

**INTERNATIONAL PACIFIC SALMON
FISHERIES COMMISSION**

PROGRESS REPORT

No. 11

**CYCLIC DOMINANCE IN ADAMS RIVER
SCKEYE SALMON**

BY

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NEW WESTMINSTER, B. C.

CANADA

1964

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FISHERIES COMMISSION

APPOINTED UNDER A CONVENTION
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THE SOCKEYE AND PINK SALMON FISHERIES IN
THE FRASER RIVER SYSTEM

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ABSTRACT

Large and regular fluctuations in the abundance of sockeye salmon, occurring in a quadrennial pattern are a feature of Fraser River sockeye salmon and of the Adams River stock in particular. This phenomenon has been termed "cyclic dominance". In the case of Adams River sockeye, great, stable, disparities in the abundance of the annual runs indicate the existence of dominance maintaining agents. Depensatory predation acting during the lacustrine life-history stage was considered to be the maintaining mechanism. A model which simulates dominance in Adams River sockeye was formulated and tested. The model indicated that dominance could be developed and maintained in a simple system involving depensatory mortalities. Finally, implications of quadrennial dominance to the management of the fisheries were considered.

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INTRODUCTION

Major fluctuations in abundance are a common feature of the population dynamics of Pacific salmon. Often these fluctuations seem to occur at random but in a few cases regular periods of abundance and scarcity are evident. Historically, large catches of Fraser River sockeye salmon, Oncorhynchus nerka (Walbaum) have been made regularly at four year intervals. In recent years, these great quadrennial catches have been caused by the presence in the fishing areas of sockeye belonging to the Adams River stock originating in the Shuswap Lake area, part of the Fraser River system (FIGURE 1). After passing through the fisheries these "dominant" populations of Adams sockeye appear on their spawning grounds. During intervening years, the annual populations of spawners are invariably much smaller. In fact, the largest or dominant population belonging to the Adams River stock may be as much as a thousand times more numerous than the smallest of the "off years". Contributions of these fish to Fraser River commercial fisheries vary accordingly. Henry (1961) has computed that the Adams River stock contributed 8.5 million sockeye (81 per cent) to a total catch of 10.5 million in the Fraser River fishery in 1958 but in 1956 the contribution was less than one per cent out of a total of 1.8 million.

Evidence for the recurrence at quadrennial intervals of dominant populations, is available for most stocks of Fraser River sockeye, but currently the differences between largest and smallest annual populations are not as great as in Adams River sockeye. Some stocks which were decimated as a result of migration blocks in the Fraser River at Hell's Gate during the period 1911 to 1913 are now increasing and seem to be developing population structures which may exhibit the extreme dominance presently shown by the Adams stocks.

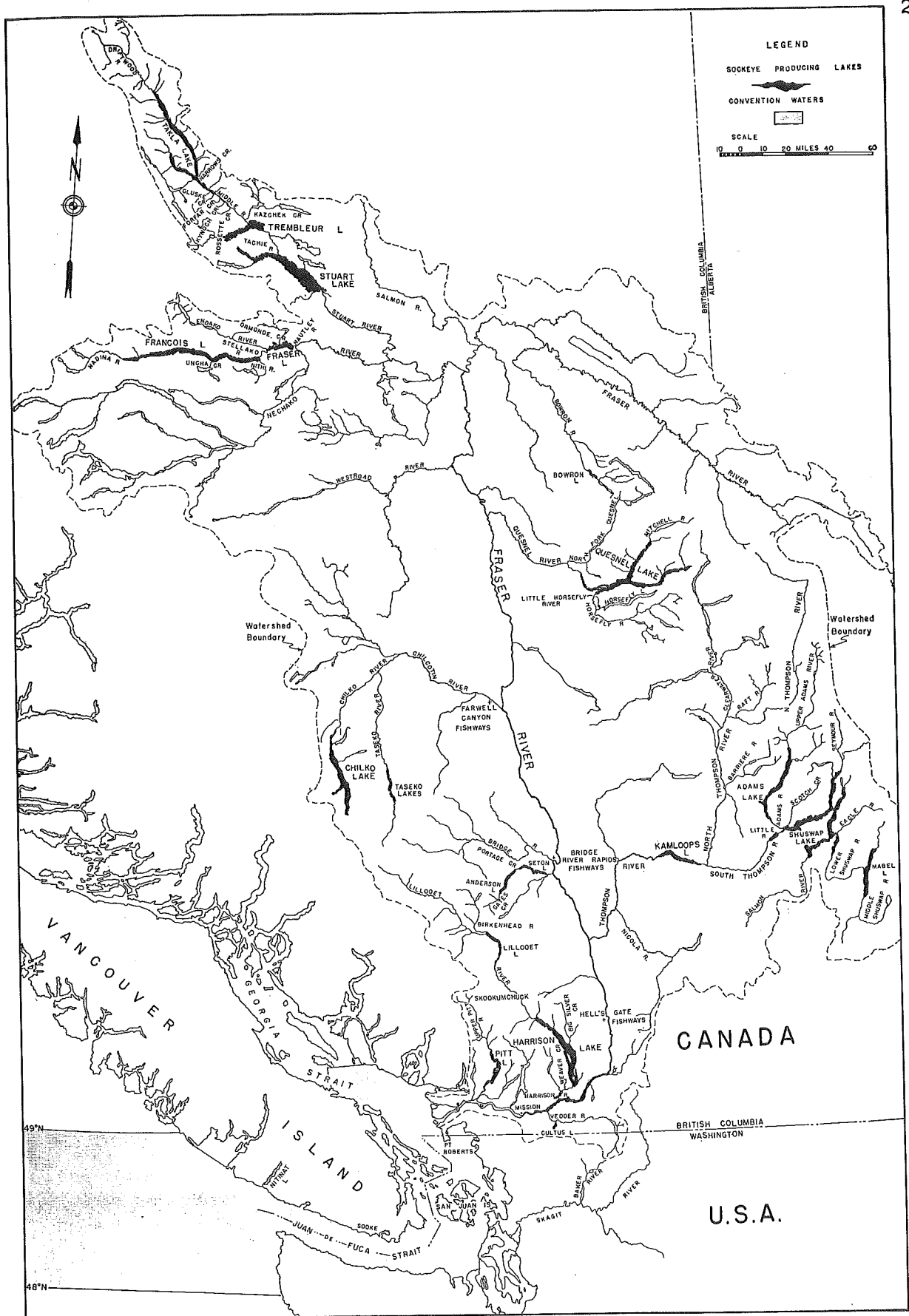


FIGURE 1 - Fraser River watershed showing areas utilized by major populations of spawning sockeye salmon.

The present great fluctuations in the annual abundance of Adams River sockeye are a major factor in the economy of the Fraser River fishery and therefore of considerable importance to the management of this fishery.

Without knowledge concerning the causes of this phenomenon of cyclic dominance, management procedures actually designed to increase average quadrennial catches might result in a reduction rather than an increase in quadrennial production. One major purpose of this paper is to organize the available information on dominance in such a manner that management policies may be indicated.

The first part of the paper will summarize the history of dominance in Fraser River sockeye salmon with particular reference to the Adams River stock. This will be followed by a section dealing with the nature of the phenomenon as exhibited in Adams River sockeye. The stage in the life-history in which dominance maintaining agents are most likely to act on the Adams stock will then be considered. The type of mortality acting to maintain off year populations of Adams sockeye at low levels of abundance will be considered in other sections. The hypotheses presented were designed to account for the maintenance of cyclic dominance in the Adams stock. Other hypotheses may be more appropriate to other stocks.

Life-histories, environments, and population dynamics of sockeye salmon will be related to the phenomenon of cyclic dominance. To test the credibility of the proposed hypotheses, the performance of a model designed to simulate the characteristics of the Adams River stock will be related to the natural phenomenon. Finally the information presented will be discussed as it applies to the management of the fisheries.

HISTORY OF FRASER RIVER SOCKEYE RUNS

For convenience, the history of Fraser River sockeye salmon can be divided into three periods: A period prior to the commencement of a significant commercial fishery; a period from the beginning of this fishery until 1917 when the original pattern of annual runs disappeared; and, finally, the modern period which includes the development of a new pattern of abundance.

Information concerning cyclic dominance before 1873 was drawn from documents of the Hudson's Bay Company. Pertinent extracts from these documents are on file in the library of the International Pacific Salmon Fisheries Commission.

Information concerning the second period (1873 to 1917) and part of the third (1917 to 1942) was obtained from two sources, Rounsefell and Kelez (1938) and Thompson (1945). Recent data concerning the third or modern period has been obtained from the Annual Reports of the International Pacific Salmon Fisheries Commission. These Salmon Commission records include estimates of the abundance of spawners as well as catch data.

The Abundance Pattern Prior to 1873

The earliest reference to salmon abundance in the upper Fraser River was made by Alexander Mackenzie (1801) on August 6, 1793. On the Fraser, near the mouth of the West Road River (Blackwater River) he noted: "The salmon were now driving up the current in such large shoals, that the water seemed, as it were, to be covered with the fins of them."

Obviously by their abundance, the fish observed by Mackenzie were sockeye. It is also interesting to note that 1793 is on the same sequence of years (1901, 1905, 1909, 1911 and 1913) as the dominant runs occurring during the

early days of the commercial fisheries (to be discussed in the next section). The major stocks originating from tributary systems upstream from the mouth of the West Road are the Stuart and Fraser-Francois Lakes stocks.

Records from Fort Langley, near the mouth of the Fraser River show that salmon were abundant in 1829, 1857 and 1869, years on the old pre-1917 dominant sequence. Information concerning other years of this sequence at Fort Langley was missing. Salmon were apparently moderately abundant in 1830, the year following a year of abundance. No data for other years of this sequence were available. Data for the third sequence of years were recorded in 1827, 1851, 1855, 1859, 1863 and 1867. Salmon were apparently abundant in 1827 but the runs were either moderate or small in the other years of this cycle. In the fourth sequence, data were recorded in 1828, 1856, 1868 and 1872. Salmon were scarce in each of these years. It is apparent from the Fort Langley records that salmon were consistently abundant during the 1829-1869 sequence, the pre-1917 dominant series, but with the exception of 1827 either scarce or only moderately abundant on the other three sequences of years.

These Fort Langley records do not make a clear distinction between the species of salmon, however in 1829 it was possible to infer that reference was being made to an abundant sockeye run. About the middle of September 1829, the presence in the river of a different kind of salmon was noted. By the description, these fish were pink salmon. Prior to this, the abundant species must have been sockeye. Further evidence suggesting that sockeye were the abundant salmon species noted on the 1829-1869 sequence is available from the relative scarcity of salmon noted on the other odd year sequence (1827 to 1867). If pink salmon were the abundant species on the 1829-1869 cycle they would also be abundant on the 1827-1867 sequence, since this species

exhibits biennial dominance. These Fort Langley records, therefore, indicate that Fraser River sockeye in general exhibited cyclic dominance prior to the development of a commercial fishery and that this dominance was stable for many generations.

More complete records are available from Fort Alexandria which was located on the Fraser River about ten miles downstream from the mouth of the Quesnel River (FIGURE 1). These records would refer to the following major stocks: the Quesnel, Stuart and Fraser-Francois.

Prior to the development of the commercial fishery the fur traders in north-central British Columbia were extremely dependent on dried salmon for winter food for both men and dogs. Salmon were eagerly awaited; a large run caused universal relief and a failure was a serious matter. Salmon were captured in weirs, nets and sometimes speared. Estimates of relative abundance at Fort Alexandria are shown in TABLE 1. These estimates have been arranged into four series of years.

TABLE 1 - Estimates of the relative abundance of salmon at Fort Alexandria on the Fraser River, 1827 to 1869 (++++ abundant run, ++ moderate run, + small run).

Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance
1825		1826		1827	+	1828	+
1829	++++	1830		1831	+	1832	
1833	++++	1834		1835		1836	
1837	++++	1838	++	1839		1840	
1841	++++	1842	++	1843	+	1844	+
1845	++++	1846		1847	+	1848	++
1849	++++	1850	++	1851	+	1852	+
1853	++++	1854	+	1855	+	1856	+
1857	+	1858	+	1859		1860	+
1861	++++	1862		1863		1864	+
1865	++++	1866		1867		1868	+
1869	++++	1870		1871		1872	

Although these determinations of relative abundance involve personal interpretation there can be little doubt that sockeye were, with the exception of 1857, abundant in the upper Fraser in all years of the 1829-1869 quadrennial cycle, the same dominant sequence as indicated by the Fort Langley records for the whole Fraser River system. Sockeye were either scarce or only moderately abundant on the other three series of years. It is again evident that sockeye stocks native to the upper tributaries of the Fraser were dominant on the same sequence of years (1829-1869) before the development of a commercial fishery as was the case after the fishery became intense (1897) and before the original pattern was destroyed by the Hell's Gate blockades during the 1911-1913 period. Apparently the run of 1857 failed in the upper river but not in the lower tributaries (see the previous discussion of the Fort Langley records).

The records from the individual tributary systems, although not so complete indicate the same pattern, dominant populations on the same sequence as indicated by the Fort Langley and Fort Alexandria records.

Fort St. James records (TABLE 2) refer to sockeye native to the streams of Stuart, Trembleur and Takla Lakes. It is apparent that stocks in this area were dominant on the same sequence from 1825-1873. Some evidence for a subdominant series (1822-1854 sequence) exists. Sockeye at Fort St. James were generally scarce on the other two cycles. Apparently the dominant run of 1857 was a failure, confirming the Fort Alexandria information. Again it is apparent that dominance existed prior to the establishment of an intense commercial fishery.

TABLE 2 - Estimates of the relative abundance of Stuart River system sockeye stocks from Fort St. James records, 1820 to 1873 (++++ abundant run, ++ moderate run, + small run).

Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance
1821		1822	+	1823	++	1820	+
1825	++++	1826	++	1827	+	1824	+
1829	++++	1830	++	1831	+	1828	+
1833	++++	1834		1835		1832	
1837		1838		1839		1836	
1841	++	1842	++	1843	+	1840	+
1845	++++	1846	++	1847	+	1844	+
1849	++++	1850	++	1851	+	1848	++
1853	++++	1854	++	1855	+	1852	+
1857	+	1858		1859		1856	
1861		1862		1863		1860	
1865		1866		1867		1864	
1869		1870		1871		1868	
1873	++++	1874				1872	

A similar pattern existed in the Fraser-Francois Lakes system (TABLE 3). Records from both Fort St. James and Fort Fraser indicate that salmon were usually abundant in the area on the 1825-1873 cycle. The two chief sockeye spawning streams in this system are the Stellako and Nadina Rivers. Salmon also tended to be numerous on the 1824 sequence but the 1825 sequence runs were clearly dominant. Extremes of abundance were not as common in the Fraser-Francois Lakes system as they were in the Stuart system. The fur traders at Fort St. James were sometimes able to get dried salmon from Fort Fraser at Fraser Lake when the runs to the Stuart River system failed. However the Babine district, part of the Skeena system, seldom had a salmon failure and provided fish for north-central British Columbia when the upper Fraser River stocks failed.

TABLE 3 - Estimates of the relative abundance of Fraser-Francois Lakes system sockeye stocks from the Fort St. James and Fort Fraser records, 1820 to 1873 (++++ abundant run, ++ moderate run, + small run).

Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance
1821		1822	+	1823	++	1820	+
1825	++	1826		1827	+	1824	++
1829	++++	1830		1831	+	1828	++
1833		1834		1835		1832	
1837		1838		1839		1836	
1841	++++	1842	+	1843	+	1840	
1845		1846	+	1847	+	1844	++
1849		1850		1851		1848	++
1853		1854		1855		1852	++
1857		1858		1859		1856	
1861		1862		1863		1860	
1865		1866		1867		1864	
1869	++++	1870		1871		1868	
1873	++++					1872	

In another tributary system, the Thompson, there is strong evidence for dominant populations occurring on the 1825-1873 sequence, evidence for the occurrence of subdominant runs on the 1826 sequence and scarcity on the 1827 and 1828 sequences (TABLE 4).

TABLE 4 - Estimates of the relative abundance of Thompson River system sockeye stocks from Kamloops records, 1822 to 1859 (++++ abundant run, ++ moderate run, + small run).

Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance	Year	Relative Abundance
1821		1822	++	1823		1824	+
1825		1826	++	1827	++	1828	
1829		1830		1831	+	1832	
1833		1834		1835		1836	
1837		1838		1839		1840	
1841	++++	1842	++	1843	+	1844	
1845	++++	1846		1847		1848	
1849		1850	++	1851	+	1852	
1853		1854	+	1855		1856	+
1857		1858		1859	+	1860	

Two important conclusions can be drawn from the evidence provided by these Hudson's Bay Company records. First, dominant populations occurred in upper Fraser River sockeye stocks before the development of an intense commercial fishery. Stocks native to the Thompson River system, present home of the now dominant Adams River stock, also exhibited dominance. A second important conclusion is that dominance was stable. Records for the upper Fraser suggest that dominance occurred as early as 1793 and continued on this same sequence without deviation. (Sockeye may have been scarce in some of the upper Fraser tributaries in 1857 but were again abundant in 1861.)

The Abundance Pattern, 1873 to 1917

Prior to 1897 the catches reflected factors in the development of the fishery more than fluctuations in abundance and, in the absence of other suitable records, the pattern of abundance during the 1873-1897 period cannot be determined. Beginning in 1897 and continuing until 1913 large packs of over a million cases were made at four year intervals (FIGURE 2). The years of these great catches were 1897, 1901, 1905, 1909 and 1913. On two occasions, 1901 and 1913, the annual pack was over two million cases. Since the average number of fish per case in 1913 was about 13, this would represent a catch of approximately 30 million sockeye. Between these years of large catches, except for the year 1899, much smaller annual packs occurred (TABLE 5).

The great catches made on the 1897 cycle were composed of major stocks dominant on this cycle, the original 1793-1873 sequence. Documents of the British Columbia Department of Fisheries, chiefly the correspondence of J. P. Babcock, reveal that stocks inhabiting the upper tributaries of the Fraser River were dominant on this 1897 sequence. Adults were abundant on the Shuswap district spawning grounds in 1901, 1905 and 1913. Large numbers

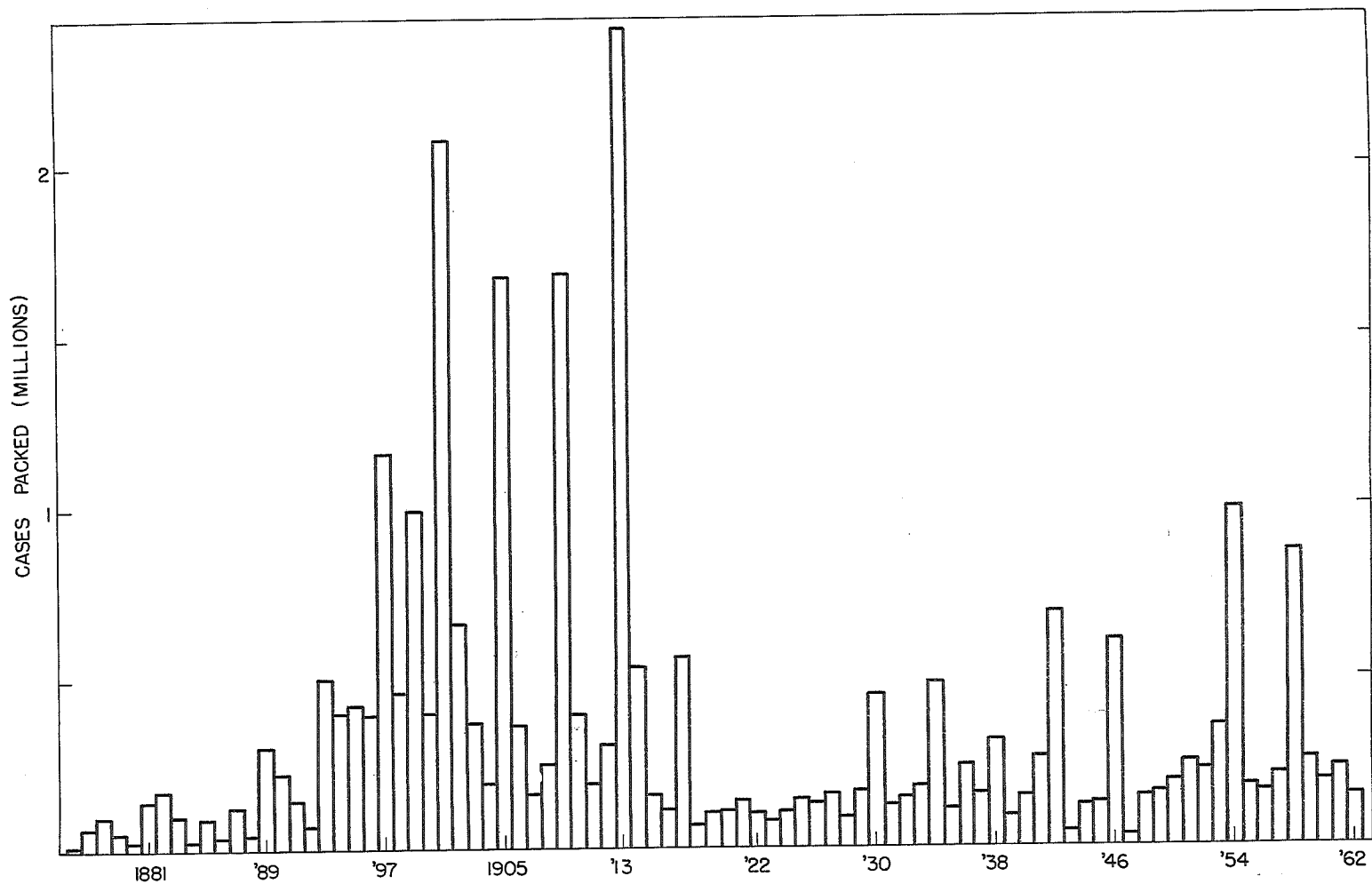


FIGURE 2 - Fraser River sockeye salmon packs (48-pound cases), 1876 to 1962.

TABLE 5 - Annual packs of Fraser River sockeye salmon in 48-pound cases arranged into quadrennial cycles of years, 1897 to 1913.

Year	Pack	Year	Pack	Year	Pack	Year	Pack
1897	1,162,048	1898	468,000	1899	998,909	1900	402,417
1901	2,081,554	1902	667,980	1903	372,059	1904	196,594
1905	1,675,935	1906	367,681	1907	162,035	1908	250,162
1909	1,688,334	1910	399,636	1911	192,231	1912	309,647
1913	2,412,700						
Mean	1,804,114		475,824		431,309		289,705

of sockeye were reported in Quesnel River in 1901 when a dam near the lake outlet impeded migration. However the run recovered and was again large in 1905 and reached 4,000,000 in 1909. The run in 1913 was much reduced by the Hell's Gate obstruction, and only 500,000 reached the spawning grounds. The sockeye runs to the Chilcotin showed a similar pattern. The 1905 and 1909 annual populations were large but the 1913 run was little better than the moderate runs which occurred in 1908 and 1912. From observations made at Fort St. James, it was concluded that runs of sockeye to the Stuart Lake system were large in 1905 and 1909 but sockeye were scarce in 1913. Similarly, in the Fraser-Francois Lakes system, the annual populations were large in 1905 and 1909 but poor in 1906 and 1907, the second and third off year sequence respectively. Runs were of moderate size in 1904 and 1908, the fourth off year sequence.

Pertinent extracts from these documents are on file in the library of the International Pacific Salmon Fisheries Commission.

Based on the above information it is evident that the quadrennially dominant catches prior to 1917 must have been composed primarily of these upper river stocks which were all dominant on the 1793-1913 sequence.

The Abundance Pattern Since 1917

After 1913 catches of Fraser River sockeye declined sharply and have not as yet regained their former size (FIGURE 2). Primarily as a result of blockades in the river caused by railroad construction in the Fraser Canyon, the great upriver runs were destroyed (Thompson, 1945); however, beginning in 1930 a new pattern of cyclic dominance in the catches can be noted (FIGURE 2). Packs in 1930 and 1934 were well above average for the post-1917 period. The catch declined in 1938 but this decline has been explained by Thompson (1945). The poor return in 1938 was associated with blockade conditions at Hell's Gate in 1934. Large packs were made in 1942, 1946, 1954 and 1958. The packs of 1950 and 1962 were unusually low; the runs were small for natural reasons (Internat. Pacific Salmon Fish. Comm., 1951 and 1963). Annual packs from 1930 to 1962 are summarized in TABLE 6.

In contrast with the pre-1917 situation, the comparatively large catches made on the 1930 cycle were composed primarily of fish belonging to one stock, the Adams River stock, inhabiting the Shuswap Lake district. Prior to 1917, two stocks of sockeye originated in the Shuswap Lake area, an early and a late migrating stock, both of which were dominant on the 1901 cycle of years (Thompson, 1945). The early migrating stock was composed of fish spawning in the Seymour River, Scotch Creek and the Upper Adams River among others. The late migrating stock spawned primarily in the Lower Adams River with smaller proportions spawning in Little and South Thompson Rivers.

