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FACTORS IN THE POPULATION BIOLOGY OF THE SOCKEYE SALMON OF THE SKEENA RIVER

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INTRODUCTION

The Skeena River system is currently the third largest producer of sockeye salmon (*Oncorhynchus nerka* (Walbaum)) in British Columbia, Canada. The mixture of sockeye stocks comprising the annual 'run' has supported an intensive commercial fishery for nearly 60 years, over which period the average yield to the fishery has been about 881 000 fish. Fishing for sockeye is traditionally with gill-nets operated in the river mouth and seaward for a distance of roughly 20 miles. The catch is largely 4- and 5-year-old fish that went to sea in their second year (4_2s and 5_2s), although other age groups are represented.

The individual stocks of the Skeena River run are produced in twenty-one lakes and associated tributary streams located throughout the drainage. By far the largest and most important of these is the Babine Lake watershed, which currently provides the spawning area of about 90% or more of the total that escape from the fishery.

Past studies demonstrate or suggest the following main features of the population biology of the Skeena stocks.

(1) Decrease in size of the run. The sockeye catch declined gradually from an average level in excess of one million fish in early years to about half a million in recent years.

(2) Change in the relative abundance of the stocks. The decline of non-Babine Lake stocks has been relatively faster than that of Skeena River sockeye generally.

(3) Relation of number of parents to number of progeny. Shepard & Withler (1958) and Shepard *et al.* (1964), describe for Skeena sockeye of ages 4_2 and 5_2 a reproduction curve with an almost linear ascending limb and a very precipitous descending limb generally after the Ricker type (Ricker 1954).

(4) Inheritance of age of return. Sockeye salmon die after spawning and therefore correlations between the age of the parents and the age at which their progeny spawn have particular significance. There is a positive correlation between age of parents and the age of return of their progeny (Milne 1955; Godfrey 1958).

(5) 'Cyclical' changes in brood success. Both 5-year and 4-year 'cycles' of highly successful broods have been apparent in past years (Godfrey 1958). An initial 5-year cycle was followed by a shift to a 4-year cycle.

The purpose of this paper is threefold: (1) to examine these features of the population biology of Skeena River sockeye; (2) to indicate factors that may have contributed to influencing the population changes; and (3) to assess, with a computer simulation, whether a synthesis of the contributing factors provides an explanation for the observed history of the population.

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As background to this analysis, the first two sections of the paper outline the salient features of the Skeena River and its sockeye salmon population.

THE SKEENA RIVER AS A SOCKEYE ENVIRONMENT

(1) *Description of sockeye-producing areas*

The Skeena River drainage covers an area of roughly 19 000 square miles lying in the west–central portion of British Columbia between 54° and 57° north latitude (see Fig. 1). The climate varies from the moderate temperatures and heavy precipitation of the coast to the more extreme temperature and light precipitation of the interior plateau. (See Brett (1951) for a more detailed description of geography and climate.)

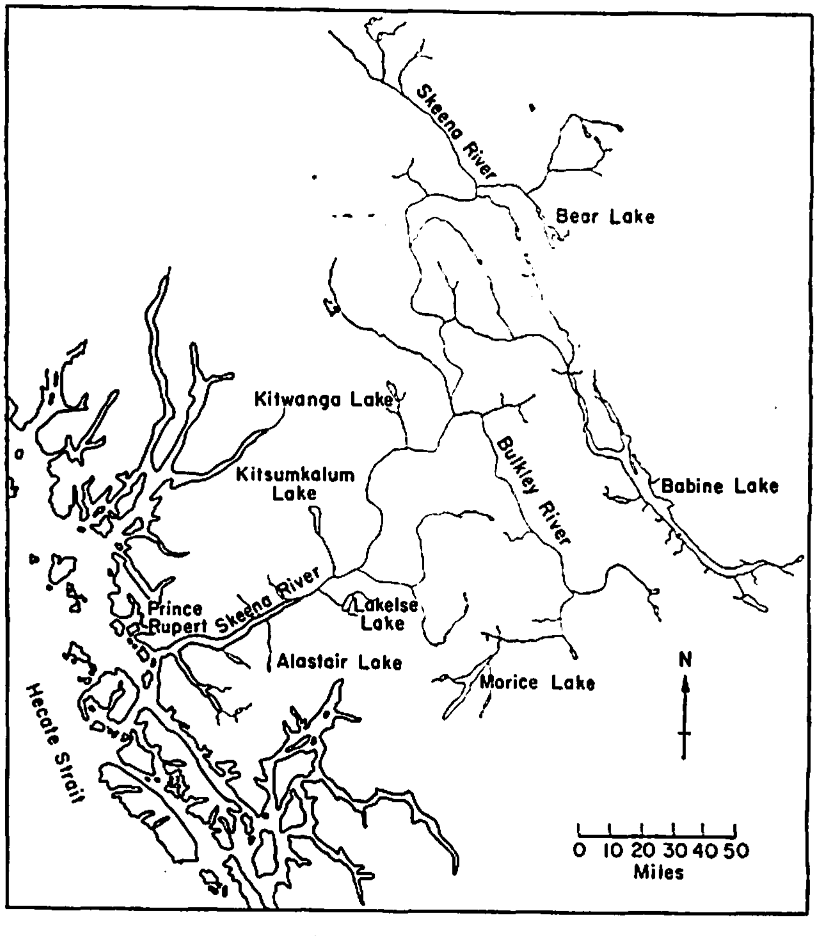

FIG. 1. Skeena River drainage showing sockeye-producing lakes.

Throughout the drainage there are twenty-one lakes which, together with their associated spawning areas, produce sockeye. Brett (1952) provides a general description of many of these lakes and their tributary streams. Further detail has been reported by Brett (1946), McConnell & Brett (1946), Brett & Pritchard (1946 a, b), Foskett (1947 a, b), Withler (1948) and Withler, McConnell & McMahon (1949).

Babine Lake is by far the largest in the Skeena River system, with a surface area of about 186 square miles. The principal spawning grounds are the outflowing Babine River near the lake outlet and the Fulton River, which empties into the central portion of the lake. Sockeye also spawn in accessible portions of all tributary streams, most of which are located in the central and southern parts of the lake basin.

Morice Lake is the only lake of importance in the Bulkley River system—the largest Skeena tributary. It has an area of about 37 square miles (second in size to Babine Lake), and the Nanika River is the principal tributary and spawning ground.

The remaining sockeye-producing lakes are relatively small, each less than 20 square miles in area, and are located throughout the Skeena River drainage from tidewater to as far as 400 miles upstream. Sockeye spawn in their tributary streams or in some instances in the lakes themselves. Lakelse, Bear, Alastair, Kitwanga and Kitsumkalum Lakes are the largest and the most important producers in this group of smaller lakes.

(2) *Life history of the sockeye stocks*

Skeena sockeye return from the sea, spawn and die in either their third, fourth, fifth or sixth year. The fertilized eggs are deposited in the gravel of a stream bed or lake bottom in the late summer or autumn. The young remain in the gravel until the following spring when they emerge to take up lake residence. Seaward migration occurs in the spring, either 1 or 2 years later. Return to freshwater as adult fish takes place after 1–3 years at sea.

The age of the adult and the age at which the fish migrated to sea can be read from scale and/or otolith patterns. Common practice is to divide sockeye into age groups on the basis of age of returning adult (from time of egg fertilization) and age of seaward migration. For Skeena sockeye there are five principal groups. These are:

(a) 3_2s (invariably males), which migrate to sea in their second year and mature in their third,

(b) 4_2s and 5_2s, which migrate to sea in their second year and mature at 4 or 5 years of age, and

(c) 5_3s and 6_3s, which migrate to sea in their third year and mature at 5 or 6 years of age

Table 1. *Percentage age composition of the Skeena River sockeye catch by 10-year periods*, 1912–61

Period	% by age group					Average annual catch (pieces)
	4_2	5_2	5_3	6_3	Other	
1912–21	41·4	47·2	7·6	3·9	0	1 137 951
1922–31	53·5	35·0	9·4	2·1	0	1 232 649
1932–41	57·8	29·7	9·5	3·0	0	801 688
1942–51	34·6	54·7	7·2	3·5	<0·1	733 514
1952–61	57·4	35·0	5·0	2·6	<0·1	497 913

Most Skeena sockeye return at 4 and 5 years of age, after a marine sojourn in the central portion of the Gulf of Alaska. Table 1 provides estimates of the numbers and proportions of each age group in the commercial catch for 10-year periods from 1912 to 1961. Estimates are based on samples taken usually weekly throughout each fishing season. Values for 4_2 and 5_2 fish are from Shepard & Withler (1958) and Shepard *et al.* (1964). Values for other age groups were calculated on a comparable basis.

Because the catch is made almost entirely by gill-nets, and some selection for size and therefore age of fish occurs (see later section), the age composition of the catch cannot be considered representative of the age composition of the total run (catch plus escapement). This is especially true in respect to 3_2s, which, because of their small size, are largely unharvested by the commercial nets. Differential selection of the older age groups is less severe but nevertheless substantial, the 5- and 6-year olds being harvested at greater rates than 4s. The catch data are nevertheless useful in indicating any substantial change in relative abundance of the different ages over the years.

Throughout the period 1912–61, the Skeena run has comprised largely 4_2 and 5_2 sockeye, which made up 89% of the catch, with sub 3 fish (i.e. those migrating to sea in their third year) (5_3s and 6_3s) most of the balance. The 4s (4_2s) and 5s (5_2+5_3) have contributed equally to the catch (48·44 and 48·54% respectively). Sub 2s ($4_2+5_2+6_2$) were 88·93% of the total; sub 3s (5_3+6_3) were 11·07%. There was considerable variation in the proportions of 4s and 5s over the five decades, the 4_2s ranging from 34·6 to 57·8% and the 5_2s from 29·7 to 54·7%. The proportion of sub 3s was more consistent for the first 40 years (10·7–12·5%) but dropped to 7·6% in the last 10 years.

The age compositions of individual stocks are summarized in Table 2. These data are available from scale and otolith samples taken from fish either on, or en route to, specific spawning areas. The Babine stock is almost entirely composed of 4_2 and 5_2 sockeye. Non-Babine stocks taken as a group are the main contributors of 6-year-olds and of the sub 3 age groups.

MAIN FEATURES OF POPULATION BIOLOGY

(1) *Decline in size of run*

The decrease in the total run of sockeye to the Skeena River was gradual throughout the period 1910–48 (Milne 1955). The trend line suggested a decline in catch to about 50% of that in early years. More recently, the catch has levelled off at about 500 000 sockeye per year, although this average reflects the effect of a landslide into the Babine River on the spawning runs of 1951 and 1952 (Godfrey *et al.* 1954), and subsequent changes in fishing regulations designed to restore the affected stocks. Additionally, regulation of the fishery in recent years has aimed at providing better chances of escaping, and catches have been accordingly reduced during the period of rehabilitation (see later section on overexploitation by the commercial fishery). Despite these qualifications, there is evident a persistent decline in abundance of sockeye stocks from the historic levels of the early part of the century when catches averaged in excess of a million fish.

Fig. 2 indicates the changes in abundance from 1908 to 1964 based on the analyses of Shepard & Withler (1958) and Shepard *et al.* (1964). There are sharp fluctuations in annual abundance, but in making interpretations we should keep in mind the peculiarities of salmon life history. The abundance in each year is the sum of the 4s produced by the brood of 4 years previous and the 5s of 5 years previous. There is thus *a priori* reason for supposing that any recurrent peaks of abundance at regular 4- or 5-year intervals would be related to age composition. In the early series of years there are peaks of abundance in the years 1910–14–19–24–30. There is a further group of peaks in 1940–45–48–52. Abundance after 1952 reflects in part the effects of the landslide on the Babine River and regulatory measures. Typical, then, of the Skeena sockeye abundance is a rather erratic fluctuation with major peaks at intervals of between 3 and 5 years. Because of the dependence of the peaks on the success of the various brood years it is useful to rearrange the data according to brood year success, which is done in a later section.

