behaviour of the control groups indicates that most of the fish

TABLE XIX Comparison of the homing performance of control and displacement groups of early stream (E.S.) for 1966 and 1967 and Pinkut Creek for 1966 sockeye.

	Numbers of Control Fish			Chi-Squares		Numbers of Displaced Fish			Chi-Squares	
	Released	Recovered		1966 E.S. x 1967 E.S.	E.S. x Pinkut	Released	Recovered		1966 E.S. x 1967 E.S.	E.S. x Pinkut
		In Streams	In Stream of Origin				In Streams	In Stream of Origin		
				Early Streams - offshore within 16 km						
1966	150	129	110	0.0		400	309	204	0.7	
1967	40	31	26			41	33	26		
Total	190	160	136		1.1	441	342	230		8.0**
				Early streams - off streams within 16 km						
1966	183	162	133	0.1		284	211	92	5.5*	31.1**
1967	265	199	169			472	302	178		14.9**
Total	448	361	302		2.4	756	513	270		27.1**
				Early Streams - all releases within 16 km						
1966	283	244	200	0.1		684	520	296	0.5	
1967	265	199	169			513	335	204		
Total	548	443	369		1.7	1197	855	500		20.7**
				Early Streams - all releases						
1966	333	292	247	0.4		982	713	355	5.6*	36.0**
1967	265	199	179			513	335	204		13.4**
Total	598	491	426		1.0	1495	1048	559		30.6**
				Pinkut Creek - all releases						
1966	100	58	58			250	135	124		

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* Differ at 5% level of significance

** Differ at 1% level of significance

used in the sockeye displacement experiments were destined to spawn in the stream at which they were originally captured. The distributions of the displacement groups at recapture sometimes differed markedly from that of their controls (Table XVIII). In what follows, the data have been analyzed to identify factors which might be involved.

Sex and State of Maturity

The proportions of ripe males and females in control groups did not differ significantly from the proportions in displacement groups (Table XX). Comparisons of the numbers of displaced fish returning to their stream of origin revealed no consistent, significant differences in the return of males and females or, within sexes, in the return of those fish classified as green at the time of tagging and those fish classified as ripe. The only significant chi-square value was for 1967 Four Mile Creek males -- ripe males from these displacement groups returned to the stream of origin at a significantly higher rate than green males.

In 1966, sockeye first entered the early streams about July 27 with peak entries occurring about August 10 in most streams (August 7 in Four Mile Creek which appeared to be a few days earlier than most). Thus, most of the displaced early stream fish were taken from the first half of their respective spawning runs. Overall, 91.7% of the males and 28.5% of the females displaced from early streams in 1966 were ripe at the time of tagging (Table XX).

In 1966, spawning in Pinkut Creek began approximately August 15, but did not peak until September 16 to 18 (information supplied by Resource Development Branch, Department of Fisheries of Canada). The fish used in the displacement experiments were seined off the mouth September 2 and 3,

TABLE XX Comparisons of a) the number of ripe and green male and female sockeye in control and displacement groups.
b) the homing performance of males and females.
c) the homing performance of ripe and green males and ripe and green females.

	Number of Controls				Number Displaced				Total				Chi-Squares Control x Displaced		Number Displaced Fish Recovered at Source				Chi-Squares		
	Male		Female		Male		Female		Male		Female				Male		Female		Sex	Maturity	
Source	Ripe	Total	Ripe	Total	Ripe	Total	Ripe	Total	Ripe	Total	Ripe	Total	M.	F.	Ripe	Total	Ripe	Total		M.	F.
1 9 6 6																					
Pierre	120	124	25	127	349	389	116	408	469	513	141	535	0.5	3.2	119	133	41	158	1.1	0.0	0.4
4 Mile	20	22	7	28	83	84	19	66	103	106	26	94	0.1	0.1	35	36	9	20	1.6	0.9	2.7
Gullwing	19	20	2	13	20	20	4	14	39	40	6	27	0.0	0.6	8	8	0	1	3.3	-	0.4
Early Stream Total	159	166	34	168	452	493	139	488	611	659	173	656	0.2	3.1	162	177	50	179	0.0	0.0	0.2
Pinkut	52	53	0	47	129	132	8	118	181	185	8	165	0.0	3.1	65	66	1	63	0.1	0.2	2.7
1 9 6 7																					
Sockeye	27	37	2	38	58	77	1	74	85	114	3	112	0.0	1.5	15	17	0	12	0.7	1.5	0.2
Pierre	13	44	1	46	22	92	0	89	35	136	1	135	0.4	2.3	13	52	0	35	2.8	0.3	-
4 Mile	23	33	0	27	42	56	1	54	65	89	1	81	0.1	0.4	29	31	1	26	0.2	5.4*	0.5
Gullwing	19	22	1	18	26	41	1	39	45	63	2	57	1.1	0.4	15	18	1	23	0.9	3.5	0.8
Total	82	136	4	129	148	266	3	256	230	402	7	385	0.3	1.9	72	118	2	96	1.5	1.4	0.7

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* Differ at 5% level of significance.

about 14 days before the peak of spawning. Overall, 97.7% of the displaced males and 6.8% of the displaced females were ripe at tagging. The proportion of ripe males in the Pinkut Creek displacement groups did not differ significantly ($\chi^2 = 0.4$, $p > .05$) from that of the 1966 early stream displacement groups but the proportion of ripe females was significantly lower ($\chi^2 = 18.4$, $p < .01$).

The fish displaced in 1967, all from early streams, were seined off the mouths of streams in late July, before any appreciable numbers of fish had entered. The Pierre Creek groups, the most numberous, were captured the day before any sockeye entered that stream, about 14 days before spawning peaked in the early streams. The overall proportion of ripe males in the 1967 early stream displacement groups (55.6%) was significantly lower than that of the 1966 early stream displacement groups ($\chi^2 = 28.4$, $p < .01$) and the 1966 Pinkut Creek displacement groups ($\chi^2 = 22.3$, $p < .01$). The proportion of ripe females (1.2%) was also significantly lower than that of the 1966 early stream ($\chi^2 = 65.9$, $p < .01$) and Pinkut Creek displacement groups ($\chi^2 = 8.5$, $p < .01$).