TABLE 6 - Annual packs of Fraser River sockeye salmon in 48-pound cases, 1930 to 1962.

Year	Pack	Year	Pack	Year	Pack	Year	Pack
1930	455,856	1931	128,158	1932	150,980	1933	182,664
1934	488,878	1935	117,499	1936	244,359	1937	160,531
1938	321,435	1939	97,807	1940	152,715	1941	269,884
1942	690,437	1943	49,340	1944	125,529	1945	132,835
1946	611,310	1947	35,930	1948	152,091	1949	161,176
1950	197,968	1951	252,551	1952	230,452	1953	354,420
1954	988,301	1955	180,513	1956	168,348	1957	219,383
1958	868,770	1959	258,737	1960	195,422	1961	235,428
1962	150,282						
Mean	530,360		140,067		177,487		214,540

Thompson states: "The disappearance of the early run into Adams Lake is consistent with the widespread failure of 1913 and of subsequent years in that cycle sequence. So too, is the diminution of the late run of the same years." Thompson also suggested that failure of the old late run to regain its former level may have been caused by the effects of a dam located at the outlet from Adams Lake. Sharp fluctuations in water level may have resulted in drying and freezing of redds in the winter and scouring of the gravel at other seasons. Regardless of the cause or causes, after 1913 both the early and late stocks inhabiting the Shuswap district were virtually eliminated; however, beginning in 1922, the late stock showed signs of a definite increase in abundance but has developed cyclic dominance on the 1922 sequence, not on the original pre-1917 dominant sequence. The presence of

established dominance in this stock first became obvious in the catch of 1930 (FIGURE 2). Thompson associated the increase, commencing with the 1922 population, with the abandonment of the dam and the attainment of favorable fall water levels in Adams River.

Quantitative estimates of populations of spawners belonging to the Adams River stock began in 1938, and are presented in TABLE 7.

TABLE 7 - Annual estimated spawning populations of Adams River sockeye, 1938 to 1962.

Year	No. Spawners	Year	No. Spawners	Year	No. Spawners	Year	No. Spawners
1938	776,000	1939	32,000	1940	12,000	1941	50
1942	2,568,000	1943	10,000 ¹	1944	2,000	1945	67,000
1946	2,352,000	1947	200,000	1948	15,000	1949	22,000
1950	1,268,000	1951	145,000	1952	11,000	1953	222,000
1954	2,066,000	1955	64,000	1956	8,000	1957	307,000
1958	2,274,000	1959	135,000	1960	2,000	1961	66,000
1962	1,151,000						
Mean	1,779,000		98,000		8,000		114,000

¹The 1943 estimated population appears too small to have given rise to the 1947 population. At this late date the accuracy of the 1943 estimate cannot be verified.

The scarcity of spawners in 1941 was caused by blockade water levels at Hell's Gate during the migration period (Internat. Pacific Salmon Fish. Comm., 1943). Other stocks originating in streams above Hell's Gate were also affected. It might, at first, seem anomalous that a spawning population of only 50 fish be followed by one of 67,000. In fact, the

great majority of the 1945 population present on the spawning grounds was composed of three-year-old jack sockeye arising from the population which had spawned in 1942.

Regardless of this inconsistency, it is apparent that populations spawning quadrennially on the 1938 cycle were much larger than those which were present during the other three cycles of years.

The development of new dominant populations in upper river stocks other than the Adams is not so apparent. These populations remained at low abundance levels for a much longer period than the Adams stock, apparently because they migrated through the Fraser Canyon earlier and were affected more seriously and more frequently by the prevailing adverse water levels at Hell's Gate. As demonstrated by Talbot (1950), most of these remaining major stocks increased rapidly after 1945. Apparently dominant populations are again developing. In the Quesnel and Stuart stocks, these new dominant populations are on the original 1793-1917 sequence. For some reason the Chilko stock was less seriously affected by the Hell's Gate obstruction than other upper river stocks and two cycles of runs were larger than the remaining two. These were the 1940 and 1941 sequences; however in 1941 the Chilko stock was seriously affected by blockade conditions in the Fraser Canyon. Since then, the 1940 sequence has predominated. Sockeye spawning in the Stellako River, part of the Fraser-Francois Lakes system has had since 1945 larger than average annual populations present on the spawning grounds on the 1946 sequence.

The general statement can be made that in all major stocks inhabiting tributaries above Hell's Gate, one sequence of annual populations tends to be more abundant than the other three. However, these larger than average populations currently do not occur on the same sequence in all stocks.

The history of Fraser River sockeye salmon from 1793 to the present time leads to the conclusion that quadrennial dominance is a common feature of Fraser River sockeye salmon dynamics and of the Adams River stock in particular. Populations present on the quadrennial sequence, 1793 to 1917 were generally far more abundant than those occurring on the other three quadrennial sequences. When this pattern was destroyed extreme dominance developed again in the Adams River stock, on the 1930-1962 sequence, a change from the original 1793-1917 sequence.

MAINTENANCE OF DOMINANCE

The most important feature of well developed dominance is the great, consistent disparity between dominant and off year populations. Consistent dominance is apparent in catch data from the pre-1917 years (FIGURE 2) and in the Adams River escapement data (TABLE 7). This consistency in size is even more apparent and the disparity more pronounced when the number of precocious adults or "jacks" belonging to dominant populations is removed from the annual populations immediately preceding the dominant sequence of years (FIGURE 3). Transformations to logarithms, base ten, were made to reduce the great annual differences, thus facilitating presentation.

Adams River escapements show three distinct abundance levels, the highest level (dominant populations), an intermediate level (subdominant populations) and a low level (the remaining two off year series). The dominant cycle of populations will be referred to as Cycle I, the subdominant as Cycle II, the next off year as Cycle III and the last as Cycle IV.

Two explanations are available for the maintenance of dominance¹. It could be argued that consistent disparity is largely due to chance. One annual population initially may have had favorable survival conditions and subsequently maintained its position because similar favorable conditions

¹ Any regular four year cycle of physical events seems such a remote possibility that it may be dismissed.

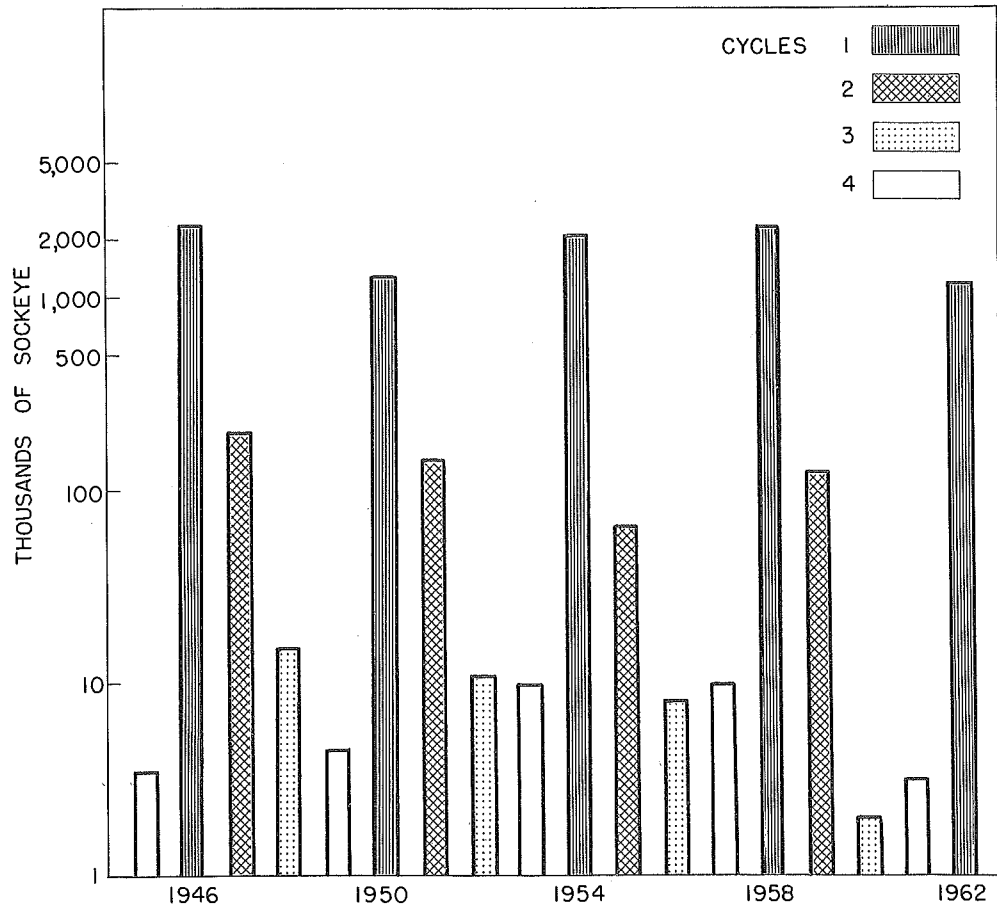


FIGURE 3 - Annual parental populations of Adams River sockeye salmon. Jacks are not included in estimates of Cycle IV abundance.

did not occur for other annual populations. In this situation dominance would be maintained until an unusual set of conditions either increased the abundance of one or more of the smaller annual populations or decreased dominant abundance. The other possibility is that one or more factors might act to limit off year abundance, i.e. dominance is relatively stable and the abundance pattern is actively maintained.

In assessing these two possibilities, three considerations are pertinent relative to the present apparent stability of the various annual populations of Adams sockeye: First, the effects of a slight increase in average survival during the incubation of Cycle II eggs; second, rates of increase which have applied in recent years to other stocks of Fraser River sockeye not fully utilizing spawning and rearing areas; finally, the rate of increase apparently applying during the period 1922 to 1938.

Effect of Increased Survival

Because the dominant population utilizes the same spawning and freshwater rearing areas, it would be expected that the various off year populations would have potentialities for increase. Hunter (1959), among others, has shown that survival of pink and chum salmon eggs may be density-dependent (and as will be shown in a later section, fry survival was lowest from the largest Chilko Lake sockeye spawning population). If all other mortalities remained constant, off year populations should show frequent increases in abundance. These increases should appear as definite upward trends in off year population levels. Such trends were not apparent (FIGURE 3); however, a relatively small increase in average survival could have produced in four generations a great change in the abundance of Cycle II sockeye. If

we assume that one million female sockeye is an average optimum dominant population and that survival during incubation for a subdominant population of 50,000 females is 12 per cent and for a dominant population of one million females, six per cent, all other things equal, a subdominant spawning population of 50,000 females would increase to over 250,000 in four generations. A similar argument can be applied to Cycle III and Cycle IV sockeye. That none of these populations have shown marked increases since 1922 is not consistent with knowledge concerning density-dependent survival rates during spawning and incubation. Any increased survival that may have occurred during this phase has apparently been compensated by increased mortalities at some other stage in life.

Rates of Increase in Other Stocks of Fraser River Sockeye

Sockeye populations migrating upstream in the Fraser in 1945 were the first to benefit by the construction of the fishways at Hell's Gate in the Fraser Canyon (Talbot, 1950). Stocks which had been at low abundance levels but had potentially large spawning and rearing areas benefited most and showed major increases. The Early and Late Stuart stocks and the Quesnel stock increased rapidly (Talbot, 1950). Since Cycles II, III and IV Adams sockeye were only occasionally affected by blockade levels at Hell's Gate prior to 1945 (Thompson, 1945), their case was similar to that of the above mentioned stocks. Large spawning and rearing areas were available but were not fully utilized. One would have expected that increases similar to those shown for Stuart and Quesnel sockeye would have applied to Adams fish of Cycles II, III and IV soon after the cause of the initial decline was no longer effective (presumably about 1920).

Application of Quesnel rates of increase to the 1945 Cycle III Adams population gives surprising results: in 1948, 15,000 fish would have been present; in 1952, 100,000; 1956, 525,000; finally, in 1960, the escapement would have been 1,130,000. In fact, the population was only about 2000. Moreover, the opportunity for increases to occur were apparently present for almost 40 years; not just 12 years as in the case of Quesnel sockeye.

Rate of Increase in Cycle I Adams Sockeye

Thompson (1945) lists the Adams River spawning population in 1922 as 20,000 fish. By 1926 this had increased to 300,000. Numerical estimates of spawning abundance were not made again until 1938 when it was estimated that approximately 800,000 sockeye were present on the spawning grounds (Internat. Pacific Salmon Fish. Comm., 1951). By 1942 the spawning population was over two million. These increases in Cycle I populations were obviously rather rapid. For instance, between 1922 and 1926 the increase was fifteenfold and between 1926 and 1938 approximately twofold. This shows that sockeye populations and Adams River stock sockeye in particular can increase in abundance at rapid rates under suitable conditions.

It is concluded, therefore, that the consistent low levels of abundance exhibited by Cycle II, III and IV populations has a low probability if no stabilizing influences exist.

Inherent Differences in Survival

Assuming that dominance maintaining agents exist, off year populations may be maintained at low levels by differences in the reproductive potential of each sequence of populations. If such genetic differences exist one would need to conclude that each cycle was genetically isolated. Isolation

cannot be demonstrated nor can the possibility be rejected since the required degree of isolation is unknown. However it can be shown that exchanges of genetic material do take place between annual populations (TABLE 8). For example, some five-year-old fish from Cycle I populations contribute to Cycle II populations. A very large fraction of the fish present on the spawning grounds during the year preceding the return of a dominant population are precocious adults derived from the preceding Cycle I spawning (TABLE 8). These jack populations are, however, about 99 per cent males therefore their contribution is much less than their numbers would suggest. Only about 3000 of the jacks in 1957 were females which deposited eggs. Even so it can be seen that a large fraction of the eggs deposited by females in Cycle IV years are derived from Cycle I populations. In addition, 3_2 males may contribute genes to both 3_2 and 4_2 females to some unknown degree.

In summary, exchanges of genes do take place and these exchanges may tend to reduce genetic differences between annual populations. No firm conclusion can be reached because insufficient data are available, however some direct evidence is at hand concerning the reproductive performance of annual populations of Adams River sockeye. For example, unequal sex ratios, pre-spawning mortality, egg retention and differences in egg abundance are all factors which could cause annual differences in reproductive potential.

It is unlikely that a paucity of males in a natural spawning population would limit the number of fertile eggs deposited. Mathisen (1955) has shown that for Bristol Bay sockeye, fry survival was only slightly reduced even at ratios of 15:1 in favor of females.

TABLE 8 - Age composition of annual Adams River spawning populations.

YEAR OF SPAWNING	TOTAL POPULATION	4 ₂		3 ₂		5 ₂		5 ₃	
		Number	Per Cent	Number	Per Cent	Number	Per Cent	Number	Per Cent
1954	2,065,000	2,059,000	99.7	6,000	0.3	0	0	0	0
1955	65,020	61,000	93.8	780	1.2	670	1.0	2,570	4.0
1956	8,050	6,000	74.5	1,100	13.7	890	11.1	60	0.7
1957	307,130	3,000	0.6	305,000	99.3	130	0	0	0

If there were relatively few females produced by Cycle II, III and IV populations, it is possible that these populations would be stabilized at lower levels of abundance. Shown in TABLE 9 are the average percentage compositions by sex of each cycle of populations. Each cycle percentage was computed from three annual populations. For example, the Cycle I percentages were derived from totals of males and females from 1950, 1954 and 1958 populations. Estimates of both male and female jack abundance were also included in each total. Inclusion of jacks (Cycle I, 3₂'s) with the Cycle IV population accounts for the very unequal sex ratio during years when Cycle IV 4₂'s spawn, since jacks are relatively very abundant and about 99 per cent of them are males.

TABLE 9 - Sex compositions of each cycle of Adams River sockeye, adult spawners 1949 to 1960.

CYCLE	PERCENTAGE	
	Male	Female
I	47.7	52.3
II	37.0	63.0
III	52.5	47.5
IV	97.8	2.2

Neglecting Cycle IV for the moment, it is evident that only Cycle II populations differ greatly from a 1:1 ratio and this deviation is in the direction of fewer males. Hartman and Conkle (1960) suggested that even a highly unbalanced sex ratio favoring females might result in only minor decreases in ultimate egg survival from each female. They also suggested that such a population might yield a considerable increase in potential

production over one of equal size but with a more even sex ratio. It seems probable then that unequal sex ratios in Cycles II and III populations are not a factor resulting in unequal relative reproductive potential.

Earlier, it was suggested that Cycle I jacks contribute little to Cycle IV spawning populations because of the great predominance of males. Therefore the true productivity of Cycle IV is determined by the number of females, both jacks and older fish. In this case it is evident that the unequal sex ratio does limit the abundance of Cycle IV sockeye; however this limitation is a result of dominance rather than a cause since the inequality is brought about by the great numerical abundance of Cycle I populations. The actual sex ratio of four and five-year-old fish present on the Cycle IV sequence for four generations has been 1:1.8 in favor of females.

In some areas considerable numbers of sockeye die unspawned (Internat. Pacific Salmon Fish. Comm., 1954). These mortalities have been associated with unusually warm stream temperatures and possibly other factors. No similar mortalities have been noted among Adams River annual populations occurring either at random or in any sort of pattern.

Another factor which could affect potential egg deposition to the detriment of small populations is greater egg retention by females of Cycles II, III and IV. Female carcasses have been examined from 11 annual populations and it was found that eggs were almost completely expressed in all years. Any slight differences in egg retention would have been offset by relatively minor fluctuations in sex ratio or in the size of females.

Ward (1952) found that the mean egg number for an Adams River sockeye 564 mm. long in 1950 (Cycle I) was 3320. In 1951 (Cycle II) a fish of the

same length contained 3550 eggs. The 1950 sample was composed of 79 fish whereas 39 fish formed the 1951 sample. These differences could result from the relatively small and perhaps unrepresentative samples or in environmentally controlled differences in the condition of the fish rather than from any genetic differences in the egg count-length relationship. Regardless of which of the above is correct, the data indicate that, if anything, the Cycle II population had more eggs per female. Small differences such as these could be masked by annual variations in mean size and again by differences in sex ratios. Although no data are available for fish belonging to Cycles III and IV it would seem unlikely, in view of the above, that differences in the body size-egg number relationship between annual populations could greatly affect the number of eggs deposited by an Adams River sockeye in any systematic manner.

The absence of any differences in potential egg deposition which would result in differences between cycles in relative production and the rather low probability for inherent differences in viability, lead to the conclusion that factors other than genetic should be considered as agents for maintaining the cycles at different levels of abundance.

Nature of Mortalities

Neave (1953) has suggested that mortalities affecting salmon populations are of three types, directly density-dependent, inversely density-dependent and those independent of population density. He has applied the terms "compensatory", "depensatory" and "extrapensatory" to these classes of mortalities. This terminology will be used below.

Because dominance, once formed, appears to be relatively stable, it follows that on the average, total mortality coefficients from generation

to generation are equal for all four cycles. It is clear that for dominance to be maintained Cycles II, III and IV by comparison with Cycle I, must be affected by compensatory mortalities. If this were not so, the small populations would increase in abundance, presumably to the level of dominant populations.

It is possible that this relative depensation could occur at any one or several of the life-history stages.

In following sections, the type of mortality applying during each stage in sockeye life-history will be discussed, but first, the several stages will be defined:

- (1) The spawning-incubation stage -- taken here to include arrival on spawning grounds, spawning (egg deposition), death of adults, incubation and hatching of eggs, emergence of fry, and migration of fry into the lake.
- (2) The lacustrine stage -- dispersal of fry throughout the lake and the lacustrine residence period.
- (3) The marine stage -- the migration of smolts down the tributaries of the Fraser River, entry into the Strait of Georgia, dispersal in the eastern North Pacific Ocean and the return of the maturing fish to coastal areas.
- (4) The adult stage -- a relatively short period between entry into coastal waters and arrival on the spawning grounds. During most of this latter period, sockeye are subjected to commercial fishing and a food fishery conducted by Indians.

It is important to note that in these various life-history stages the different cycles have only limited opportunities for affecting each other directly. For example, when Cycle I eggs are in the gravel, Cycle IV fry

are in the lake; and as Cycle I fry emerge and disperse, Cycle IV smolts are leaving the lake. Similarly, Cycle II overlaps Cycle I during the seven or eight months of fall to spring. Except for this short period, the cycles are virtually completely separated in their freshwater life-history. Several ages of Adams sockeye are resident in the North Pacific at the same time but they inhabit the same regions at the same time to only a limited extent (Kasahara, 1961). Accordingly it is appropriate to first examine the life-history stages for compensatory effects, without reference to the possibility of direct interaction between cycles.

Spawning-Incubation Stage

Compensatory mortalities are probably the most important type affecting survival during the spawning-incubation period. Neave (1953) has discussed in some detail the sources of mortality during this stage for pink salmon, Oncorhynchus gorbuscha, and chum salmon Oncorhynchus keta. Most of these mortality sources also apply to sockeye although not to the same degree. For example, extrapensatory effects are less frequent and more consistent since the freshwater environment of sockeye is much more stable than that of coastal streams which are subject to flooding, where pinks and chums generally spawn. Pritchard (1948) and Hunter (1959) have shown, for pink and chum salmon, that survival during the spawning-incubation stage is compensatory. No such data are available for Adams River sockeye, since fry production has not been measured; however, data for the Chilko stock of Fraser River sockeye are shown in FIGURE 4.

The trend line indicates that fry production from the largest egg depositions was generally lower than from the smaller depositions. This relationship in turn indicates that mortality rates were positively density-dependent or compensatory in effect.

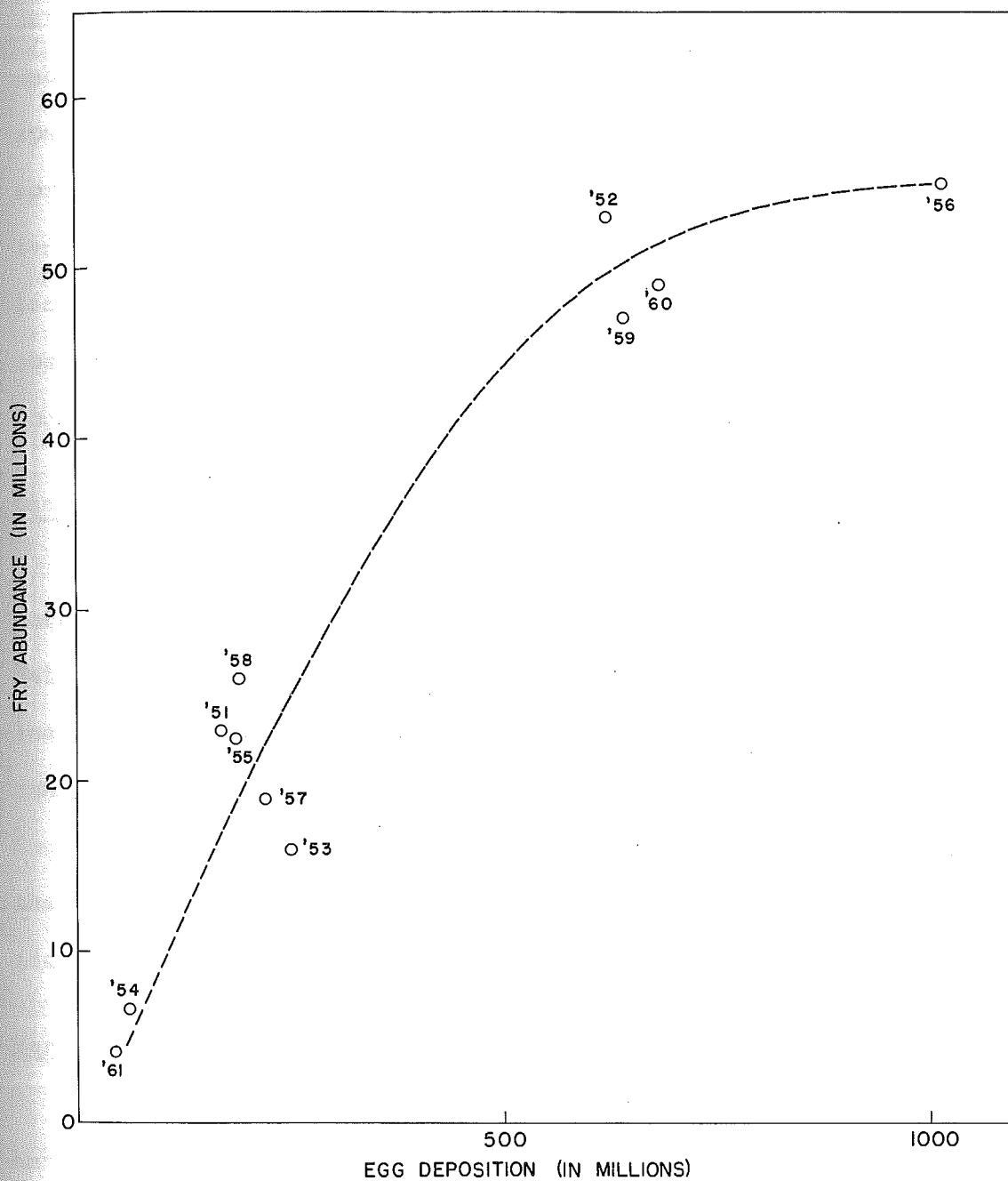


FIGURE 4 - Relationship of Chilko Lake sockeye fry production to the number of eggs deposited (broods from 1951 to 1961).

