Spawning Stock Size and Resultant Production for Skeena Sockeye[1]

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ABSTRACT

For age 4 and 5 Skeena sockeye, plots of total production of adults from individual brood years against number of parent spawners gave a reproduction curve with an almost linear ascending limb and a very precipitous descending limb. Maximum reproduction (2.4 million sockeye) was achieved at spawning levels of slightly over 0.9 million; the maximum sustained yield (1.4 million) was provided by spawnings of 0.9 million. The stock is very sensitive both to small changes in fishing intensity, and to random variations in survival caused by density-independent environmental fluctuations. Therefore the attainment of high sustained yields by application of a constant optimum exploitation rate is not practical. Regulation to provide the optimum number of spawners each year would more likely provide the highest average yield. Observed fluctuations in commercial catches over the past 50-odd years can be accounted for by changes in annual rates of exploitation. Still higher yields might be attained if individual components of the composite stock studied could be managed separately.

INTRODUCTION

THE SKEENA RIVER is currently the third largest producer of sockeye salmon (*Oncorhynchus nerka*) in British Columbia. Over the past 50 years it has produced an average annual yield to the fishery of 79,439 48-lb. cases of sockeye, or about 953,000 individual sockeye per year. The Skeena sockeye are exploited mainly by gill-nets within a radius of 40 miles of the river mouth and within the lower reaches of the river itself. In the Skeena River system there are some 16 lakes which support sockeye. Of these, by far the most important is the Babine-Nilkitkwa watershed which accommodates about 75% of the annual escapement to the Skeena system as a whole.

Past studies (Milne, 1955; Godfrey, 1958) have shown that there is a positive relationship between the size of the catch in the parent year and the contribution of progeny of that year to the commercial catch. This relationship suggests that the number of adults returning to the fishery from a given brood year may be dependent upon the abundance of spawners in the parent year. The purpose of the present paper is to examine the available information in more detail and to characterize the relationship, if any, between the abundance of spawners and the size of the resulting stock.

HISTORY OF THE FISHERY

The history of the Skeena sockeye fishery, from its inception in 1877 up to 1948, has been described in detail by Milne (1955). It began in 1877 with the establishment of the first cannery. In that year about 3,000 48-lb. cases of sockeye (approximately 37,500 fish) were packed, and about 40 boats were

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employed. From 1877 to 1910, the number of boats and canneries increased progressively, the expansion in effort being rewarded with increasing returns (Fig. 1, Table I). In the peak year 1910, a catch of 185,000 cases (about 2,750,000 sockeye) was obtained by a fleet of some 850 gill-netters.

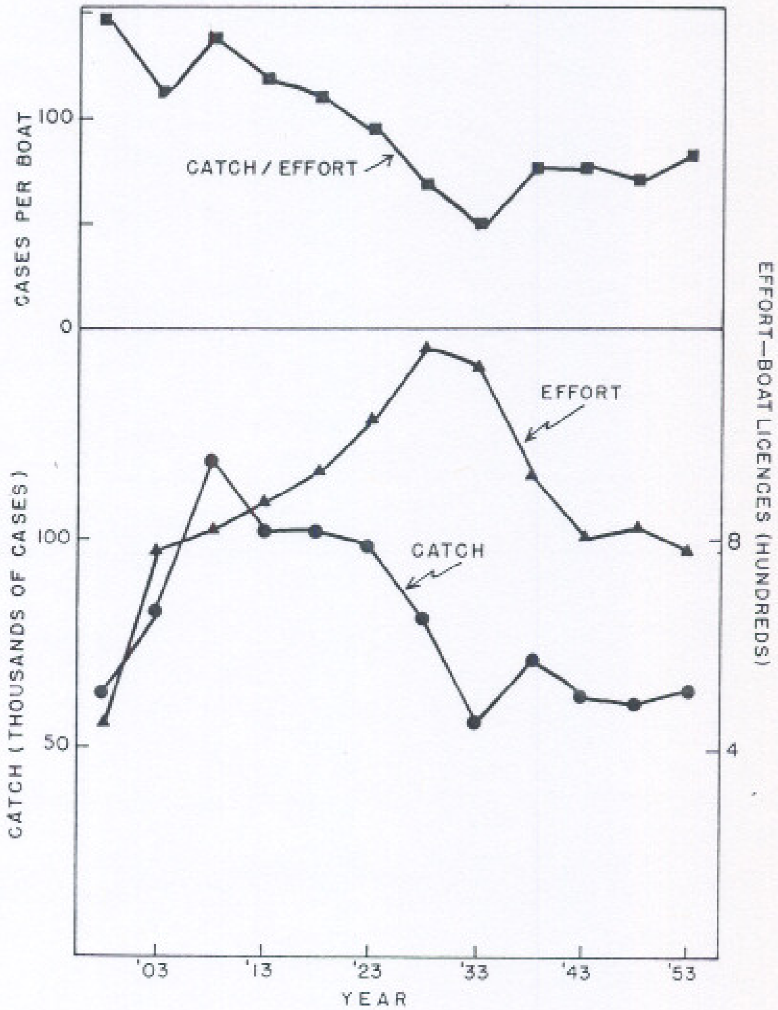

FIGURE 1. Catch, effort, and catch per unit effort for Skeena sockeye, 1896 to 1955 (averaged in 5-year periods).