Condition at Time of Recapture

Ricker (1959b)records a number of instances in which salmon on spawning migrations temporarily entered streams which they subsequently left to spawn in another. This suggests the possibility that unspawned fish captured and recorded during stream surveys might be making brief excursions and will ultimately spawn elsewhere. If so, stream recaptures which include a large proportion of unspawned fish might indicate a rate of homing different from that which actually occurs. In 1967, many of the fish from which tags were recovered were classified as either spawned (wholly or partially) or unspawned at the time of capture. Of 120 fish classified as spawned, 45 (37.5%) were taken in streams other than the stream of origin compared with 40 (34.8%) of the 115 fish classified as unspawned. The figures for the two groups do not differ significantly ($\chi^2 = 0.1$, $p > .05$).

Displacement Distance

The percentage of fish recaptured in the stream of origin tended to decline with increasing displacement distance (Figure 18). The highest percentages were recorded for control groups, released at the capture site. With the exception of displacement groups 4c and 4d which exceeded their control (4a), the per cent return of early stream displacement groups was lower than that off the associated control. The average per cent return of groups displaced less than 16 km (10 mi) was 58.0%. Within this distance, the percentage return of individual groups was extremely variable, from 4.8% (group 12c) to 81.6% (group 5c). The extreme variability suggests that factors other than distance were involved. The average return of early stream fish transferred over 16 km was 31.5% from 8.5% (2c) to 51.7% (1b).

The per cent return of Pinkut Creek groups consistently exceeded those of early stream fish displaced comparable distances (Figure 18).

In some of the comparisons which follow, only data for groups displaced less than 16 km have been considered in order to partially obviate the effects of displacement distance.

Character of Release Site

Early stream sockeye released at neutral areas offshore had a significantly higher ($\chi^2 = 3.9$, $p < .05$, Table XVIII) rate of return to the stream of origin (67.5% of stream recaptures) than those re-

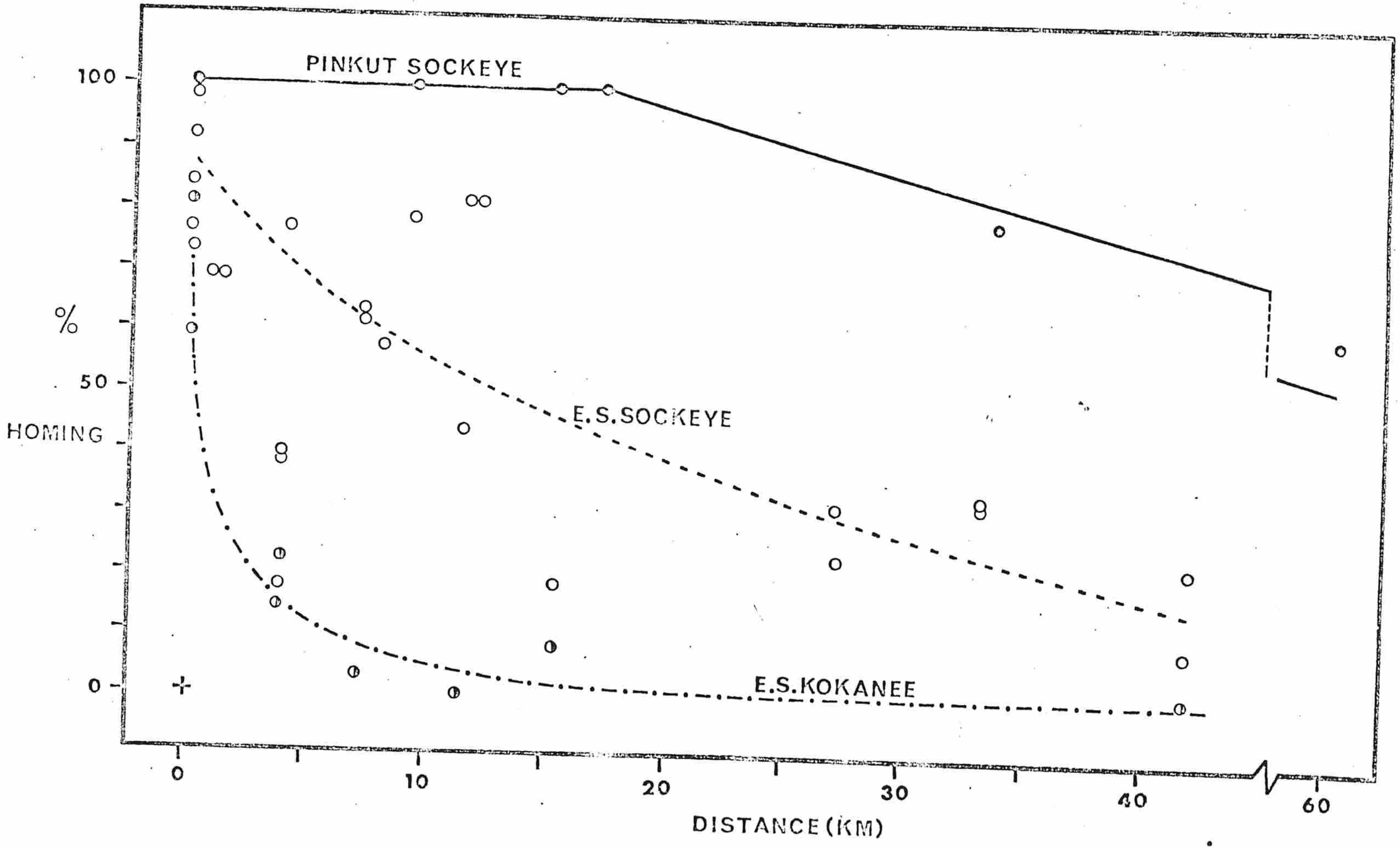

Figure 18. Effect of distance on homing performance of displaced Early Stream (E.S.) and Pinkut Creek fish.

leased within the influence of streams other than the stream of origin (56.4% of stream recaptures made at stream of origin).