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Table 2. *Age composition of Skeena River sockeye stocks*

Stock	No. of years of sampling	Total no. sampled	Mean proportions by age groups							4_2+5_2	5_3+6_3	Sub 2s	Sub 3s
			3_2	4_2	5_2	6_2	5_3	6_3	Other				
Babine Lake	9	2045	1·7	45·7	49·1	1·6	0·7	1·1	0·1	94·8	1·8	98·0	1·8
Morice Lake	9	2456	0·5	11·0	17·6	0·4	44·9	25·5	0·7	28·6	70·4	29·5	70·5
Lakelse Lake	8	1671	0·1	21·0	76·2	0·1	0	2·5	0	97·3	2·5	97·5	2·5
Bear Lake	4	97	–	–	–	–	–	–	–	–	–	100·0	0
	4	193	0	40·9	59·1	0	0	0	0	100·0	0	100·0	0
Alastair Lake	3	61	–	–	–	–	–	–	–	–	–	64·2	35·8
	1	39	0	2·6	5·1	0	87·2	5·1	0	7·7	92·3	7·7	92·3
Kitwanga Lake	1	45	–	–	–	–	–	–	–	–	–	84·5	15·5
Sustut Lake	2	22	–	–	–	–	–	–	–	–	–	90·0	10·0
	1	90	0	24·4	44·5	1·1	16·7	13·3	0	68·9	30·0	70·0	30·0
Johanson Lake	1	10	–	–	–	–	–	–	–	–	–	90·0	10·0
	1	35	0	0	0	0	31·4	65·7	2·9	0	0	0	97·1
Asitka Lake	1	7	–	–	–	–	–	–	–	–	–	85·7	14·3
Stephens and	3	11	–	–	–	–	–	–	–	–	–	83·4	16·6
Swan Lakes	1	6	0	100·0	0	0	0	0	0	100·0	0	100·0	0

(2) *Change in relative abundance of the stocks*

The Babine Lake stock consists almost entirely of sub 2 ($4_2 + 5_2$) sockeye while non-Babine stocks contain substantial proportions of sub 3s ($5_3 + 6_3$). Any large change in relative abundance of the two stocks would thus be reflected in the abundance of the two fresh-water age groups.

Estimates of the annual number of spawners to individual sockeye-producing areas are available after 1946 (Brett 1952, and Canada Department of Fisheries file reports). Figures for Babine Lake in all years except 1948 are from counts at a fish fence. Estimates for other areas are much less precise but are considered adequate to reveal substantial changes in abundance. From 1946 to 1963 the average total Skeena escapement has remained at a fairly stable level between nearly 500 000 and 650 000 spawners (Fig. 3), but Babine Lake escapement has increased both in numbers and in proportion. During the 1946–48 period the Babine escapement averaged 427 000—about 70% of the total. In the most recent period, average escapement was 600 000 or 93% of the total. A corresponding decrease occurred in escapement levels to non-Babine lakes, which seems to be paralleled by a decrease in occurrence of sub 3 sockeye in the catch. (From Table 1, sub 3 fish were 10·7% in 1942–51; 7·6% in 1952–61.) Evidently, non-Babine stocks are at low levels of production by comparison with those of Babine Lake.

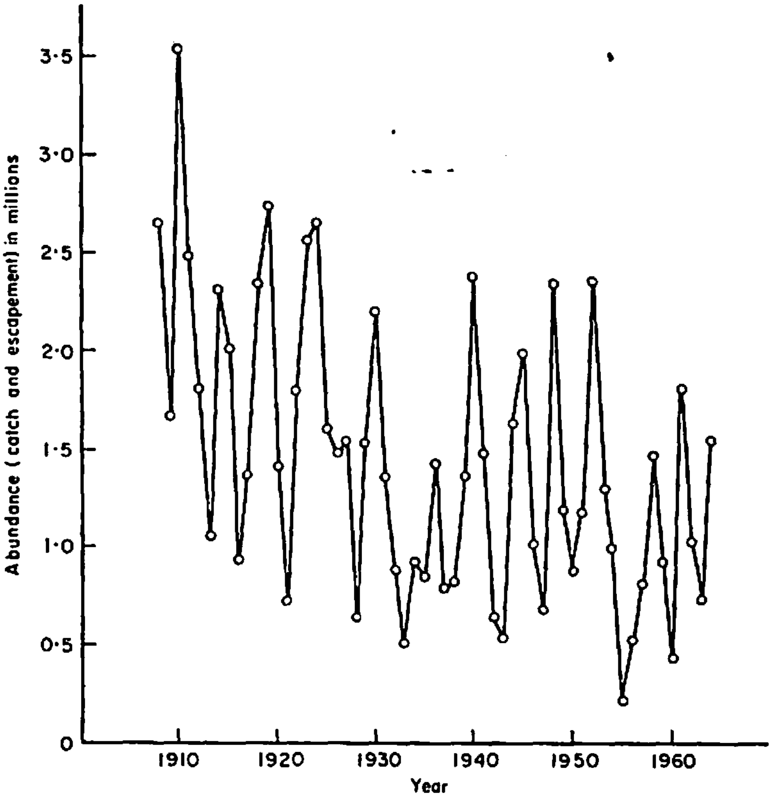

FIG. 2. Abundance of Skeena River sockeye salmon from 1908 to 1964, based on estimates provided by Shepard & Withler (1958) and Shepard *et al.* (1964).

(3) *Relation of number of parents to number of progeny*

The relation between spawning stock size and resultant yield for sub 2 Skeena sockeye has been described by Shepard & Withler (1958) and Shepard *et al.* (1964). Addition of sub 3 fish does not materially influence the shape of the curve for the sub 2s (Fig. 4). The wide variability is perhaps in part contributed by errors in estimation as well as a variety of factors influencing abundance, but additionally the Skeena stock comprise several races and the resultant curve is composite (Anon. 1962). The empirical curve based on running means shows a sinuous left-hand limb with a rate of return that is almost constant over a wide range of stock sizes. The abrupt descent of the right limb is perhaps in part an artifact of the smoothing procedures. Unless the stock is increasing indefinitely in size, it is statistically inevitable in a given series of observations that the largest escapements should be associated with returns that were smaller (the rate of exploitation is relatively constant). Extension of the right limb to suggest decreasing

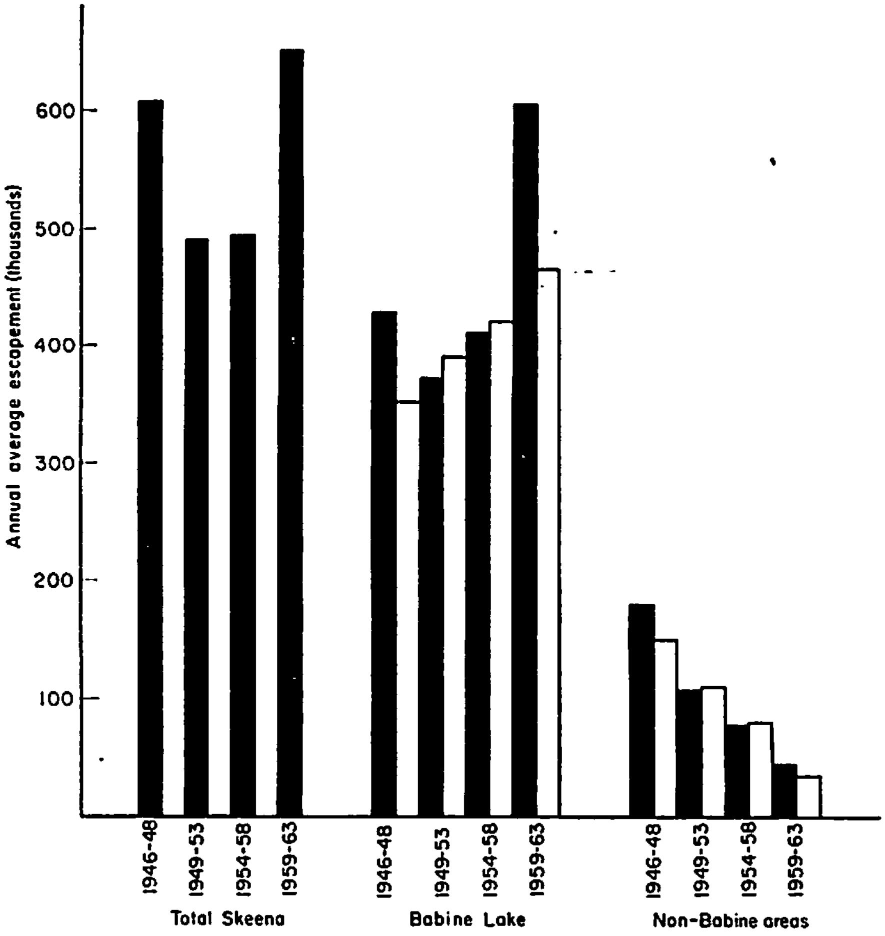

FIG. 3. Annual average spawning escapements (■) for 1946–48 and succeeding 5-year periods for Babine Lake, non-Babine areas, and the proportions each contributed to the total (□).

return with increased stock size beyond 1·25 stock units would certainly not seem justified.

Because the Skeena population is made up of the two groups, Babine and non-Babine, several attempts were made to devise two component Ricker-type reproduction curves which in combination would give the stock-recruit relation of Fig. 4 (modified to include sub 3s). Algebraically, the objective is to fit to the points of Fig. 4, a 'least-squares' line described by

$$Z = A_1 w_1 e^{a_1(1-w_1)} + A_2 w_2 e^{a_2(1-w_2)}$$

where Z is the production of progeny arising from w_i parents, where a_1 and a_2 are the 'compensation coefficients' for the two stocks and A_1 and A_2 are coefficients for converting the stock sizes into population sizes.

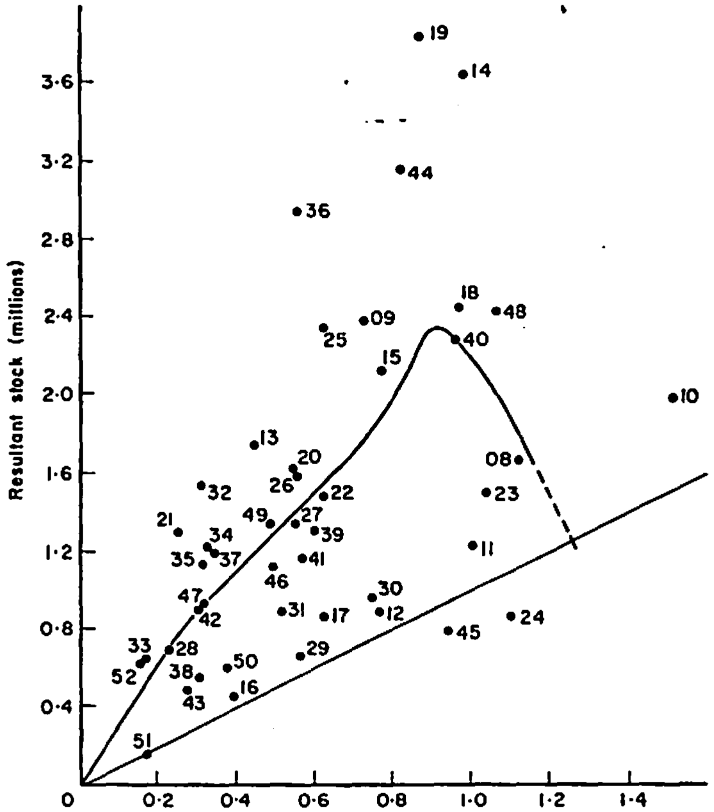

FIG. 4. Numbers of 4_2 and 5_2 Skeena sockeye (catch + escapement) plotted against numbers of parent spawners. Figures in the body of the graph indicate brood years. (From Shepard & Withler 1958.)