Qualitative observations also indicate that the effect of mortalities during spawning and incubation are compensatory. Large numbers of dead unburied eggs are apparent in holes in Adams River during and after the spawning period of Cycle I sockeye. Cycle I fry have been observed in the spring trapped in blind side channels. In addition, some Cycle I adults tend to spawn in areas both in Adams and Little Rivers which are apparently less suitable than those utilized by Cycle II, III and IV spawners. These observations would also suggest that mortality coefficients for this stage would be smaller for off year populations.

Lacustrine Stage

Evidence concerning the relationship between population density and survival during the lacustrine stage is not available for the Adams stock. Neither annual fry populations entering Shuswap Lake nor smolt populations leaving have been enumerated, therefore estimates of lacustrine survival cannot be made. On the other hand, there is no evidence either from the Shuswap district or from other sockeye producing areas which would preclude the existence of a compensatory relationship for the lacustrine stage of Adams sockeye.

Marine Stage

Foerster (1954) found a significant inverse relationship between the annual abundance of smolts leaving Cultus Lake and the survival to adults returning to the lake. These data indicate that the overall effect of mortalities applying after the fish leave the lake until they return as adults is compensatory. By definition both the marine and adult stages are covered during this period. Similar data were available from Chilko Lake sockeye (Henry, 1961) but annual racial catches were known and could be

added to populations enumerated on the spawning grounds thus giving estimates of the abundance of survivors at the end of the marine stage. These Chilko data are shown in FIGURE 5. They indicate that smolt to adult mortalities have a compensatory effect. High survival rates never applied to large populations although survival was low for two small populations. This relationship, however, seems to be fortuitous. Marine survival of Chilko sockeye is highly correlated with weighted Fraser River spring discharge. Using Multiple Regression, where $X_1 = \log_{10}$ Chilko smolt abundance, $X_2 =$ weighted Fraser River discharge at Hope (FIGURE 1) during seaward migration and $Y =$ percentage survival from one-year-old smolts to returning 4₂ adults (racial catch plus escapement) the following partial correlation coefficients were computed:

$$r_{y1.2} = -0.569, P > 0.05; r_{y2.1} = 0.865, P < 0.01; r_{12.y} = -0.323, P > 0.05.$$

These results indicate that marine survival is more highly correlated, linearly, with discharge conditions than it is with smolt abundance. The standard partial regression coefficients show, in linear correlation, that discharge is over twice as effective in predicting survival than is the abundance of seaward migrating smolts ($b'_1 = 0.302$, $b'_2 = 0.750$). Although the linear regression of survival on smolt abundance is not significant, it does account for 32 per cent of the total variability, and the sign of the partial correlation coefficient is negative, demonstrating an inverse relationship between abundance and survival rate, indicative of compensation rather than depensation.

This analysis shows that for one stock of sockeye and during the period studied (broods from 1949 to 1958 inclusive) marine mortalities were predominantly of the extrapensatory type. Their effect was primarily

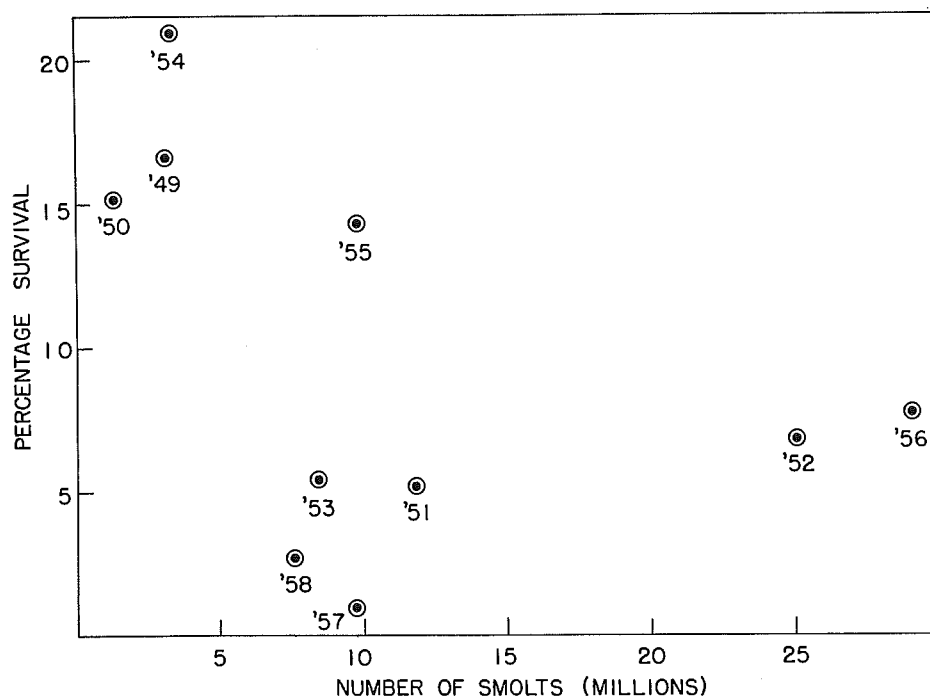


FIGURE 5 - Relationship between abundance of one year lake resident Chilko Lake sockeye smolts and survival to returning 4₂ adults (broods from 1949 to 1958).

independent of population density. There was no evidence indicating that depensation occurred.

Adult Stage

During the adult stage in Fraser River sockeye life-history (the period extending from arrival in inshore waters to arrival on the spawning grounds) the chief source of mortality is the commercial fisheries. In general, during this stage, effects of natural mortality are minor in comparison with fishing mortality. Exceptions occur such as natural mortality resulting from blockades along the migration route but in most years these effects can be ignored.

Recently it has been possible to estimate the annual catch made from each stock of Fraser River sockeye made in Convention waters (Henry, 1961). The relationships between survival from these fisheries and total annual adult abundance for the Chilko, Stellako, Early Stuart and Adams stocks are shown in FIGURE 6.

There is evidence that fishing mortality on Chilko sockeye has been of the depensatory type. Except for 1960, the survival rate from the fisheries was generally lower for small populations. For the Chilko stock the apparent effect of the fisheries is depensatory; fishing mortality rate is inversely related to population size.

A different relationship is evident for Stellako sockeye. Generally survival rates from the fisheries were lower for the larger populations (e.g. 1959 and 1954). The overall effect of the fisheries on this stock is compensatory. Very little relationship seems to exist between population size and survival from the fisheries for the Early Stuart and Adams stocks. Small populations have both high and low survival rates. The largest

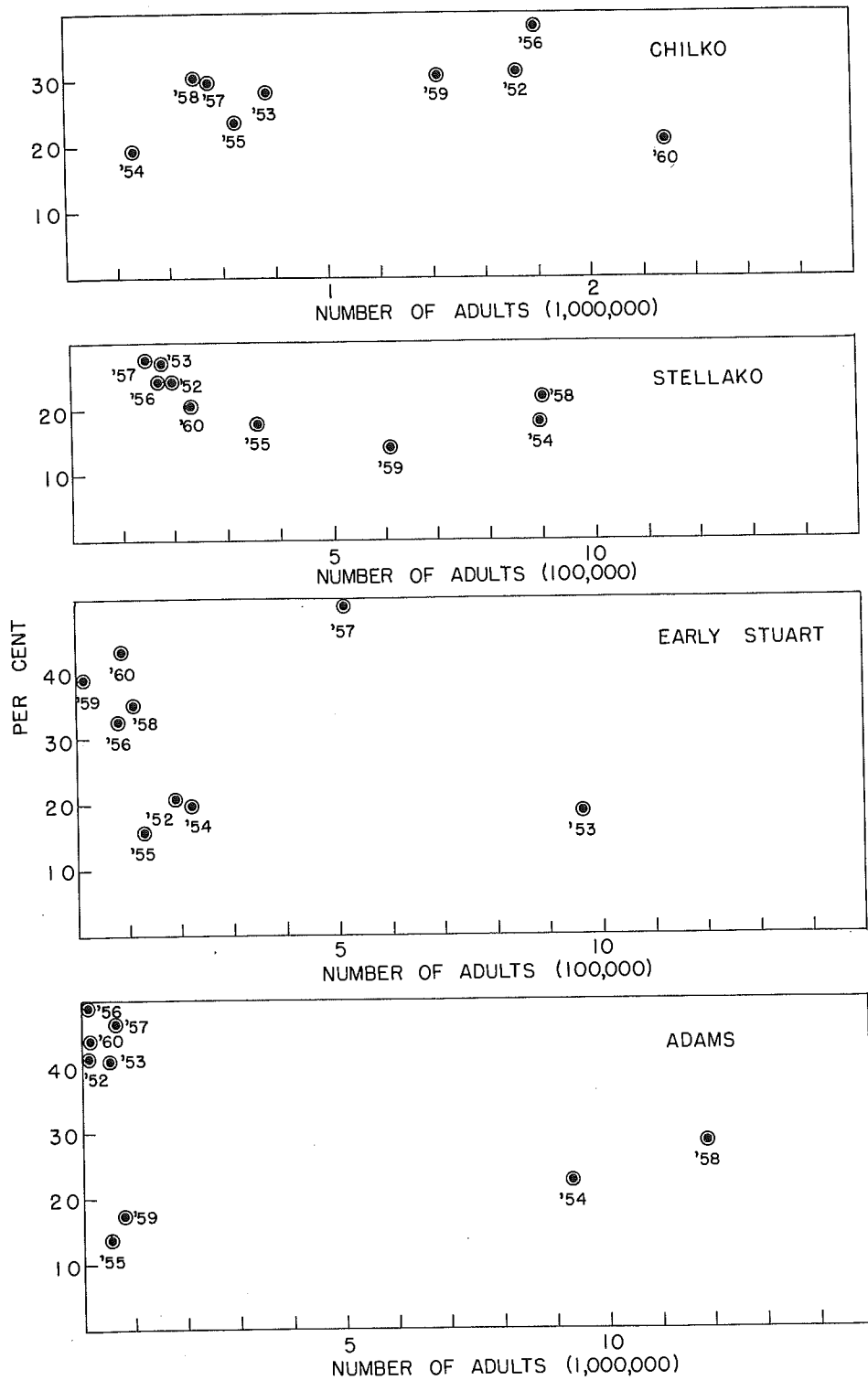


FIGURE 6 - Relationship between the number of adults of several races of sockeye entering Fraser River commercial fisheries and per cent racial survival from the fisheries (1952 to 1960).

populations have either low or intermediate survival rates.

The effect of the fisheries on these four stocks is obviously quite variable. This variability can be expected because annual racial management requirements vary and because social and economic conditions and the relative abundance of other stocks and species all affect the intensity of the fisheries both annually and seasonally. It can be concluded that the fisheries have no consistent density-dependent effect over the whole range of population sizes on the major stocks of Fraser River sockeye. Management policies applied to the Adams River stock will be discussed in a later section.

In only one stage in sockeye life-history is the relationship between survival rate and population density clearly evident. Compensatory type mortalities apply during the spawning-incubation stage. Data are not available concerning the pattern during the lacustrine stage. For one stock, Chilko sockeye, the total effect of marine mortalities has been independent of population size. For another, Cultus Lake, the total effect for both the marine and adult stages has been compensatory, although, as in the case of Chilko sockeye, the relationship between smolt abundance and survival may be fortuitous. As stated, the effects of the fisheries seem to be highly variable. In no stage in the life-history of Fraser River sockeye is there consistent evidence for the occurrence of depensation. By default, since there are no data for this stage, the lacustrine stage seems to be one, in the case of the Adams stock, in which depensatory mortalities are most likely to act to maintain dominance. Fortunately other independent evidence is available concerning the location of dominance maintaining agents affecting Adams River sockeye.

Other Evidence

Hunter (1959) has suggested that dominance among sockeye stocks may be maintained by factors acting during the spawning-incubation period. He suggested that survival might be reduced in one or more subsequent years by after-effects produced by dead eggs of the dominant population. If true, one would expect among Adams sockeye, the population following the dominant to be smallest. Instead, Cycle II populations have been invariably next in size to Cycle I populations (FIGURE 3). In addition, it is unlikely that effects would hold-over with increasing intensity for three years. Hold-over effects, as described by Hunter (ibid.), would probably cause a shorter cycle, possibly biennial.

Data from Chilko Lake sockeye, presented in FIGURE 4, throw additional light on the topic. Note that in 1956 egg deposition was heavy - over one million eggs - yet survival in 1957 was moderately high. In only one case, 1953, was survival low following the heavy 1952 deposition. Spawning in the Chilko River occurs in a limited area and in years such as 1948, 1952, 1956 and 1959 density of spawners was high. For example, it was estimated that the average density in 1952 in some areas averaged 3.2 fish per square yard for the season (Internat. Pacific Salmon Fish. Comm., Interim report on the Chilko River watershed, 1949). One would expect that hold-over effects after such heavy spawning would be apparent if they existed.

Taken with the survival-density data presented previously it is unlikely that depensation either of an immediate or hold-over type occurs during the spawning-incubation stage.

The marine and adult stages are also unlikely sites for depensation. As shown, dominance existed before the commercial fisheries. On this basis, the fisheries acting on adults is an unlikely maintaining agent although it may accentuate an already existing abundance pattern.

It is now clear that Pacific salmon originating in many different North American streams inhabit the same general areas during the marine stage. For example, sockeye tagged in the central Gulf of Alaska in 1962 were identified later in streams flowing into Bristol Bay and as far south as the Fraser River (Neave et al., MS.). It seems probable that sockeye stocks from many different river systems are associated at least to some degree during part of their marine life. A mortality agent acting at sea to maintain sockeye of one stock dominant on a different cycle from some other stock would have to act selectively. This possibility seems unlikely.

Henry (1961) has provided data concerning the close association of two stocks of Fraser sockeye during the first year of marine life. He found that the growth of Chilko fish during their first year of marine life was depressed when dominant Adams populations were at sea. This reduced growth was independent of Chilko marine survival. The depressing effect of the dominant Adams populations suggests a close spatial association of the two stocks during this early marine period. An association would give both stocks the opportunity to be similarly affected by dominance maintaining agents. That this has not occurred can be seen from annual estimates of the abundance of adult spawners for the two stocks (see Internat. Pacific Salmon Fish. Comm., 1956 to 1961 inclusive). The largest Chilko populations coincide with Cycle II and III Adams populations which are small in comparison. If the Chilko stock was being affected by the agents maintaining dominance among Adams sockeye, the abundance fluctuations of the two stocks should be at least partially in phase. In the present circumstances, for dominance maintaining agents to be active during this period of marine life it would again be necessary to postulate a selective action. Adams fish would have to be favored in some years and not in others.

The lacustrine period as a site for the action of dominance maintaining agents has logical attractions in the case of the Adams stock. It is a stage in which one stock is usually geographically isolated from other Fraser stocks. It represents a resource which is shared by the four cycles. Moreover, it is the stage where there are possibilities for direct interaction between cycles, for the lake residence period is the only time when two cycles are in the immediate area at the same time.

Further evidence concerning the site of agents maintaining dominance in the Adams stock is available from a study of growth and abundance data collected from two stocks which spend their lacustrine period in Shuswap Lake. Sockeye spawning in Adams River and sockeye spawning in the Seymour River (FIGURE 1) both spend their lacustrine life in Shuswap Lake although both are separated temporally and spatially during the spawning-incubation period. Seymour sockeye spawn approximately a month earlier than Adams sockeye and the adults are dead before Adams sockeye begin to arrive in the Shuswap district in numbers.

It will be shown in a subsequent section that Adams first year or lacustrine growth is highly correlated with indices of lacustrine population density. The average number of first year scale circuli of Seymour and Adams sockeye are also highly correlated ($r = 0.900^{**}$, d.f. = 12) but Seymour lacustrine population density is not highly correlated with Seymour lacustrine growth ($r = -0.131$); however Adams population density indices are highly correlated with Seymour growth ($r = -0.857^{**}$, d.f. = 12). Partial correlation and standard partial regression coefficients obtained from a Multiple Regression Analysis were: $r_{y1.2} = -0.858^{**}$, $r_{y2.1} = 0.162$, $b'_1 = 0.879$ and $b'_2 = 0.086$.

where $X_1 = \log_{10}$ Adams parental abundance, $X_2 = \log_{10}$ Seymour parental abundance and $Y =$ Seymour average first year scale circuli number.

Seymour lacustrine growth, independent of Seymour abundance, was highly correlated with Adams lacustrine abundance. In fact, Adams abundance was about ten times as effective in predicting Seymour growth as was Seymour abundance. These data indicate that the two stocks are interacting in Shuswap Lake, at least during years when Adams fish are more abundant than Seymour fish. Probably the two stocks actually intermingle to some unknown degree. It could be argued that they are spatially separate but are feeding on a common, mobile food supply. This possibility is unlikely because Ward (1957) showed that there were consistent differences in the availability of plankton in different parts of Shuswap Lake, indicating that plankton populations were not freely intermixing. For this reason it seems likely that the two stocks of sockeye are competing and intermingling in the same parts of the lake. Direct evidence supports this conclusion. Large numbers of fingerlings which, by their great abundance, must have belonged to Cycle I Adams populations have been seen and sampled in all parts of Shuswap during times when Cycle I populations have been resident in the lake. In these years it is highly likely that Seymour fish would come into contact with Adams fish. The same could also be true for Adams Cycle II and Seymour juveniles.

If, as seems likely, the two stocks intermingle, it is possible that they would be similarly affected by dominance maintaining agents. In this case one would expect dominant Seymour populations to occur and to coincide in time with the dominant Adams populations. There is evidence (TABLE 10) that the abundance patterns of the two stocks are coming into phase. Annual

TABLE 10 - Annual estimated spawning populations of 4₂ Seymour River sockeye, 1946 to 1962.

Year	No. Fish	Year	No. Fish	Year	No. Fish	Year	No. Fish
1946	2,600	1947	10,000	1948	3,000	1949	11,000
1950	11,000	1951	24,000	1952	6,300	1953	5,700
1954	26,000	1955	9,500	1956	2,600	1957	11,000
1958	78,000	1959	52,000	1960	2,900	1961	3,600
1962	58,000						
Mean	35,120		23,875		3,900		7,825

populations occurring in the 1946-1962 series of years are, on the average, larger than those occurring during any other cycle of years. These populations coincide with Cycle I Adams populations (TABLE 3). The next series of years, 1947 to 1959, has a smaller average population but larger than the averages of the remaining two series of years. This 1947-1959 series coincides with subdominant or Cycle II Adams populations (TABLE 3).

The present Seymour abundance pattern apparently began to be established about 1950 (TABLE 10). Before this time there was no evidence for dominance. The reason for the lack of a dominant run prior to 1950 is not clear but may be associated with a general low level of abundance caused by unfavorable migration conditions in the Fraser which recurred until 1945 when the fishways at Hell's Gate became operative. The data shown in TABLE 10 indicates that a trend towards the establishment of a dominance pattern now exists among Seymour River sockeye and its characteristics appear to be the same as for the Adams River stock.

In subsequent sections data will be examined concerning the actual mortality producing mechanisms which act during the lacustrine life of Adams sockeye. On the basis of these studies an attempt will be made to develop a hypothesis involving one or more of these lacustrine mechanisms as dominance maintaining agents.

COMPETITION

One of the obvious potential causes of dominance is competition between the young of the various cycles as they pass through the period of lake residence. For example, Cycle I populations may deplete the food supply to such an extent that survival of Cycle II, III and IV lacustrine populations is reduced. Another possibility is that Cycle I populations may indirectly affect the food supply utilized by populations of other fishes. Ricker (1950) has suggested that "residuals", the non-anadromous offspring of sockeye, may interact with juvenile anadromous fish. He has suggested that residuals of the dominant brood would be more abundant than residuals of other cycles. These dominant residuals would then interact either as competitors or predators with the fry, fingerlings and smolts of Cycles II, III and IV populations.

Sockeye may compete with other species of fish for food; in fact these other competitors may be more abundant and more effective than non-anadromous forms of sockeye such as kokanee or residuals. Possible competitor species are abundant in Shuswap Lake.

If compensatory mortalities were resulting from competition for food or space one would expect that a measurable effect would be observed in the growth pattern. Cycle I populations should have the highest lacustrine growth rate, Cycle II next highest and Cycles III and IV the lowest. The

absence of this pattern does not mean that competition is not resulting in depensation but the probability of competition as a maintaining agent is greatly reduced. Annual lacustrine growth and abundance data are examined below.

Fluctuations in Lacustrine Growth

If competition were a causal agent for the observed relationship between annual populations, one would expect the size of individual juvenile sockeye to be related to their survival potential. It would also be expected that the average size of members of each annual lake resident population would be directly related to their abundance.

Samples of smolts are available only from dominant and subdominant sockeye populations. The smolt populations of the other two cycles are invariably so small that sampling them is virtually precluded for purely practical reasons. The relationship is shown in FIGURE 7 between the average fork length of annual smolt samples and the logarithms of the abundance of the parental population (used as indices of lacustrine abundance).

It will be noted that values from representatives of only two cycles - the dominant and subdominant - are presented. However, even in the absence of additional data it is apparent that smolts of the smaller subdominant cycle are larger than those of the dominant populations ($r = -0.89^*$). Foerster (1944) found a similar significant negative correlation between the annual average weight of smolts and their estimated abundance at Cultus Lake. Burgner (1962) has reported that unusually large sockeye escapements have resulted in reduced growth of juveniles in the Wood River lakes, Iliamna Lake and Chignik system, all located in Alaska.

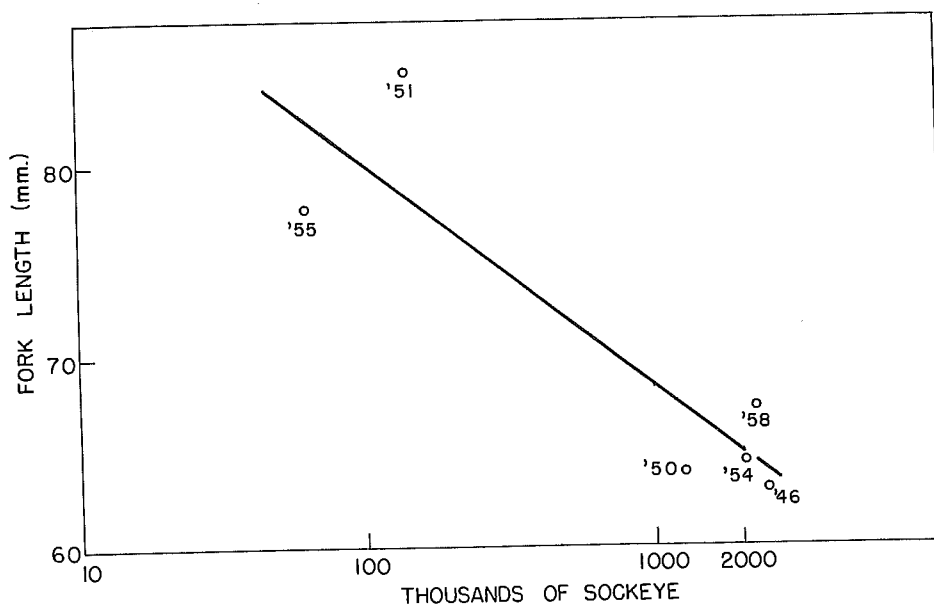


FIGURE 7 - Relationship between the length of Shuswap Lake smolts and parental abundance.

If competition among Cycle I juveniles caused lowered food abundance, and this depletion held-over until the next year, Cycle II smolts would be even smaller than those of the dominant cycle. This is not the situation since smolts of subdominant populations are significantly larger than those of any dominant brood.

Clutter and Whitesel (1956) demonstrated a significant relationship between the total lacustrine scale circuli counts of juvenile sockeye and their length and weight. For this reason, lacustrine circuli counts from adult scales can serve as indices of growth during the period of lake residence.

The use of adult scales to determine growth during lake residence has two advantages over direct measurements of smolt or fingerling size. First, adults are concentrated on spawning grounds and scales are available for all annual populations of sockeye, not just the two largest. Secondly, spawning ground scale samples provide good estimates of overall lacustrine growth. This is not necessarily the case when samples are obtained either from lake residents or from the seaward migrating population. Certain sections in Shuswap Lake are more productive than others (Ward, 1957) and juvenile sockeye are probably more abundant in some areas than in others. These two facts result in variations within one annual population in pre-smolt size. A smolt or pre-smolt sample taken at one location or at a particular time during downstream migration may not be representative of the total population. This difficulty could be overcome by stratified sampling but sampling of this type, in practice, would be difficult. On the other hand, after leaving the lake, the fish must tend to become thoroughly mixed. This would seem to be particularly the case during the oceanic phase of the life-history. Thus, a sample of adult scales provides a better average

picture of growth conditions during the period of lake residence.