This difference can be attributed to a tendency for fish released off the mouths of streams to enter those streams. In total, 13 groups of early stream fish were displaced to streams within 16 Km of the stream of origin. In every instance, the per cent of displaced fish entering the release stream exceeded the per cent of fish from the associated control entering the same stream. One hundred eighty-five (36.2%) of 511 recovered displaced fish were found in the release stream compared with 27 (4.4%) of the associated control fish. This difference is highly significant ($\chi^2 = 149.5$, $p < .01$). At the same time, the tendency for displaced fish to enter streams other than the stream of origin or release stream was no greater ($\chi^2 = 0.0$, $p > .05$) than that of controls: 68 (11.1%) of 6.4 recovered control fish and 56 (11.0%) of 511 recovered displaced fish entered such streams.

Three comparable transfers were performed with Pinkut Creek sockeye; two offshore (8b and 8c) and one to the mouth of a nearby stream (8d). In each instance, all recoveries were made at Pinkut Creek.

Tendency for Fish to Enter Stream Similar to Stream of Origin

Displaced early stream fish not returning to the stream of origin tended to enter other early streams rather than either the Fulton River or Pinkut Creek, the two large streams in the Main Lake area (Table XXI). Of the 43 early stream fish which did enter the Fulton River and Pinkut Creek in 1966, 34 (79.1%) were from five groups released at the mouths of one or the other of the two streams. The average distance of these displacements was 26.1 km (9.4 to 33.4 km). In 1967 no early stream fish were released off Fulton or Pinkut and only one fish was recaptured in either of the streams.

Few displaced Pinkut Creek fish were recovered eleswhere and the nearest comparable stream, the Fulton River is 50.3 km away. No conclusions as to the tendency for Pinkut Creek fish to enter streams of similar kind are possible with the available data.

TABLE XXI . Comparison of the distribution in streams of recoveries of sockeye salmon displaced from early streams (1966 and 1967) and from Pinkut Creek (1966).

	Number Released	Number Recovered in Streams	% Recoveries In			
			Stream of Origin	Early Streams	Fulton	Pinkut
			Early Streams			
1966	981	713	49.9	43.9	2.5	3.7
1967	522	333	58.2	41.5	0.3	0.0
			Pinkut Creek			
1966	250	165	93.4	4.8	1.8	---

Direction of Displacement

During 1966 and 1967, seven groups of early stream sockeye were displaced to localities not more than 16 km north of their streams of origin (groups 1c, 4c, 5c, 5d, 5e, 11b, 12b) and seven groups to localities not more than 16 km south (1d, 5f, 6d, 6e, 11c, 12c, 13c). In each instance three localities were offshore and four at the mouths of strems. The fish to the north were displaced a greater average distance (12.2 km) than those displaced south (7.2 km). A higher proportion of the fish displaced north returned to their stream of origin than those displaced south (Table XXII). However, the difference in return, though suggestive, is not significant ($\chi^2 = 3.2$, $p \geq .05$).

TABLE XXII . Comparison of the homing performance of early stream sockeye displaced north and south of their stream of origin.

	Number Released	Number Recovered in Streams	Recovered in Stream of Origin		Chi-square
			Number	%	
North	417	302	182	60.3	3.2
South	390	275	135	49.1	

Comparison of 1966 and 1967 Early Stream Displacements

Although the control groups associated with the 1966 and 1967 early stream displacement groups did not differ significantly in their return of recapture fish to the stream of origin, there was a significant difference in the return of displacement groups themselves (Table XIX). This is true even when the kinds of displacement groups being compared are restricted by distance (groups displaced more or less than 16 km) or by character of release site (those displaced off streams or offshore).

Comparison of Early Stream and Pinkut Creek Displacement

All Pinkut Creek data have been lumped, regardless of displacement distance or character of displacement site because there are too few data to warrant further categorization. Recovered Pinkut Creek control fish returned to the stream of origin at a rate which did not differ significantly from that of early stream control groups (Table XIX). However, in all comparisons, data for fish recovered in streams indicate that displaced Pinkut Creek sockeye returned to the stream of origin at a rate significantly higher than that of displaced early stream fish.

With one possible exception, there is no evidence that the Pinkut Creek data have been greatly influenced by the low recovery rate. The recovery of control groups (58.0%) and displacement groups (54.0%) did not differ significantly ($\chi^2 = .22$, $p > 0.05$). There was no significant difference ($\chi^2 = 0.3$, $p > .05$) between control and displacement groups in the numbers of recovered fish found in the stream of origin (58 of 58 controls, and 124 of 135 displaced fish). If a large number of Pinkut Creek sockeye had entered early streams, they should have been more easily detected than those which returned to Pinkut Creek. The data are therefore more likely to be biased against a high return percentage than for it. The one instance in which recovery data may have been markedly influenced involves group 9b, displaced 60.3 km to the Fulton River. This stream is larger and even more difficult to collect than Pinkut Creek and it is likely that the proportion of the displacement group which entered is higher than the data indicate.

Kokanee Displacement Experiments

Kokanee from Four Mile Creek and Pierre Creek (Table XXIII) were caught in traps near the mouths of these streams just when upstream movements of kokanee were beginning to decline. Of the experimental kokanee captured at Pierre Creek (Table XXIV) an overall 98.1% of the males and 17.9% of the females were ripe at tagging. The corresponding figures for Four Mile Creek kokanee are 97.1% for males and 7.7% for females. The proportion of ripe

TABLE XXIII. Releases and recoveries of experimental groups of kokanee, 1966. Blank in Chi-square column indicates no test made; double asterisk indicates that means differ at 1% level of significance.