With the wide variability, several combinations of two Ricker-type reproduction curves seemed almost equally compatible with the empirical stock-recruit relation, even with the restriction that the Babine stock should have a replacement level of population size approximately twice that of the non-Babine stock ($A_1 \approx 2A_2$). Moreover, it seemed difficult to reconcile the observed returns in the lower ranges of stock sizes, which imply compensation coefficients of less than 2·0 for either stock, with the high returns at stock sizes of tainly not seem

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0·8–1·0 million spawners, that suggest a coefficient at least for the Babine stock in excess of 2·75. If it is assumed that the rates of exploitation were somewhat higher than has been estimated during the years from 1918 to 1928, some of the returns from the large stock sizes would be modified in such a way as to suggest that the compensation coefficient could be about 1·75 for the Babine stock.

(4) *Inheritance of age of return*

The empirical relation between the proportion of 4s in a brood year and the proportion of 4s in the progeny of the brood is shown in Fig. 5 and Table 3. The correlations presented by Milne (1955) and Godfrey (1958) provide evidence that to some degree the age of return of sockeye salmon is related to the age of their parents at spawning. However, the correlation coefficients which Godfrey calculated, while significant, were relatively small ($\log_{10}$ of catches of parents of age 4 and $\log_{10}$ of catches of progeny of age 4, $r = 0{\cdot}39$. $0{\cdot}01 < P < 0{\cdot}05$, similarly for age 5, $r = 0{\cdot}60$, $P < 0{\cdot}01$). With the differential selection of 5-year-olds by gill-nets, these correlations in catch figures might be misleading. Assuming that the selection in favour of 5s is at the rate of 1·5 to 1, the proportions of 4s and 5s in the escapement estimates of Shepard & Withler (1958) may

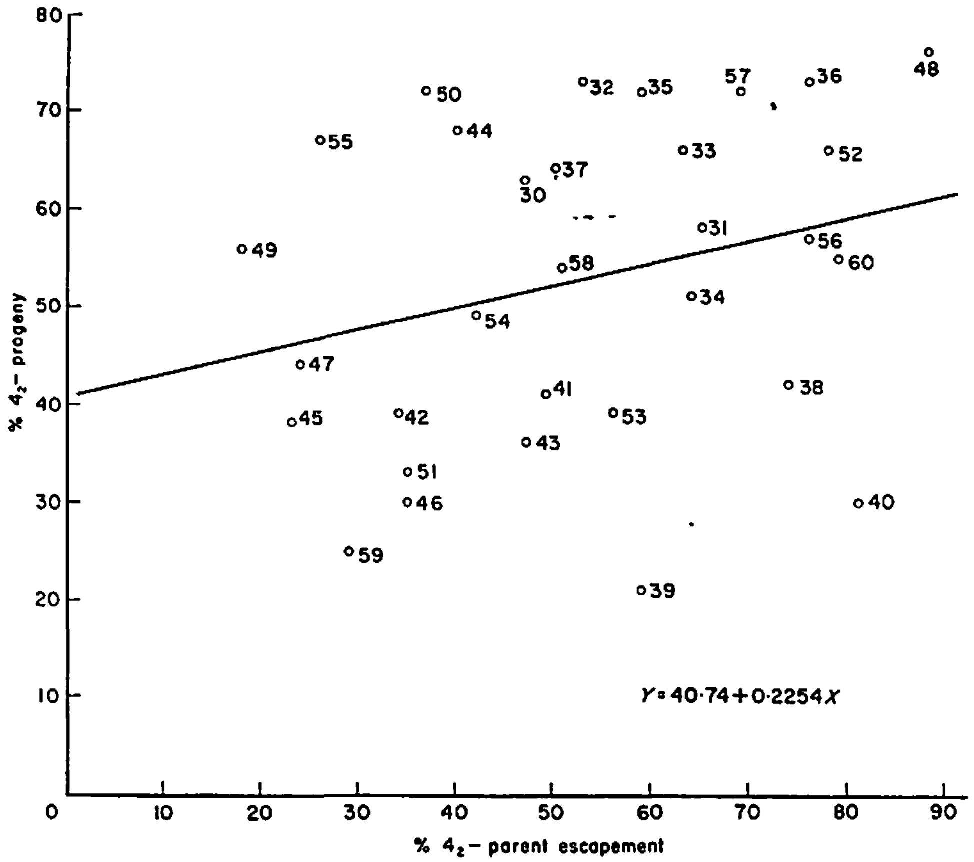

FIG. 5. Relation between the percentage of 4_2s in the parent escapement and the percentage of 4_2s in the resulting progeny. Figures in the body of the graph indicate brood years.

be recalculated as a basis for correlation between proportion of 4s in a brood year with proportion of 4s in the progeny.* This correlation is significant but is also small ($r = 0{\cdot}36$, $0{\cdot}01 < P < 0{\cdot}05$) and the relation is virtually unaffected by addition of the size of the escapement as an additional independent variable. Apparently age of the parent is only partially effective in influencing the age of return of the progeny.

Table 3. *Escapements and returns of* 4_2 *and* 5_2 *sockeye salmon of the Skeena River for the brood years* 1930–60

Brood year	Escapement × 10³†				Returns			
	Total	4_2‡	5_2‡	% 4_2	Total	4_2‡	5_2‡	% 4_2
1930	742	348	394	47	981	617	364	63
1	510	332	178	65	889	518	371	58
2	310	164	146	53	1556	1136	420	73
3	173	109	64	63	640	420	220	66
4	320	205	115	64	1220	626	594	51
5	310	183	127	59	1183	850	333	72
6	556	422	134	76	2944	2156	788	73
7	340	170	170	50	1202	763	439	64
8	297	220	77	74	535	227	308	42
9	598	353	245	59	1318	273	1045	21
1940	963	828	135	86	2285	683	1602	30
1	572	280	292	49	1183	486	697	41
2	305	104	201	34	905	356	549	39
3	272	128	144	47	477	171	306	36
4	824	330	494	40	3156	2163	993	68
5	940	216	724	23	795	218	577	38
6	486	165	321	34	1112	334	778	30
7	307	74	233	24	911	397	514	44
8	1066	938	128	88	2427	1846	581	76
9	480	86	394	18	1363	759	604	56
1950	382	143	239	37	601	430	171	72
1	163	55	108	34	184	61	123	33
2	158	123	35	78	637	421	216	66
3	700	392	308	56	1349	524	825	39
4	511	214	297	42	1325	654	671	49
5	87	23	64	26	379	252	127	67
6	370	281	89	76	540	307	233	57
7	448	305	143	68	2179	1569	610	72
8	819	414	405	51	799	418	357	54
9	799	234	565	29	1482	381	1125	25
1960	273	215	58	79	774	426	348	55

† Basic escapement-return figures from Shepard & Withler (1958, 1964).

‡ Estimated from age composition of catch, 1930–55; from catch and test fishing data, 1956–57; from catch and test fishing data, 1958 on, using corrections for test fishing selection (K. V. Aro, personal communication).

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* The recalculated escapement of 4s is given by

$$E_4 = B\left[\frac{1{\cdot}5\,(B+D)}{(1{\cdot}5\,B+D)\,F} - 1\right]$$

where F is the rate of exploitation on an annual basis, the per cent taken by the fishery

B is the apparent escapement of 4s, or $\frac{(1-F)}{F}$ (catch of 4s)

D is the apparent escapement of 5s, or $\frac{(1-F)}{F}$ (catch of 5s)

The corrected escapement of 5s is given by $B+D-E_4$.

Alternatively, the mechanisms underlying the inheritance of age of return may be considerably more complicated than is implied by simple correlation coefficients between brood years and their yield. With the simplest dominant–recessive inheritance, based on a single pair of alleles, and an initial age composition of equal numbers of each age, it would require a great many generations to effect a virtual elimination of 5s by their differential selection in the fishery. Moreover, there are other lines of evidence suggesting factors which might operate in the opposite direction. Observations of spawning behaviour (Hanson & Smith 1967) indicate that larger and older males (5s) serve disproportionately more females of any age. To make matters even less straightforward, Bilton (personal communication) has assembled evidence that larger (and hence usually older) fish produce larger eggs, which in turn produce larger fry. On the average, fish which return as adults at younger ages were larger at the time of their seaward migration. Thus, in some circumstances 5s may perhaps in some measure be responsible for the production of 4s and 4s may perhaps be the parents of 5s.

Lack of understanding of the mechanisms which determine the age of return is a serious deficiency in any speculation concerning the population biology of Skeena sockeye salmon. For the present, the only firm basis on which to build is the weak correlation suggesting that age of return is determined, at least in part, by the age of the parents.

(5) *Cyclic changes in brood success*

Godfrey (1958) examined annual catches of 4_2 and 5_2 sockeye and noted 'cycles' of success in the production by the various brood years. Among 5_2 sockeye there were peak catches separated by 5-year intervals resulting from the broods of 1909, 1914 and 1919. Among 4_2 fish there were peak catches separated by 4-year intervals resulting from the broods of 1932 to 1948.

A more complete examination of patterns in success of broods is available from annual estimates of the total abundance (catch plus escapement) of 4_2s and 5_2s given by Shepard & Withler (1958) and Shepard *et al.* (1964). These data, arranged to show the returns from each brood year (Fig. 6), reveal the same 5-year and 4-year series of peaks as in Godfrey's catch data. When 4_2s and 5_2s are combined, peaks in abundance occurred at 5-year intervals from the brood years from 1909 to 1919.

In the years between 1919 and 1932 there was no regular pattern of changes in production and only one major peak (1925) in brood year success. In 1932 there began a series of peaks at 4-year intervals which persisted until 1948.

Surprisingly, the age composition of the spawning populations of the peak brood years varied substantially (see Fig. 5 and Table 3). For example, the 1914 brood year contained 25% 4s and the resultant production was 48% 4s. The 1919 brood year was 34% 4s and it eventually produced almost equal numbers of 4s and 5s, the former contributing almost two-thirds of the near peak in abundance in 1923 and the latter more than two-thirds of the peak abundance in 1924. In 1932, the apparent initiating year of the sequence of big brood years at 4-year intervals, the spawning population was 53% 4-year-olds; in 1936 it was 76%; and, in 1940, up to 86%. In 1944, however, the return of 4s was small, being numerically smaller than the number of 4-year-old parents in the 1940 brood year. Thus, the large 'cycle year' run in 1944 contained a majority of 5-year-olds (60%), which originated in 1939 from a spawning population that not only was relatively small but consisted of almost 60% 4-year-olds! As a further surprise, the 1944 run subsequently produced a large number of 4-year-old progeny, which made up 88% of the 1948 spawning escapement. This 1948 brood in turn produced a large number of 4-year-