During the early period of expansion, the increasing exploitation of salmon stocks throughout British Columbia prompted application of conservation measures. By 1894, province-wide regulations had been issued covering the licensing of boats, the type of gear to be used in fishing, and the areas in which fishing was permitted. From 1900 to 1910 concern over the heavy fishing in the Skeena area resulted in a limitation of the number of licences issued to 850 per

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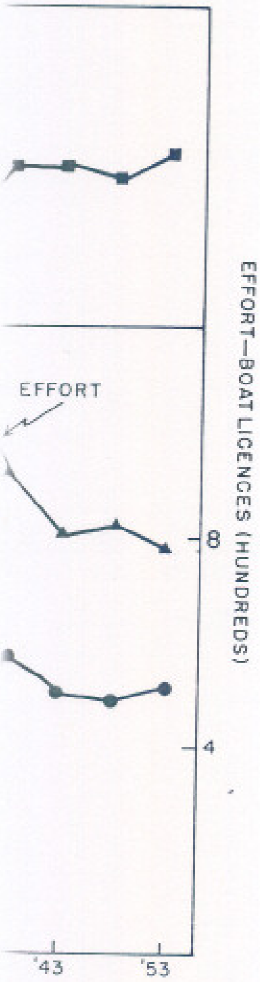

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season, and to stricter enforcement of existing regulations concerning the area of fishing (see figure 1 of Milne, 1955) and the time of fishing (a 24-hour weekly closed period existed during this period).

Beginning in 1915, the number of boats was permitted to increase again and, by 1933, a peak total of 1,218 boats was licensed to fish the Skeena. Not only did the number of boats increase but, from 1924 to 1935, the mobility of the fleet was greatly increased by the replacement of sails by gasoline engines. To counter the increase in effort increasingly stringent regulations were imposed. During the period 1910 to 1936, the upriver boundary had been moved about 8 miles seaward and the weekly closed period had been lengthened from 24 to 48 hours.

From 1910 to 1936 both the catch and the catch per unit effort declined steadily so that, during the 5-year period from 1931–1935, the annual average pack was about 56,000 cases, only 46% of that obtained during the peak 5-year period, 1906–1910 (Fig. 1).

Due largely to the poor return per boat in the mid-1930's, which made maintenance of a large fleet impractical, the number of boats fishing began to drop after 1935 and, by 1941–1945, the fleet averaged only 803 boats per year, compared to the peak average of 1,175 per year in 1931–1935.

Following this decrease in number of boats fishing, the catch climbed slightly and, for the 1941–1945 period, an average annual catch of some 62,000 cases was obtained. With the decrease in number of boats, there was an increase in catch per unit effort of about 50%.

From 1936 to 1954 both the average catch and the average catch per boat remained relatively constant at about 50% of what prevailed during the peak period 1906–10. The catches from 1955 to 1957 were much lower than any since 1885. These lower catches were due to severe restriction of the fishery during the years of return of progeny from broods depleted by the 1951–52 rock slide in the Babine River (Godfrey *et al.*, 1954, 1956).

From 1941 to the present the gear and boats have continued to increase in effectiveness. In 1942 the mechanical drum, which greatly speeds the picking up of nets and permits the fishermen to make more sets, was adopted by the fleet. In 1955, nylon gill-nets, which are said to be about twice as effective as other nets for river fishing, replaced linen nets. These increases in effectiveness were again accompanied by increased restriction. In 1949, the upstream boundary was moved 3 miles farther seaward. In 1953, a special one-week closure was imposed near the peak of the run. During the period 1955–1957 there have been a number of special closures of the fishery during the fishing season, and an extension of the basic weekly closed time from 48 to 72 hours.

In assessing variations in fishing effort, an important consideration in the long-term development of the Skeena fishery has been the participation of fishermen of Japanese origin. As demonstrated by Milne (1955), Japanese have been more effective fishermen than either whites or Indians. Their greater effectiveness is due to the fact that they fish more days of each fishing season and more hours per day. In the early part of the century Japanese fishermen formed a major component of all British Columbia gill-net fishermen. For example, in 1916, 2,506 of

TABLE I. Estimates of catch, escapement, and total returning stock for Skeena 4_2 and 5_2 sockeye, 1902 to 1957, and estimated units of effort and computed exploitation rates, 1908 to 1957. Where there is no entry, data are not available.

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
Year	PACK	CATCH			EFFORT					RATE OF UTILIZATION		SPAWNING ESCAPE-MENT	RESULTANT STOCK		
		4_2	5_2	Total 4_2+5_2	Total boats	Japanese boats	Gas boats	Drum boats	Total boats (weighted)	Instantaneous i	Annual a	P_n	4_2	5_2	Total (S_n)
	cases	*thousands of fish*			*boat licence units*							*thousands of fish*			
1902	117,677	...	...	...	...	...	0	0	...	...	...	...	...	...	...
3	50,968	...	...	...	...	...	0	0	...	...	...	...	...	...	...
4	93,404	...	...	...	...	...	0	0	...	...	...	...	...	...	...
5	84,717	...	...	...	781	...	0	0	...	...	...	...	...	...	...
6	86,394	...	...	...	870	...	0	0	...	...	...	...	...	...	...
7	108,413	...	...	...	700	...	0	0	...	...	...	...	...	...	...
8	139,846	...	...	1,527[1]	863	518[2]	0	0	1,010	0.80	0.55	1,124	1,138	520	1,658
9	87,901	...	...	960[1]	850[3]	510[2]	0	0	994	0.79	0.55	706	575	1,805	2,380
1910	187,246	...	...	2,045[1]	850[3]	510[2]	0	0	994	0.79	0.55	1,506	613	1,308	1,921
1	131,066	...	...	1,431[1]	850	510[2]	0	0	994	0.79	0.55	1,054	781	458	1,239
2	92,498	626	413	1,039	850	510[2]	0	0	994	0.79	0.55	765	513	381	894
3	52,927	316	286	602	850	510[2]	0	0	994	0.79	0.55	444	1,062	675	1,737
4	130,166	337	993	1,330	850	510[2]	0	0	994	0.79	0.55	979	1,775	1,882	3,657
5	116,553	461	772	1,233	962	577[2]	0	0	1,126	0.89	0.59	771	953	1,207	2,160
6	60,923	282	252	534	868	521[2]	0	0	1,015	0.80	0.55	393	273	177	450
7	65,700	552	198	750	788	473[2]	0	0	922	0.73	0.52	623	575	273	848
8	123,322	994	378	1,372	889	533[2]	0	0	1,040	0.82	0.56	970	1,603	849	2,452
9	184,945	629	1,242	1,871	1,153	692[2]	0	0	1,349	1.07	0.66	868	1,847	1,991	3,838
1920	90,869	161	712	873	954	572[2]	0	0	1,116	0.88	0.59	546	782	841	1,623
1	40,018	368	113	481	1,109	665[2]	0	0	1,298	1.03	0.64	244	849	447	1,296
2	100,615	1,010	172	1,182	1,091	642	0	0	1,271	1.00	0.63	625	1,093	394	1,487
3	131,731	1,053	484	1,537	900	578	0	0	1,070	0.85	0.57	1,043	1,213	284	1,497
4	144,732	438	1,115	1,553	941	385	18	0	1,022	0.81	0.56	1,098	389	469	858
5	77,785	501	496	997	1,067	327	65	0	1,115	0.88	0.59	624	1,141	1,205	2,346
6	82,307	656	268	924	1,129	295	75	0	1,158	0.91	0.60	554	1,084	498	1,582
7	83,988	752	244	996	1,195	295	162	0	1,227	0.97	0.62	549	920	424	1,344
8	34,524	245	179	424	1,208	295	257	0	1,249	0.99	0.63	224	482	197	679
9	77,714	696	286	982	1,143	295	263	0	1,192	0.94	0.61	565	336	341	677