Experiment	Group	Date (Aug.)	Stream of Origin	Site of Release	Distance (km)	Number Released	Number Recovered											Total	χ^2
							Fulton	Tachek	Sockeye	Kew	Pierre	Twain	Pinkut	¼ Mile	4 Mile	Gullwing	Shass		
1	1a	12	4 Mile	4 Mile	0.0	100								1	26	5		32	
	1b	12	4 Mile	Gullwing	4.0	100								3	9	25	3	40	**
	1c	12	4 Mile	Pierre	4.9	100					25	2						27	**
2	2a	13	Pierre	Pierre	0.0	98				3	13	6						22	
	2b	13	Pierre	Sockeye	15.4	99			16	3	2	4						25	**
	2c	13	Pierre	Offshore 1	11.5	100			3	16		3						22	**
	2d	13	Pierre	Twain	3.8	100					3	18						21	**
	2e	13	Pierre	Offshore 5	7.2	98					1	30						31	**

TABLE XXIV. Comparison of the number of ripe male and female kokanee in control and displacement groups from Pierre and Four Mile Creeks, 1966.

Creek	Number of Controls				Number Displaced				Total				Chi-squares	
	Male		Female		Male		Female		Male		Female			
	Ripe	Total	Ripe	Total	Ripe	Total	Ripe	Total	Ripe	Total	Ripe	Total	M.	F.
Pierre	55	55	3	43	259	262	29	135	314	317	32	178	0.0	3.7*
Four Mile	80	81	0	19	124	129	7	71	204	210	7	90	0.3	1.9
TOTAL	135	136	3	62	383	391	36	206	518	527	39	268	0.0	5.2*

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* Means differ at 5% level of significance

females in the Pierre Creek displacement groups was significantly higher ($\chi^2 = 3.7$, $p < .05$) than the proportion of ripe females in the Pierre Creek control groups but there was no significant difference in the proportions of ripe males. There were no significant differences of this kind between Four Mile Creek control and displacement groups.

The recovery rate for kokanee was low in comparison with that of sockeye: 27.3% of 198 control fish and 27.6% of 597 displaced fish. The proportion of recovered, displaced fish which were found in the stream of origin was also low, only 9.1% overall. The recovery rate declined rapidly with distance (Figure 18). Even control fish, which had already entered the stream once, and which were released within its influence, returned to the stream of origin at a rate which was low in comparison with that of control sockeye from the same streams: 18.8% of the recovered kokanee controls from Four Mile Creek and 40.9% of those from Pierre Creek were recaptured in streams other than the stream of origin.

DISCUSSION

Homing in spawning salmonid fishes has been the subject of recent discussion by McCleave (1967), Hartman and Raleigh (1964) and Hasler (1966). McCleave defines three types of homing in spawning fish:

1) Reproductive homing -- the return of adults to spawn in the same location in which they were hatched;
2) Repeat homing -- the return of adults to spawn in subsequent breeding seasons at the location of initial spawning;
3) In-season homing -- the return of displaced adults, within the same breeding season, to the location of initial choice.

A high degree of reproductive homing appears to be characteristic of salmonid fishes. In some instances, the evidence for reproductive homing is direct, in others, it is inferred. It is generally assumed that repeat and in-season homing are associated with a disposition on the part of the fish to return to the place of its genesis as often as it spawns and in the face of obstacles such as displacement. Thus, high incidences of repeat and in-season homing are a consequence of reproductive homing.

Evidence to date suggests that the sockeye salmon, Oncorhynchus nerka, and its freshwater form, the kokanee, home to about the same degree as other salmonids. Foerster (1968) has reviewed the evidence for reproductive homing in this species using data resulting from releases of marked fingerlings. Much of the data is unsatisfactory, but it does suggest a high incidence of reproductive homing. Vernon (1957), using morphological and scale data, defined three races of kokanee localized in specific areas of Kootenay Lake, B. C. He was not able to determine the degree of homing to specific tributary streams but he did conclude that more than 97% of the kokanee he examined spawned in the area of the lake in which they had their origin. Hartman and Raleigh (1964) conducted a series of displacement experiments with sockeye salmon at Brooks Lake and Karluk Lake, Alaska, which indicated in-season straying of less than 7%. The authors concluded that sockeye in these lakes had a highly developed homing tendency.

The hypothesis which formed the basis for these experiments was that the tendency to enter and spawn in streams other than the home stream would be greater for sockeye adapted to spawning in unstable streams (i.e., the early streams in the Main Lake area of Babine Lake) than for sockeye adapted to spawning in relatively stable streams (e.g., Pinkut Creek). It was supposed that this would be reflected indifferences in the homing performance of fish displaced, in-season, from streams of the two kinds.

The distributions of recaptured control fish indicated that most of the sockeye used in the displacement experiments at Babine Lake would have spawned in the streams in or off which they were originally captured. The distributions of recaptured displacement fish often differed markedly from that of their associated control group (Table XVIII). A number of factors have been shown to affect the homing performance of the sockeye, especially the early stream sockeye, displaced at Babine Lake. The displaced fish most likely to return to the stream of origin were those displaced short distances (less than 16 km) and released offshore, away from the direct influence of streams. Fish displaced long distances and released off the mouths of streams, especially streams similar to the stream of origin, were less likely to return. The majority of those straying under these circumstances entered the release stream.

There is some indication that direction of displacement may have also affected returns. The per cent of fish displaced north which returned to the stream of origin was higher, though not significantly, than that of fish displaced south. A related observation was that most of the fish from early stream control groups which were recaptured in streams other than the stream of origin had moved south. This was true of fish captured in traps in streams and those captured by seine off the mouths of streams. The former had already chosen and entered a stream and would presumably have spawned there had they not been intercepted and handled. The latter might be expected to contain a higher proportion of fish which were only temporarily associated with the fish schooling off the stream and would have eventually gone elsewhere to spawn.

These data suggest a tendency to southward movement in early stream sockeye. Such a tendency might be learned or innate. Sockeye enter Babine Lake at its northernmost end and must travel south for several days before reaching the streams of the Main Lake area where this study was conducted. If these migrating sockeye follow the shoreline they must move in a southward direction through the Nilkitkwa - North Arm area of the lake. A southward oreintation could be learned during this early part of the lake migration. There is, however, a possibility that a southward orientation during lake migration is an innate characteristic of Main Lake early stream sockeye. Groot (1967) has presented strong evidence of innate directional orientation among seaward migrants in the Babine Lake system.