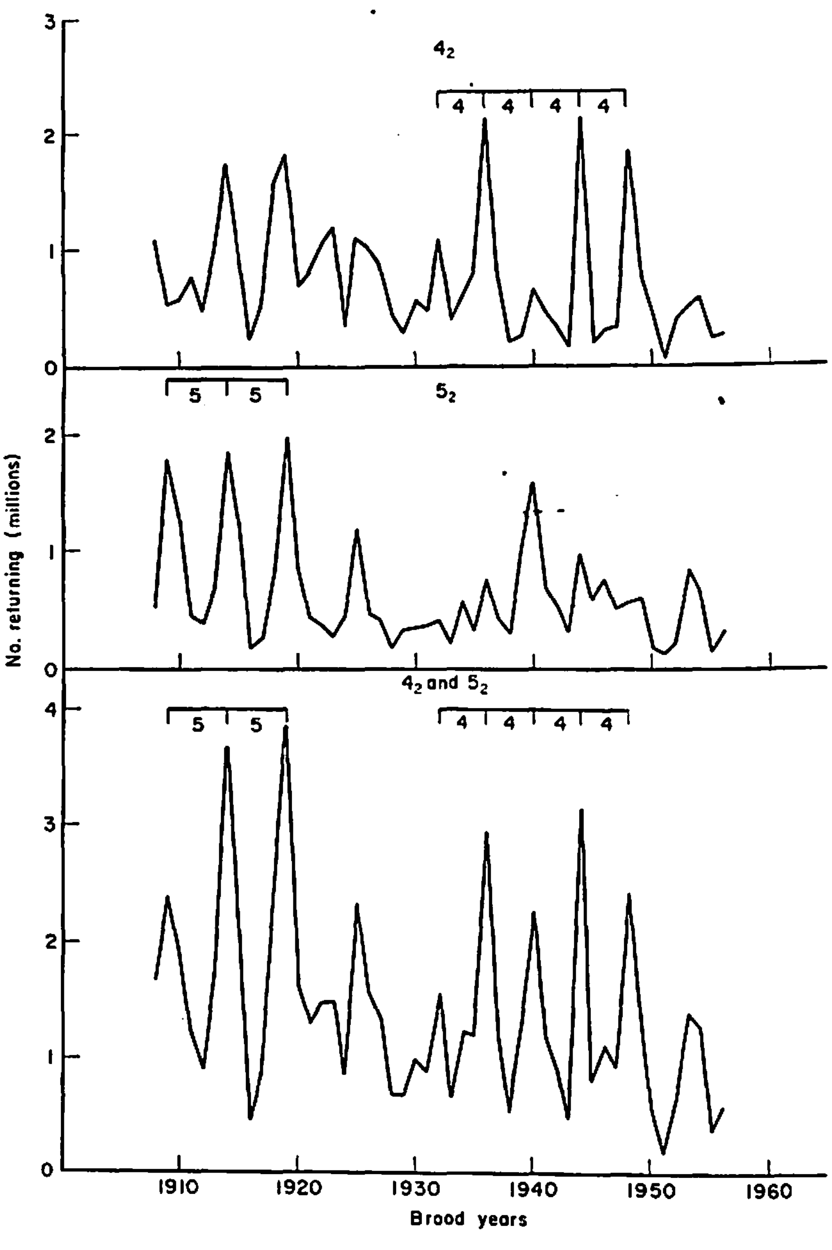

FIG. 6. Number of 4_2s, 5_2s and the total returning from each of the brood years 1908–56.

old progeny in 1952, which made up 78% of the brood of that year.[*] Thus, in the middle of this apparent 4-year 'cycle', there was a radical change and then a reversal, in the proportion of 4-year-old fish in the spawning escapements.

[*] These age compositions are based on catch statistics and are accordingly biased by selective effects of the fishery. In every instance except after 1958 the proportion of 4s is probably higher than that indicated. If it is assumed that selection of 5s is at the rate of 1·5 to 1, the percentages of four-year-olds in the brood cycle years were: 1932—79%; 1936—92%; 1940—96%; 1944—58%; 1948—95%. For 1939 it was 79%.

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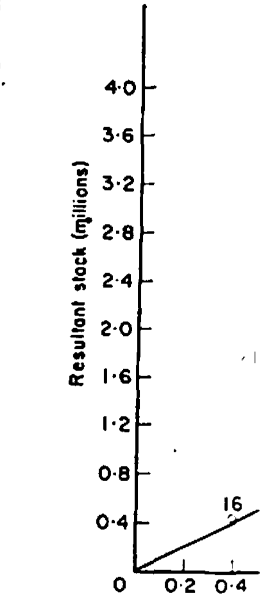

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While it is apparent that 4-year-old fish seem to predominate in the brood successes at 4 year intervals, it is evident that an explanation of this series of successes cannot depend solely on the simple notions that 4-year-old parents produce progeny which mature at 4 years of age and that a large brood always produces a large brood. On the other hand the relation of brood successes to age of return is too striking to be fortuitous.

An additional feature of the relation between spawning stock size and yield is the greater rate of return from the brood years of the sequences of brood year successes. Fig. 7 isolates data of Fig. 4 for two sets of brood years, those for the 1908–20 brood years, which include the 5-year peaks in 1909, 1914 and 1919; and the brood years 1931–53, which include the 4-year peaks from 1932 to 1948. For the earlier period, although the production rates from the brood years 1909, 1914 and 1919 were higher than most others, there is insufficient evidence to conclude that this was not due to chance alone.

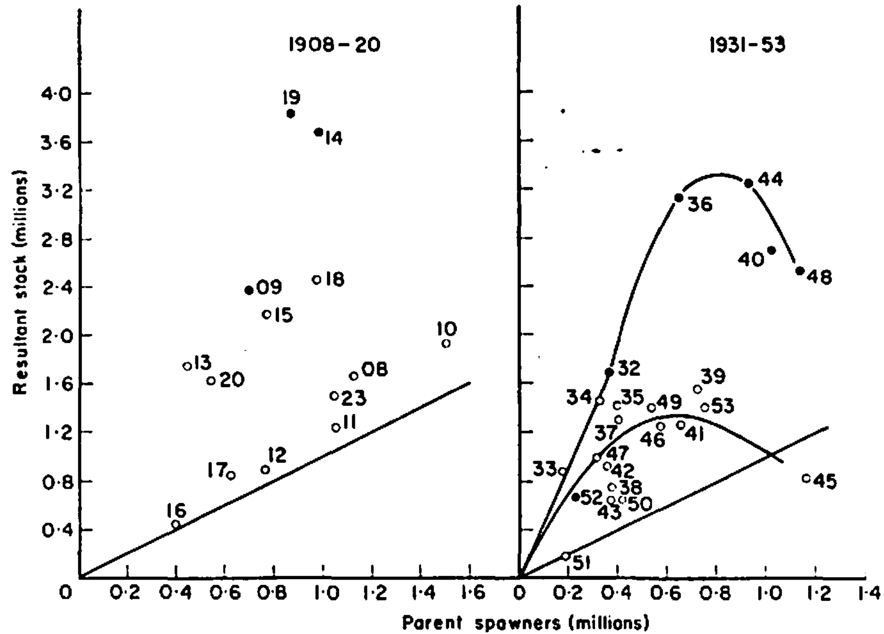


FIG. 7. Relation between number of parent spawners and resultant stock of progeny during the periods 1908–20 and 1931–53. Years in which brood success was apparently recurrently high are shown with solid circles. Figures in the body of the graph indicate brood years.

A larger number of points are available for the later period when the 4-year peaks occurred. Two reproduction curves, fitted by eye, one to the parent–progeny relation in the peak years and the other to the years between, emphasize the apparent differences in rate of return. For the peak years the rate of return is at least twice as great as for the years between where the parent spawners exceed an abundance of 0·6 stock units. The apparent reproductive advantage of the cycle years appears to have been lost when, in 1952, parent spawners were reduced to a very low level by the Babine River slide. The return from this brood was no higher than that of broods of the same order of size in the non-peak years.

POSSIBLE CONTRIBUTING FACTORS TO POPULATION CHANGES

(1) *Features of the commercial fishery*

(a) *Overexploitation*

Throughout the history of the Skeena fishery there have been restrictive measures in type of gear, season, weekly fishing times and fishing area. Increased effectiveness of fishing gear was countered mainly by reducing weekly fishing times and seaward movement of fishing boundaries. The net effect of the regulations, until recent years, has been a strong tendency for removal by the fishery of a fixed proportion of the annual run, in the period 1920–39 about 60% and from 1940 to 1950 about 50%. In recent years, management has aimed at providing an optimum sized escapement each year (i.e. one which on the average will produce the largest catch over the long term) although immediate economic considerations are recognized.

The reproduction curve shown in Fig. 4 suggests a maximum sustained yield at a rate of exploitation of 57%, and because the left-hand limb is relatively straight, any greater rate of exploitation would push the stock to progressively lower levels. In their analysis Shepard & Withler (1958) concluded that the observed decline in yield followed a 'pattern that would be expected as a consequence of the observed changes in rate of exploitation with the spawner-return relationship'. The gross decline in abundance thus reflects a history of exploitation at rates slightly greater than the combined stocks can support.

(b) *Selection in the commercial fishery*

It is widely recognized that, because of the manner in which gill-nets catch fish, they operate selectively. Their selective action in the Skeena fishery is described by Withler (1945) and Milne (1955). Precise measurement of the selective effect of the fishery requires detailed assessment of catch and escapement statistics. The former is complicated by week to week variation in racial and age composition of the run and of the times, places and duration of the fishery. Seasonal changes in the type of nets used ('tangle' nets, with more mesh per length of net are used in the latter part of the sockeye season for pink salmon) and the long-term transition from linen to synthetic fibre nets are further complicating factors. Precise measurement of the size of the escapements and of their race and length composition is also formidable. With so many contributing sources of error, detailed analysis of selection effects has been relatively unrewarding. It is nevertheless apparent that the gross statistics of catch and escapement reflect a strong selection of 5_2 sockeye by comparison with 4_2 sockeye. For example, for the years 1962–65, escapements to the Babine fence, which are over 90% of the total, show a preponderance in the proportion of 4s by comparison with the commercial fishery (Table 4). While the relative rates of exploitation in Table 4 are not corrected for non-Babine fish, they indicate a substantial selection of 5s over 4s of the order of magnitude of 1·5 to 1. The selective effect apparently varies with the proportion of 4s in the run and the rate of exploitation, being greatest when the former is intermediate and the latter high. Presumably selection also extends to 6_3 fish in comparison to 4_2s and perhaps to large 4_2 fish by comparison with small 4_2s.

(c) *Differential harvesting of stocks by the commercial fishery*

The extent to which individual stocks have been exploited may be examined by comparing the times when the stocks are present in the fishing area and the periods when fishing has been permitted.

Table 4. *Numbers of* 4_2 *and* 5_2 *sockeye in Skeena catch and Babine escapement for the years* 1962–65, *with approximate estimates of selective exploitation of* 5_2 *fish*

Year	Catch (in thousands)		Escapement Babine fence (thousands)		Relative rates of exploitation		Ratio of relative rates of exploitation	Proportion of 4s in run	Total rate of exploitation (whole system)
	4	5	4	5	4	5	5/4		
1962	163	321	349	264	0·318	0·549	1·726	0·467	0·442
1963	101	41	534	133	0·159	0·236	1·484	0·786	0·176
1964	185	581	290	605	0·389	0·490	1·260	0·286	0·462
1965	138	156	516	158	0·211	0·497	2·355	0·676	0·304