FIGURE 8 shows the relationship between total freshwater circuli counts of Adams sockeye, determined from samples of the adult spawning population, and the logarithm of the parental escapement. It is evident that circuli counts were lowest for largest populations and highest for the smallest. From the relationships, established by Clutter and Whitesel (1956), between juvenile sockeye length, weight and circuli counts it can be concluded that growth was lowest for Cycle I populations and highest for the off years.

On the basis of growth data it seems unlikely that competition is resulting in depensation. On the contrary, growth and abundance are inversely related, indicating that the effects of competition are compensatory.

It is possible, in certain circumstances, for mortalities resulting from competition to result in depensation. Intense competition early in life could result in mortalities of the depensatory type which would be difficult to detect. Survivors might compensate for early poor growth. If the critical period occurred prior to scale formation, no record of reduced growth would be apparent from subsequent scale studies.

Fry, fingerlings and smolts of dominant populations could cause a reduction in the abundance of zooplankton during a short critical period in the spring when alevins of subdominant populations were first entering Shuswap Lake. Direct competition for food might occur between Cycle I smolts and Cycle II fry. In this fashion, subdominant populations might suffer a high mortality rate early in life. Survivors of such a reduction might not show any of the effects of intensive competition. The amount of food available would probably increase very quickly in the late spring and early summer and growth of the now relatively scarce juvenile sockeye would be rapid. Major increases in zooplankton abundance on most Shuswap

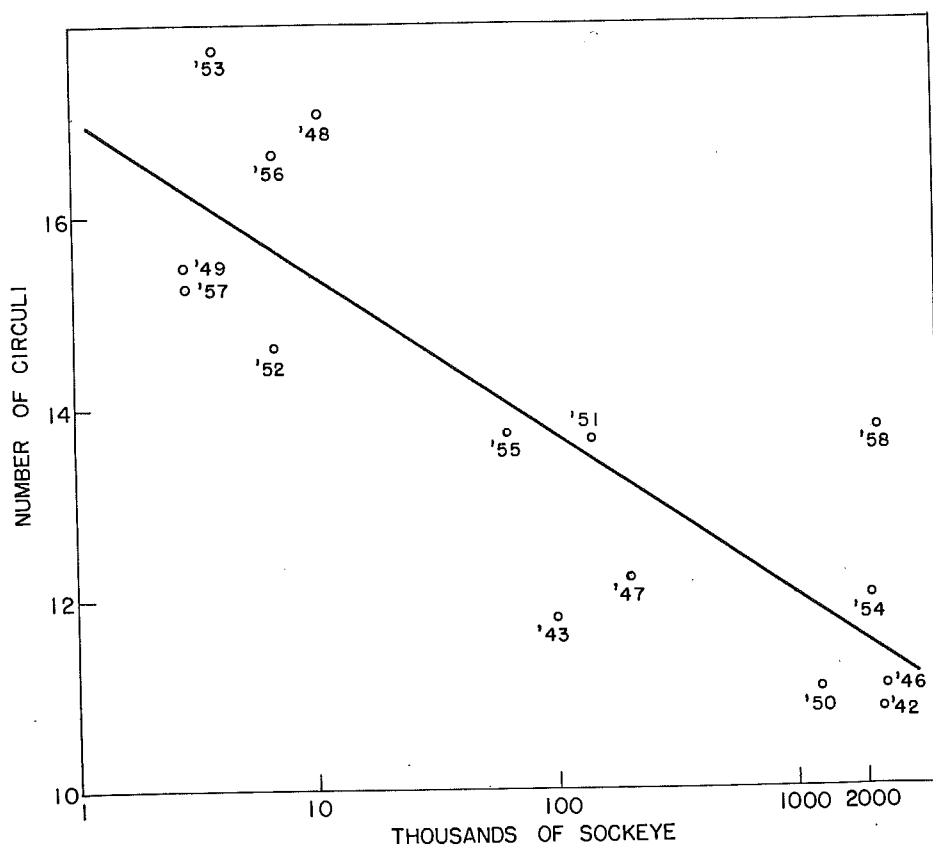


FIGURE 8 - Relationship between the average number of lacustrine scale circuli and Adams River sockeye parental abundance.

Lake sampling stations in late spring and early summer have been demonstrated by Ward (1957). This series of events could result in smolts of subdominant broods being larger than those of dominant populations although relatively fewer in number.

There is a major objection to the extension of this hypothesis. It accounts only for Cycle II fish being less abundant than Cycle I. It can offer no explanation for the reduced abundance of the other two cycles. In these circumstances, one would expect a biennial cycle rather than a quadrennial dominance pattern.

Fluctuations in Food

Additional evidence supporting the conclusion that competition does not cause mortalities that result in depensation can be obtained from comparisons of annual indices of zooplankton abundance. Assuming that zooplankton samples were representative of the food of juvenile sockeye, it would be expected that zooplankton indices would be low during years when Cycles II, III and IV populations were resident in Shuswap Lake. This situation would indicate that less food was available to these off year populations. Ward (1957) on the basis of zooplankton samples showed that even if it was assumed that a dominant population of fingerlings reduced availability of zooplankton, an abundance level was attained during the succeeding year comparable to that which had occurred in the lake during the season immediately preceding the one in which the dominant population was resident. On the basis of these data, it was concluded that a food shortage was not a factor controlling dominance unless it acted during a short critical period. Ricker (1937) demonstrated that the abundance of Daphnia declined earlier in the season when a large sockeye population was present in

Cultus Lake than normally, but he concluded that there was no hold-over effect from this cropping.

Subsequent to the publication of the data and conclusions of Ward (1957), additional information on zooplankton abundance has been collected (TABLE 11). Discrepancies between values shown above for the years 1954, 1955 and 1956 and those previously presented by Ward have resulted from averages being calculated over slightly different annual periods.

TABLE 11 - Average annual volumes of zooplankton sampled from four stations on Shuswap Lake, 1954 to 1959.

Year	No. of Samples	Mean Centrifuged Zooplankton (ml)	Standard Error (ml)
1954	44	0.96	± 0.08
1955	56	0.53	± 0.04
1956	60	0.93	± 0.06
1957	48	1.18	± 0.09
1958	52	1.39	± 0.09
1959	52	1.06	± 0.10

It will be noted that in both 1955 and 1959, years when dominant populations were lake resident, the averages were lower than during the immediately preceding years. In the case of 1955, the following year (1956) has a higher value. These data may indicate that dominant populations had a cropping effect, but, as previously concluded, there is no evidence of a hold-over effect. Note that the average zooplankton volume for 1959 was considerably higher than values obtained when much smaller populations were resident in Shuswap Lake. These data indicate that fluctuations in food availability are not an obvious cause for the observed relationship between annual populations of Adams River sockeye.

Competition with Non-Anadromous Forms

In view of the relationship between population density and lacustrine growth shown in FIGURE 8, it is not likely that lacustrine competition, either inter- or intraspecific could result in depensation and, therefore, the maintenance of dominance. This general conclusion receives additional support when the growth of Adams sockeye is compared with the growth of non-anadromous sockeye (FIGURE 9). Growth of kokanee native to the Eagle River (FIGURE 10) is low when Cycle I sockeye populations are resident in the lake. During years in which off year populations are resident both kokanee and sockeye growth increases, suggesting more favorable growing conditions in the lake when Cycle I populations are absent.

If kokanee or non-anadromous sockeye in general were competing with off year sockeye populations to limit the abundance of these off year populations, one would expect a cycle of abundance in the non-anadromous fish which would coincide with the Adams dominance pattern. As Ricker (1950) has suggested, non-anadromous forms with the same abundance pattern as sockeye would compete with increasing intensity with each of the three remaining cycles of Adams River sockeye.

Indices of abundance of non-anadromous O. nerka are shown in TABLE 12. Blank spaces indicate that no estimates were made.

These estimates of non-anadromous O. nerka spawning populations can only be used as indices of abundance since they are based on counts of live fish, not on enumeration by tagging as in the case of the larger sockeye populations. Counts were made by a standard method of observation each year and differences in the indices reflect real differences in abundance.

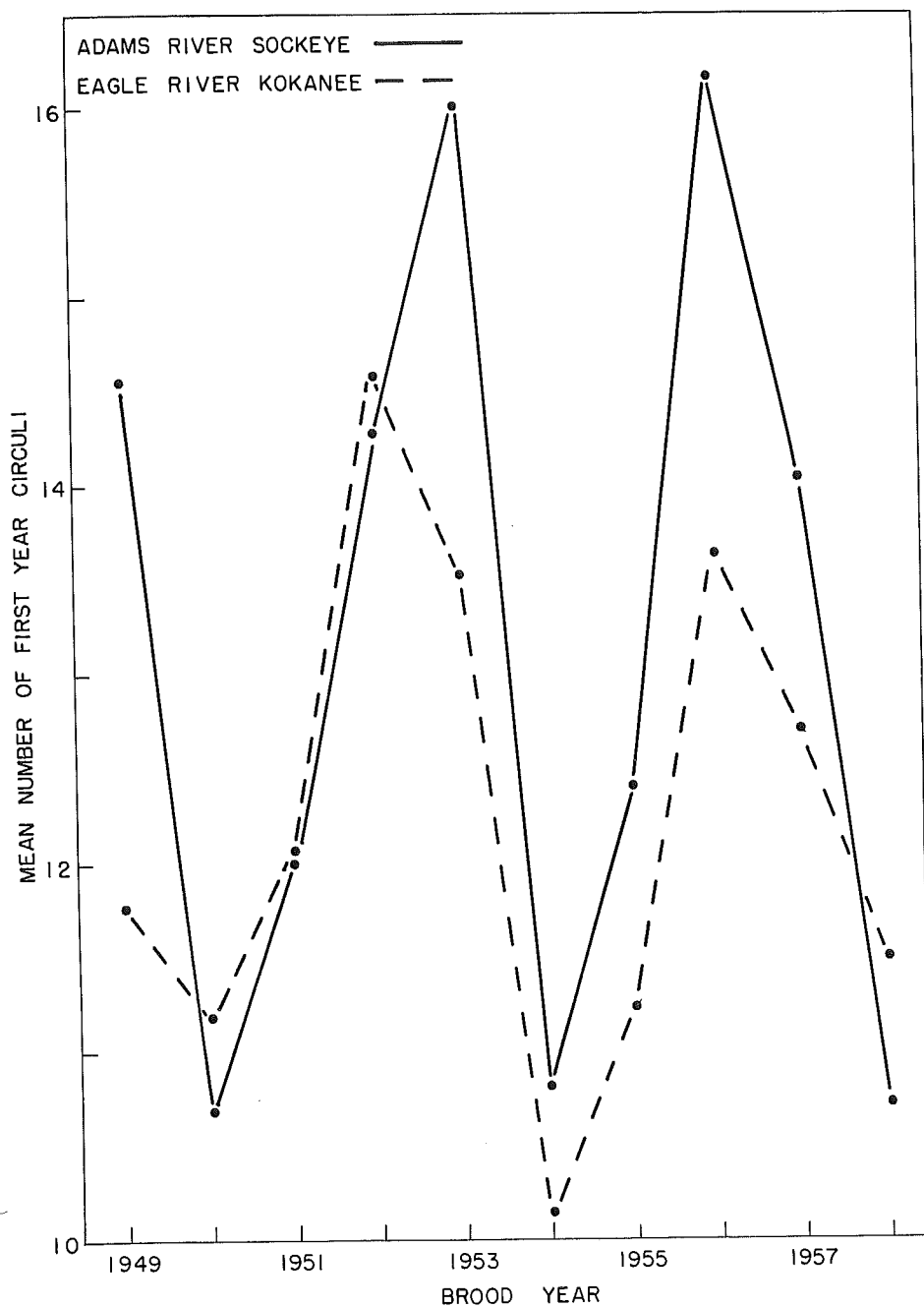


FIGURE 9 - Relationship between first year circuli counts of Adams River sockeye and Eagle River kokanee.

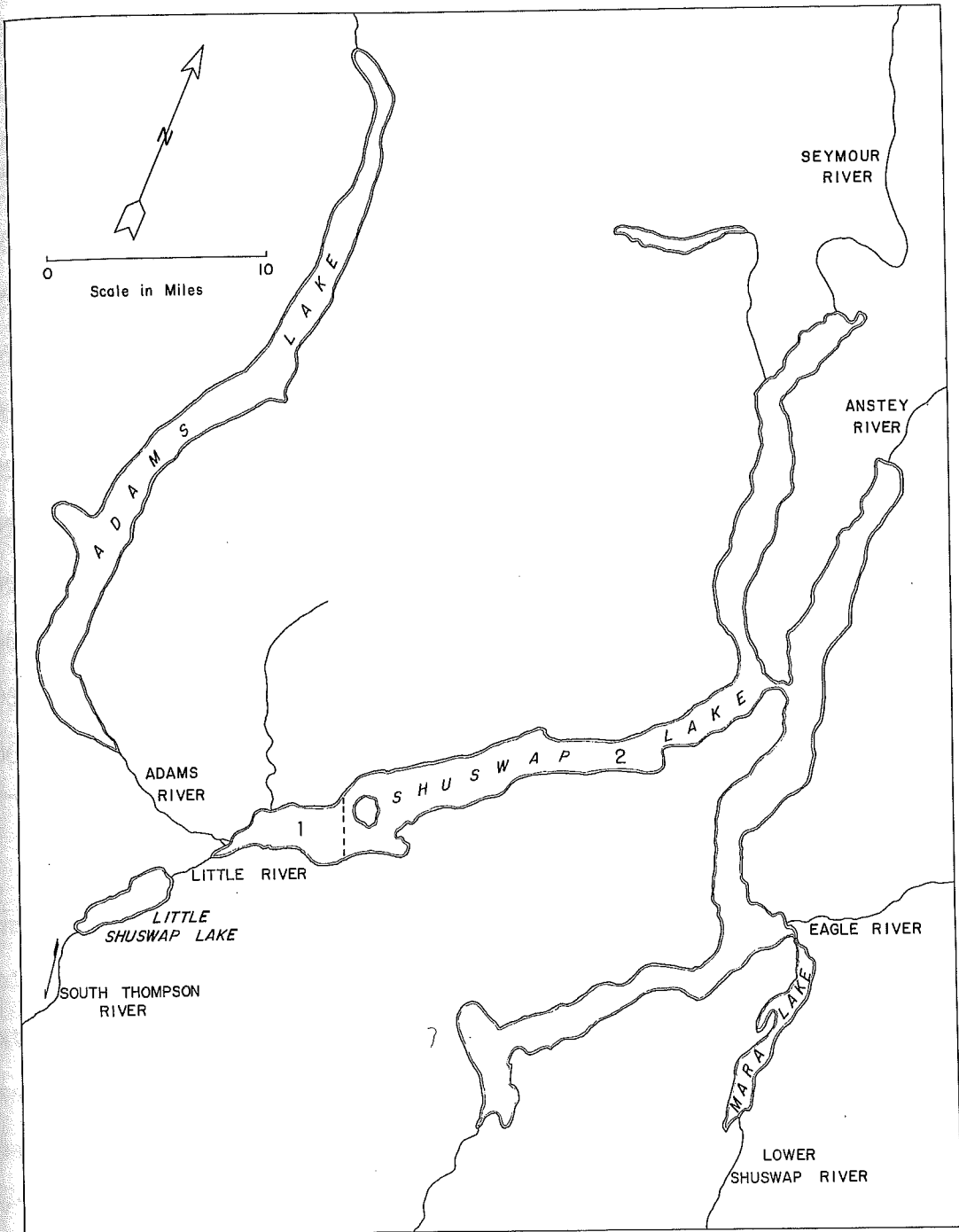


FIGURE 10 - Shuswap Lake showing the major tributaries and the trout sampling areas.

TABLE 12 - Annual indices of the abundance of the major spawning populations of non-anadromous O. nerka in the Shuswap Lake district, 1953 to 1962.

YEAR OF SPAWNING	NUMBER OF FISH			TOTAL NUMBER
	Eagle	Lower Shuswap	Anstey	
1953	230,000	9,000	35,000	274,000
1954	48,000	112,000	2,000	162,000
1955	84,000	67,000	5,000	156,000
1956	44,000	124,000	0	168,000
1957	207,000	115,000	10,000	332,000
1958	78,000	87,000	6,000	171,000
1959	8,000+	---	3,000	11,000+
1960	33,000	---	---	33,000
1961	210,000	38,000	---	248,000
1962	75,000	337,000	2,000	414,000

7

It will be noted that the Eagle River populations had three large runs occurring in 1953, 1957 and 1961. The smallest Adams sockeye populations coincided with these large kokanee populations; however, too few years of data are available to draw any conclusions. The relationship may not be stable; but it is evident that these three broods of kokanee spent their first year of residence in Shuswap Lake when competition from sockeye was at a minimum. Evidence from scale analyses indicates that Lower Shuswap kokanee do not spend their whole life in Shuswap Lake therefore comparisons with Adams sockeye growth are not pertinent. Lower Shuswap abundance indices do not indicate regular fluctuations.

Non-anadromous sockeye did not have an abundance pattern similar to sockeye. There is no evidence for the existence of superabundant year-classes which would compete with and differentially affect off year sockeye survival.

Residuals in Shuswap Lake

Ricker (1950) proposed that dominant populations may produce large residual populations which compete with successive broods of anadromous juveniles reducing their growth and causing increased mortalities. The relationship between growth and population density, presented earlier (FIGURE 8) makes this hypothesis improbable unless the high mortality rate resulting from this competition occurred early in the lacustrine life of each off year lacustrine population. Further, there is no evidence for the presence of large numbers of residuals in Shuswap Lake.

Ricker suggests that slow growth favored delayed migration; therefore, not only should the total number of non-migratory dominant fingerlings be large, but relative to the other cycles, the proportion should be larger because lacustrine growth rate is lower for Cycle I fingerlings (FIGURE 8). Shown in TABLE 13 are proportions of one and two-year lake resident fish in four adult broods.

TABLE 13 - Adams River sockeye spawning populations of one and two year-lake resident fish of the same brood as calculated from age analyses of scales.

BROOD YEAR	TOTAL ESCAPEMENT	ONE YEAR RESIDENTS		TWO YEAR RESIDENTS	
		Number	Per Cent	Number	Per Cent
1950	2,280,428	2,277,857	99.9	2,571	0.1
1951	68,473	68,417	99.9	56	0.1
1952	6,983	6,983	100.0	0	0
1953	3,323	3,323	100.0	0	0
Total	2,359,207	2,356,580	99.9	2,627	0.1

Apparently, dominant Adams populations do not produce a large fraction of two-year resident anadromous fish; however it is still possible that dominant populations produce large numbers of non-anadromous fish.

A sample of 193 migrating juvenile sockeye was taken in the central area of Shuswap Lake in the spring of 1953. Only six (3.1 per cent) were two-year-old fish arising from the dominant population spawning in 1950. This direct evidence, although based on a small sample, indicates that few juveniles of a dominant population remain in Shuswap Lake more than one year. Further, it seems probable that most of the two-year-old fish sampled in 1953 would have gone to sea that spring and returned in 1955 as 5₃ adults. From TABLE 13 it can be determined that 5₃ fish (brood of 1950, shown as two-year residents in TABLE 13) present in the spawning population of 1955 formed 3.8 per cent of the total. This approximates the percentage of two-year-old juveniles in the 1953 lake sample. On the basis of this evidence it seems unlikely that dominant populations of Adams sockeye give rise to significant numbers of residual or non-anadromous sockeye.

The characteristics which were originally used to distinguish between residuals and kokanee, self-perpetuating, non-anadromous populations (Ricker, 1938), have been shown (Ricker, 1959) to be invalid; therefore no separation can yet be made on the basis of morphological differences. However sockeye have behavioral differences which are pertinent to the problem of identification of the two forms in Shuswap Lake. Non-anadromous sockeye spawn in streams flowing into the eastern basins of Shuswap Lake (FIGURE 10). The streams supporting the largest populations are: Eagle River, Lower Shuswap River and Anstey River (TABLE 12). Adams River sockeye spawn primarily in Adams and Little Rivers. Only very occasionally are non-anadromous sockeye observed in these streams. Numerous authors, among

them Thompson (1945), have shown that Pacific salmon and sockeye in particular, return as adults to their streams of origin. In order for the non-anadromous sockeye native to Shuswap Lake to be residuals they would have to travel almost exclusively to "foreign" streams for spawning. Since this lack of homing is improbable, one can conclude that sockeye native to Eagle, Lower Shuswap and Anstey Rivers are kokanee, the self-perpetuating non-anadromous form of the species.

Available evidence suggests that residuals, the non-anadromous offspring of anadromous sockeye, are scarce if present at all in Shuswap Lake. They cannot be considered as important competitors with juveniles of the anadromous form.

Regardless of the effects of competition on dominant populations during lacustrine life the evidence cited above indicates that differential mortalities resulting from competition are not a dominance maintaining agent, at least in sockeye of the Adams River stock.

PREDATION

Predation often results in mortalities which have a depensatory effect, when the combined effects of both the functional (eating more) and numerical (survival and breeding) responses, expressed as a rate, are inversely related to population density. Hollings (1959) has shown both in field and laboratory studies that predation can have a depensatory effect on sawfly larvae. Hunter (1959) found that depensation occurred in populations of juvenile pink and chum salmon. Mortality rates from predation were inversely related to the initial abundance of fry. Evidently predation during the lacustrine stage of sockeye could result in depensation. If so, predation could be the dominance maintaining mechanism.

In following sections information concerning predation in Shuswap Lake will be presented. The rainbow trout, Salmo gairdneri, is an abundant and widely distributed piscivorous species in Shuswap Lake. Beginning in 1953, staff of the International Pacific Salmon Fisheries Commission, with the cooperation of the Fish and Game Branch of the Department of Conservation and Recreation of British Columbia, collected data from anglers' catches made in Shuswap Lake. A total of 8455 rainbow trout caught by anglers was sampled. Other predator species are also resident in the lake but are either relatively rare or are difficult to sample. It is, therefore, necessary to keep in mind that rainbow trout, although abundant, are only one of several species of salmon predator. For instance, stomach analyses show that lake trout, squawfish, ling and dolly varden char all take juvenile sockeye. Several bird species are also known to eat juvenile sockeye.

Life-History of the Rainbow Trout of Shuswap Lake

Rainbow trout appear to utilize all major inlet streams for spawning where both fry and yearling trout have been observed. Age and growth studies using scales have been rather unsuccessful. Presence of accessory checks and reabsorption of margins during spawning complicates analyses. So much personal interpretation is involved, that the age of most of the scales cannot be adequately justified. However on the basis of readable scales, it is apparent that the annual catch is composed of Age II, III and IV fish with older fish present but comparatively scarce. Spawning occurs in the spring, usually for the first time at 3 or 4 years of age. The relative scarcity of fish older than 4 years of age suggests that a heavy mortality occurs after spawning. Carl, Clemens and Lindsey (1959) report that males often mature one year earlier than females. This sex difference may also

apply to Shuswap Lake rainbow trout.

Anglers have been attracted to Shuswap Lake to fish for rainbow trout both by their abundance and by their comparatively large size. Fish weighing in the vicinity of five pounds are quite common and fish up to 25 pounds are occasionally captured.

Food of Rainbow Trout

Deviations from the average volume of the stomach contents of rainbow trout caught in Shuswap Lake near the mouth of Adams River are shown in FIGURE 11. There has been considerable seasonal and annual variation in the average volumes. In the summer and fall of 1955 stomach contents were above average. During both these periods fingerlings of a Cycle I population were available and during the fall, eggs of a Cycle II population were present (TABLE 14). In the spring of 1956 the average volume was again above average when Cycle I smolts and Cycle II fry were abundant. During the summer and fall, after Cycle I smolts had gone to sea, Cycle II fingerlings dispersed throughout the lake and relatively few eggs from a Cycle III population were available to trout. During these seasons stomach content volume was below average. But in the spring of 1957, the average volume was again high when Cycle II smolts were abundant and concentrated in the outlet area (TABLE 14). Volumes were again below average during the summer and fall of 1957 and during the spring and summer of 1958 when only Cycle III and IV sockeye were present. In the fall of 1958, Cycle I adults were spawning and the average volume of stomach contents was again high. In the spring of 1959, Cycle I fry were entering the lake from Adams and Little Rivers (FIGURE 10) and stomach content volume was again above average. Cycle IV smolts would also be leaving the lake at this time. Surprisingly, volumes

FIGURE 11 - Seasonal deviations from the mean stomach content volume (2.5 ml.) of rainbow trout caught in Shuswap Lake near the mouth of Adams River. Sample sizes are shown in brackets.