In addition to a southward tendency which would aid them in returning to their stream of origin, fish displaced to the north may be able to utilize environmental cues such as landmarks. They are retracing part of their original migration route from the north while fish displaced south are more likely to be entering unfamiliar territory. Helle (1966) has shown that pink salmon (O. gorbuscha) displaced along the route of their original migration home better than those displaced off-route.

Another factor, for which definitive data is not available but which is likely to have affected returns, is the state of maturity of displaced fish. Other studies of in-season homing in salmonids suggest that there is an inverse relationship between spawning readiness and homing performance (Lindsey et al., 1959; Helle, 1966; McCleave, 1967; and Groves et al, 1968). In the Babine Lake experiments there was no consistent significant difference, within groups, in the return of ripe and green sockeye, male or female (Table XX). This can mean that either there is no correlation between homing performance and spawning readiness or that the criterion used, expressibility of sex products, is not a sufficiently precise measure of spawning readiness to be useful in distinguishing the spawning readiness of same-sex fish <u>within</u> groups. The latter appears the most likely possibility. This does not exlude the possibility that significant differences in the per cent ripe fish are indicative of real differences in the spawning readiness <u>between</u> groups, i.e., that the within-group and between-group correlations are different. It is not possible to test this with the available data. The experiments differed in too many ways, other than per cent ripe fish, which are known to affect homing performance.

In any case, there were differences in the per cent of ripe fish in various groups which may have had some influence on homing performance. Most of the 1966 early stream sockeye were captured in traps after they had entered streams while the 1966 Pinkut Creek and 1967 early stream fish were seined off the mouths of streams before entering, at a slightly earlier stage in the spawning migration. As might be expected, a significantly higher proportion of the 1966 early stream fish were ripe at the time of capture. They also had the poorest homing performance of the three major groups (Table XIX). These data suggest that differences in state of maturity may account for at least part of the difference in the homing performance of the early stream and Pinkut Creek sockeye displaced in 1966. However, a consideration of the 1967 early stream results suggests that this effect may not be very great.

The experimental techniques employed in the 1967 early stream transfers were virtually identical to those employed at Pinkut Creek in 1966. In each case, the fish were seined off stream mouths, very early in their respective spawning seasons, approximately two weeks before spawning peaked. The per cent ripe sockeye, male and female, in the 1967 early stream groups was significantly lower than that of Pinkut Creek groups. Even so, the homing performance was more like that of the 1966 early stream sockeye than like Pinkut Creek sockeye (Table XIX). This suggests that most of the difference in the homing performance of early stream and Pinkut Creek sockeye is not associated with differences in state of maturity.

The homing performance of displaced Pinkut Creek Sockeye is in accord with what is known of the homing performance of other populations of the species. The homing performance of early stream sockeye displaced under similar circumstances is much poorer. This difference may be due to undetected differences in either experimental technique or in the physiological state of the displaced animals. Another possibility is that there is an innate difference in the homing performance of sockeye from Pinkut Creek and the early streams. Evidence is increasing that much of the migratory behaviour of sockeye populations is subject to genetic control. Raleigh (1968) has shown that the tendency for sockeye fry to move either upstream or downstream from spawning areas in streams is inherited. Calaprice (personal communication) has recently demonstrated that the relationship is a simple dominant-recessive one. Groot (1967) presents persuasive evidence that the orientation of sockeye smolts leaving the Babine system is innate.

There is some indication of species differences in homing performance. The pink salmon (O. gorbuscha) has an invariable two year life cycle so that there is no overlap in the spawning returns of different year classes such as commonly occurs among salmonid fishes. Without overlap age of maturity, a spawning failure in any one year might totally eliminate a population of the species. This could be partly compensated for by straying from nearby streams where spawning survival was better. Thus, a high degree of straying might have survival value for this species.

In an early study involving marked pink salmon fry from McClintock Creek, B.C., Pritchard (1939) found little evidence of straying.

However, in a more recent experiment, Parker (1967) marked 331,000 fry leaving the Bella Coola River in B.C. In the spawning year, the Bella Coola and other nearby spawning streams were searched for marked fish. Parker estimated that 31% of the marked fish spawned in streams other than those of the Bella Coola system. Harry and Olson (1963) presented strong, though not conclusive, evidence that pink salmon stray to Saskin Creek, Alaska, from other nearby streams.

Vernon (1962) notes the rapid expansion of pink salmon in the upper Fraser River area. No pink salmon had spawned above Hell's Gate for 35 years prior to 1945 when a fish ladder was established at Hell's Gate. He presents evidence that in years of large spawning populations, the proportion of fish spawning above Hell's Gate is greater than in years of low population levels. In the former years, the main Fraser population spawning below Hell's Gate, expands upstream.

Vernon contrasts the capacity of Fraser River pink salmon to emigrate and re-establish major populations in barren areas with that of sockeye salmon. The latter have shown little capacity to re-invade areas whose original populations were decimated by the Hell's Gate blockade.

While it seems likely that the sockeye salmon, as a species, has a greater tendency to home than the pink salmon, there remains the possibility that individual populations of sockeye differ in this respect.

Lindsey _et al._ (1959) suggest that reproductive homing functions first, to ensure that eggs are deposited in an area capable of rearing the young and, second, to balance the number of fish utilizing a spawning area against its reproductive capacity. This ensures that developing eggs are not destroyed by adverse conditions, not apparent at the time of spawning, which are regularly associated with particular streams (high temperatures, low water, flooding, freezing, predation, etc.). It follws that homing is most advantageous in relatively stable spawning environments.

Mayr (1963) has pointed out that "A species may evolve a specially adapted population in any ecologically 'marginal' area, whether this is in the centre of the species range or at its periphery." Straying might be expected to be high in newly colonized regions at the fringes of a species range. The individuals comprising such populations are themselves strays or the offspring of recent strays and the environments are often marginal. Success under such conditions may be dependent on a high innate tendency to stray, a willingness to spawn in any suitable environment, whether the parent stream or some other. The same argument can be applied to marginal environments well within the species range.