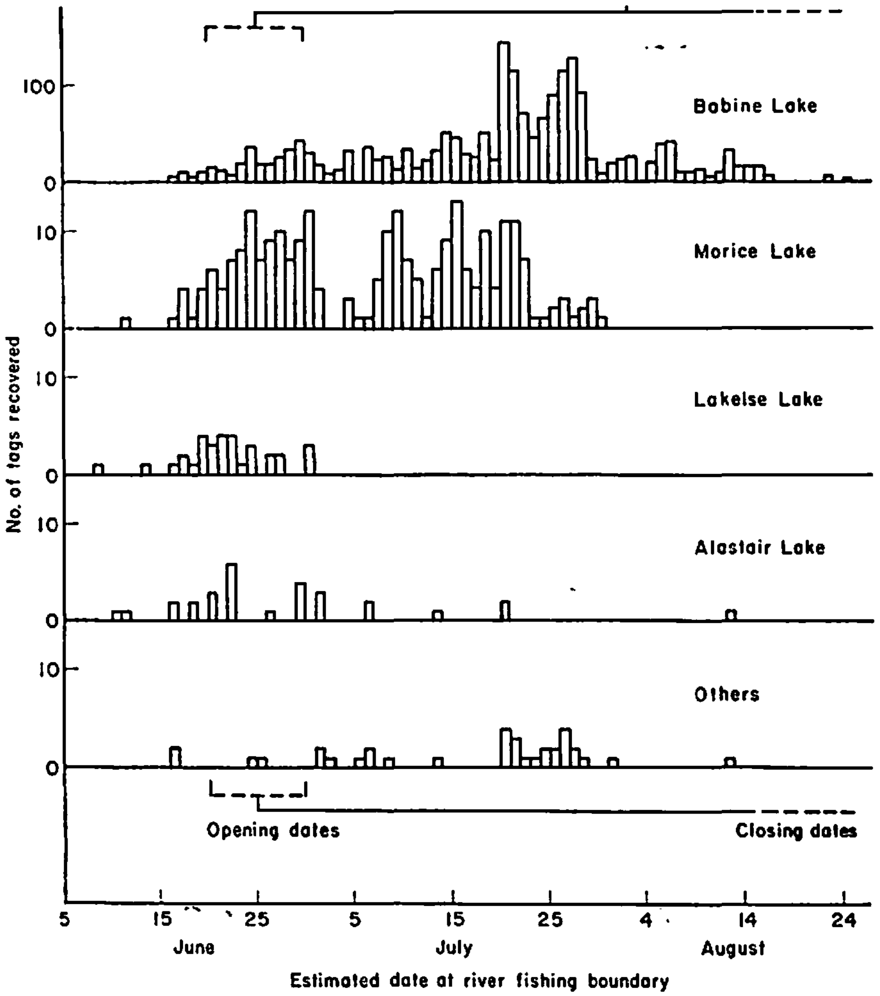


FIG. 8. Estimated date of passage through the fishing area of sockeye salmon, which from subsequent tag recovery could be assigned to various Skeena River rearing areas. Based on data from Aro (unpublished).

Dates of passage of fish through the fishing area are indicated by past tagging and recovery programmes. In 9 past years sockeye were tagged in the fishing area and later recovered on the spawning grounds. Fig. 8 is drawn from data summarized by Aro (unpublished). Tag recoveries for all years have been grouped, and as proportionate tagging or recovery did not occur, the figure indicates only the periods when the stocks have been observed in the fishing area. Fishing opening and closing dates are from Canada Department of Fisheries records.

It is apparent that for all stocks some fish may escape upriver before the season opens. In the case of the Babine Lake and 'others' it appears that most of the fish are available to the fishery each year. The earliest part of the Morice Lake stock may have been relatively lightly fished in those years when the opening occurred nearer the end of June. Considerable proportions of the Lakelse and Alastair Lakes sockeye appear to pass through the fishery area before the end of June. In years when the opening was as late as 30 June, the tagging data indicate that almost all the Lakelse stock and a majority of the Alastair Lake fish would escape exploitation.

(2) *Differential yield of Babine and non-Babine stocks*

Skeena sockeye are produced in a large number of lake areas spread over a large and diverse geographical region. Differences in the yield of these lakes for sockeye would be expected. Some limnological features such as surface area, mean and maximum depth, shore area development and temperatures are summarized by Godfrey (1955) for a number of lakes. For the most part these data are sufficient only to place the lakes into very general categories of type and provide little indication of productivity for sockeye. A better indication is gained by comparing the numbers of sockeye produced per unit lake-surface area.

Table 5. *Relative densities of sockeye in some Skeena lakes*

Lake	Surface area (ac)	Average escapement (1946–48)	Fish per acre
Babine	114816	427 000	3·7
Morice	25600	70 000	2·7
Swan, Stephens	8896	12 000	1·4
Bear	4608	30 000	6·5
Kitsumkalum	4352	8 000	1·8
Lakelse	3520	9 000	2·6
Alastair	1472	11 000	7·5

In Table 5 average escapements from 1946 to 1948 are used as a relative measure of sockeye yield for the most important lakes. Escapements in the 1946–48 period were chosen for two reasons. Firstly, there was little change in the effect of the fishery on the stocks in those years (annual rates of exploitation varied between 0·50 and 0·52) and therefore escapement size provides a useful index of abundance. Exceptions are Lakelse and Alastair lakes stocks, which in past years have escaped commercial fishing to a considerable extent by virtue of their relatively early period of migration through the fishing area. To put Lakelse and Alastair ratings on a more comparable basis, escapements to these areas have been halved. Secondly, non-Babine escapements were at a high level relative to more recent years and probably more representative of long-term yield.

Values given in the table indicate a density index ranging from 1·4 sockeye/ac to 7·5/ac.

Two of the non-Babine lakes (Bear and Alastair) appear to be more productive of sockeye than Babine Lake. However, the relatively low yield of Morice Lake, which historically was the most important contributor to the non-Babine group, suggests that non-Babine producers taken as a whole are somewhat less productive for sockeye than Babine. Independent evidence of differences in the potential of the various lakes for producing sockeye would be desirable, but is not available.

(3) '*Dominance*' *effects*

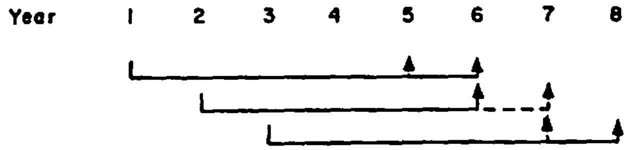
The peaks in brood success observed on the Skeena appear to be too persistent—particularly the 4-year sequence from the brood years 1932 to 1948, to result from chance alone. A similar and more pronounced pattern, termed 'dominance' in the Fraser River sockeye, has attracted considerable attention (e.g. Ricker 1950; Ward & Larkin 1964).

In the simplest case, a stock may be made up almost exclusively of 4-year-olds. A river system is then inhabited by four virtually distinct populations or 'lines', each occurring on one of the four years of a cycle. If one of the four populations is consistently much larger than the others, it is termed dominant. The dominant line enjoys some continuing relative advantage in abundance because (a) of some innate characteristic, (b) the other three lines somehow stimulate production in the fourth, or (c) it somehow suppresses the other three lines, either directly or through some mediating factor.

Of many possible mechanisms that have been considered (genetics, competition, cannibalism, disease, conditioning) predation in freshwater seems most likely as a major contributing factor to dominance (Ricker 1950; Ward & Larkin 1964). Juvenile salmon, both fry and smolts, are particularly susceptible to predation during the course of downstream movements when they are concentrated in what is tantamount to a funnel. In these circumstances a wide variety of seasonal predators are capable of eating to capacity over a wide range of prey densities. By cropping a relatively fixed quantity they may exert a depensatory effect (Neave 1953) from year to year, removing a greater proportion from smaller populations. Additionally, when prey are very abundant, a 'numerical' response of the predators (and in the case of predaceous fish this may take the form of increased survival and growth rates) may be inflicted largely upon the succeeding year class or two. This line of argument was used by Ward & Larkin (1964) as an explanation for the 'dominance' in Adams River sockeye.

There is a variety of other lines of speculation which suggest possibilities that the presence of a large run in a particular year might adversely influence the production of young from the brood of the following year or few years. For example, parasites with short life histories may increase in abundance when there is a large number of fingerlings in the lake. The possibilities of fouling of spawning gravel by large numbers of dead eggs have been mooted. It is necessary that any explanation should take account of the curious life history of sockeye salmon for, where they are almost purely 4-year-olds, there is little direct contact between the various lines. The search is for a freshwater factor which would tend to respond slowly to salmon densities, accumulating its effect during the years of big runs and inflicting it on succeeding broods.

The foregoing considerations are apparently confounded when, as in the case of the Skeena, a large proportion of the run is 5-year-olds. Any good year of production should be reflected both 4 and 5 years later, and it would seem that any disparity between lines would quickly be eliminated by the contributions of the large years to the small. However there are also possibilities for much more complex patterns of fluctuation. For example, if it is assumed for the moment that age of return is inherited, then varying proportions of 4s and 5s in a series of brood years, coupled with varying success of the brood years, may fortuitously result in a small run in a year following a large run. Suppose the following combination: a successful brood year (say year 1) spawned predominately by 5s, followed by a successful brood year (year 2) spawned mostly by 4s, followed by a poor brood year (year 3) spawned mostly by 5s. With this sequence, year 7 is a very low year preceded by a very large year, a situation in which depensatory effects would presumably be large.



In model studies of these mechanisms we have observed that where 5s are a sufficiently large proportion of the population, there are many possibilities for complex cycles of 20 years—multiples of 4- and 5-year cycles. These studies will be reported elsewhere in detail; for the present purpose a single example (Fig. 9) illustrates the type of cyclical pattern that may be generated.

The upper portion of Fig. 9 illustrates the first 20 years and the last 20 years, of a 300 year simulation of a population with an initial age composition of 7% 3s, 31% 4s, 60% 5s and 2% 6s. The population is influenced strongly by unbuffered depensatory effects, age of return is inherited, there is no fishery and there are no climatic effects simulated by random normal deviates. The simulation is thus deterministic. The disparity in population sizes in the initial years is tenfold. The algebraic structure of the model is as outlined by Larkin & Hourston (1964).

The striking feature of this simulation is the super-imposed 4-year cycle on a 5-year cycle which results in recurring 20-year cycles in which the 'peaks' of abundance (counting the second of 2 equal years as the peak) are separated by 3, 2, 2, 4, 4 and 5 years respectively.

The lower portion of Fig. 9 is the same simulation with random climatic effects added. A similar basic cyclical pattern is evident (this is apparent if year 282 in the upper histogram is matched with year 286 in the lower). The 'peaks' are much more exaggerated, and the comparable intervals between the peaks in this particular 20 years (starting at year 287) are the same as in the deterministic simulation.

Thus it would be expected that depensatory processes acting on mixed-age compositions would generate quite complex patterns of population fluctuation. It is significant in these particular simulations that if the proportion of 5s falls below about one-third, 5s are quickly eliminated by losses incurred in the years between the big years of abundance of 4s. The value of 'about one-third' has no particular significance, because it reflects the values chosen for the various parameters which determine the severity of the depensation process, and if it was less severe the critical proportion of 5s would be lower. Nevertheless, the point is made that the stability of an age composition is related to depensatory effects. Where the losses are severe, it would not be expected that a small proportion of 5s would long persist.

There are no direct field observations which confirm the existence of depensatory mortality from predators or other causes in the Skeena system. A considerable body of anecdotal evidence confirms the activity of predators in exploiting sockeye fry, when, during their migration lakeward, they may be extremely vulnerable. The list of occasional predators even includes such unlikely species as the robin (*Turdus migratorius* L.). There is as much anecdotal evidence to the contrary, and the obvious need is for further observation.

To turn to less flimsy speculation, the small native food fishery on the Skeena may contribute to depensatory losses, particularly in local situations. In the period 1935–48 (data from Shepard & Withler 1958) the native fishery in the Skeena as a whole took a smaller percentage catch from the larger runs. Over a range of escapements from 302 000 to 1 185 000 it took approximately from 2·4 to 17·6%, and though there is wide variability, the percentage catch tended to be greatest on the smaller runs (Table 6).