	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	0	1,298	1.03	0.64	244	849	447	1,296
2	100,615	1,010	172	1,182	1,091	642	0	0	1,271	1.00	0.63	625	1,093	394	1,487
3	131,731	1,053	484	1,537	900	578	0	0	1,070	0.85	0.57	1,043	1,213	284	1,497
4	144,732	438	1,115	1,553	941	385	18	0	1,022	0.81	0.56	1,098	389	469	858
5	77,785	501	496	997	1,067	327	65	0	1,115	0.88	0.59	624	1,141	1,205	2,346
6	82,307	656	268	924	1,129	295	75	0	1,158	0.91	0.60	554	1,084	498	1,582
7	83,988	752	244	996	1,195	295	162	0	1,227	0.97	0.62	549	920	424	1,344
8	34,524	245	179	424	1,208	295	257	0	1,249	0.99	0.63	224	482	197	679
9	77,714	696	286	982	1,143	295	263	0	1,192	0.94	0.61	565	336	341	677

1930	130,952	694	771	1,465	1,202	295	637	0	1,287	1.02	0.64	742	617	364	981
1	93,029	552	299	851	1,076	295	607	0	1,171	0.92	0.60	510	518	371	889
2	52,624	299	263	562	1,119	295	760	0	1,226	0.97	0.62	310	1,136	420	1,556
3	27,693	215	126	341	1,218	295	669	0	1,304	1.03	0.64	173	420	220	640
4	54,558	389	215	604	1,164	295	740	0	1,264	1.00	0.63	320	626	594	1,220
5	52,879	316	222	538	1,053	295	842	0	1,177	0.93	0.61	310	850	333	1,183
6	81,960	670	219	889	970	295	882	0	1,108	0.88	0.59	556	2,156	788	2,944
7	41,023	231	231	462	850	295	840	0	997	0.79	0.55	340	763	439	1,202
8	46,988	382	134	516	1,049	295	1,043	0	1,196	0.94	0.61	297	227	308	535
9	68,388	459	321	780	844	295	841	0	992	0.78	0.54	598	273	1,045	1,318
1940	116,505	1,229	190	1,419	926	295	922	0	1,073	0.85	0.57	963	683	1,602	2,285
1	81,183	450	465	915	981	295	976	0	1,128	0.89	0.59	572	486	697	1,183
2	29,976	111	215	326	775	0	774	774	860	0.68	0.49	305	356	549	905
3	28,259	131	148	279	749	0	749	749	831	0.66	0.48	272	171	306	477
4	67,855	321	491	812	725	0	725	725	805	0.64	0.47	824	2,163	993	3,156
5	103,940	243	801	1,044	787	0	787	787	874	0.69	0.50	940	218	577	795
6	52,928	89	450	539	877	0	877	877	973	0.73[4]	0.52[4]	486	334	778	1,112
7	32,511	58	319	377	750	0	750	750	833	0.69[4]	0.50[4]	307	397	514	911
8	101,268	1,125	159	1,284	833	0	833	833	925	0.73	0.52	1,066	1,846	581	2,427
9	65,937	125	569	694	886	2	886	886	985	0.81[4]	0.55[4]	480	759	604	1,363
1950	47,479	105	389	494	800	90	800	800	938	0.73[4]	0.52[4]	382	430	171	601
1	61,694	219	429	648	791[5]	...	791	791	...	0.78[6]	0.54[6]	163	61	123	184
2	114,775	949	264	1,213	860[5]	...	860	860	...	0.73[6]	0.52[6]	158	421	216	637
3	65,003	342	262	604	813[5]	...	813	813	...	0.62[6]	0.46[6]	701	524	...	...
4	60,817	206	289	495	778[5]	...	778	778	...	0.70[6]	0.50[6]	510	...	...	...
5	14,649	24	93	117	663[5]	...	663	663	...	0.76[6]	0.53[6]	100	...	...	...
6	14,663	126	19	145	...	...	...	...	...	0.30[6]	0.26[6]	361	...	...	...
7	25,428	191	73	264	...	...	...	...	...	0.43[6]	0.35[6]	448	...	...	...