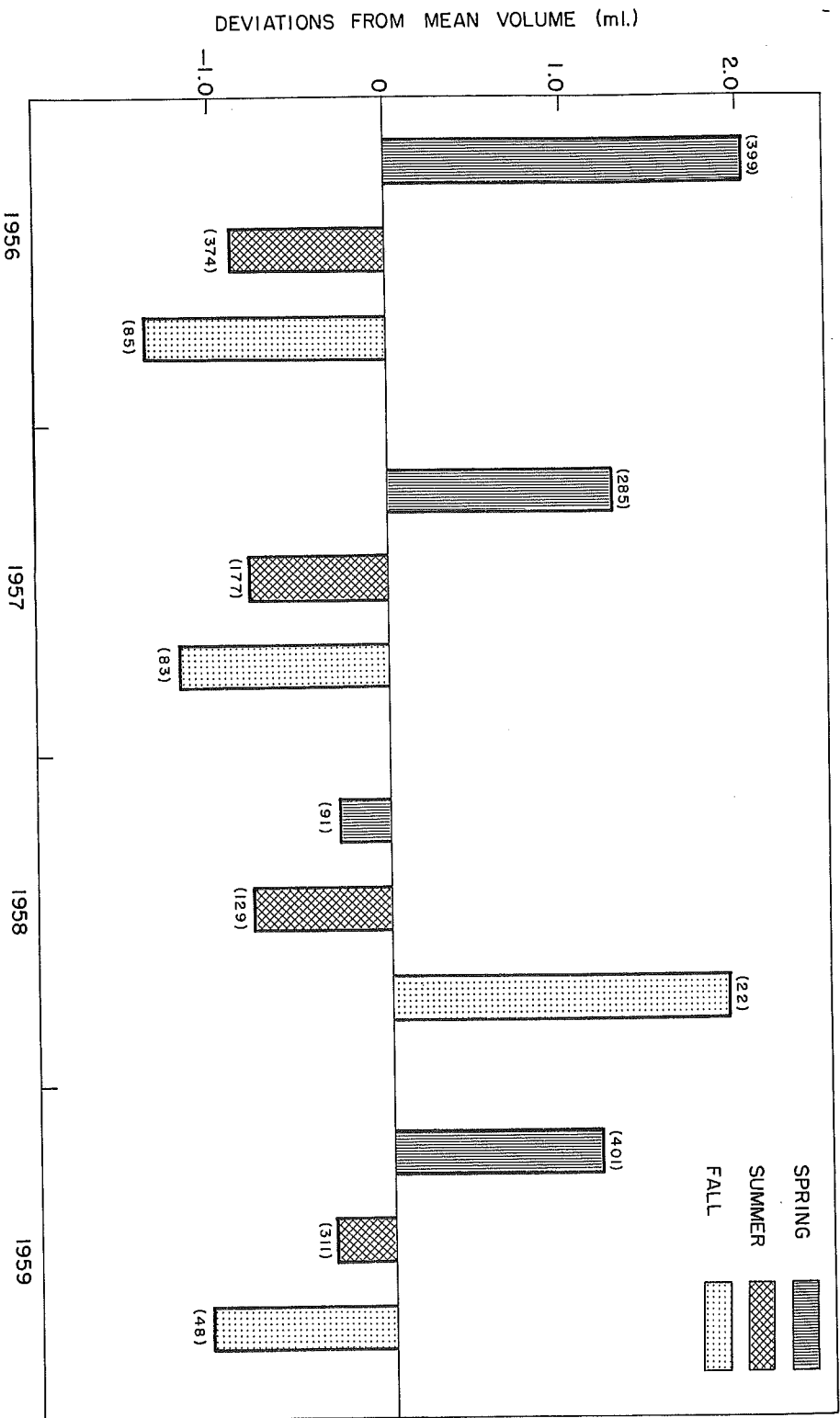


TABLE 14 - Types of sockeye and relative abundance present seasonally and annually in western Shuswap Lake, Adams and Little Rivers.

Year	Spring	Summer	Fall	Winter
1	Cycle III smolts Cycle IV fry low	Cycle IV fingerlings low	Cycle IV fingerlings Cycle I eggs high	Cycle IV fingerlings Cycle I eggs high
2	Cycle IV smolts Cycle I fry high	Cycle I fingerlings high	Cycle I fingerlings Cycle II eggs high	Cycle I fingerlings Cycle II eggs high
3	Cycle I smolts Cycle II fry high	Cycle II fingerlings moderate	Cycle II fingerlings Cycle III eggs moderate	Cycle II fingerlings Cycle III eggs moderate
4	Cycle II smolts Cycle III fry moderate	Cycle III fingerlings low	Cycle III fingerlings Cycle IV eggs low	Cycle III fingerlings Cycle IV eggs low

in the summer and fall of 1959 were below average, although Cycle I sockeye fingerlings and Cycle II eggs were relatively abundant (TABLE 14).

These seasonal variations in stomach content volume of rainbow trout seem to be associated, with two exceptions, with the relative abundance of juvenile sockeye in the area. From FIGURE 12 it is evident that juvenile sockeye during these same periods formed a significant fraction of the food of rainbow trout.

In the summer of 1955 sockeye eggs formed the major diet item. These eggs were deposited in Adams River in the fall of 1954 by a dominant sockeye population. Subsequently, these eggs, which were either unfertilized at deposition or later died, were swept down into Shuswap Lake where they lodged and served as trout food until the fall of 1955. Sockeye eggs also

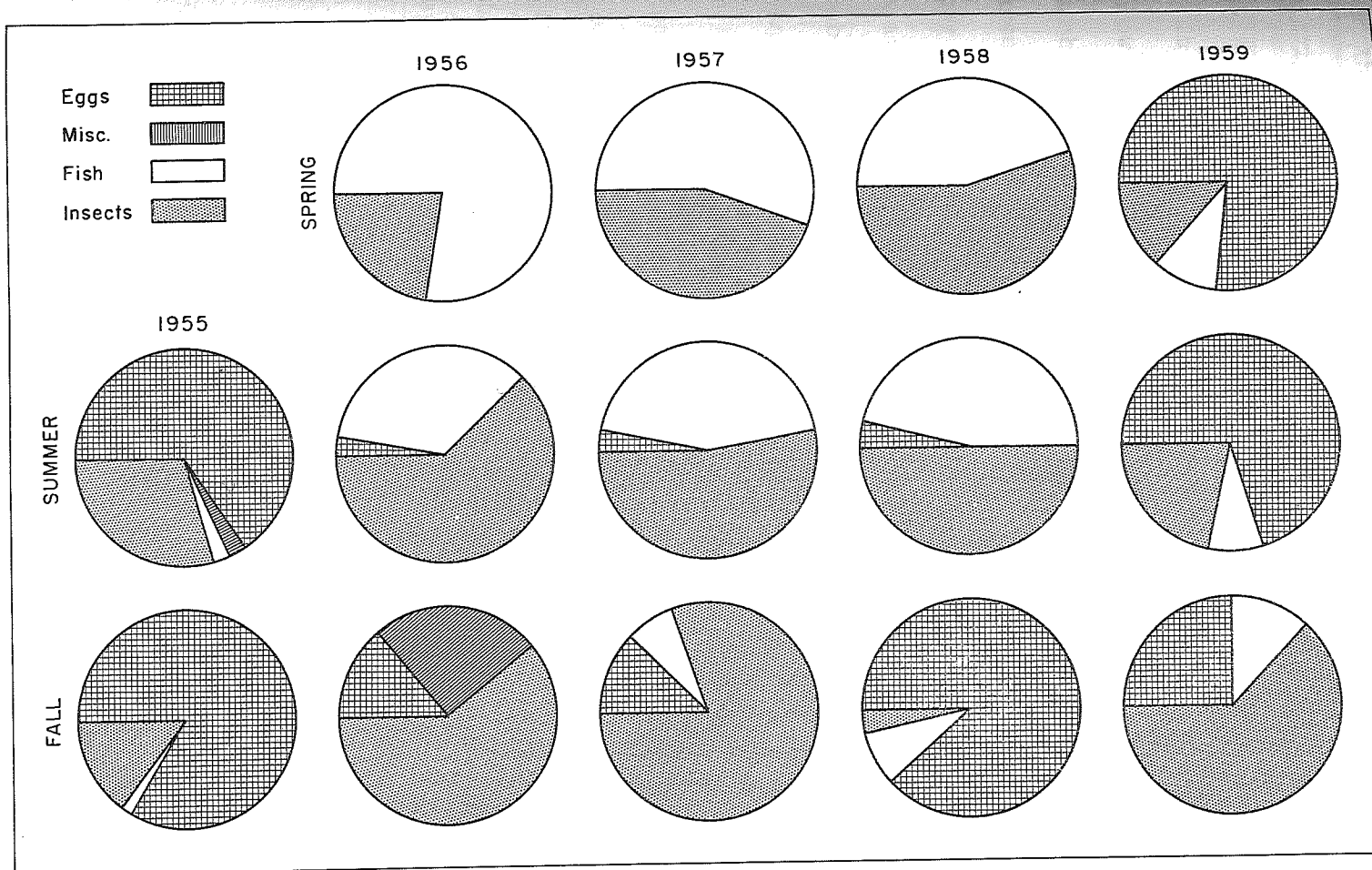


FIGURE 12 - Stomach contents by volume of rainbow trout captured in the Adams River area of Shuswap Lake, 1955 to 1959. Segments of the circles represent proportions of each major item.

formed the chief diet item of trout in the fall of 1955. Some of these eggs originated with the subdominant population, spawning during that fall.

In the spring of 1956, fish were the most important diet item of rainbow trout. The fish component formed 73 per cent of the total volume of stomach contents. Juvenile O. nerka (i.e. sockeye, but possibly including some kokanee), predominantly the progeny of the 1954 dominant population, composed 63 per cent of the total volume. The 10 per cent difference between total fish and juvenile O. nerka was unidentified fish remains which again was probably chiefly juvenile O. nerka. Insects formed a significant portion of the total stomach contents. In the summer of 1956 the contribution of fish to the total was much reduced, probably because by this time most of the smolts of the dominant population had migrated to sea. Apparently, a few eggs were available in early September (September was included within the summer period). It will be noted that insects formed the bulk of the diet. The situation was essentially unchanged during the fall of 1956, except that the egg component had increased in importance.

Fish were again very important in the spring of 1957. Nine per cent of the total stomach contents was identified as juvenile O. nerka and much of the remainder of the unidentified fish component was undoubtedly juvenile O. nerka, probably smolts arising from the 1955 subdominant population. The composition and relative abundance of items in stomach contents of trout was essentially similar during both the summers of 1956 and 1957. Fish were an important item of the diet but insects were the major item. In the fall of 1957 insects predominated. This predominance may have reflected the scarcity of eggs available to trout when an off year population was on the spawning grounds (TABLE 14).

Fish were an important item of the diet during the spring of 1958, although insects were the major contributors to total stomach contents. Fish and insects were the two major items of diet during the summer of 1958. The appearance of a dominant population on the spawning grounds during the fall of 1958 was reflected by an 88 per cent contribution of sockeye eggs to the total volume.

Stomach contents during 1959 were qualitatively similar to those for 1955. Sockeye eggs were the major component of the diet. The chief difference between the two years occurred in the fall samples. Insects were more important in 1959 than in 1955, or conversely, sockeye eggs were less important during the fall of 1959 than they were in 1955.

Considering the data as a whole, sockeye when abundant seemed to be a preferred dietary item. Fish were important during spring periods. Much of the fish remains were not identified, but juvenile O. nerka was the only species which was consistently present. It is probable, therefore, that much of the unidentified material was the remains of O. nerka. It was not possible to distinguish between juvenile sockeye and kokanee, so a portion of these remains may have belonged to the non-anadromous form of the species. It should be noted, however, that the trout included in these samples were captured near the lake outlet. In the spring, sockeye smolts are concentrated in this area as they migrate to sea and fry enter the lake here from their native streams. It would seem that concentrations resulting from fry and smolt migrations must account for the high percentage of fish in trout stomachs during the spring periods of 1956, 1957 and 1958.

Fish were also an important item during summers of years when sockeye eggs were scarce, but insects were the major dietary items. In general, the data presented in both FIGURE 11 and FIGURE 12 indicate that insects

were a subsistence item, to be utilized when other perhaps more desirable foods were scarce.

Small trout were not as piscivorous as large trout. Trout less than 300 mm. in fork length ate relatively few fish but utilized insects and sockeye eggs, when present, to a greater degree than larger trout. Since many sockeye eggs eaten by trout are either dead or unfertilized it is probable that these small trout did not have much effect on the rate of survival of any of the four cycles of sockeye. Larger trout (longer than 300 mm. fork length) utilized fish and sockeye eggs when available. Seasonal deviations from the average volume of fish and sockeye eggs found in rainbow trout over 300 mm. are shown in FIGURE 13. Stomach contents in 1955 were not classified by fork length of fish and, therefore, cannot be shown. In general the situation described in FIGURE 11 (which represents variations in total stomach content volume) is duplicated. When sockeye as juveniles were scarce, fish as an item was below the average volume. It is significant that fish volumes were high in spring periods when juvenile sockeye entering and leaving the lake tended to concentrate in the sampling area. Even in the spring of 1958 when both fry and smolts were scarce (TABLE 14) the volume of fish consumed per trout was hardly below the overall average.

Several conclusions can be drawn from the data concerning food of rainbow trout caught in the western region of Shuswap Lake. First, juvenile sockeye form an important diet item of rainbow trout (FIGURE 12). Among larger trout (over 300 mm. fork length), sockeye were only partly replaced in the diet when they were scarce. This conclusion can be verified by comparing data in FIGURE 11 and FIGURE 13. When fish material was at a low level in stomachs, average total stomach content volume was

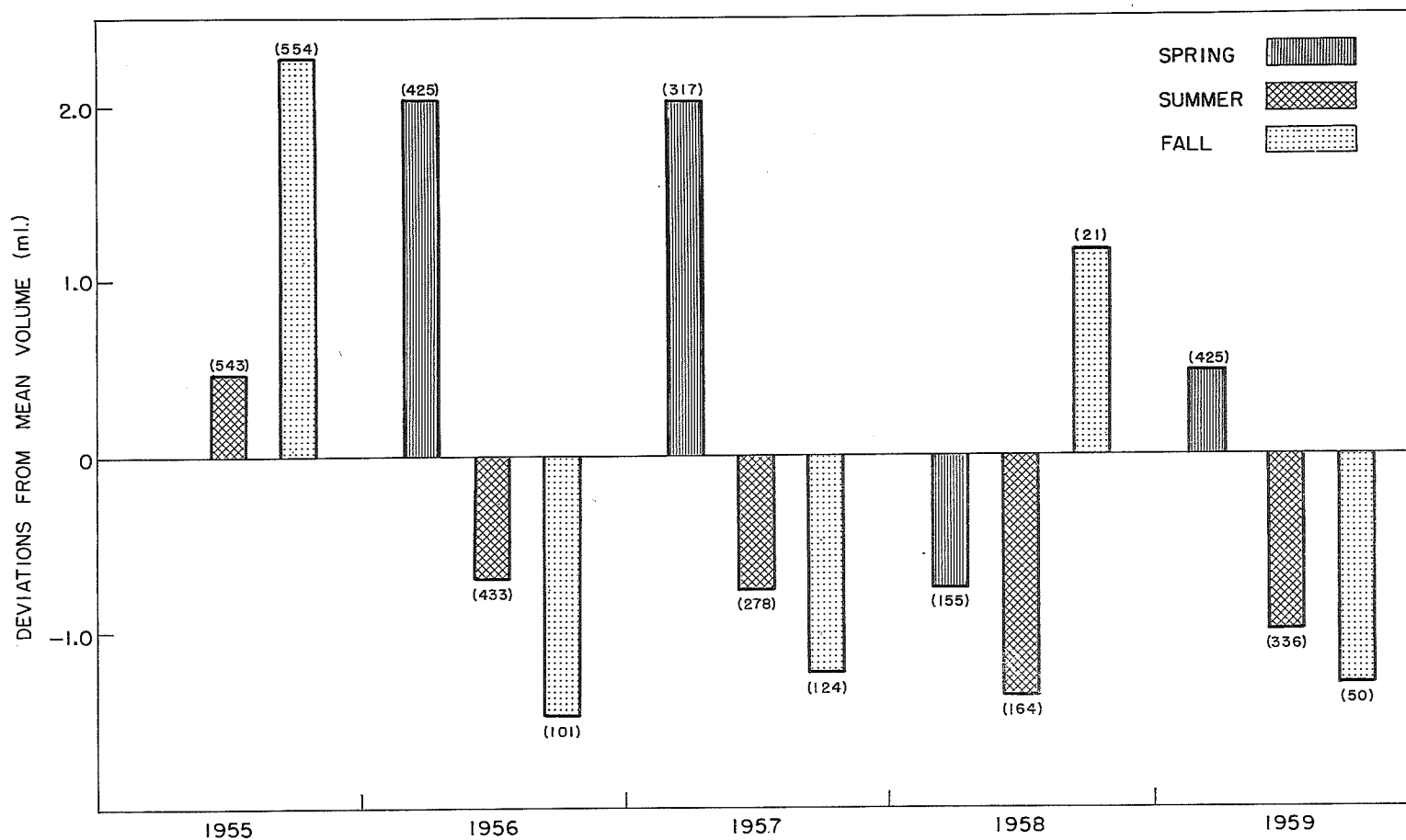


FIGURE 13 - Seasonal deviations from the mean volume of fish remains found in stomachs of rainbow trout 300 mm. and longer caught in Shuswap Lake near the mouth of Adams River. Sample sizes are shown in brackets.

also low. These data lead to the general conclusion that rainbow trout over 300 mm. are an important piscivorous species utilizing juvenile sockeye as food.

Fluctuations in the Condition of Rainbow Trout

Anglers report that in some years and in some areas, particularly in the vicinity of the mouth of Adams River, rainbows are "fat". In other years it is reported that they are "thin". These fluctuations are alleged to be associated with the abundance of sockeye.

Shown in TABLE 15 are the annual numbers of rainbow trout from anglers' catches which supplied the measurements used in studies of condition. Each fish was weighed to the nearest one-tenth of a pound and measured (fork length) to the nearest millimeter. Later, weights were transformed to grams. Data are grouped into two subsamples, the Adams River area (Area 1) of Shuswap Lake and the other lake regions (Area 2). The location of the two areas by number can be seen in FIGURE 10.

Data collected in the Adams area are considered first; following this, data from Area 2 are compared with findings from the Adams area.

Differences Between Sexes

Differences between the sexes in condition were examined for significance by application of the method of covariance analysis to \log_{10} length - \log_{10} weight data. The first test utilized a sample of fish taken during October, 1957; the next utilized data from fish collected during May, 1958; and the third, data from fish collected during July and August, 1958.

TABLE 15 - Annual samples of trout lengths and weights from the Adams River area and other lake areas available for use in comparisons.

Year	Adams River Area	Other Lake Areas
1953	241	217
1954	97	43
1955	1,081	63
1956	1,167	298
1957	756	203
1958	850	102
1959	793	121
1960	440	604
Total	5,425	1,651

Results of tests for homogeneity of regression coefficients and for homogeneity of adjusted mean weights are shown below in TABLE 16.

TABLE 16 - Significance of differences between the sexes of rainbow trout in regression coefficients (\log_{10} weight on \log_{10} fork length) and in adjusted mean weights for three periods.

PERIOD	SAMPLE SIZE		REGRESSION COEFFICIENTS		ADJUSTED MEAN WEIGHTS	
	Male	Female	Value of F	Probability	Value of F	Probability
October, 1957	65	57	1.77 n.s.	> 0.10	1.38 n.s.	> 0.10
May, 1958	40	34	0.40 n.s.	> 0.10	3.00 n.s.	> 0.10
July-Aug., 1958	35	35	0 n.s.	—	1.50 n.s.	> 0.10

The null hypothesis concerning homogeneity of regression coefficients was accepted (Robson and Atkinson, 1960). The test for homogeneity of adjusted mean weights of males and females was, therefore, valid. It was concluded that there was no significant difference between the adjusted \log_{10}

weights of male and female rainbow trout in any of the tests. It was concluded that differences in condition between sexes was not a source of error in studies of variation in condition of rainbow trout.

Variations in the Regression Coefficients of Annual Samples

Annual regressions of \log_{10} weight on \log_{10} length for samples of trout captured in the vicinity of the mouth of Adams River from 1953 to 1960 were tested for homogeneity of regression coefficients. The F ratio ($F = 1,083^{**}$) was significant at the 1 per cent level. If regression coefficients varied with length and if the annual samples varied in length, significant differences in regression coefficients might be avoided by subdividing annual samples into length groups. Three length groups were chosen, 200 to 299 mm., 300 to 399 mm. and 400 mm. and over. The results of tests for homogeneity of annual regression coefficients for each length group were as follows: (1) 200 - 299 mm., $F = 14^{**}$; (2) 300 - 399 mm., $F = 113^{**}$; (3) 400 mm. and over, $F = 114^{**}$. It was concluded that annual length group \log_{10} weight - \log_{10} length regression coefficients were not homogeneous.

Since the homogeneity of regression coefficients could not be assumed, some measure of condition other than adjusted mean weights was required. A suitable alternative appeared to be annual weights at a common length. These weights were computed from the individual annual \log_{10} weight - \log_{10} length regression lines. A limitation to this procedure was that inferences concerning annual variations in weight were restricted to those variations occurring at the selected lengths; however, inferences might be valid if consistent patterns in weight variations occurred between the means of length group regression lines. For example,

one might infer that trout were in better condition in 1955 if the computed weights at the mean lengths of the 200 - 299 mm. group, the 300 - 399 mm. group and the 400 mm. and over group were all higher than in other years. Annual and seasonal comparisons of these computed weights are made in following sections.

Annual Variations in Computed Weights of Rainbow Trout Captured in the Adams River Area

Annual computed weights at the overall mean length of each length group are shown in TABLE 17. An overall mean length is the mean of \log_{10} lengths, all years, for a particular size group. For example the overall mean length for the 200 - 299 mm. length group (data shown in TABLE 17) is 2.427. This value was computed from the sum of all 889 \log_{10} lengths of fish falling within this length grouping. Annual deviations from the overall mean weight of each length group have been plotted in FIGURE 14. Insufficient fish in the 200 - 299 mm. group were sampled in 1954; therefore, no reliable regression line could be calculated.

In 1955 and 1959 when dominant populations were resident in Shuswap Lake, computed weights were above average in all three length groups. With the exception of fish in the 300 - 399 mm. group captured in 1954, all fish were below average weight in other years.

The consistently high computed weights in 1955 and 1959 for all three length size groups indicated that the condition of trout of all lengths was above average in these two years. Referring back to TABLE 14 and FIGURE 12, it will be noted that juvenile sockeye were abundant and that they formed an important food item.

TABLE 17 -- Annual computed weights at the overall mean lengths of three length groups of rainbow trout caught in the Adams River area of Shuswap Lake.