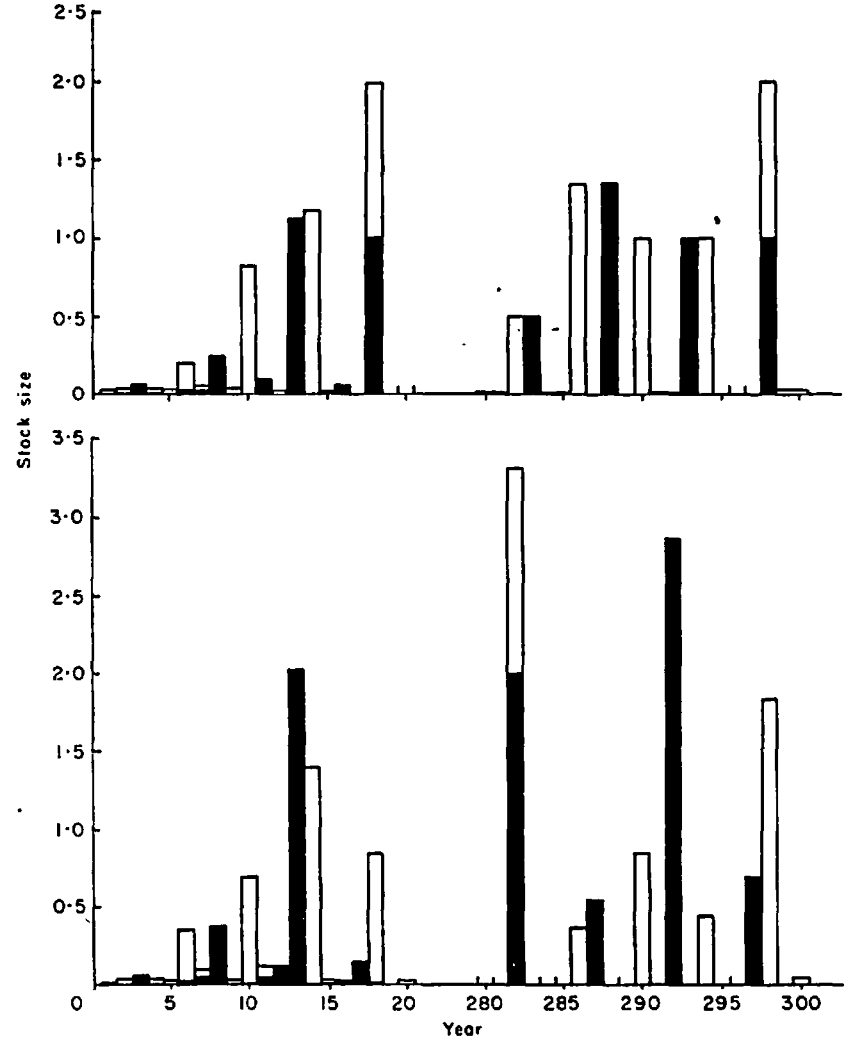


FIG. 9. Fluctuations in abundance of 4-year-old (□) and 5-year-old (■) salmon in computer-simulated populations in which depensatory mortality produces 'dominance' effects. Upper figure without and lower figure with climatic effects simulated by random normal deviates. See text for explanation.

The native fishery at Moricetown Falls on the Bulkley River takes sockeye of the Morice Lake stock when they are confined in a narrow stretch of river below a natural obstruction. In recent years a fishway installation has assisted migration and enabled assessment of the fishery. Although water levels influence the vulnerability of the salmon (Palmer 1964 unpublished), it is apparent that exploitation rates are at least as high on small runs as on large, and are perhaps higher (Table 7).

Table 6. *Estimated escapements (thousands) and Indian food catches of* 4_2 *and* 5_2 *sockeye for the Skeena River for* 1935–48, *listed in order of decreasing size of escapement (data rearranged from Shepard & Withler* (1958))

Year	Escapement	Catch	% caught	
1946	1185	28	2·4	'Large' runs: Mean % caught = 8·51 % caught, total = 7·78
1940	1070	137	12·8	
1945	1044	36	3·4	
1944	916	48	5·2	
1939	664	71	10·7	
1941	636	58	9·1	
1936	618	99	16·0	
1947	514	36	7·0	'Small' runs: Mean % caught = 12·06 % caught, total = 11·78
1937	378	56	14·8	
1935	344	51	14·8	
1948	343	30	8·8	
1942	339	40	11·8	
1938	330	58	17·6	
1943	302	29	9·6	

Similarly, the food catches by natives at Babine Lake may be related to the series of escapement counts for the Babine River fence, just a short distance downstream from the native fishery (Table 8). Since 1946 the escapements to the fence have ranged from 71 000 to almost a million, while the food catch has varied narrowly from just over 10 000 to less than 40 000. The fishery obviously tends to take a relatively constant number over a wide range of escapements, only at the lowest escapements taking a smaller number, though a greater percentage of those available.

Table 7. *Escapements and percentage catch of sockeye at Moricetown Falls, Bulkley River, for years in which data are available*

Years of relatively large escapement			Years of relatively low escapement		
Year	Escapement	% catch	Year	Escapement	% catch
1945	70 000	38·0*	1961	18 000	18·0
1951	53 600	8·0	1966	16 000	25·0
1946	50 000	26·2	1962	11 500	10·7
1947	24 000	21·2	1964	10 500	33·3
1965	22 000	13·5	1963	6 100	58·0*
Mean		21·38	Mean		29·0
Excluding 1945		17·23	Excluding 1963		21·75

* Years of relatively low water level when fish were apparently very vulnerable. Data for 1945–63 from Palmer (1964), for 1964–66 from files of Department of Fisheries, Canada. Data for 1966 preliminary. Catch includes 35% allowance for fish injured but not captured.

It is important to emphasize that the much larger commercial fishery, by taking a fixed percentage of the annual run, would serve to exaggerate any differences in productivity among various years. If the runs of smaller years were less productive it would be expected that they would be more readily depressed, increasing the disparity between the large and small years. Further, it is obvious that any pressures for less stringent regulation of the fishery would be more intense in years of a small run. While it is difficult to document these effects for the earlier years in the history of the Skeena fishery, the possibility that they occurred should not be overlooked. The recent history of the Skeena fishery has certainly been characterized by strong representations for more fishing time in years of small runs.

MODEL FOR SIMULATION OF SKEENA SOCKEYE STOCKS

If the major factors responsible for the population fluctuations of Skeena River sockeye salmon are as have been outlined, their synthesis in a single model should provide the basis for a simulation of the history of population changes. While the simulation may be far from adequate, it should serve the purposes of (1) verifying that the purported mechanisms involved have the potential, when quantified, of producing the sort of population behaviour which has been observed and (2) perhaps indicating corollaries that suggest new lines of investigation.

Table 8. *Escapements at the Babine River fence and Indian food catches for 1946–65, ranked in order of size of escapement*

Year	Escapement (in thousands)	Catch	% caught	
1961	942	31 436	3·34	'Large' escapements: Mean % caught = 3·43 % caught, total = 3·38
1964	828	19 655	2·37	
1958	812	38 580	4·76	
1959	783	16 727	2·13	
1953	687	26 913	3·92	
1948	650	26 278	4·05	
1963	588	20 021	3·40	'Medium' escapements: Mean % caught = 4·29 % caught, total = 4·16
1965	580	18 840	3·48	
1962	548	18 122	3·31	
1954	494	21 849	4·43	
1949	461	28 525	6·18	
1946	445	20 052	4·50	
1957	433	20 434	4·72	
1950	364	27 449	7·54	'Small' escapements: Mean % caught = 10·09 % caught, total = 9·02
1956	355	30 584	8·62	
1952	349	34 404	9·86	
1960	262	16 754	6·39	
1947	261	26 109	10·00	
1951	141	19 036	13·50	
1955	71	10 423	14·70	

Structure of the model and values of parameters

The general model of Larkin & Hourston (1964) was adapted for simulation of Skeena sockeye population processes. The two stocks, Babine and non-Babine, were harvested by a joint fishery taking a constant percentage (55%) of the run, with selection for 3-, 4-, 5- and 6-year-olds at rates of 0·0 to 1·0 to 1·4 to 1·4 respectively. The escapements were then assigned in relation to abundance of the two stocks, and egg depositions (in stock units) calculated with factors of 0·0, 0·951, 1·152, 1·152 for 3-, 4-, 5- and 6-year-olds respectively. The factor of 0·0 for 3-year-olds arises from the fact of their all being males;

those for other ages were based on egg-counts of various ages of females taken in 1965. The sum of the products of the egg deposition factors and the age composition proportions must equal approximately unity for initial conditions and the factors were computed accordingly. The initial age compositions were estimated from catches for the period 1912–22 (Table 9), assigning sub 3 fish to non-Babine stocks, assuming similar proportions of 4_2 and 5_2 fish in Babine and non-Babine stocks, a fixed proportion of 5% 3-year-olds in all stocks, and an initial ratio of abundance for 4_2 and 5_2 fish of 0·8 Babine to 0·2 non-Babine. The resulting approximate age distributions used for initial conditions were:

	3	4	5	6
Babine	0·05	0·49	0·46	0
Non-Babine	0·05	0·30	0·54	0·11

The catch in the period 1912–22 was in the ratio of 900 000 Babine fish to 370 000 non-Babine and this ratio was taken as reflecting initial relative abundance. Initial values for the sizes of the two stocks were each placed at one stock unit (equilibrium). The replacement equilibrium for the combined stocks as given by Shepard & Withler (1958) is approximately 1·2 million. Thus the starting sizes of the runs were put at 920 000 Babine and 380 000 non-Babine.

Table 9. *Estimated numbers of sockeye of different ages in Skeena River gillnet area catches*, 1912–22

Year	4_2	5_2	5_3	6_3	Total
1912	619 367	399 591	79 918	26 640	1 125 516
1913	316 291	281 994	45 729	15 242	659 256
1914	337 390	993 426	103 092	37 488	1 471 396
1915	461 550	772 047	92 310	33 568	1 359 475
1916	267 574	285 120	83 343	92 116	728 153
1917	552 069	197 911	82 384	30 302	862 666
1918	994 468	378 253	96 784	36 405	1 505 910
1919	628 517	1 242 386	182 429	78 564	2 131 896
1920	160 947	711 831	65 426	75 239	1 013 443
1921	368 230	112 659	28 812	12 101	521 802
1922	1 009 852	171 690	143 437	19 560	1 344 539

In each generation the escapement was used as a basis for determining the proportions of the progeny which would eventually return as adults at various ages. The brood was then processed in sequence through: a compensatory stage, a freshwater environmental 'influence', a depensatory stage and a shared marine environmental 'influence'. The assumptions involved in each of these steps are critical in determining the machinery of the simulation and are detailed below.

The *mechanism determining age of return* was as in the model of Larkin & Hourston (1964)—simply that fish of any particular age produce offspring which return at the same age. The age composition of the spawning populations, approximately weighted by the egg deposition factors, thus determines the proportions of the brood returning at various ages. The proportion of 3-year-old males was held constant.

The *compensatory stage* was a modified Ricker-type relation of the form:

$$Z = (1-D)e^{-a_2(w-1)} + D, \quad w > 1$$
$$Z = we^{a_1(1-w)} \quad , \quad w < 1$$

where Z is the production of progeny from w adults, a_1 is the compensation coefficient, the value of D specifies the asymptotic number of stock units of parents, beyond which

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For the model simulation, the Babine stock was assigned a competition coefficient (a_1) of 1·75, and a value of (a_2) of 1·75. For the non-Babine, both a_1 and a_2 were set at 1·25. For both stocks the value of D was set at 0·75. These values are all compatible with the empirical stock-recruit relationship, but are really only guesses that seem reasonable. The a_1 values determine that the Babine stock would support a maximum sustained yield at a rate of exploitation of about 67%; non-Babine 52%.

The *freshwater environmental influence* was of the form devised by Ricker (1954) in which scaled random normal deviates (augmented in absolute value by unity) are used as multipliers or divisors depending on sign. The scaling factor used (Q) was appropriate for producing a five-fold ratio of extremes about an average production (Z) with 95% confidence ($Q = 0{\cdot}61803$),* which seemed approximately to reflect the variation in egg-to-smolt survival in Babine Lake for the broods of 1956–62 (H. D. Smith, personal communication).