[1]Estimated assuming 10.9 4_2 and 5_2 fish per case (the average number of 4_2 and 5_2 fish per case for the 1916–1925 period).
[2]Assuming that 60% of the gill-net licences were issued to fisherman of Japanese origin (see text, p. 1012).
[3]No record available. Boat licences were assumed to be 850.
[4]See Table II.
[5]Licences no longer issued by area. Boat figures derived from Fishery Officer's estimates of number of boats fishing.
[6]Derived from catch, escapement statistics similar to those in Table II.

the 4,615 gill-net licences issued in the province were taken out by Japanese fishermen (Anon., 1918, p. 240). On the Skeena, although accurate records are not available for the years prior to 1922, it is probable that about 60% of the gill-net fleet was manned by Japanese. Between 1922 and 1926 the number of Japanese fishermen was reduced by licence limitations from about 60% of the total Skeena fishermen to about 35%; and from 1926 to 1941, when the total licences issued for the Skeena varied between 844 and 1,218, the number of licences issued annually to Japanese remained at 295. In 1941, as a consequence of wartime regulations, all Japanese left the Skeena area. They began to return to the Skeena fishery in 1949 and at present again form a substantial segment of the Skeena gill-net fishermen.

ESTIMATION OF STOCK SIZE AND ABUNDANCE OF SPAWNERS

In order to determine the relationship between the number of spawners and the resultant total stock, it is necessary to obtain two pieces of information: first, the abundance of the total stock returning from the seeding of a given year; and second, the number of fish spawning in the parent year. To estimate the magnitude of the total returning stock, it is necessary to determine the contribution of each brood year to both the commercial catch and the escapement. On the Skeena, sockeye predominantly mature at 4 and 5 years of age. Thus the total stock of returning adults produced by the spawners in year n would be the number of 4-year-old fish in both the catch and escapement in the year $n + 4$ and the number of 5-year-old fish in the catch and escapement in year $n + 5$. Data on both the magnitude of the commercial catch and on its age composition are available since 1912. However, reliable data on the abundance and age composition of spawners are available only since 1946 (e.g. Brett, 1952).

Estimates Prior to 1946 and in 1948

Without direct measures of the characteristics of the spawning populations prior to 1946, it becomes necessary to estimate the size of annual sockeye escapements and their age compositions by indirect means. For the years in question, such estimates could be derived if the annual rate of exploitation and the number of fish in the catch, and the age composition of both the catch and escapement, were known.

ESTIMATION OF ANNUAL EXPLOITATION RATES

For the period 1946 to the present, relatively accurate estimates of the rate of utilization and the age composition of the escapement are available from catch statistics and from examination of fish on the spawning grounds. The number of boats fishing on the Skeena is also known for this period. If it is assumed that the instantaneous rate of fishing in any year is proportional to the number of boats operating in that year, and knowing the number of boats operating in both the recent and earlier periods, it is possible to estimate annual exploitation rates in years prior to 1946.

In establishing the rate of exploitation in recent times, it is necessary to restrict consideration to years in which the pattern of the fishery (with respect to length of fishing season and to duration of weekly closed periods) was essentially similar to that which existed in the pre-1946 period, and in which reliable measures of the size of spawning escapements were available. The years 1946, 1947, 1949, and 1950 fulfil these requirements.[2] Estimates of the rate of exploitation and instantaneous rate of fishing for these years are given in Table II (columns VII and VIII). From these data it is seen that in the years in question the rate of exploitation averaged slightly over 50%.

In determining the number of units of effort (here the number of boats fishing) for each year, the number of licences issued (see Table I) can be used as the measure of the number of boats fishing each season. However, because the effectiveness of gear has varied over the period under study, and because the proportion of Japanese fishermen also has changed, direct use of boat licence data would provide biased measurements of rates of exploitation. It is therefore necessary to adjust the boat licence data for changes in fishing effectiveness of gear and fishermen. Milne (1955) has examined the comparative effectiveness of fishermen of different racial origins and of the effectiveness of gasoline boats (commonly called 'gas' boats) as compared to sail boats, and has used these data to arrive at weighted measures of fishing effort (adjusted numbers of boats). He accepts as his unit of effort 1 gas boat operated by a white or Indian fisherman. To account for the lesser effectiveness of sail operations he applies a factor of 0.9 to sail boats and to adjust for the greater effectiveness of the Japanese, applies a factor of 1.5 to all boats operated by Japanese licence holders. Because the introduction of mechanical net drums occurred suddenly (in 1942), there are no data available to assess the difference in effectiveness between boats equipped with drums and others. However, the increased effectiveness of drum operation is provided primarily by the ability of the operators to haul their nets more quickly and thus to make more sets per unit time. This advantage is very similar to that conferred by the addition of the gas engine to the old sail boat hulls, in permitting gas boat operators to make more drifts over favoured fishing grounds (bars) per unit time. Without more precise data it is most reasonable to assume that mechanical-drum gas boats had about the same degree of increased effectiveness over non-drum gas boats. Thus, a factor of 1.11 would be assigned to drum-equipped boats.

In Table I, the number of gill-net boats licensed for the Skeena area since 1908 are listed (column VI). By applying the factors described in the foregoing paragraph, weighted numbers of boats have been derived and are given in column X of Table I.

Using these weighted numbers of boats as the measure of effort, estimates of the rates of exploitation for the period 1908–1945 and in 1948 were derived as

[2]Escapement estimates are not reliable for 1948 (due to a washout of the Babine adult counting weir), nor in 1951 and 1952 (due to the destruction of a large part of the escapement by the Babine River rock slide). From 1953 on, the seasonal pattern of the fishery has been altered by a series of special closures and strikes.

TABLE II. Rates of utilization and fishing effort for Skeena sockeye; 1946, 1947, 1949 and 1950.