YEAR	200 - 299 mm.			300 - 399 mm.			400 mm. and over		
	Sample Size	Computed Weight		Sample Size	Computed Weight		Sample Size	Computed Weight	
		Mean Log ₁₀ (grams)	Geometric Mean (lbs.)		Mean Log ₁₀ (grams)	Geometric Mean (lbs.)		Mean Log ₁₀ (grams)	Geometric Mean (lbs.)
1953	54	2.304	0.44	121	2.610	0.90	66	2.989	2.15
1954				56	2.665	1.02	41	2.984	2.13
1955	130	2.382	0.53	460	2.664	1.02	491	3.073	2.61
1956	115	2.332	0.47	526	2.636	0.95	526	3.038	2.41
1957	180	2.325	0.46	256	2.624	0.93	320	3.020	2.31
1958	343	2.334	0.47	417	2.630	0.94	90	2.999	2.20
1959	45	2.387	0.54	563	2.699	1.10	185	3.090	2.71
1960	22	2.264	0.41	183	2.614	0.91	235	3.044	2.44

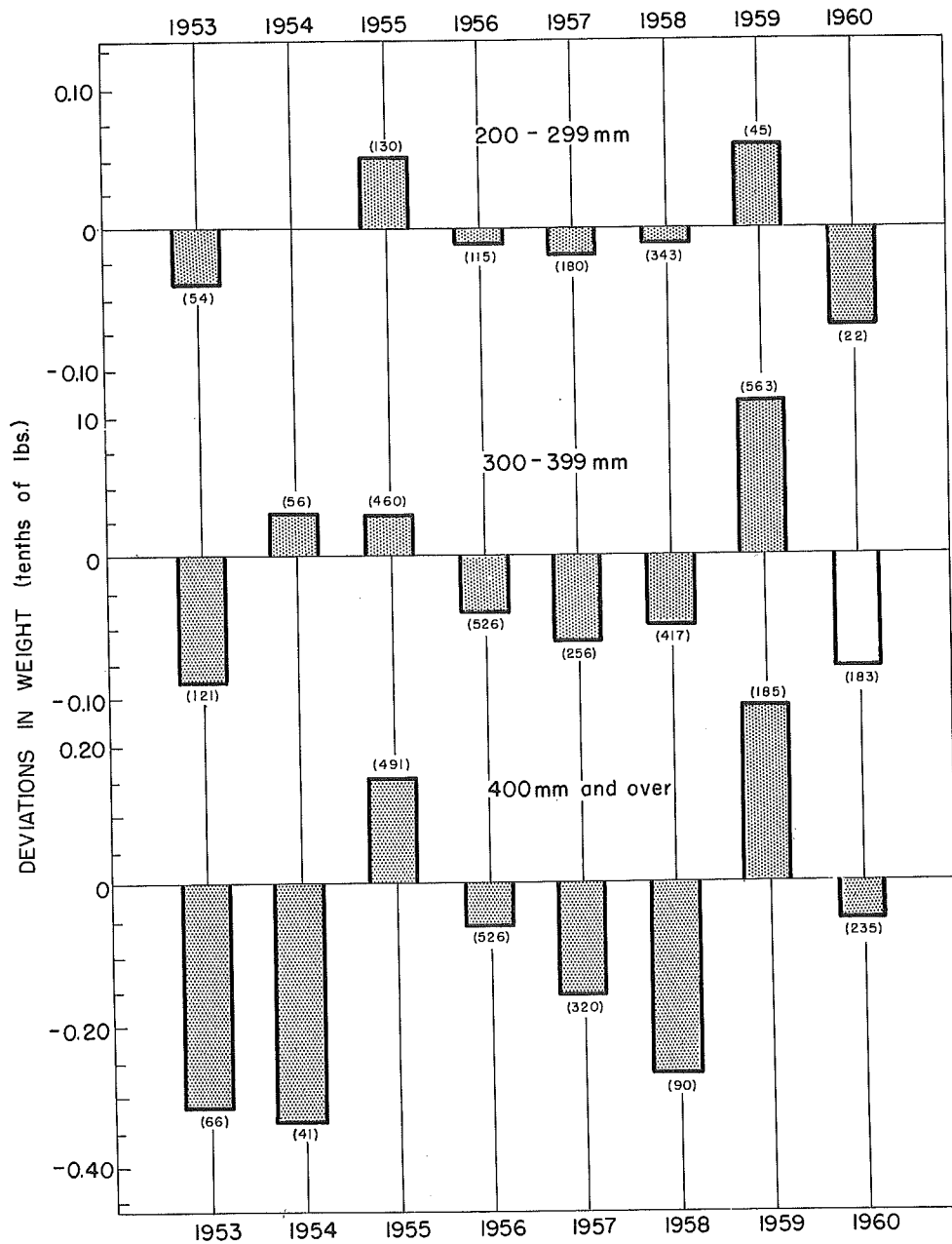


FIGURE 14 - Annual deviations from the overall mean weight of each of three length groups of rainbow trout from the Adams River area of Shuswap Lake.

Seasonal Variations in Computed Weights of Rainbow Trout Captured in the Adams River Area

Samples beginning with that of the summer of 1955 are sufficient to allow seasonal changes in computed weights of rainbow trout taken in the Adams River area to be studied. The annual samples were divided into the following three seasonal categories: Spring - April, May and June; Summer July, August and September; Fall - October and November.

It was intended that these groupings as well as being seasonal would separate phases in the life-history of sockeye. For example, the spring period includes fry emergence, distribution in the lake and most of the downstream smolt migration. If trout sampled in June had been included with the summer period, part of the up-lake migration of fry and part of the smolt migration would have been included in the summer period. Similarly, the fall period includes the adult migration on the spawning grounds and the deposition of eggs. The inclusion of September with the summer period puts the earliest part of the migration and spawning period in the summer category.

Seasonal computed weights for each length group are shown in TABLE 18. Deviations from the overall mean weight of each length group are shown in FIGURE 15. Insufficient data were available after the summer of 1959 concerning fish in the 200 - 299 mm. group; therefore, regression lines were not computed.

Trout belonging to all size groups in 1955 and 1959 were heavier than the average. As shown in TABLE 14, juvenile sockeye of dominant population were resident in the lake during these years. Fish of the 200 - 299 mm. group were slightly below average in weight for the years 1956, 1957 and 1958. The two larger size groups exhibited a somewhat different pattern

TABLE 18 - Seasonal computed weights at the overall mean length of three length groups of rainbow trout caught in the Adams River area of Shuswap Lake.

YEAR	SEASON	200 - 299 mm.			300 - 399 mm.			400 mm. and over		
		Sample Size	Computed Weights		Sample Size	Computed Weights		Sample Size	Computed Weights	
			Mean Log ₁₀ (grams)	Geometric Mean (lbs.)		Mean Log ₁₀ (grams)	Geometric Mean (lbs.)		Mean Log ₁₀ (grams)	Geometric Mean (lbs.)
1955	Summer	87	2.453	0.63	209	2.669	1.03	174	3.077	2.63
	Fall	43	2.380	0.53	251	2.660	1.01	317	3.066	2.57
1956	Spring	28	2.311	0.45	203	2.663	1.01	262	3.076	2.63
	Summer	57	2.334	0.48	208	2.627	0.93	159	2.989	2.15
	Fall	30	2.335	0.48	115	2.615	0.91	105	2.990	2.15
1957	Spring	36	2.299	0.44	123	2.615	0.91	198	3.038	2.41
	Summer	101	2.328	0.47	85	2.627	0.93	89	2.991	2.16
	Fall	43	2.338	0.48	48	2.636	0.95	33	3.018	2.30
1958	Spring	69	2.339	0.48	73	2.625	0.93	27	2.994	2.17
	Summer	62	2.333	0.47	123	2.631	0.94	40	2.981	2.11
	Fall	212	2.344	0.49	221	2.635	0.95	23	3.004	2.22
1959	Spring	22	2.387	0.54	268	2.702	1.11	126	3.093	2.73
	Summer	22	2.396	0.55	260	2.700	1.10	46	3.088	2.70
	Fall				35	2.678	1.05	13	3.079	2.65
1960	Spring				94	2.624	0.93	168	3.054	2.50
	Summer				54	2.619	0.92	48	3.019	2.30
	Fall				35	2.579	0.84	19	3.005	2.23

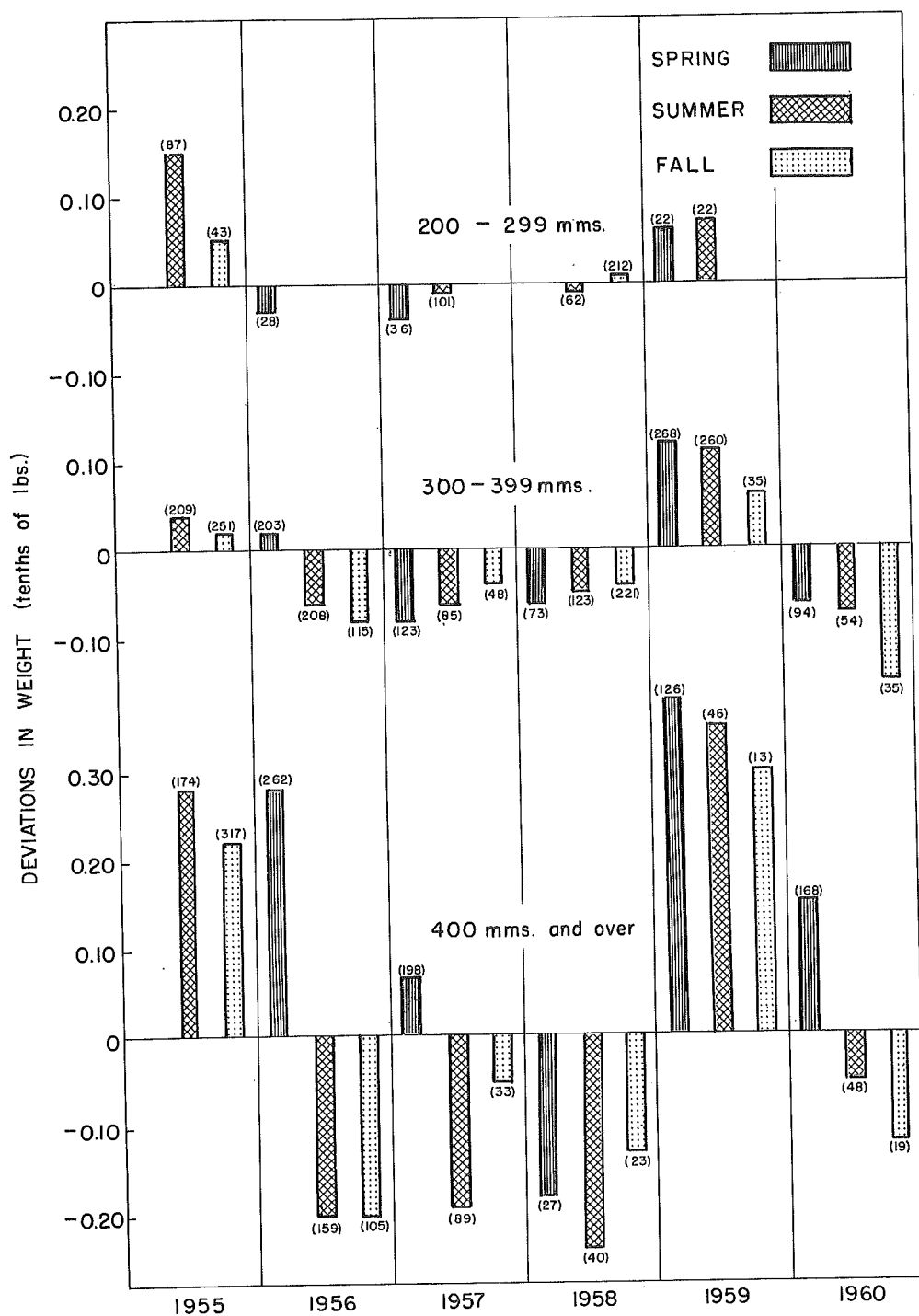


FIGURE 15 - Seasonal deviations from the overall mean weight of each of three length groups of rainbow trout from the Adams River area of Shuswap Lake.

of fluctuations. The intermediate size group, 300 - 399 mm. were above average during the spring of 1956 but were substantially below average during the spring of 1960. The largest size group, 400 mm. and over, were above the average weight both in the spring of 1956 and the spring of 1960. It is suggested that the relatively good condition in the springs of 1956 and 1960 of the two largest size groups resulted from predation upon abundant smolts belonging to a dominant population and Cycle II fry.

The consistency exhibited by the three size groups in the pattern of deviations indicates that, with minor exceptions and to varying degrees, trout of all lengths represented in the anglers' catches were responding in a similar manner to a causal agent. These seasonal changes in weights were apparently associated with the relative abundance of sockeye eggs, fingerlings and smolts. When sockeye were abundant condition of trout was relatively good. When sockeye were scarce condition of trout was below average and average volume of stomach content was also generally low (FIGURE 11). This situation held after the spring of 1956 until the spring of 1959 when eggs and fingerlings again became abundant.

Seasonal Variations in Computed Weights of Rainbow Trout from the Remainder of Shuswap Lake

The Adams River area forms only a small fraction of Shuswap Lake. Large numbers of rainbow trout were captured in other sections of the lake, but samples were much more difficult to obtain because individual camp landings were small and more camps had to be visited.

Seasonal computed weights for the mean length of all fish combined are shown in TABLE 19. Deviations of these weights from the overall mean weight are shown in FIGURE 16.

TABLE 19 - Computed weights of rainbow trout caught in Area 2 of Shuswap Lake, 1955 to 1960.

YEAR	SEASON	SAMPLE SIZE	COMPUTED WEIGHT	
			Mean (\log_{10} gm.)	Geometric Mean (lbs.)
1955	Summer	56	2.975	2.08
1956	Spring	245	2.948	1.96
	Summer	53	2.947	1.95
1957	Spring	143	2.913	1.81
	Summer	58	2.963	2.03
1958	Spring	36	2.926	1.86
	Summer	52	2.950	1.96
1959	Spring	64	2.921	1.84
	Summer	52	2.962	2.02
1960	Spring	253	2.946	1.95
	Summer	306	2.934	1.89

Variations in weight were minor and not closely related to sockeye abundance. Although weights were above average in the summers of 1955 and 1959 when juvenile sockeye were numerous they were also above average in the summers of 1957 and 1958 when sockeye were scarce. Evidently trout in these up-lake areas were not as dependent on sockeye as a food source as were trout in the Adams River area of Shuswap Lake.

Few eggs of Cycle I populations were available to trout in this up-lake area because few sockeye spawn in tributary streams located in this part of the lake; therefore an important factor causing fluctuations in trout weight

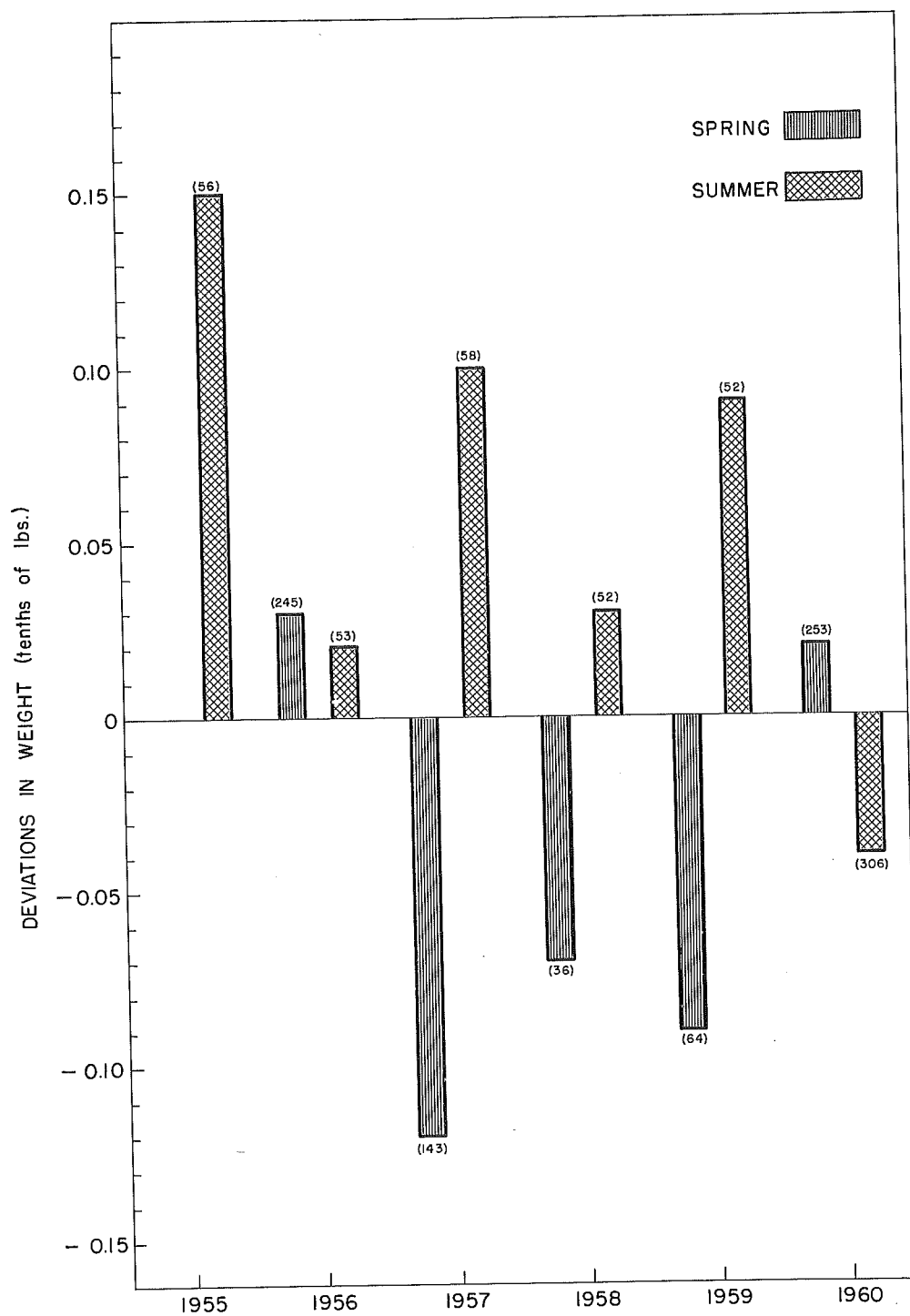


FIGURE 16 - Seasonal deviations from the overall mean weight of rainbow trout from Area 2 of Shuswap Lake.

was absent. Kokanee were more abundant in the eastern basins thus providing a relatively constant food source which would tend to maintain trout weight when sockeye were scarce.

A Possible Interaction Between Sockeye and Predator Populations

Dominant Cycle I populations were apparently established in the Adams River sockeye stock during the 1922-1930 period. As a result, a general increase in predator abundance might also have occurred during the same period. An upper limit on such an increase could have been established by the feeding demands of predators during periods of sockeye scarcity, i.e. during periods when only off year sockeye populations were resident in the area. An increase in predator abundance would have the effect of increasing the mortality rate applying to small sockeye populations but by the limitation imposed by these small prey populations on increases in predator abundance, the mortality rate might remain lower for large sockeye populations. In this way, a relatively stable cyclical abundance pattern could be maintained in the sockeye stock.

Circumstantial evidence supporting this hypothesis is available in the present situation. When sockeye are abundant, the condition of rainbow trout in the western part of Shuswap Lake is above average. When sockeye are scarce they are only partially replaced in the diet and the condition of trout is lower (FIGURES 14 and 15). This combination of effects suggests first, that trout may be more abundant as a result of the food provided by the dominant run and secondly, the small off year populations may limit the ultimate size of the trout population by influencing trout survival, growth and fecundity.

Detailed information concerning the total effects of predation is unavailable. However it is possible to envisage the role which rainbow trout might play in maintaining dominance in Adams River sockeye. The consequences to the abundance of trout of this dependence, in the western part of the lake, on sockeye may be several. In general, trout of a size greater than 300 mm., which show the greatest relation to sockeye abundance, are at least II and more likely III years old or older. During the years when sockeye are abundant as food, these ages of fish presumably grow faster and have higher rates of survival than comparable trout in the off sockeye years. This greater survival carries over into the off years, from the viewpoint of trout, aggravating the relative shortage of sockeye as food, and from the viewpoint of sockeye exposing them to a disproportionate predation. The reverse is true for the dominant run, which arrives after two years of poor condition and presumably low survival for large trout. The majority of trout spawn for the first time between ages III and V and few survive to spawn for a second time. There is thus little likelihood of a carry-over to the next dominant sockeye cycle of trout year-classes which had benefitted from the previous dominant or subdominant years.

There is a possibility that fluctuations in egg deposition may be involved in producing some sort of damped fluctuation in trout abundance. In years following a big sockeye run there might be a greater egg deposition by trout. During the off years for sockeye, starvation (as judged from condition) may influence survival of trout. There may also be effects on egg production (Scott, 1962). To the limited extent that egg deposition is a factor influencing the size of the trout

population, there would seem to be a mechanism available for regular fluctuations in the size of year-classes of trout which in some degree reflected the regular sequence of abundance of sockeye. However, this potential adjustment of trout populations to sockeye abundance is probably diluted by varying ages of trout at spawning, factors influencing survival of young trout, the use of alternate sources of food, and a variety of other secondary modifying factors. The most reasonable generalizations about the interaction of sockeye and trout populations would seem to be: (1) the trout population present is more abundant than it would be if there were no dominant sockeye populations and (2) Cycle I populations of sockeye create conditions for favorable survival of trout which persist to have effects on Cycle II, III and IV populations of sockeye. A mechanism of this kind would tend to increase the probability of depensation occurring and it would tend to be self-regulating since the predator population would be limited by mortality during the two years when sockeye are scarce.

The pronounced changes in the weight of trout in the western end of the lake are clearly dependent on the location of the major sockeye spawning streams and the lake outlet. In central and eastern sections, juvenile sockeye when present are probably more widely dispersed and less vulnerable than in the outlet area where fry enter the lake and smolts are concentrated prior to their seaward migration. Trout resident in these central areas would presumably avail themselves of alternate foods.

Juvenile sockeye belonging to small populations would seem to be particularly vulnerable in the western extremity of the lake. When fry first enter Shuswap Lake from Adams and Little Rivers they are concentrated

in shallow water near the outlet (FIGURE 10). Even after they begin the up-lake migration they still remain concentrated in shallow water. This behavior would seem to make small populations more vulnerable to predation than if the fish entered the lake in a more centrally located, less constricted area and if they immediately dispersed widely in a horizontal plane throughout the lake. Small smolt populations must also tend to be concentrated in this western area. The outlet region might act as a funnel concentrating schools and thus making small populations available to predators. Both the entry of fry into the lake and the seaward smolt migration occur during the spring period; therefore the depensatory effects of predation would be expected to be intense at this time. Predation on sockeye eggs and alevins in the rivers is less likely to be an effective depensatory mechanism since these are phases when other natural mortalities are at a maximum. Many of the eggs taken would not have survived to hatch. Unfertilized eggs and eggs already dead are most available to stream predators. It is also probable that the availability of eggs as food is directly related to population size. Relatively more eggs from Cycle I populations are available to be eaten. In general, it is probable that mortalities from egg and alevin predation have a compensatory effect.

On the basis of these considerations, it would seem that depensatory effects are limited both in time and space and indeed are exaggerated thereby. The western part of the lake seems to be the most likely site and spring periods seem to be the most likely times for dominance maintaining agents to operate.

In a previous section it was suggested that the Seymour stock now shows a dominance pattern similar to the Adams. It is evident that if the juveniles of the two stocks mix when dominant Adams runs are present in the lake, Seymour populations of this cycle will be buffered and will suffer a similar low mortality rate due to predation. Predation on Cycle II Seymour fry populations might be buffered by the presence of Cycle I Adams smolts and pre-smolts. A general migration of predators towards the outlet area along with Adams smolts would offer this type of protection to Seymour Cycle II fry. When Cycles III and IV Adams populations are resident in Shuswap Lake no protection would be afforded to Seymour fry and survival might be lower than for Cycles I and II populations. Seymour smolts, as far as is known, would be affected in the same way as Adams smolts since all smolts must pass through the western section of the lake.

Direct evidence supporting the predation theory as presented above is scant. Trout in the western part of Shuswap Lake utilize sockeye, their condition varies relative to sockeye abundance and it is probable that there has been some long-term numerical response on the part of the trout but there is no direct evidence suggesting that trout or predators in general take a higher proportion of Cycles II, III and IV sockeye than they do of Cycle I. There is, therefore, no direct evidence for the existence of a depensatory agent. Additional studies on the effects of predators on prey populations of varying densities seem necessary.

Effect of Predation on Sockeye Populations

Although direct evidence concerning the relationship between trout predation and prey density is not available, an indirect approach to determining this relationship can be made. First it is necessary to convert theoretical juvenile sockeye populations to indices of biomass so that the contributions of different cycles present during the same period can be summed and then related to both the functional and combined functional and numerical response of the predators. Approximate values for the abundance of individuals for each cycle of Adams River sockeye determined from the average number of adult females belonging to each cycle are shown below:

	<u>Cycle I</u>	<u>Cycle II</u>	<u>Cycle III</u>	<u>Cycle IV</u>
Eggs	1×10^6	50,000	4,000	4,000
Fry	1×10^5	5,000	400	400
Smolts	20,000	1,000	80	80

Survival to the fry stage was assumed to be 10 per cent and from eggs to smolts, 2 per cent. These values are obviously crude indices, since survival from eggs to fry is probably directly density-dependent and from fry to smolts inversely density-dependent, however, the differences between cycles is so great that errors due to compensation and depensation are relatively minor in comparison.

These abundance indices can be converted to biomass indices by multiplying each index by an appropriate average weight for sockeye in that stage. The average weight of a mature egg may be taken as 0.1 gm., a recently emerged fry as 0.25 gm., a summer fingerling 1.5 gm., a fall fingerling 3.0 gm., a dominant smolt 3.2 gm. and an off year smolt 6 gm. Again there will be cyclic differences in some of these weights but the great numerical differences between cycles at all stages will make such

errors relatively unimportant. Biomass indices for three seasons and a complete sequence of years is shown in TABLE 20.

TABLE 20 - Indices of the seasonal biomass of Adams River race sockeye for four consecutive years.