Similarly, the *shared marine environmental influence* was scaled to produce an eight-fold ratio of extremes ($Q = 0{\cdot}91421$). This range was suggested by the observed variability in smolt-to-adult survival of Babine sockeye for the brood years 1956–61.

However, this range, combined with that for the freshwater influence, results in a ten-fold range of extremes, and produced, in the first simulation, population fluctuations which masked any other effects in the simulation. The *observed* range of variation in survivals from egg-to-smolt and smolt-to-adult may be misleadingly large because it presumably reflects depensatory effects as well as climatic effects. For the second simulation it was decided to restrict the range of random environmental effects to the five-fold ratio of extremes produced by the simulated freshwater influence.

The *depensatory stage* is critical for the generation of cyclical patterns of abundance and may reflect any mechanism which tends to result in a greater mortality in less abundant year classes.

For the purpose of the model the procedure of Larkin & Hourston (1964) was followed, with the depensatory process:

$$\begin{aligned} M &= Re^{a_3(R-1)}, && R<1 \\ M &= R\ , && R>1 \end{aligned}$$

where M is the production of young salmon which reach the sea, R is the production of fry and a_3 is a coefficient of depensation.

The value of a_3 was made a function of the densities of the previous three year classes, with coefficients of 0·5, 0·3 and 0·2, viz:

$$a_3 = 0{\cdot}5\ E_{t-1} + 0{\cdot}3\ E_{t-2} + 0{\cdot}2\ E_{t-3}$$

where E_{t-i} ($i = 1, 3$) are the escapements of adults of the 3 previous years.

This procedure is a gross way of representing depensatory effects, literally specifying that small year classes will suffer greater losses when preceded by large year classes.

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* Plus or minus two standard deviations ($\sigma = 1$) enclose approximately 95% of unit normal deviates. If the ratio of extreme multiplier to extreme divisor is to be X-fold, then the scaling factor Q may be obtained from:

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

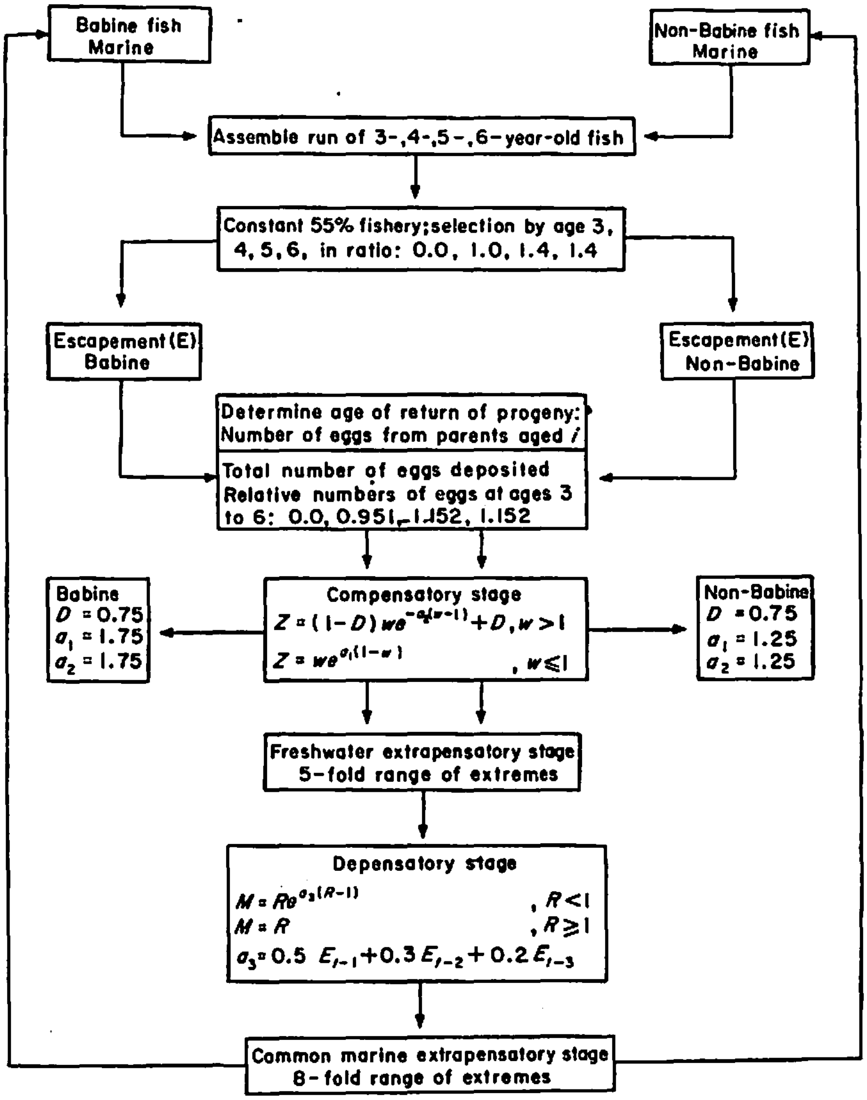

FIG. 10. Diagrammatic representation of sequence of processes in the model of Skeena salmon population biology. See text for explanation.

In the absence of more precise knowledge of the mechanisms involved, this type of procedure is essentially only a useful device for simulation studies.

The sequence of processes involved in the model is summarized in Fig. 10. The simulations were computed with an IBM 7040 machine at the University of British Columbia computing centre. The programme for the model was written in FORTRAN IV.

RESULTS OF SIMULATION

The results of the simulation are summarized in Table 10 and Fig. 11. Because the simulation involves random effects there is rather little point in looking for exact replication of the history of the Skeena population, and emphasis in interpretation is on the form of the population fluctuation.

Table 10. *Abundance and catch in computer simulations of Skeena River sockeye salmon populations*

	Abundance			Catch		
Decade	Babine	Non-Babine	Ratio	Babine	Non-Babine	Ratio
1–10	917 320	307 800	2·98	567 317	188 284	3·01
11–20	1 249 440	210 140	5·95	498 022	111 380	4·47
21–30	1 040 440	150 480	6·91	557 819	82 634	6·75
31–40	759 240	148 200	5·12	408 547	80 813	5·06
41–50	710 980	147 136	4·83	381 333	80 218	4·75
51–60	1 138 480	159 220	7·15	617 380	87 048	7·09
61–70	913 900	79 040	11·56	502 470	43 374	11·58
71–80	817 380	97 660	8·37	449 545	53 725	8·37
81–90	983 060	145 160	6·77	540 700	79 856	6·77
91–100	932 900	116 280	8·02	513 226	63 985	8·02

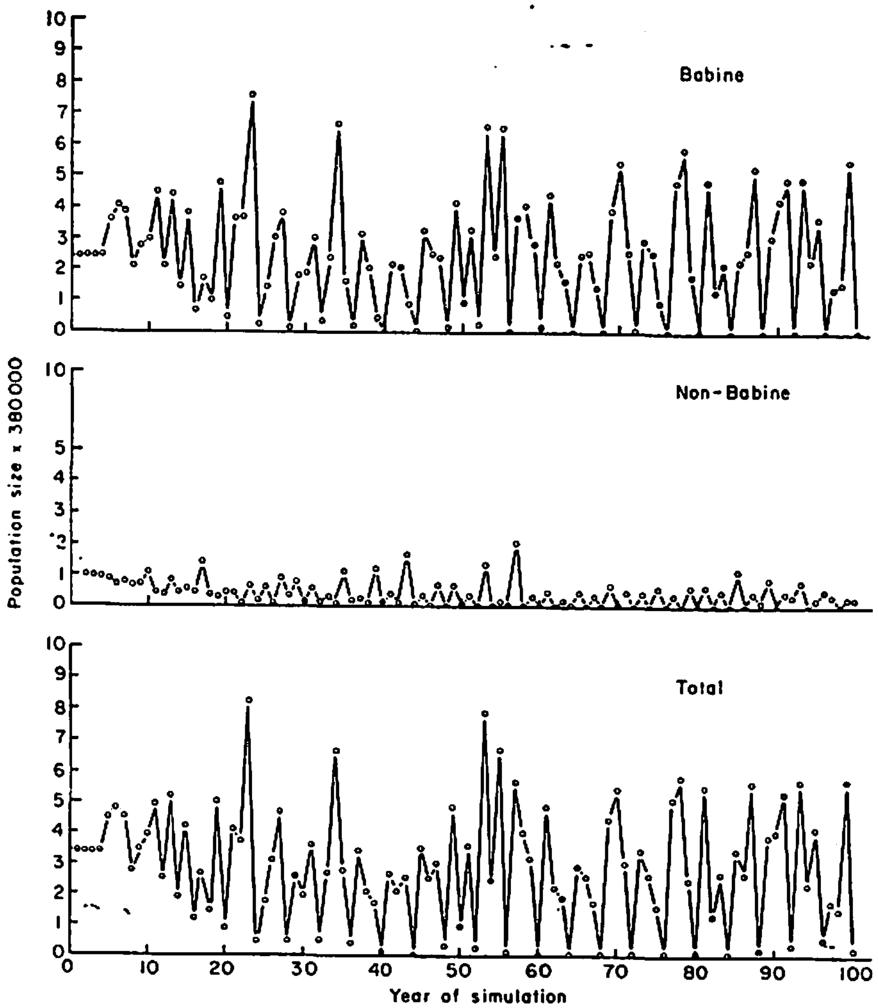

FIG. 11. Fluctuations in abundance of Skeena sockeye salmon, and the component Babine and non-Babine stocks, in a computer simulation.

Decline in abundance is indicated and, in the first 50 years of the simulation, is attributable to the decline of both Babine and non-Babine stocks. Thus the catch in the decade 41–50, corresponding approximately to the real years 1951–60, declined to about 450 000. This initial decline was followed in the next two decades by a continued decline of the non-Babine stocks, but a recovery of the Babine stocks. In consequence, the decades 51–60 and 61–70 witnessed a rapid fall in the relative proportion of non-Babine fish. The parallel to the natural situation is striking but the reasons for the changes in the computer simulation seem to be in part of somewhat different origin.

In the simulation, the decline in non-Babine stocks in part reflects that the rate of exploitation (55%) slightly exceeds the maximum which they can sustain (52%), but an additional factor is the selective action of the fishery on 5-year-olds and 6-year-olds. The latter were virtually eliminated by year 50, and the former were reduced to about 2% of the total, which was to be expected considering that age of return was inherited and the fishery selectively removed the older fish. The immediate effect of this selective removal is to reduce the annual egg deposition, but an additional and lasting effect is the virtual elimination of 5s which follow years of large abundance of 4s. Thus after year 22, the non-Babine stocks show in the simulation a regular 2-year 'cycle', with two dominant lines of 4-year-olds, and two 'off' lines of 4-year-olds. Similarly the Babine stock 5s were eliminated by the series of low years at 4-year intervals beginning in year 16. Depending on the year of origin of 5s, they may not immediately suffer the effects of depensation because they are with a large number of 4s, but in 5, 10, 15 or 20 years their return inevitably coincides with a year of low return of 4s and each such coincidence depresses them to very low levels.

By contrast, in the natural situation, the decline in abundance and the decline in the relative proportion of non-Babine fish was not accompanied by a rapid elimination of 5s, the decade 1942–51 being marked by a greater proportion of 5s than in years previous. Quite evidently there are factors of inheritance of age of return, or environmental determinants of age of return that sustain the proportion of 5s in the natural populations.

The same weakness in the simulation is reflected in the short-term pattern of fluctuation. While the simulation gives suggestions of peaks at from 3- to 5-year intervals, as occur naturally, the striking feature is the recurrent 4-year lows beginning at year 20, which do not occur naturally. Presumably any tendency in this direction, if it occurs in nature, is prevented by the persistence of large numbers of 5s.