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Year	Commercial catch	Indian[1] catch	Spawning escapement	Total[2] escapement (III+IV)	Total stock (II+V)	Rates of utilization[4] (II/VI)		Boats	Japanese boats	Weighted boats[3]	Unit rate of fishing (VIII/XI)
	thousands of fish					a	i	no.	no.	no.	c
1946	644	39	555	594	1238	0.52	0.73	877	0	973	0.00075
1947	385	41	345	386	771	0.50	0.69	750	0	833	0.00083
1949	766	48	569	617	1383	0.55	0.81	886	2	985	0.00082
1950	527	43	443	486	1013	0.52	0.73	800	90	938	0.00078
Average						0.52	0.74	828		938	0.00079

[1]Catch of sockeye in Indian food fisheries above the commercial fishing boundary.
[2]Total escapement is composed of all fish escaping the commercial fishery (i.e. catch of upstream Indian food fishery plus spawners).
[3]During this period all boats were equipped with mechanical drums. Appropriate weighting factors have been applied (see page 1013).
[4]The annual rate, a, is the catch divided by the total stock; the instantaneous rate, i, is equal to $-\log_e(1-a)$.

follows: In the period 1946–1950, for which the rate of exploitation is known with some precision, the average rate, 52.3%, was effected by an average of 932 weighted boats.[3] Converted to an instantaneous rate of fishing, this exploitation rate becomes 0.740. Thus the average instantaneous rate of fishing per boat is calculated as $0.740/932 = 0.00079$. In column XI of Table I the weighted boat values have been multiplied by this estimated unit rate of fishing to arrive at estimates of the total rate of fishing in each year. In column XII these are converted to arithmetic rates of exploitation (fraction of the population caught).

These rates of exploitation were computed without regard to the possible influence of changes in fishery regulations on the effectiveness of the fleet. The main changes during the period under study were movements of the up-river fishing boundary (in 1925, 1935 and 1948). Available data indicate that the changes that did occur probably did not exert extreme effects on effectiveness. For example, the rate of exploitation prior to the 1948 boundary change was very similar to that observed in the period immediately following the shift (Table II). As a consequence, no corrections have been made to the effort data to account for changes in regulations in the pre-1946 period.

ESTIMATION OF AGE COMPOSITION AND CATCH ABUNDANCE

In studying the relation between the abundance of the total stock and the size of parent spawning escapements, it would be expected that the most precise relationship would be achieved if statistics for a single stock could be employed. As mentioned earlier, however, the Skeena sockeye population is composed of several different stocks and precise separation of the single most important stock (that of the Babine-Nilkitkwa area) is not possible. Nevertheless, differences in the age composition of the runs to some lakes permit some restriction in the number of stocks that must be treated as a unit.

Examination of the age composition of the catches (summarized annually in the British Columbia Provincial Fisheries Reports, 1912 to 1957) indicate that the majority of adult sockeye in the catch are 4- and 5-year-old fish that have spent one year in fresh water (4_2's and 5_2's). However, every year there are also substantial numbers of fish of 5 and 6 years of age that have spent two years in fresh water (5_3's and 6_3's). Recent observations of scales from fish taken on the spawning grounds indicate that most of these 5_3's and 6_3's spawn in the Morice and Alastair Lake systems and that the runs to these two areas contain relatively few 4_2 and 5_2 individuals. The spawning runs to Morice and Alastair Lakes have comprised, on the average, about 13% of the total Skeena spawning escapement in recent years. Of sockeye utilizing the remaining lake systems, about 85% utilize the Babine-Nilkitkwa watershed. Thus, if the 5_3 and 6_3 fish are omitted from estimations, the resultant relationship between escapement and return will reflect more accurately the performance of the single most important stock in the Skeena system.

[3]Correction factors used in Table I were also applied in column XI of Table II.

In Table I, columns III and IV, the estimated numbers of 4_2 and 5_2 fish in each year's catch are listed and the total given in column V. These data were derived using essentially the same method as was outlined by Godfrey (1958, p. 333). However, some adjustments were made to correct for errors in sampling procedures. In the early years especially, it was found that sampling was not carried out in proportion to seasonal changes in the abundance of the catch. To correct for this, the annual age compositions were recalculated by weighting the observed weekly estimates of age composition according to the weekly abundance of the catch. In general, these recalculations necessitated only relatively small changes in earlier estimates of age composition (e.g. Godfrey, *loc. cit.*).

ESTIMATION OF SPAWNERS AND RETURNING STOCK

With the above information on the rates of exploitation, data on the abundance and age composition of the catch may now be utilized to provide estimates of the abundance of spawners in the years prior to 1946 (and 1948), and of the abundance of the returning stock produced by the spawnings of those years.

Estimates of total escapements in the pre-1946 period and in 1948 would be derived as follows:

(1) $$E_n = C_n \left(\frac{1-a}{a}\right)$$

Where: E_n = total escapement in year n,
C_n = total catch in year n (4_2's and 5_2's),
a = annual rate of exploitation in year n.

However, the escapement figures derived in expression (1) include a number of sockeye that would be taken in the Indian food fishery before reaching the spawning grounds. In Table III, available data on Indian food catches are compared with the total estimated escapement for the period 1935–1948. The data indicate that during this period the Indian catch comprised 9.2% of the total escapement. To arrive at an estimate of the total *spawning* escapement, it is therefore necessary to apply a factor of 0.9 to expression (1). The size of the spawning stock is therefore calculated as:

(2) $$P_n = 0.9\, E_n = 0.9\, C_n \left(\frac{1-a}{a}\right)$$

Where: P_n = total spawners in year n.

Estimates of spawning escapements for the pre-1946 period and in 1948 are listed in column XIII of Table I.