Straying is more likely to have significant effects in the gene pool in small populations, like those of the early streams. The influx of small numbers of strays may constitute a large proportion of a small population but the same number might constitute a genetically insignificant proportion of a large population. Lindsey et al.(1959) have discussed this point in considering homing among rainbow trout (Salmo gairdneri) at Loon Lake, B.C.

The discussion so far has been based on the sockeye experiments. The kokanee experiments were not sufficiently extensive to allow any definite conclusions about their homing ability in comparison with that of sockeye.

The homing performance of the kokanee, all from Pierre and Four Mile Creeks, was much poorer than that of sockeye from the same streams. Even the control kokanee, trapped in the stream and released at its mouth, strayed at a much higher rate than sockeye controls. There are a number of possible explanations. The kokanee were captured late in the respective spawning runs and were probably closer to spawning than the sockeye used in displacement experiments. They were much smaller in size than the sockeye and Groves _et al_ (1968) have shown that chinook salmon (_O_. _tsawystcha_) are less likely than larger fish to return to a home stream after displacement. Small fish may not have sufficient energy reserves to undertake a long return journey after displacement. Possibly they are more affected by handling during trapping.

Displacement experiments are at best an unsatisfactory method of determining rates of straying. The hypothesis that sockeye salmon from marginal streams stray to a high degree should be tested by marking experiments involving fry. These experiments should be carried out over a number of years so that the distribution of returns during years of good spawning conditions can be compared with returns during years of poor spawning conditions. This will give some indication of the extent to which a tendency to stray is innate and the extent to which it can be influenced by environmental conditions in the spawning streams.

SECTION V

GENERAL DISCUSSION

The available evidence suggests that the sockeye and kokanee of Babine Lake do not constitute two distinct species. The hypothesis which most readily encompasses the available information is that the sockeye and kokanee in the early streams of the Main Lake area are part of the same, polymorphic population.

The modern concept of species, the so-called "biological species", is that of "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr, 1963). As indicated, the decisive criterion is the reproductive isolation of populations. Observations in the early streams of the Main Lake area, where the two forms spawn sympatrically, indicates that hybridization, particularly that involving female sockeye and male kokanee, is common (Section III). There are no effective premating isolating mechanisms. Though the rate of hybridization cannot be determined directly (because hybrids cannot be distinguished morphologically from the parental types) it would appear to be high enough to bring about a breakdown in the species border in the absence of effective postmating isolating mechanisms such as hybrid inviability.

Ford (1964) has commented on the increasing recognition of the role of polymorphism in the genetics of natural populations. Ford (1940) defined genetic polymorphism as the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation. Most genetic polymorphisms are balanced, "being maintained by contending advantages and disadvantages at a level determined by the relative strength of the opposing selective forces to which they are subject. Thus they assure permanent diversity." (Ford, 1964).

Sockeye enjoy a number of advantages over kokanee:

1. Sockeye have the opportunity to utilize the greater resources of the oceanic environment, among them longer growing season and more abundant food. As a result, sockeye at maturity are larger than kokanee.

2. The larger size of sockeye results in numerous advantages:
   a. greater fecundity (Table X).
   b. larger egg size (Fig. 8) resulting in larger fry (Fig. 5) with presumably better survival.
   c. greater choice in spawning sites because they are able to utilize a wider range of bottom materials and tolerate a greater range of water velocities.
   d. better preparation of the spawning nest with increased gravel permeabilities (Section III) and, presumably, greater egg-to-fry survival.
   e. greater success in securing mates (Table XVII).

The major disadvantages of sockeye in comparison with kokanee are:

1. Increased mortality associated with the journey to and from the ocean including increased natural hazards and mortality from fishing.

2. Inability to utilize spawning grounds under extreme low water conditions.

3. Possibly, a greater vulnerability to predation, especially in small, shallow streams.

Of the disadvantages listed, the first applies equally to any of the Babine Lake sockeye populations. The second and third apply, in particular, to the early streams.

While there is evidence that kokanee can enter and spawn in areas unavailable to sockeye (Section III), there is, as yet, no direct evidence that kokanee are less subject to predation in streams. However, differential predation on larger fish is suggested by the following:

1. The major predators in the Babine Lake area, the black and grizzly bears and the bald eagle, generally take fish as the latter move through shallow riffles. In such situations sockeye are at a disadvantage because their backs often protrude from the water and because they are more likely to become stranded if panicked.

2. There are more hiding places suitable for kokanee than for sockeye. Kokanee utilize small holes under banks, roots, etc., which are too small for sockeye.

3. Kokanee have greater maneuverability in confined areas than sockeye. In my own experience, kokanee are much more difficult to net than sockeye.

4. It was my impression, during three summers of work, that predator-killed sockeye were much more numerous than predator-killed kokanee.

Kokanee are rare or absent in the larger streams at Babine Lake, suggesting that there selection consistently favours sockeye. However, in the variable environment of the early streams, kokanee, because of their small size, may sometimes enjoy a selective advantage. If the conditions favouring kokanee (low water levels, obstructions and, possibly, differential predation) recurr with sufficient regularity, kokanee will continue to persist in spite of what, at first glance, would appear to be overwhelming advantages to sockeye.

A kokanee/sockeye polymorphism would enable the early stream populations of O. nerka to maximize the utilization of the available spawning grounds. Why, however, is the polymorphism confined almost exclusively to early stream populations in the Main Lake area? One possible explanation is that the offspring of female kokanee, which suffer from an initial size disadvantage, cannot tolerate intense intraspecific competition such as occurs in high-density nursery areas like the North Arm. Thus, a sockeye/kokanee polymorphism might be a viable strategy only in areas like the Main Lake, where low densities of sub-smolt sockeye offspring limit intraspecific competition.

A high incidence of straying among spawning fish, sockeye and kokanee, would also serve to increase the utilization of available spawning grounds. Fish returning to a parent stream which was dry or otherwise unsuitable could utilize other, nearby streams. In addition, frequent straying would bring about rapid recolonization of those streams whose populations have been previously depleted by difficult environmental conditions. This strategy would only be effective if some of the early streams were available, as refuges, during even the dryest years. The four Type I early streams would seem to fulfill this function. Though they may suffer partial spawning failures, they are almost always accessible to a portion of the early run. They could act as refuge streams during a succession of dry years, and as centers from which the population could expand when conditions subsequently improved. If something of this kind does occur, there must be considerable interchange of individuals and genetic material as the available early stream spawning area expands and contracts from year to year. Quite possibly, the O. nerka, sockeye and kokanee, spawning in the early streams constitute a single, panmictic population, a population quite different from those utilizing the large, stable streams.