It was not our intention in undertaking the simulation to give ourselves too many 'tries'. In a model employing so many variables there are inherent dangers in continued trials that rationalize new values for the parameters, or which amount to a search for a particular sequence of random numbers. The simulation presented above was the third attempt. The first attempt used the empirical relation of Fig. 5, between proportion of 4s in the parent spawning population and the proportion of 4s in the progeny. In the course of other unrelated model studies we realized that such a procedure in part defeats the purpose of the simulation. While it would inevitably result in a preservation of the proportion of 5s, it would shed no light on understanding (or lack of same) of the consequences of postulated mechanisms. The regression would merely provide that given 0% adult 4s, one would predict 41% 4s in the returns of the progeny; given 100% 4s the expectation is for 63% 4s in the progeny. We accordingly chose to assume for the purpose of the simulation that age of return was inherited simply, despite the weak correlation supporting this contention. The second attempt incorporated such large environmental effects that any potentially meaningful fluctuations were masked. To these we have

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alluded already. It was obvious that the range of effects suggested by the data on survival from egg-to-smolt and smolt-to-adult potentially included depensatory effects as well as environmental influences. Accordingly, the random factors were changed to include only the freshwater influence.

The third attempt, which has been presented, is thus virtually free from manipulation based on hindsight. It underlines a lack of understanding of some obviously essential features of the population biology, chief among which is the mechanism(s) determining age of return of sockeye salmon. Equally apparent is the fact that the depensatory mechanism proposed by Ward & Larkin (1964) as an explanation for dominance in the Adams River run of the Fraser does not provide any simple explanation for the patterns of abundance in the mixed populations of 4s and 5s such as occur on the Skeena. Unfortunately, the almost complete lack of field data on the interrelations between sockeye salmon and other species of organisms (particularly other fish species) necessitates a gross simulation procedure for what is probably a fairly complex natural situation. Although the field evidence for compensatory processes summarized in the Ricker stock-recruit relationship is more extensive, there is nevertheless rather little information available that details the density-dependent processes that are presumably involved. Competition for spawning sites among adults, losses in spawning redds from oxygen deficiencies caused by excessive numbers of eggs, competition for food amongst juveniles and many other possible effects all seem reasonable but have not been adequately documented as bases for compensatory mortalities. It is quite possible that at low densities of adults there are depensatory effects which relate to social behaviour of any of a variety of kinds (Allee 1938). It is also useful to question whether environmental effects are adequately described by a log-normal distribution as treated in this paper and in those of Ricker (1954) and by Larkin & Ricker (1964).

Impressive as the accumulation of statistical evidence may be, it is apparent that much further study is required of the natural history of sockeye salmon and their relations with their physical and biological environment as a basis for understanding the fluctuations in their abundance.

ACKNOWLEDGMENTS

Miss Dolores Doidge cheerfully undertook much of the technical tedium of this study and is warmly thanked. Dr D. H. Chitty was an encouraging and excellent critic whose advice was most helpful.

SUMMARY

1. A commercial fishery at the mouth of the Skeena River, British Columbia, has yielded an average of 881 000 sockeye salmon per year since 1908. The catch is largely 4- and 5-year-old fish that went to sea in their second year. The individual stocks of the Skeena River run are produced in twenty-one lakes and tributary streams, the largest being the Babine Lake watershed which currently provides 90% of the total yield.

2. The purpose of this study was to examine features of population biology, to indicate factors that may have contributed to them, and to assess with a computer simulation, whether a synthesis of the contributing factors explains the observed history of population changes.

3. The main features of the population biology have been the following.

(i) A decline in the total size of the run. This occurred gradually between 1910 and

1948, and was associated with a decline in catch of about 50%. More recently the catch has been about 500 000 sockeye per year. In the short term, abundance has fluctuated over a four- or five-fold range, with major peaks in abundance at 3–5 year intervals.

(ii) Since 1948 there has been a decline in the non-Babine stocks from 30 to 7% of the total.

(iii) The relation between spawning stock size and resultant production for Skeena sockeye is a composite curve reflecting the component stocks. The variability of these makes statistical separation of the component curves difficult. Compensation coefficients of 1·75 and 1·25 for Babine and non-Babine stocks respectively, seem reasonable values in the Ricker type formulation of the stock-recruit relationship.

(iv) There is a weak correlation ($r = 0{\cdot}36$) between the proportion of 4-year-old fish in the present spawning stock and the proportion of 4-year-old fish in the progeny. Ignorance of the mechanisms which determine age of return makes the weakness of the correlation not surprising.

(v) Cyclic recurrence of high brood-success occurred at 5-year intervals up to 1919, irregularly between 1919 and 1932 and at 4-year intervals between 1932 and 1948. The age composition of the spawning populations that produced peaks, varied substantially. Although 4-year-old fish predominated in the brood successes at 4-year intervals, simple notions that 4-year-old parents produce 4-year-old progeny and that a large brood always produces a large brood are inadequate as explanation.

4. Possible contributing factors to population changes are the following.

(i) The commercial fishery was regulated to remove about 60% of the annual run between 1920 and 1939, and 50% from 1940 to 1950. The relation between spawning stock size and production suggests a maximum sustained yield at a rate of exploitation of 57%, and the decline in abundance thus reflects a history of slight over-exploitation. The fishery does not harvest precocious 3-year-old males, and selectively removes 5-year-olds at a rate 1·5 times that of 4-year-olds.

Dates of passage suggest that some of the non-Babine fish may have been relatively unexploited; in general there is no pronounced seasonal differential effect that would account for decline of the non-Babine stocks.

(ii) Sparse information on the rearing capacity of the various lake systems suggests that the non-Babine stock may have less productive environments than the Babine.

(iii) The observed variations in brood success may reflect the effect of big spawning populations on those of following years. Of many possible mechanisms predation in fresh water seems most likely as a mediating factor in the dominating effect of large runs. This depensatory effect, or some similar effect, may maintain 4-year-cycles, each of a very large run followed by three small runs, provided the population is predominantly 4-year-old fish. With the large proportion of 5-year-old fish on the Skeena, dominance effects would be more complex, producing 20-year cycles as multiples of superimposed 4- and 5-year cycles.

5. A model for the simulation of Skeena sockeye stocks was developed as follows.

(i) If these are the major factors responsible for the population fluctuations of Skeena River sockeye salmon, their synthesis in a single model should provide the basis for a simulation of the history of population changes. The general model of Larkin & Hourston (1964) was adapted for this purpose.

(ii) The simulation showed decline in total abundance of an appropriate order of magnitude and decrease in the relative abundance of non-Babine stocks. However, the simulation involved rapid elimination of 5-year-old fish, reflecting the selective action

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of the fishery in conjunction with inheritance of age of return, whereas in the real history 5-year-olds have persisted as a major age group in the run. Additionally, the short-term pattern of fluctuation was different in the simulation from that in nature, showing recurring 4-year lows, related to the predominance of 4-year-olds and the simulated dominance effect.

(iii) The simulation was kept virtually free from manipulation based on hindsight and may therefore be a fair reflection of present understanding of the population biology of Skeena sockeye salmon. It underlines a lack of understanding of mechanisms determining age of return; and a lack of field studies on the possible existence of depensatory mortality from predation or other causes.

REFERENCES

Allee, W. C. (1938). *The Social Life of Animals.* London.

Anon. (1962). Report on salmon stocks of the Pacific Coast of Canada with reference to article III(1)(a) and IV of the International Convention for the High Seas fisheries of the North Pacific Ocean. *Bull. int. N. Pacif. Fish. Commn*, 9, 1–67.

Brett, J. R. (1946). Lakes of the Skeena River Drainage. IV. Kitsumgallum Lake. *Prog. Rep. Pacif. Cst Stns*, 69.

Brett, J. R. (1951). A study of the Skeena River climatological conditions with particular reference to their significance in sockeye production. *J. Fish. Res. Bd Can.* 8(3), 178–87.

Brett, J. R. (1952). Skeena River sockeye escapement and distribution. *J. Fish. Res. Bd Can.* 8(7), 453–68.

Brett, J. R. & Pritchard, A. I. (1946a). Lakes of the Skeena River drainage. I. Lakelse Lake. *Prog. Rep. Pacif. Cst Stns*, 66,

Brett, J. R. & Pritchard, A. I. (1946b). Lakes of the Skeena River drainage. II. Morice Lake. *Prog. Rep. Pacif. Cst Stns*, 67.

Foskett, D. R. (1947a). Lakes of the Skeena River drainage. V. Bear Lake. *Prog. Rep. Pacif. Cst Stns*, 70.

Foskett, D. R. (1947b). Lakes of the Skeena River drainage. VI. The lakes of the upper Sustut River. *Prog. Rep. Pacif. Cst Stns*, 72, 28–32.

Godfrey, H. (1955). On the ecology of Skeena River whitefishes, *Coregonus* and *Prosopium*. *J. Fish. Res. Bd Can.* 12(4), 499–542.

Godfrey, H. (1958). A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. *J. Fish. Res. Bd Can.* 15(3), 331–54.

Godfrey, H., Hourston, W. R., Stokes, J. W. & Withler, F. C. (1954). Effects of a rock slide on Babine River salmon. *Bull. Fish. Res. Bd Can.* 101.

Hanson, A. & Smith, H. D. (1967). Mate selection in a population of sockeye salmon (*Oncorhyncus nerka*) of mixed age-groups. *J. Fish. Res. Bd Can.* 24(9), 955–77.

Larkin, P. A. & Hourston, A. S. (1964). A model for simulation of the population biology of Pacific salmon. *J. Fish. Res. Bd Can.* 21(5), 1245–65.

Larkin, P. A. & Ricker, W. E. (1964). Further information on sustained yields from fluctuating environments. *J. Fish. Res. Bd Can.* 21(1), 1–7.

McConnell, J. A. & Brett, J. R. (1946). Lakes of the Skeena River drainage. III. Kitwanga Lake. *Prog. Rep. Pacif. Cst Stns*, 68.

Milne, D. J. (1955). The Skeena River salmon fishery, with special reference to sockeye salmon. *J. Fish. Res. Bd Can.* 12(3), 451–85.

Neave, F. (1953). Principles affecting the size of pink and chum salmon populations in British Columbia. *J. Fish. Res. Bd Can.* 9(9), 450–91.

Palmer, R. N. (1964). *A re-assessment of Moricetown Falls as an obstruction to salmon migration.* Department of Fisheries of Canada.

Ricker, W. E. (1950). Cyclic dominance among the Fraser sockeye. *Ecology*, 31, 6–26.

Ricker, W. E. (1954). Stock and recruitment. *J. Fish. Res. Bd Can.* 11(5), 559–623.

Shepard, M. P. & Withler, F. C. (1958). Spawning stock size and resultant production for Skeena sockeye. *J. Fish. Res. Bd Can.* 15(5), 1007–25.

Shepard, M. P., Withler, F. C., McDonald, J. & Aro, K. V. (1964). Further information on spawning stock size and resultant production for Skeena sockeye. *J. Fish. Res. Bd Can.* 21(5), 1329–31.

Ward, F. & Larkin, P. A. (1964). Cyclic dominance in Adams River sockeye salmon. *Prog. Rep. int. Pacif. Salm. Fish. Commn*, 11, 1–116.

Withler, F. C. (1945). *An investigation of the distribution of age groups and sexes of sockeye salmon throughout the fishing season at the Skeena River.* M.S. in the Department of Zoology Library, University of British Columbia, Canada.

Withler, F. C. (1948). Lakes of the Skeena River drainage. VIII. Lakes of the Lac-Da-Dah Basin. *Prog. Rep. Pacif. Cst Stns*, 74.

Withler, F. C., McConnell, J. A. & McMahon, V. H. (1949). Lakes of the Skeena River drainage. IX. Babine Lake. *Prog. Rep. Pacif. Cst Stns*, 78.

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