For the pre-1946 period and for 1948, the total resultant stock (i.e. the catch and the escapement arising from the spawning in a given brood year) was estimated as follows:

(3) $$S_n = \frac{C_{4n+4}}{a_{n+4}} + \frac{C_{5n+5}}{a_{n+5}}$$

numbers of 4_2 and 5_2 fish in
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Where: S_n = total resultant stock arising from the spawning of year n,
C_{4n+4} = catch of 4_2 fish in year $n + 4$,
C_{5n+5} = catch of 5_2 fish in year $n + 5$,
a_{n+4} = annual rate of exploitation in year $n + 4$,
a_{n+5} = annual rate of exploitation in year $n + 5$.

Values for S_n are listed in column XVI of Table I.

TABLE III. Total Skeena Indian food catches of sockeye and total estimated escapements of 4_2 and 5_2 fish for the years 1935–48. Catches shown are from data of Pritchard (1948); they exclude catches made on the Bulkley River system, where the sockeye are predominantly 5_3 and 6_3 fish bound for Morice Lake.

Year	Indian catch	Estimated total escapements
	thousands of fish	
1935	51	344
1936	99	618
1937	56	378
1938	58	330
1939	71	664
1940	137	1070
1941	58	636
1942	40	339
1943	29	302
1944	48	916
1945	36	1044
1946	28	1185
1947	36	514
1948	30	343
Average	56	620

ESTIMATES FOR 1946 TO 1957 (EXCLUDING 1948)

For the period from 1946 on (except 1948) spawning stock estimates were based on Babine River weir counts and stream survey estimates for all other Skeena spawning grounds except those of Morice and Alastair Lakes.[4] Total escapements from the commercial fishery were derived by adding the spawning ground estimates to Indian food catches (excluding those taken on the Bulkley River, migration route for Morice Lake spawners). The estimates of spawning escapements are listed in column XIII of Table I.

Examination of length frequency distributions of spawning fish to obtain gross indices of age composition indicates, that in most years, the age composition of the spawning stock roughly parallelled that of the commercial catch. However, in the years 1946, 1947 and 1950, there was apparently a higher proportion of 4_2's in the escapement than in the catch. For the period 1946–1954 the age composition of the escapement was taken to be the same as that in the catch, except for the 3 years mentioned above, for which the proportion of 4_2's in the escapement was

[4]See p. 1015.

adjusted upward. From 1955 to 1957, special closures of the fishery (as mentioned earlier) distorted the normal seasonal pattern of fishing, making it impossible to use catch age composition data for estimating age composition of spawners. In these years, age composition data concerning the escapement were derived by examination of scales from samples of sockeye taken by a research boat fishing throughout the season above the commercial fishing boundary.

From these data the contributions to both the catch and escapement, of the spawning in a given brood year, were determined and the estimates listed in columns XIV, XV and XVI of Table I.

RELATION BETWEEN SPAWNERS AND RESULTING STOCK

For the period 1908–1957, estimates have been derived of the annual abundance of spawners and of the total stock of returning adults produced from these spawnings. Consideration has been restricted to 4_2 and 5_2 fish, which are predominantly sockeye originating in a single large lake system, the Babine-Nilkitkwa. In Fig. 2, the estimated number of fish produced from the spawnings of individual brood years is plotted against the abundance of spawners in the parent year. A diagonal line has been drawn to indicate the locus of points wherein the total resultant stock would just equal the number of fish spawning in the parent year. Hence, points lying above this "45-degree line" represent cases where the total resultant stock was greater than the number of parent spawners, and points below the line indicate brood years in which the total return was less than the number of spawners in the parent year.

In general, the return and the number of spawners have tended to vary together; small spawnings have tended to provide small returns, and, although the resultant stocks vary widely at high spawning levels, the largest returns have been obtained from larger—though not the largest—seedings. In only two brood years of the 45 examined were the returns smaller than the number of parent spawners. In other words, in only two years did the spawning stock fail to replace itself.

To characterize the relationship described above, the points have been fitted empirically by the trend line shown in Fig. 2. This line was derived by ranking escapement-return data according to the abundance of spawners (net escapement), then by determining the moving mean by fives for associated escapement-return values. The moving mean values of the resultant stock were then plotted against the appropriate moving mean values for the parent escapements, and a line drawn by eye through the points (Fig. 3).

The shape of the trend line in Figures 2 and 3 indicates that, for spawning escapements from 0.2 million to 0.9 million increasing escapements on the average provided increasing returns. Between 0.9 and 1.0 million spawners, the maximum return was achieved; at escapement levels beyond 1.0 million, the absolute magnitude of the return decreases.

The above relationship indicates that, for that portion of the Skeena stock under study, the abundance of spawners is one of the most important factors determining the production of sockeye. The almost direct linear relation between spawning population and average return in the ascending limb of the curve