Year	Spring	Summer	Fall
1	Cycle III Smolts 480 Cycle IV Fry <u>100</u> 580	Cycle IV Fingerlings 600	Cycle I Eggs 100,000 Cycle IV Fingerlings <u>1,200</u> 101,200
2	Cycle IV Smolts 480 Cycle I Fry <u>25,000</u> 25,480	Cycle I Fingerlings 150,000	Cycle II Eggs 5,000 Cycle I Fingerlings <u>300,000</u> 305,000
3	Cycle I Smolts 64,000 Cycle II Fry <u>1,250</u> 65,250	Cycle II Fingerlings 7,500	Cycle III Eggs 400 Cycle II Fingerlings <u>15,000</u> 15,400
4	Cycle II Smolts 6,000 Cycle III Fry <u>100</u> 6,100	Cycle III Fingerlings 600	Cycle IV Eggs 400 Cycle III Fingerlings <u>1,200</u> 1,600

As discussed previously, during spring periods the bulk of these biomasses will funnel through the Adams River mouth region of Shuswap Lake. During the summer periods sockeye fingerlings will be present in the area but the population as a whole will be widely dispersed throughout the Shuswap Lake. This situation also applies to fingerlings during annual fall and winter periods. Only a portion of the fall egg biomass will be available to trout predators because most eggs will be buried in the gravel. For this reason only spring and summer periods will be considered.

The first step in studying the relationship between predators and prey density will be to determine the functional response of rainbow trout over 300 mm. during two seasons of a four year sequence. Measures of relative predation are average volumes of fish material found in the stomachs of trout over 300 mm. These values are plotted against biomass estimates in FIGURE 17.

The data indicate that the volume of fish in trout stomachs increases with an increase in sockeye biomass, however the relationship does not appear to be linear. The volume at high prey densities is not much greater than at low prey densities. Assuming a constant abundance of trout, one could conclude that a smaller fraction of a large biomass was taken by trout than from a small biomass. In this situation mortality rates from trout predation would be inversely related to prey density, which of course, is depensation.

Although as stated, major fluctuations in the annual abundance of trout in Shuswap Lake as a whole are unlikely, there may be a kind of numerical response on the part of rainbow trout. Large biomasses may tend to attract and concentrate more trout than smaller biomasses. In this event the overall effect of predation on the prey populations might be that a constant percentage of the prey was taken (Ricker, 1954, Situation B). This possibility has been examined by attempting to obtain seasonal indices of trout abundance. If accurate indices could be obtained, average volumes of fish in trout stomachs could be multiplied by these indices to obtain indices of total predation. The only estimates of relative trout abundance available are the actual number sampled each season (see FIGURE 11 and FIGURE 12). Numbers of trout 300 mm. and over

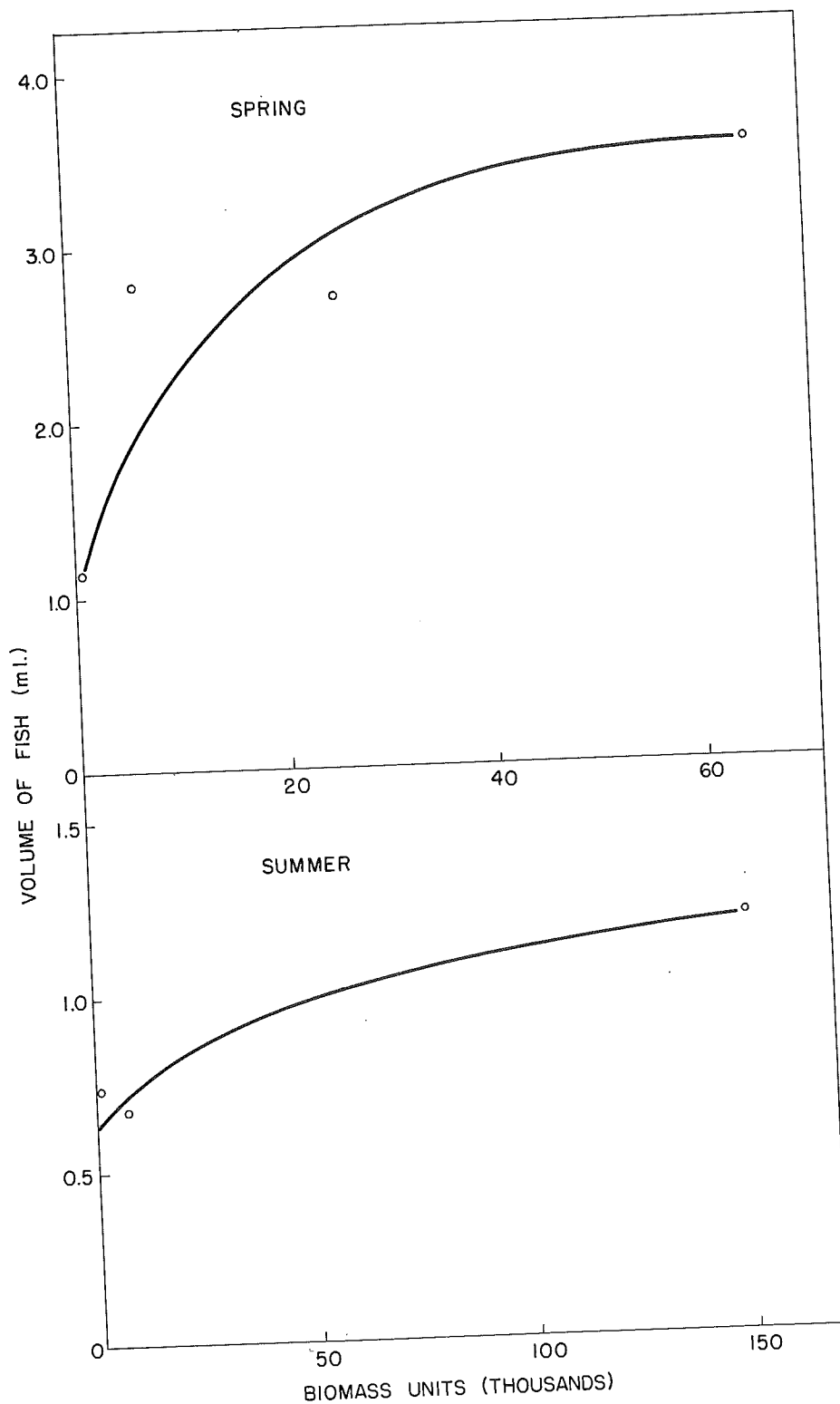


FIGURE 17 - Relationship between prey density (sockeye biomass units) and the average volume of fish in the stomachs of rainbow trout over 300 mm. from the Adams River area of Shuswap Lake. Data for four consecutive spring and summer periods are shown.

sampled in four spring and summer periods have been used to obtain indices of total predation. These values have been plotted against the appropriate biomass values in FIGURE 18. Depensation is again indicated in both graphs since the relationships are asymptotic.

The chief source of error in these data is the validity of the assumption that the actual number of trout sampled in each period was roughly proportional to the number present in the western end of the lake. In the spring of 1956, a total of 399 stomachs was examined and the average fish content per trout was 3.5 ml. The total volume of fish was, therefore, 1400 ml. At this time the sockeye biomass estimate was 65,250 units. If it is assumed that a linear relationship exists between sockeye biomass and predation and that a straight line can be fitted to the three lowest points on the spring curve of FIGURE 18, it is then possible to estimate the amount of error in the trout abundance index which would have to occur to produce the observed result at a biomass of 65,250 units. A line of "best fit" passing through the three points would predict a Y-value of 2800 ml. for an X of 65,250 biomass units. Since the average volume of fish per trout stomach was 3.5, the number of fish which would have been sampled had the relationship been linear is 800 instead of the actual 399. In order to account for the asymptotic relationship, if the true relationship was linear, it would be necessary to assume that twice as many trout should have been sampled. Possibly, more than 399 trout could have been sampled relative to the other three spring seasons, however, a twofold error seems excessive.

Although indirect evidence presented above suggests that predation by rainbow trout leads to depensation it has not been shown that total

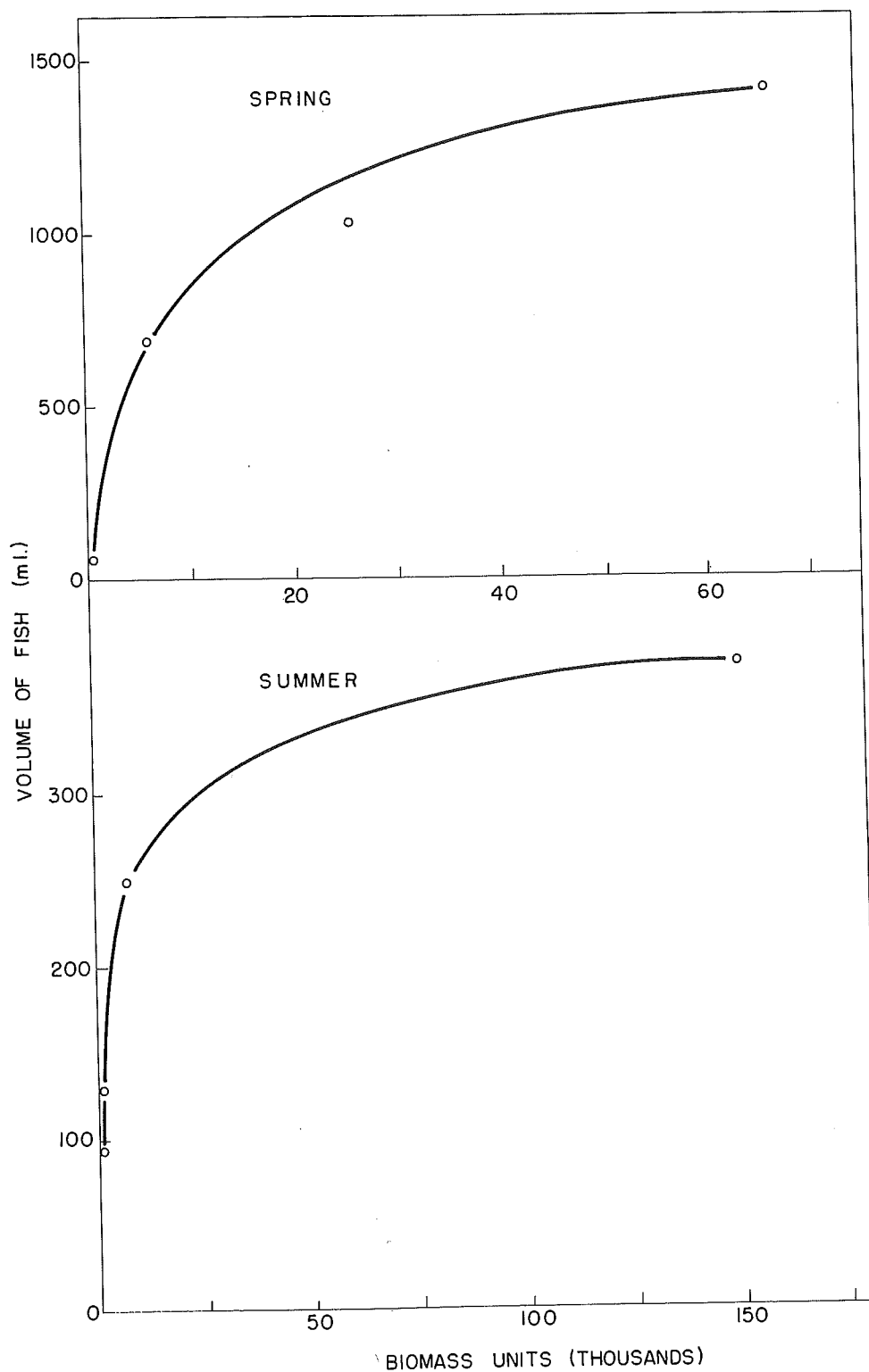


FIGURE 18 - Relationship between prey density (sockeye biomass units) and the total volume of fish found in the stomachs of all rainbow trout over 300 mm. from the Adams River area of Shuswap Lake. Data for four consecutive spring and summer periods are shown.

predation has the effect of depensation, nor has it been shown that the total effects of mortalities during the lacustrine stage result in depensation.

DOMINANCE AND SALMON POPULATION DYNAMICS

The population biology of salmon and other anadromous fishes have features in common. To a large extent the year-classes do not interact with each other; some are at sea while others are in fresh water. Death after spawning is virtually inevitable. In some cases one annual adult population contributes primarily to only one filial population; thus exchanges between populations are limited. In most stocks of Fraser sockeye, the majority of fish of all cycles return at four years of age. In consequence, each of the cycles may largely be considered a separate entity, influenced by the other cycles only at limited times and to a limited degree.

The population biology of sockeye salmon is also singular in the fairly clear division of the life-history into separate stages, each in a different environment and each potentially capable of causing a characteristic pattern of mortality. It may thus be envisaged that each stage of the life-history could be described by a "reproductive curve" depicting what the consequence would be if that stage were the only one in the life-history (Larkin et al., 1964). The stages may then be related to each other, the output of one forming the input of the next.

Formulation of Mortalities in Life-History Stages

As discussed, mortalities in the spawning-incubation stage appear to be compensatory and might be described by a reproduction curve according to the familiar equation (Ricker, 1954):

$$Z = W e^{a_1(1-W)}$$

where W and Z are, respectively, indices of parental and filial abundance. The constant a_1 is the ratio between parental populations which result in replacement reproduction and which result in maximum reproduction (Ricker, 1958). The magnitude of a_1 determines the shape of the reproduction curve. As a_1 increases, corresponding values of Z above the replacement line for given values of W also increase. Since vertical distances between the replacement line and the curve in this area represent excess stock or allowable catch, the magnitude of a_1 also determines the proportion of a stock which can be taken as a sustained catch. The dominant run of the Adams stock has demonstrated a capacity for a sustainable catch ranging between 50 and 80 per cent of the total adult population. This would suggest a reproduction curve with an a_1 value of at least two. The curve representing compensation with $a_1 = 2$ (FIGURE 19A) has the characteristic vigorous compensation which results in a steeply descending curve beyond unit stock size (this part of the curve is shown as a broken line in FIGURE 19A). This is perhaps unrealistic because it implies that there is no limit to the increasing effect of the number of spawners on the proportion of progeny which survive. It seems more likely that a wide range of parent population values beyond unit stock size would give rise to progeny populations all of approximately equal size. In fact it is observed that super-saturation of choice spawning areas is in

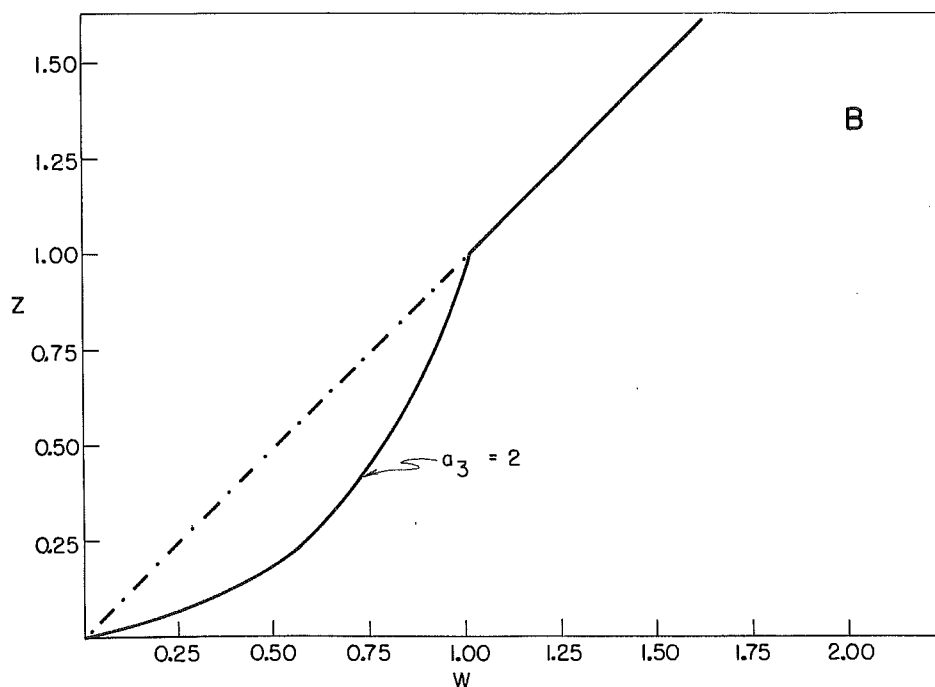
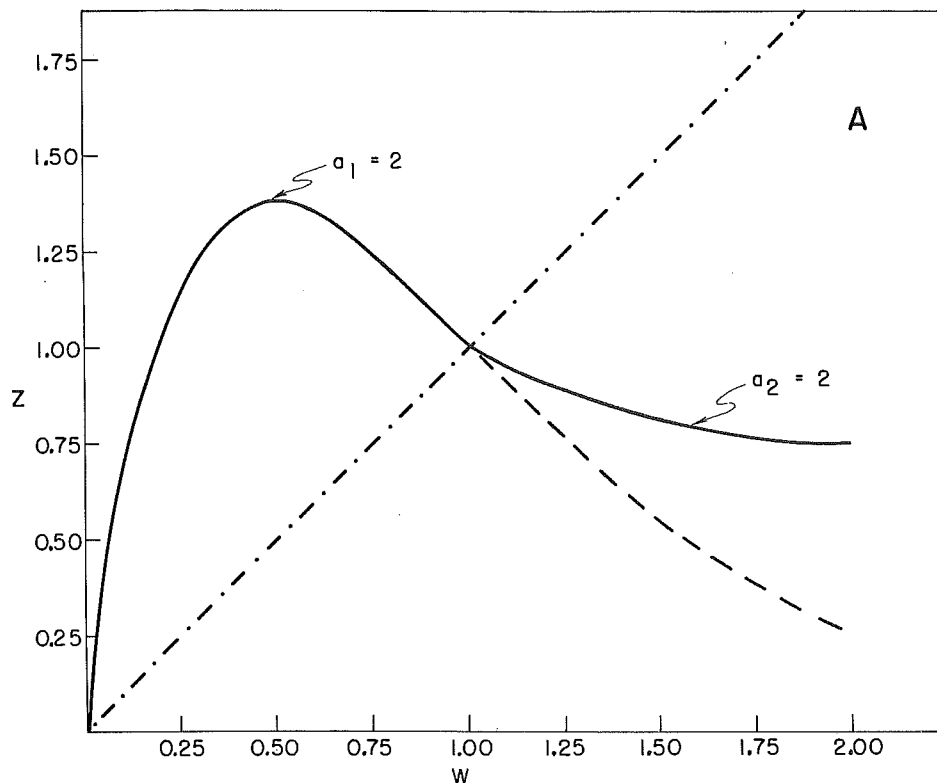


FIGURE 19 - (A) Reproduction curve based on compensation as represented by $Z = We^{a_1(1-W)}$ where $a_1 = 2$.

(B) Reproduction curve based on depensation as represented by $Z = We^{a_3(W-1)}$ where $a_3 = 2$, and where $Z = W$ when $W > 1$.

part alleviated by spawning in alternate areas, which while unproductive, may not affect survival in better spawning grounds. The empirical curve, shown as the solid curve below the replacement line in FIGURE 19A, seems to more reasonably approximate the circumstances of compensation on the Adams run spawning ground. Beyond unit stock size, stock is related to progeny by the relation:

$$Z = (1-D)e^{-a_2(W-1)+D}$$

where D, the asymptotic progeny production is 0.75.

The spawning-incubation stage is susceptible to the effects of climatic variation, although on the Adams River, physical conditions are somewhat buffered because the flow is from Adams Lake. Available records suggest that the range of effects is sufficient to produce a twofold difference in survival rates between the worst and best years. At high stock densities there appears to be a smaller range of variation. In terms of reproduction curves, the output from spawning is subject to a modification by multiplication or division with random normal deviates which in 95 per cent of cases would produce a twofold spread from highest to lowest values. The modified output may be denoted by W_f indicating the numbers of fry, expressed in stock units.

Depensation occurring during the lacustrine period and acting upon the output from the spawning-incubation stage, is conveniently represented by the converse of Ricker's compensation curve (FIGURE 19B) suggested by Larkin et al. (1964):

$$Z_s = W_f e^{a_3(W_f-1)} \quad (W < 1)$$

$$Z_s = W_f \quad (W \geq 1)$$

where Z_s is the production of smolts in stock units.

Assuming that predators are the cause of depensation, the choice of a value for a_3 is complicated by the effect of a large run on survival of the predators. If all runs of sockeye were small, it might be supposed that the predator population would be small and depensation virtually non-existent. In addition to a general numerical response of predators there may be a reinforcement of predation by short term rather than regular fluctuations in the survival of predators. For instance, a larger proportion of a year-class of trout may survive due to good feeding conditions when Cycle I fish are resident. When Cycle I sockeye are absent these predators may prey particularly effectively on one or more of the following cycles of sockeye. Presumably their condition would decline and their contribution to subsequent generations limited to the long term mean thus resulting in a fairly stable trout population. It is appropriate therefore to relate the value of a_3 to the production from previous populations, i.e.

$$a_3 = k_1 W_{(t-1)} + k_2 W_{(t-2)} + k_3 W_{(t-3)} + \dots + k_i W_{(t-i)}$$

where W_{t-i} represent sizes of adult sockeye spawning populations in previous years and k_i represent coefficients relating these runs to depensatory effects. There is evidently some limit to the number of years this kind of effect will linger, depending upon the life-history of the predator and its capacity to subsist on alternate foods or withstand starvation. In the Adams situation a choice of two or three years might seem appropriate considering the observed effects on condition of trout in years of low abundance of salmon.

A reproduction curve representing a two stage life-history in which the first stage is compensatory and the second stage is depensatory is shown in FIGURE 20.

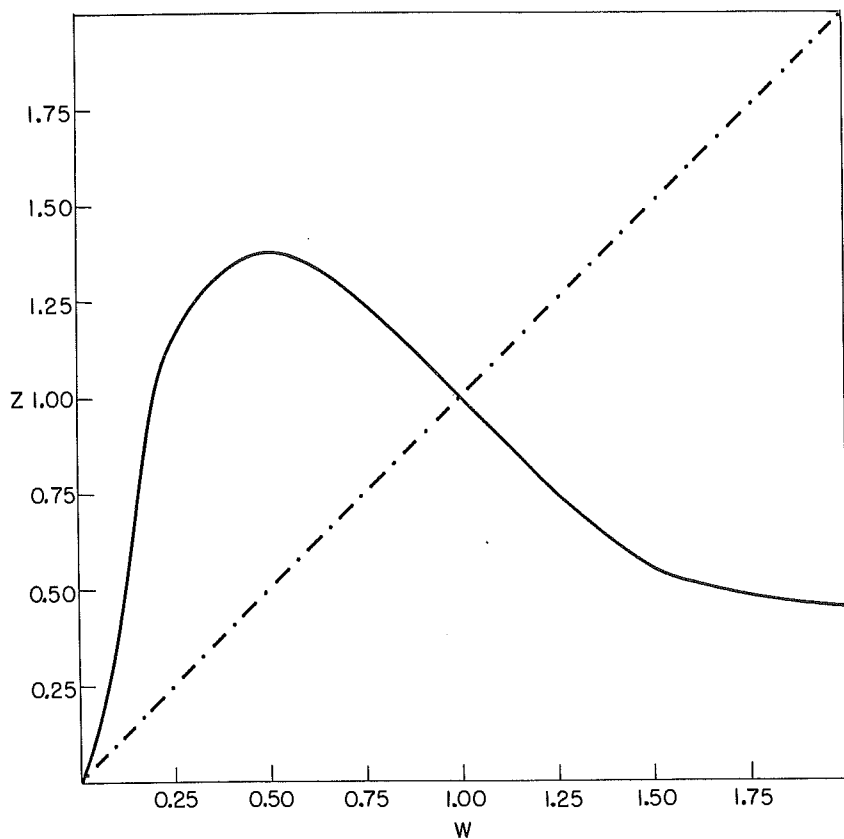


FIGURE 20 - Reproduction curve combining the effects of compensation and depensation in successive life-history stages.

A further consideration in the depensation process is the possibility of "buffering" predation by the presence of smolts of one cycle at the same time and place as the fry of the following cycle. In terms of biomass, smolts are twice as much food for trout as fry, if both fry and smolts have come from equal sized runs. Buffering probably occurs over only a limited period of time as the smolts and fry pass in their respective migrations. Estimates of the annual variations in the biomass of smolts and fry present during spring periods and the annual differences in the buffering provided by smolts can be determined from TABLE 20. Note that the maximum buffering effect by smolts applies to Cycle II fry.

Formulation of this buffering effect can be achieved simply by adding some proportion of the smolt contribution of the previous year to the fry output of a current year, processing the total through the depensation process and dividing the resultant into appropriate proportions representing fry and smolts.

Thus, first form the provisional quantity W_p from:

$$W_p = W_f + SZ_{s(t-1)}$$

where W_f is the fry output, $Z_{s(t-1)}$ is the smolt output from the previous year, (i.e. a resultant of previous depensation which has not as yet been modified by marine extrapensatory effects) and S is a coefficient describing the buffering capacity of the smolts. Then, process W_p through depensation:

$$Z_B = W_p e^{a_3(W_p-1)} \quad W_p < 1$$

$$Z_B = W_p \quad W_p \geq 1$$

The resultant Z_B represents the biomass of smolts and fry combined after depensation. To get the fraction Z_s which represents production of smolts in the current cycle after buffered predation, the value Z_B must be multiplied by the fraction W_f/W_p viz:

$$Z_s = \frac{W_f}{W_p} \cdot Z_B$$

Combining the above two equations, the output of smolts in buffered depensation is given by:

$$Z_s = W_f e^{a_3(W_p - 1)}$$

The remaining stages in the life-history of sockeye salmon from the viewpoint of population mechanics appear to be characterized by extra-pensatory mortalities (as noted above) of sufficient magnitude to cause quite substantial fluctuations in abundance. For the Adams stock the range of best to worst conditions would seem to be sufficient to cause fivefold variation in the production of adults (W) from any given production of smolts.