In summary then, a sockeye/kokanee polymorphism could be an adaptation to the peculiar spawning environment of the early streams. The hereditary mechanisms which might be involved in the maintenance of such a polymorphism are unknown. In many animals, balanced polymorphisms are maintained by switch-mechanisms which take the form of super-genes, co-adapted complexes of genes which interact and reinforce each other to produce their effects (see Ford, 1964, for a review). Ford (p. 91) states that, "If two major genes co-operate in an advantageous way, selection will favour rare structural interchanges, as well as translocations, bringing them on to the same chromosome and then the means of checking crossing-over between them. . . . This will continue until the two genes so seldom break apart that they act effectively as a single switch-mechanism; that is to say, until they have become a super-gene." The smoltification process involves a complex of behavioural and physiological responses(Hoar, 1953) suggesting the coordinated action of a series of genes, possibly a super-gene. We can envisage an array of genotypes within this super-gene, some with a greater and some with a lesser tendency to smolt.

Whatever the genetic mechanisms, it would appear that factors other than genotype can also affect the tendency to smolt. Three factors in particular appear to be important: sex, early growth and state of maturity. Females are more likely to smolt than males (Section I); the larger and/or faster growing fish of a given year class are more likely to smolt than smaller, slower growing fish (Section I); and immature fish are more likely to smolt than those in which maturation processes have already begun. (Maturation effects do not appear to be important at Babine Lake and are discussed below in connection with sockeye/kokanee populations at Lakes Cultus and Dalnee.)

Sockeye and kokanee occupy quite different environments, marine and freshwater, for a considerable part of their life history. One would expect that there would be selection within each group for, among sockeye, those fish best adapted to the marine environment and, among kokanee, those fish best adapted to the freshwater environment. This process, disruptive selection, would tend to increase genetic differences between the two forms. If the sockeye/kokanee polymorphism is to remain stable and balanced, there must be mechanisms within the population, which counteract the effects of disruptive selection so that, over the long term, gene frequencies among early stream _O. nerka_ remain relatively stable.

Several mechanisms are probably involved in maintaining the stability of the gene pool. First, there is interchange of genetic material on the spawning grounds (Section III). Second, there is probably an interchange of the progeny of sockeye and kokanee at smolting. This could come about if many of the young _O. nerka_ from the early streams lay in the middle range of genotypes for the switch-control mechanism. A large proportion of these would smolt if growth conditions in the lake were good; a smaller proportion if conditions were bad. In a year of generally poor growth conditions, many of the fish which remain in the lake, as kokanee, may be the genotypically intermediate progeny of sockeye parents. In a year of good growth conditions, genotypically intermediate kokanee progeny may leave the lake as smolts in spite of the fact that they have an initial disadvantage due to small egg size. If growth conditions in the lake do in fact influence the proportion of sockeye to kokanee within year classes, this may explain why kokanee in the early streams do not have regular cycles of abundance (Section I) even though most of them mature at the same age, in their fourth year.

Ricker (1940) and Nelson (1968a) agree that, with few exceptions, kokanee populations have been independently derived from sockeye. Nelson points out first, that kokanee are indigenous to areas that have been inhabited by sockeye and second, that the present distribution of kokanee is most plausibly explained by supposing that the agent of dispersal is the anadromous form. A switch mechanism of the kind proposed for Babine Lake would explain how kokanee could arise from sockeye progenitors. In most sockeye populations there would be some variability in the genetic constitution of the switch mechanism. Recombination could produce occasional genotypes resulting in individuals likely to remain in the lake as kokanee. The incidence of such genotypes would remain small as long as anadromous individuals benefited from a net gain in reproductive capacity resulting from the additional growth to be expected in the marine environment. However, genotypes likely to produce kokanee would be strongly selected for wherever sockeye invaded, or changing conditions resulted in, situations where a marine migration would result in a net loss in reproductive capacity. For example, situations in which:

a. the difficulties of the migration to and from the ocean exact too great a toll,

b. the large fish returning from the ocean are at some disadvantage in spawning (Babine early streams).

The balance between sockeye and kokanee producing genotypes will depend on selective forces which are unique for each situation. In many localities, selection seems to have been very strongly to one or the other extreme of the range of genotypes. At one extreme are those _O. nerka_ populations in which kokanee appear to be very rare or entirely absent. Examples are the sockeye lakes in the Bristol Bay, Cook Inlet, Prince William Sound and Kodiak Island drainages in Alaska (Nelson, 1968a). In general, spawning areas are more than adequate, growth conditions for juveniles are good, river migrations are short and easy and the lakes are close to the marine feeding grounds of the sockeye in the Gulf of Alaska. All these factors favour sockeye and these populations are among the largest in the world.

An interesting example of an all-sockeye population inhabits Owikeno Lake, British Columbia, a glacial lake draining through the three-mile long Wannock River into Rivers Inlet. Most smolts migrate seaward at age I at an unusually small size, about 60 mm fork length (Ruggles, 1965), smaller than the smolts of any other major population (Table 71; Foerster, 1968). Apparently, the lake environment is so poor that the advantage to be gained from the utilization of marine resources more than balances the additional marine mortality which is probably associated with small smolt age.

At the other extreme are the kokanee populations of lakes lying above impassable falls. In such situations, there is absolute selection against genotypes which result in a seaward migration. Any fish which does migrate cannot return and therefore can make no contribution to gene frequencies in the next generation. In time, genotypes likely to produce smolts would come to exist at very low frequencies. However, the occasional smolt could occur as the result of recombination. Such recombinations would be rare and would presumably become rarer as the population aged.