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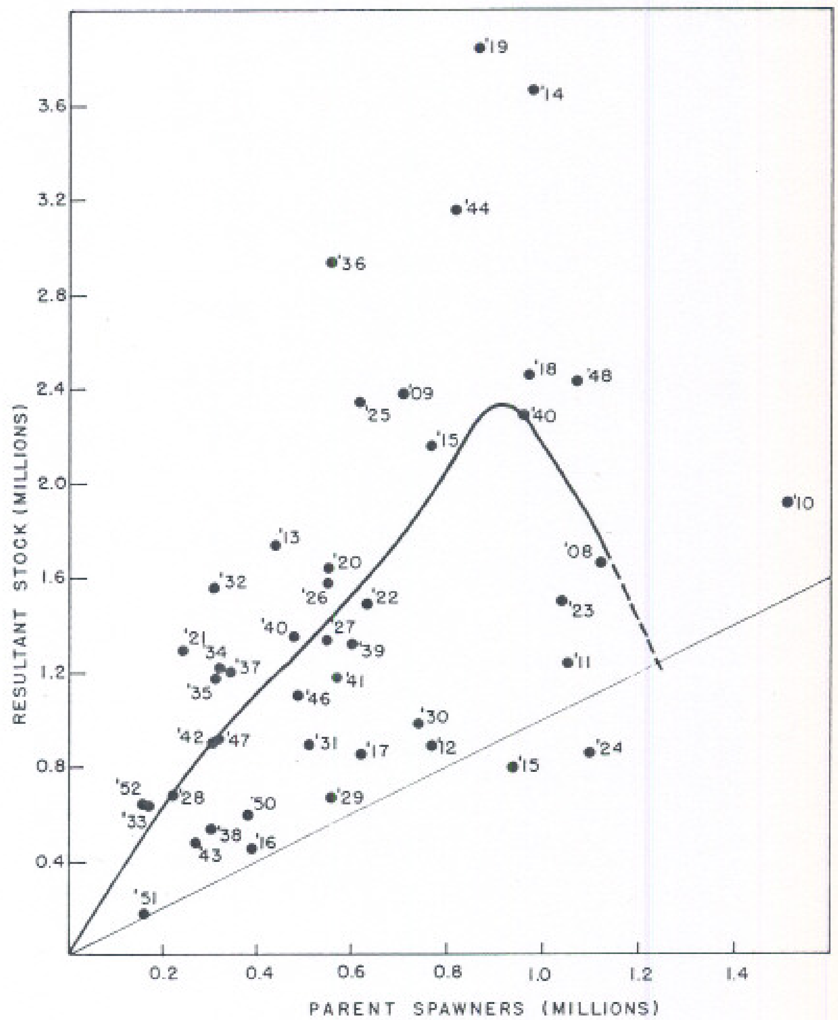


FIGURE 2. Numbers of 4_2 and 5_2 Skeena sockeye (catch plus escapement) plotted against numbers of parent spawners. Figures in the body of the graph indicate brood years. For the trend line, see Fig. 3.

indicates that for spawning populations up to 0.9 million, the capacity of the environment to produce sockeye is not limiting. However, the decrease in the size of the average return in the upper part of the curve strongly suggests that the capacity of the environment to produce sockeye is exceeded at spawning levels beyond 1.0 million.

It is probable that limitation of production at high population levels occurs during the early freshwater history of the sockeye. This limitation could either take place on the spawning grounds or in the lake nursery area. Although there are no data available to indicate that the Skeena spawning beds have been overtaxed, the amount of spawning area available to the fish is finite, and it is

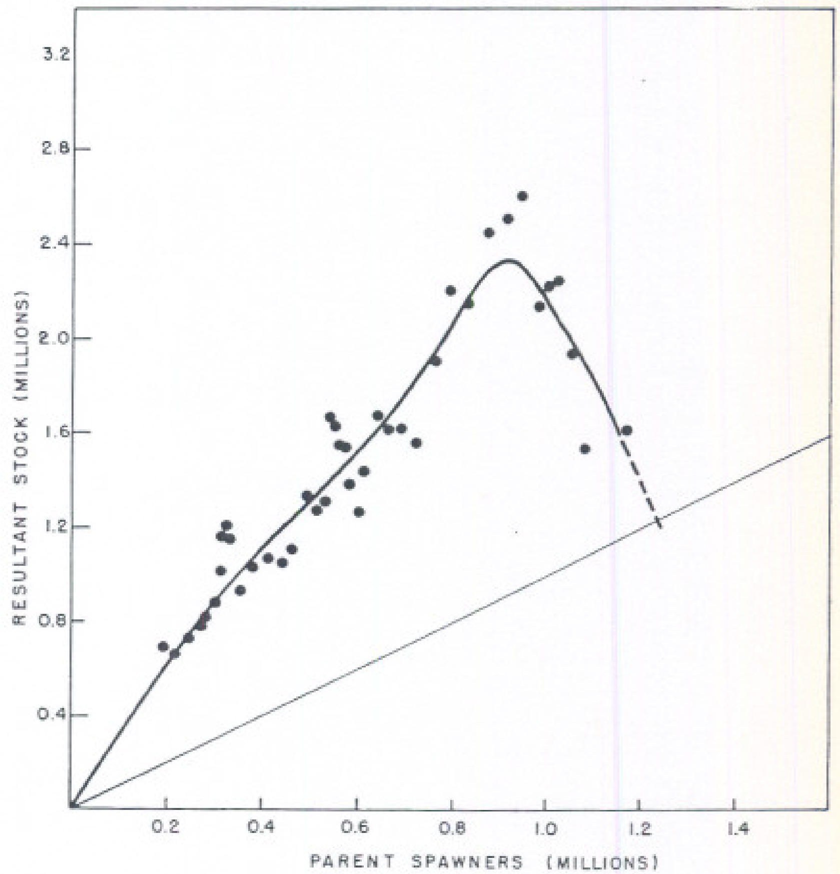
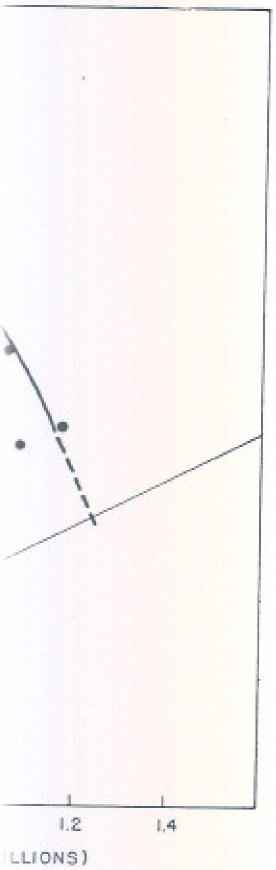


FIGURE 3. Coordinates of moving means (by fives) of ranked parent spawner and total resultant stock data, to illustrate derivation of the trend line in Fig. 2 (see text, p. 1018).

possible that in some years over-seeding may have occurred. Evidence has recently been provided to indicate that the lake nursery area of some parts of the Babine–Nilkitkwa system is sometimes sufficiently densely populated by young sockeye to result in a decrease in growth rate (Johnson, 1956). As indicated by Foerster's (1944, 1954) work at Cultus Lake, such reduction in growth (presumably as a consequence of competition for food) may result in a lowering of survival rate and a proportionately poor return of adults.