The fisheries are managed to provide optimum escapements of Adams Cycle I adults; the excess, a varying fraction depending on total abundance, is harvested as catch. The objective is to maintain parental populations at the highest level of reproductive efficiency so that all filial generations are able, under favorable conditions, to reach the maximum abundance level. Thus variations in the abundance of each filial generation are independent of its parental population.

Management objectives for the off year cycles are different. Fishing mortalities on these cycles have been maintained at the usual levels whenever possible because the long-term effects to total abundance of

special protective regulations were unknown. However, vagaries in the economy of the fisheries, the special management needs of other races and species, and random variations in off year abundance have all resulted in the effects of the fisheries being variable.

For Cycle I populations, formulation of coefficients representing the effects of the fisheries is an unnecessary complication. Lack of depensation will maintain the progeny of small total Cycle I adult populations at levels at or above optimum spawning abundance. Compensation, although reducing the abundance of the offspring of large populations is not so severe that resultant adult populations cannot attain the maximum possible size.

Similarly, the effects of the fishery on off year populations does not require formulation. The most realistic simulation would be to reduce each adult population at a fixed rate. This procedure would result in smaller parental populations suffering reduced compensatory mortalities and increased depensation. The result would be that each off year cycle would be maintained at a lower level than in the unfished state. But differences between the two equilibria would be largely obscured by extrapensatory effects.

A Model for Dominance

On the general pattern of mortalities at different life-history stages outlined in the foregoing, a model may be constructed which simulates the chief characteristics of the Adams stock of sockeye. The model represents the unfished state. Presumably, if the model is adequate, it should demonstrate the propensity for stable dominance which the Adams stock exhibits.

I. Each year's run should encounter a series of mortalities which conform in sequence to those outlined above, and which are summarized below with comments concerning values of parameters.

- (1) Compensation during the spawning incubation stage according to the relation:

$$Z = We^{a_1(1-W)} \quad Z \leq 1$$

$$Z = (1-D)e^{-a_2(W-1)} + D \quad Z > 1$$

For the Adams stock the value of a_1 should be 2 or greater.

An arbitrary value of 2 for a_2 and of 0.75 for D seems appropriate.

- (2) Modification of Z by a random normal deviate simulating an extrapensatory effect of specified magnitude. This can be accomplished by choosing random normal deviates and using them as multipliers or divisors depending on whether their sign is positive or negative. Each random normal deviate must be augmented in absolute value by 1 before being used as a multiplier or divisor (Ricker, 1954). To scale the effect to a particular range (say twofold in 95 per cent of cases) the deviates should be multiplied by a factor Q before their absolute value is increased by one. Values of Q can be obtained by solving the ratio:

$$\text{Extreme multiplier} = 2 (\text{Extreme divisor})$$

$$1 + 2Q = 2\left(\frac{1}{1 + 2Q}\right)$$

where the "extremes" are respectively 2 standard deviations from the mean and give approximately the specified 95 per cent probability. Solving, the value of Q in this example is 0.20715;

the extreme multiplier produces a value 1.41421 times as great and the extreme divisor is 0.70710 times as great, a ratio of 2:1.

The resultant of using random normal deviates as modifiers on Z may be denoted as W_f .

- (3) Depensation, involving buffering and the effect of previous runs on abundance of predators.

Buffering is given by:

$$W_p = W_f + SZ_s(t-1)$$

where the coefficient S was given values based on the biomass of smolts and the time smolts of one cycle were in contact with fry of the next (one selected value was 0.15).

Depensation leading to production of smolts, Z_s is given by:

$$Z_s = W_f e^{a_3(W_p-1)} \quad W_p < 1$$

$$Z_s = W_f \quad W_p \geq 1$$

The value of a_3 is given by:

$$a_3 = k_1 W_{(t-1)} + k_2 W_{(t-2)} + k_3 W_{(t-3)} + \dots$$

where the values of k_i can be varied (up to 5.00 as seems useful), and may not be equal.

- (4) Extrapensatory marine mortality of fivefold range of magnitude.

Accomplished in like fashion to that of item 2 above, but with

$Q = 0.61803$ (ratio of extremes, expressed as multipliers,

2.23606:0.44721 or 5:1).

II. Each year's run of adults (brood) is recruited from runs of several years previous, the proportions depending on the usual age distribution characteristics of the brood. In the case of the Adams stock, there is good reason to believe that there are differences in the proportions of various ages of spawners produced by different cycles. TABLE 21A summarizes age composition data of the runs giving the calculated proportions that each brood year received from previous years, and in TABLE 21B these age composition data have been presented again as average coefficients indicating what proportions of adults arising from production in previous years go to make up a spawning run in any particular cycle year. Thus for example, Cycle II run comprises 0.0084 of the adults produced by the run five years previous, 0.9181 of adults produced by the run four years previous, and 0.0014 (50) of the adults eventually produced by the run three years previous. All 3_2 proportions were multiplied by 0.02 to account for the very unequal sex ratio of jacks and for the relatively small number of eggs contributed by each female jack.

Performance of the Model

A computer program was written based on the foregoing sequence of mortalities and using the age distribution production coefficients of TABLE 21B. The procedure of calculation was facilitated by processing each year's run through all of the various life-history stages at once, rather than performing the operations to conform with the natural chronology (in which, for example, compensation of Cycle I eggs may occur in the same calendar year as extrapensatory mortality of Cycle III and IV fish at sea). Copies of the computer program (Fortran II) are available from the University of British Columbia Computing Center.

TABLE 21 - (A) Age composition produced by six annual spawning populations of Adams River sockeye, as based on analyses of scale samples collected from spawning populations in subsequent years. (B) Coefficients indicating the average proportion of adults produced from previous spawnings which contribute to the adult run in year n (arranged by cycle and averaged).

A

BROOD YEAR	TOTAL POPULATION	PER CENT CONTRIBUTION				
		4_2	3_2	5_2	5_3	4_3
1950	2,263,400	90.22	9.62	0.03	0.11	0.02
1951	66,300	89.76	8.81	1.34	0.08	0
1952	7,000	87.10	10.65	2.25	0	0
1953	3,800	69.60	30.40	0	0	0
1954	3,621,600	91.26	8.41	0.05	0.25	0.02
1955	131,500	93.87	5.89	0.20	0.05	0

B

CYCLE	CONTRIBUTION COEFFICIENTS		
	$n-3^1$	$n-4$	$n-5$
I	0.0018	0.9076	0.0022
II	0.0014	0.9181	0.0084
III	0.0021	0.8710	0.0225
IV	0.0061	0.6960	0.0000

¹Per cent contributions of 3_2 fish present 3 years previously were multiplied by 0.02 to adjust for unequal sex ratio of jacks and the reduced egg content of female jacks. These adjusted values were averaged.

The results of several series of computations confirm that mechanisms of the type postulated could produce sequences of adult runs which simulate the dominance pattern of the Adams River stock. The results of one such series is shown in TABLE 22. Using initial populations of 0.001 stock units (W) for Cycles II, III and IV and 0.01 for Cycle I, the small initial disparity was rapidly magnified so that within four generations of each cycle a pattern of dominance was attained. This pattern persisted for at least 30 generations (120 years). The S coefficient used to compute data in TABLE 22 was 0.15 and k_1 , k_2 and k_3 each equalled 4.0.

The output shown shows characteristics of dominance but does not closely resemble the actual numerical relationship between the Adams River cycles. The Cycle I average computed population¹ (catch plus escapement) shown in TABLE 22 is too low. This is certainly true for Cycle II and III as well. The actual average Cycle II population is approximately one-tenth as large as the average Cycle I population but the simulated population was less than one-hundredth the size of the actual Cycle II average. Simulated Cycle IV populations shown in TABLE 22 are about 98 per cent jacks, as is actually the case. The average computed populations shown were calculated from generations 4 to 30 inclusive for Cycles I, II and IV and from 5 to 30 for Cycle III: a stable situation apparently pertained during these generations (TABLE 22).

Closer approximations to the observed ratio of dominant to subdominant runs were obtained in some "segments" of computer runs using other values of S and k. For instance with $S = 0.30$ and $k_1 = k_2 = k_3 = 5.0$, the

¹ Stock units were converted to numbers of fish on the assumption that maximum reproduction of Adams River sockeye occurred from spawning populations of 1.5 million. With $a_1 = 2$, 1.5 million = 0.361 stock units.

TABLE 22 - Output from a computer run (Fortran II program) in which $S = 0.15$
 $k_1 = k_2 = k_3 = 4.0$. Values are simulations of annual adult populations of all
ages (see text).

GENERA- TION	CYCLE							
	I		II		III		IV	
	Stock Units	No. Fish	Stock Units	No. Fish	Stock Units	No. Fish	Stock Units	No. Fish
0	0.01000	41,550	0.00100	4,155	.00100	4,155	.00100	4,155
1	0.00914	37,977	0.00104	4,321	.00118	4,903	.00371	15,415
2	0.03065	127,351	0.00396	16,454	.00819	34,029	.02284	94,900
3	0.21366	887,757	0.00938	38,974	.01888	78,446	.06188	257,111
4	0.59734	2,481,948	0.00859	35,691	.01351	56,134	.19069	792,317
5	1.89669	7,880,747	0.00468	19,445	.00002	83	.16266	675,852
6	1.64029	6,815,405	0.00407	16,911	.00000	0	.11847	492,243
7	1.19473	4,964,103	0.00337	14,002	.00001	42	.07044	292,678
8	0.71026	2,951,130	0.00262	10,886	.00017	706	.17357	721,183
9	1.74672	7,257,622	0.00425	17,659	.00000	0	.07694	319,686
10	0.77584	3,223,615	0.00340	14,127	.00007	291	.15878	659,731
11	1.59983	6,647,294	0.00400	16,620	.00000	0	.06766	281,127
12	0.68238	2,835,289	0.00354	14,709	.00026	1,080	.21382	888,422
13	2.15071	8,936,200	0.00524	21,772	.00000	0	.05701	236,877
14	0.57511	2,389,582	0.00327	13,589	.00016	665	.23356	970,442
15	2.35205	9,772,768	0.00572	23,767	.00000	0	.05962	247,721
16	0.60191	2,500,936	0.00989	41,093	.00026	1,080	.04824	200,437
17	0.48468	2,013,845	0.03224	133,957	.00064	2,659	.10917	453,601
18	1.09601	4,553,922	0.02997	124,525	.00036	11,496	.08313	345,405
19	0.83857	3,484,258	0.03085	128,182	.00043	1,787	.05599	232,638
20	0.56368	2,342,090	0.02681	111,396	.00060	2,493	.14385	597,697
21	1.44660	6,010,623	0.00523	21,731	.00004	166	.09137	379,642
22	0.92108	3,827,087	0.00312	12,964	.00009	374	.06263	260,228
23	0.63000	2,617,650	0.00589	24,473	.00045	1,870	.10053	417,702
24	1.00470	4,174,529	0.00481	19,986	.00013	540	.13049	542,186
25	1.31336	5,457,011	0.00349	14,501	.00001	42	.04562	189,551
26	0.45992	1,910,968	0.00309	12,839	.00042	1,745	.15926	661,725
27	1.59673	6,634,413	0.00391	16,246	.00000	0	.05284	219,550
28	0.53288	2,214,116	0.00373	15,498	.00022	914	.12973	539,028
29	1.30367	5,416,749	0.00353	14,667	.00003	125	.17161	713,040
30	1.72989	7,187,693	0.00422	17,534	.00000	0	.09917	412,051
Average Adult Population		4,685,244		34,399		698		471,954

subdominant run from the 13th to the 21st generations (a "span" of 32 years) averaged 249,000 fish while the dominant averaged 4,444,000. However this system subsequently failed to show stable dominance, the subdominant run eventually assuming equal status with the dominant. The example serves primarily to illustrate the consequences of a certain sequence of random normal deviates (climatic conditions) on this model of dominance, rather than suggesting that the natural situation might change to one in which there were two large runs of dominant status. In general, Cycle II populations in the computer simulation could not be held stable anywhere near the observed natural level without escaping the effects of depensation and, consequently, reaching the Cycle I level of stable abundance. Modifications designed to get a better simulation of the actual relationship would be based more on mathematical requirements than on knowledge of the population dynamics of the species; therefore model changes would seem unwarranted until more is known concerning the biology of Adams River sockeye.

Even with its obvious limitations the model has produced useful results. First, as stated above, the model, based on a rather simple set of hypotheses, does produce stable dominance of the same general pattern exhibited by Adams River sockeye populations. Second, dominance of an extreme type was established within a relatively short time; (four generations) as apparently occurred in nature. Third, it became obvious from the results of the various computer runs that dominance could not be maintained for more than a generation or two without depensation. The effects of compensation and the effects of fortuitous random deviates soon brought small populations up to high levels of abundance.

Computer runs also indicated that depensation must be heavy on all the off years in addition to the subdominant if the simulated dominance is to remain stable. For instance if the third depensation coefficient (k_3) is small (less than 2) the system does not produce stable dominance, the run on Cycle IV assuming equal status with Cycle I. If the model simulates the natural mechanism, this characteristic supports the previously stated contention that the effects of gravel conditioning by Cycle I or the effects of disease resulting from contamination of the gravel by Cycle I dead eggs could not produce quadrennial dominance.

The possibilities for manipulating variables are virtually endless, and the form of the model would allow for theoretical simulation of a wide range of circumstances for different stocks of sockeye salmon. From the viewpoint of the Adams stock, even a limited number of computer runs indicate that an age distribution with a great preponderance (90%) of spawners returning at age IV is a prerequisite to quadrennial dominance. If the age distribution is changed to 59 per cent four-year-olds, 39 per cent five-year-olds and 2 per cent jacks, dominance disappears. It is also evident that rather large depensation coefficients are necessary to keep the subdominant run from becoming "dominant" also (the effects of the fisheries may be paramount under the present regime in maintaining the subdominant cycle at its current low level). Cycles III and IV suffer depensation occasioned by the previous dominant and subdominant runs and pose no threat to the stability of the existing order. However, and thirdly, a measurable buffering effect or lower depensation rate is necessary to prevent the subdominant sinking to the same low levels as the

other off years. If the model as presented is even approximately representative of the natural situation, the explanation for the observed sequence of runs of the Adams stock is more a matter of accounting for the subdominant run, than for the phenomenon of stable dominance.

Implications for Management

The explanation proposed in this paper for the phenomenon of cyclic dominance is depensatory predation. However, any theories concerning predator control, which might seem a corollary for management, must be tempered by various considerations. A program for control of all of the predators in a lake the size of Shuswap is virtually futile from the beginning. For example, an intensive effort at predator control at Cultus Lake (Foerster and Ricker, 1941), a small lake, although providing the sockeye with initial benefits, did not result in major decreases in predator abundance or in maintained increases in sockeye survival. A predator control program, even if successful, would certainly have other consequences beyond the immediate relief from predation for salmon. For instance, others of the twenty or so species of fish which occur in the lake, including kokanee might assume much greater significance as competitors. Briefly, a large scale predator control effort might set in motion a series of consequences that would not necessarily mean greater production of sockeye salmon.

Another theoretical approach to increasing catches is to raise fry production to levels above those controlled by depensation. Smolt populations and adult populations would then increase to the Cycle I level.

Gradual increases would not be successful. Each increment would quickly be eliminated by depensation, reducing smolt production to its former average level. Artificial methods of fry propagation could not produce enough additional fish to enable a small natural population to escape the limitations of depensation in one generation. Similarly, regulation of the fisheries to allow complete escapement of a Cycle III or a Cycle IV population would be unlikely to produce the desired result since fry production, even from total adult populations, would be too low.

The tendency for model simulated Cycle II populations to increase in size sufficiently to escape depensation indicates that under present conditions the effects of the fisheries may be largely responsible for maintaining natural Cycle II populations at the observed abundance level. Closure of the fisheries to allow all the adults of a Cycle II population to reach the spawning grounds might result in a fry population large enough to escape intense depensation. The immediate effect would probably be a large catch four years later but the stability of the resultant system is not known. The long-term effect might be that predator populations would be increased perhaps to the point that the offspring from a small dominant population could be seriously reduced in numbers by predation, thus returning the stock to some pattern resembling the initial dominant-subdominant situation.

This possibility seems to be supported by historical evidence. Before the development of a commercial fishery a dominant-subdominant pattern existed in the sockeye stocks of the Shuswap district (TABLE 4). Probably the cycles would return to this basic pattern following any disruption but

an intervening period of lowered production might occur (as was the case during the 1917-1930 period). In this event, it is unlikely that any major long-term gain in production could be achieved by allowing a complete subdominant escapement. Conversely, serious economic consequences would certainly result from even a brief period of low Adams River stock quadrennial catch.

Evidently, it is undesirable with the present understanding of the factors involved, to risk upsetting the existing pattern of dominance exhibited by Adams River sockeye. The current procedure of maintaining usual fishing mortalities on Cycle II adult populations is appropriate and should be continued.

SUMMARY

The occurrence of regular quadrennial fluctuations in the abundance of Fraser River sockeye salmon is of great economic importance. At present, these fluctuations are caused by regular variations in the abundance of one stock of Fraser River sockeye salmon, the Adams River stock.

The phenomenon of cyclic dominance has occurred among stocks of Fraser sockeye for many years. Information recorded prior to the establishment of a commercial fishery indicates that large populations occurred quadrennially in several stocks, one of which was the Adams. After the development of an intense fishery the dominance pattern was extreme. Between 1911 and 1913 obstructions to the migration of adults apparently caused the destruction of the original dominance pattern. Dominance again became established in the late-spawning Adams stock after 1926. This stock was now dominant on a different sequence of years, the 1926-1930 cycle. Prior to 1913 the dominant sequence had been 1901-1905.

Other stocks of Fraser River sockeye have population structures suggesting quadrennial dominance. With the possible exception of the Chilko stock, these runs have only recently (since the functioning of the Hell's Gate Fishways in 1945) increased in abundance following a long period of scarcity. Although insufficient time has elapsed for stable dominance to become established in some stocks, all major upper Fraser stocks have one annual series of populations, which on the average is more numerous than any of the other three series.

The observed stability of the annual populations of Adams River sockeye seems unlikely in the absence of maintaining agents. Compensatory mortalities acting during the spawning-incubation period would tend to increase small populations to the level of dominant populations. Other stocks of Fraser River sockeye have reacted quickly to the removal of mortalities limiting their abundance. The present dominant population, starting from a low level of abundance, achieved its present pre-eminent position within a relatively short time. In a much longer period off year populations have not increased. It was concluded that active stabilizing influences exist.

Inherent differences in reproductive potential were unlikely to be the active maintaining agents. Unequal sex ratios, differential egg retention, cyclic differences in the number of eggs per female did not indicate differences in the reproductive performance of the four cycles.

Total mortality coefficients from generation to generation were on the average equal for all four cycles since dominance is relatively stable. Therefore, for dominance to be maintained, Cycles II, III and IV, by

comparison with Cycle I, must be affected by compensatory mortalities. If not small populations would increase.

Mortalities affecting sockeye during the spawning-incubation stage in life-history are believed to be of the compensatory type, favoring increases in small populations. In the marine and adult stages the overall effect of mortalities seems to be independent of population size (extrapensatory). There was no direct evidence pertaining to the type of mortalities occurring during the lacustrine stage. Other evidence indicated that neither the spawning grounds nor the ocean were likely sites for dominance maintaining agents to be effective. Mixing of stocks at sea occurs; therefore it is difficult to believe that one stock could be differentially affected in the required manner. Since dominance existed prior to the development of an intense fishery, fishing mortality is unlikely to be the primary maintaining agent. The lacustrine stage seems the most likely site for mortalities to have a compensatory effect because stocks could be differentially affected by mortalities during this stage. Evidence was also presented, indicating that when two stocks interacted during the lacustrine stage, they had the same pattern of population fluctuations (Adams and Seymour stocks).

Smolts belonging to Cycles II, III and IV populations were larger than those belonging to Cycle I, indicating that their lacustrine growth rate was higher and their survival potential at least as good. High mortality rates occurring early in lacustrine life from interactions between seaward migrating smolts and newly emerged fry were not considered to be likely maintaining agents. In this situation a biennial rather than

a quadrennial cycle might be probable. Variations in indices of zooplankton abundance indicated that, during lacustrine life, dominant populations may have reduced zooplankton abundance, presumably by cropping, but there was no serious hold-over effect. Fluctuations in food availability were not an obvious cause for the dominance phenomenon.

Although the growth of kokanee varied relative to the lacustrine population density of Adams sockeye, there was no evidence from indices of kokanee abundance that kokanee had any effect on sockeye growth or survival.

The non-anadromous offspring of sockeye (residuals) were not abundant in Shuswap Lake and were, therefore, not likely to influence either sockeye growth or survival.

It was concluded that differential mortalities resulting from competition were unlikely to be effective dominance maintaining agents.

Analyses of the stomach contents of rainbow trout showed that they depend to a significant degree on juvenile sockeye as a food source. When sockeye were scarce, the average stomach content volume of rainbow trout captured in the western area of Shuswap Lake was below the usual value. When sockeye were scarce, they were only partially replaced in the diet of trout by other foods. Furthermore, the fish component in the diet of trout was related to the abundance of juvenile sockeye.

Rainbow trout captured in the vicinity of the mouth of Adams River in Shuswap Lake were heavier at given lengths in years when sockeye as a source of food were abundant. When annual samples were divided into seasonal subsamples, rainbow trout at given lengths were heavier when dominant populations were present in the area. These computed weights declined rapidly after sockeye smolts of dominant broods migrated from Shuswap Lake to the sea.

Deviations in computed weights of rainbow trout captured in other parts of Shuswap Lake were not so clearly related to the availability of sockeye as food as were deviations occurring in samples from the Adams River area.

Abundant food in the form of Cycle I juveniles may elicit a numerical response by increasing survival of salmon predators. Predators may be more abundant than they would be in the absence of dominant sockeye populations, thus predation on Cycle II, III and IV populations may be relatively heavy. A mechanism of this kind would increase the probability for depensation occurring and it would tend to be self-regulating because the predator population would be limited by mortality occurring during the two years when sockeye are scarce.

Indirect evidence for the occurrence of depensation was available from the relationship between estimates of sockeye biomasses present during spring and summer periods and estimates of the rate of rainbow trout predation. The relationships were asymptotic, indicating that the rate of predation declined relative to increasing prey density. This situation results in depensation.

Based on previously presented evidence and data concerning the population dynamics of Adams River sockeye, a model was formulated for the purpose of simulating relationships between parental and filial abundance. In this model, stages in sockeye life-history were described by individual "reproduction curves". Output from one stage was used as the input for the next stage so that final outputs from various parental populations could be determined. Two curves apply to the life-history of Adams sockeye. The first stage in the life-history was depicted by a

compensation curve and the second by a depensation curve. Mortalities in remaining stages were independent of population density. The output from the first stage was modified by a simulation of the effects of climatic conditions independent of population density, multiplying or dividing by random normal deviates to produce a maximum twofold spread between highest and lowest values.

The intensity of depensation occurring during lacustrine life was related to the abundance of sockeye present in previous years and to the "buffering effect" provided by smolts to fry. The effects of these factors were incorporated into the depensation stage. Output from depensation was modified by multiplication and division by random normal deviates producing a maximum fivefold variation in production thus simulating the mortalities of later stages in the life-history.

A computer program based on the model was written and tested using age composition data appropriate for the Adams stock. The results of computations confirmed that mechanisms of the type postulated could produce sequences of adult populations which simulate the dominance pattern in Adams River sockeye. Although the results did not entirely duplicate the natural phenomenon it was felt that attempts to improve the simulation would be unwarranted until additional knowledge is available.

The computer results showed that a model formulated from rather simple hypotheses can produce a fair simulation of the dominance phenomenon, in which dominance would be established rapidly, and in which dominance would soon be eliminated in the absence of depensation. Quadrennial dominance in Adams River sockeye requires that a great preponderance of spawners return at age IV.

Removal of predators in Shuswap Lake is not a practical method for increasing off year catches. Long term results of predator removals cannot be predicted. The most promising method for increasing average production would seem to be by increasing the abundance of Cycle II sockeye. This might be done by limiting catches made on a Cycle II population thus providing a large escapement. The resultant fry output might be great enough to escape the effects of depensation. Such a procedure is presently unwarranted because long-term effects cannot be predicted and, on the basis of historical evidence, might be unfavorable.

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