Horne Lake at the headwaters of the Qualicum River, B.C., is an example of a lake above impassable falls. A natural kokanee population occurs in the lake. Brent Lister (personal communication) states that occasional smolts have been captured in trapping facilities below the falls. He also states that mature sockeye have been observed in the river below the falls. Presumably, these left Horne Lake as smolts and are attempting to return.

In addition to those localities in which selection has been for one or the other extreme, there are those, such as the Babine Lake early streams, in which both sockeye and kokanee occur. However, it appears that in some lakes the situation is more complicated than that at Babine in that more than one type of kokanee can be distinguished.

Ricker (1938) described three types of non-anadromous _O. nerka_ in Cultus Lake, B. C.

1. A self-perpetuating population, having a normal sex ratio and a spawning season distinct from that of anadromous sockeye. These Ricker felt to be a natural population of true kokanee, having no present connection with other _O. nerka_ types in the lake. He has since determined (1959a) that they were almost certainly the offspring of Kootenay Lake kokanee which had escaped from the Cultus Lake hatchery. These will not be further considered in this discussion.

2. A group, the progeny of anadromous parents, experiencing below average first-year growth. These are relatively small at normal smolting age (age I). They are predominantly, though not exclusively, male and mature at ages III and IV. These are Ricker's "small size residuals". They appear to correspond to the Babine Lake kokanee.

3. A group, also the progeny of anadromous parents, experiencing above average first-year growth. These are relatively large at normal smolting age and are exclusively male. The majority mature and spawn in the autumn of their second year (age I). It is suggested that smolting is inhibited by factors associated with this precocious maturity. These are Ricker's "large

size residuals". Kokanee having these characteristics have not been identified at Babine Lake though they apparently occur in Lake Dalnee.

Foerster (1968) interprets Kroghius and Krokhin (1956) and Kroghius (1961) to the effect that both the small and large size types occur in Lake Dalnee. However, Krokhin (1967) states that kokanee comprise the fastest-growing segment of any year-class. Krokhin then presents data which show that the greatest proportion of kokanee is produced in those year-classes having the largest amount of food (crustacean plankton) available per individual, presumably because such year-classes have the greatest proportion of fast-growing individuals. Over 96% of the Lake Dalnee kokanee are males and the majority mature at age II. In this they correspond to the fast-growing kokanee at Cultus.

The almost exclusively male presence among the fast-growing type of kokanee is not unexpected if, as suggested, these arise from an inhibition of the smolting process by factors associated with precocious maturity. In effect, maturation processes would raise the threshold level for smolting. Male sexual precocity is common among salmonids. In some species males mature as parr, before the end of their first year (e.g., Atlantic salmon, Jones and King, 1952). At Babine Lake and at many other localities, some male sockeye mature at age III (as jacks) a year before the earliest females.

Nelson (1968a) reviewed the nomenclatural status of sockeye and kokanee and concluded that in view of the available information, it is advisable to designate both forms as Oncorhynchus nerka. This study strongly supports Nelson's conclusion. If, as hypothesized for Babine Lake, sockeye and kokanee are part of the same polymorphic population, they do not deserve even subspecific distinction.

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Biographical Information

NAME: Peter James McCart

PLACE AND DATE OF BIRTH: Vancouver B.C. Nov. 26, 1937

EDUCATION (Colleges and Universities attended, dates, degrees)

Univ. of Oregon	1955-1958	B.A.
Univ of Wisconsin	1958-1959	No. Degree
U.B.C.	1961-1963	M.Sc.
U.B.C.	1965-1970	Ph.D.

POSITIONS HELD:

Assistant Scientist	Fisheries Research Bd. of Canada	1963-1967
Assistant Prof.	U. of Sask., Regina	1967-

PUBLICATIONS:

See attached sheet

AWARDS:

This form is to be completed by candidates for the Master's or higher degree and submitted to the University Library Special Collections Division with the thesis.

PUBLICATIONS

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McCart thesis (1970)

✓p.1 - most Babine KO spawn in their fourth year (does this mean 3+ or 4+ ??)

✓p.5 - KO catches in standard gillnet sets from 1946 and 1958; not clear whether a "set" is a "net" or a "gang"

p.6 - discussion of early streams, (dominant KO spawn loci)

✓p.7 - estimated KO escapement 1964-1967

✓p.13 - timing of KO spawning; possibly

✓p.14 - cites Dombroski (1954) as the source of the idea that ~1% of SK smolts are age 2

p.15 size of smolts versus non-smolts, 1966-67

p.17 comparison of circuli/width of annuli for SK, KO of Four Mile Ck

p.20-22 : differences in growth of lab-raised KO and SK fry

✓p.24/25, 27 : hypural length of spawning KO, SK at 4 mile creek
- note all 3 fish (KO & SK) were males in 1965 (not 1964)
- Table IX has the raw numbers (page 27)

✓p.28 - states that none of the KO purse seined in 1966 (N = 1257) were in their fifth year (~~[illegible]~~)
- this implies that a lot of ageing was done

✓p.28 begins discussion of fecundity

✓p.29 - Table X has fecundities for 5 KO populations

✓p.30 - egg sizes of KO & SK

p.33 - sex ratios of Babine smolts (8299 1+, 57 2+)

✓p.34/35 - sex ratios of Babine KO from lake, note Table XI has gillnet data from 1957 to 1960

✓ p 53/54 Fig 11 shows seasonal periodicity of stream entry of SK, KO
to Four Mile Creek 1964-1966

✓ 55 KO can enter streams during low water, when SK cannot
KO can get through interstices of beaver dams when SK cannot

✓ 56 average stream life of KO was 12.9 days

✓ 59 differences in spawning locations (water velocity) of SK + KO redds
↳ this did not appear to be influenced by SK presence/absence

92 - ref to Johnson (1958) KO esc for 1955

✓ 108/111 - KO displacement experiments

✓ 118/119 - discussion of KO homing performance

✓ 123 - hypothesis that KO offspring cannot tolerate intense intraspecific
competition in nursery areas & this is why there are
less KO in north arm streams (where SK densities are high

✓ 125 - KO in early streams do not have regular cycles
of abundance