In examining the spawner-return relationship in Fig. 2, it is evident that the individual points scatter widely about the trend line. At spawning levels in the region of the ascending limb of the curve, the deviations of the observed returns from the trend line are smallest near the origin and tend to increase with increasing spawners. In Fig. 4 the data used in Fig. 2 have been plotted on a double logarithmic scale. Here it is seen that the logarithms of the deviations from the trend line are no greater at high spawning levels than at lower levels, indicating that the proportional variation is the same throughout the range of spawnings up



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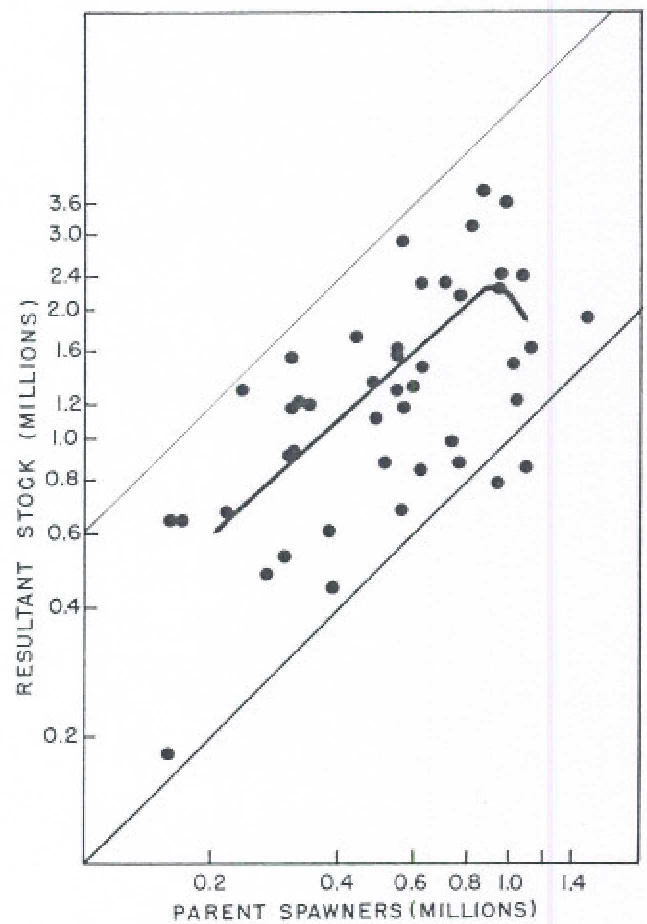

FIGURE 4. Double logarithmic plot of resultant stock against parent spawners for 4_2 and 5_2 Skeena sockeye. The lower diagonal line is the replacement line; the upper diagonal line represents the approximate upper limit of variation of the points. The trend line between diagonals was transposed directly from the trend line in Figures 2 and 3.

to 0.9 million. This pattern of variation probably results from the influence of randomly fluctuating environmental conditions which affect the survival of the sockeye independently of their abundance. Such factors would affect both large and small populations in the same proportionate manner. Examples of such factors might include adverse temperatures, or scouring of spawning grounds by floods, both of which would probably destroy the same proportion of deposited eggs whether the spawning were sparse or dense.

SPAWNER ABUNDANCE, EXPLOITATION AND YIELD

The curve derived in Fig. 2 reflects the performance of 4_2 and 5_2 Skeena sockeye over the past half century. As outlined earlier, these fish originate primarily in the Babine-Nilkitkwa system and for the purposes of the foregoing development have been considered as members of a single stock. However, the sockeye of the Babine-Nilkitkwa system actually comprise several individual runs, each having its own spawning area and characteristic time of migration. For some of these runs, the young live throughout their early freshwater life in separate basins of the system (Johnson, 1956). In general, the early-running fish tend to populate the large main area of Babine Lake, whereas later-running fish are primarily destined for spawning grounds adjacent to the outlets of Babine and Nilkitkwa Lakes. Thus, the curve in Fig. 2 represents the spawner-return relationship for a population containing several stocks, each of which would have its own spawner-return relationship. In any one year, the stocks may each be responding to a different relative level of spawning density with respect to the capacity of its own environment.

Prior to 1954, the seasonal pattern of fishing was such that all important segments of this mixed stock were fished with about the same intensity. Recently however, it has become apparent that the spawning escapements of early running stocks to the main basin tributaries of Babine Lake have been much smaller than those which would result in full utilization of the lake nursery area (Johnson, 1956). For this reason, in 1956 and 1957 the fishery has been closed during the early part of the season, disrupting the traditional seasonal pattern of fishing that had existed during the previous 50-odd years. If such regulations are effective in increasing production from this segment of the Babine-Nilkitkwa stock, then the spawner-return relationship indicated in Fig. 2 might be significantly altered.

Even though, as suggested above, changes in the traditional seasonal pattern of fishing might alter the shape of the composite curve, it nevertheless describes the responses of the mixed stock under the rather uniform seasonal fishing conditions[5] existing until very recent times.

Ricker (1954) has discussed the use of reproduction curves for studying the relationship between spawner abundance, exploitation and yield. In Figures 2 and 3, the height of the derived spawner-return curve above the replacement line indicates the number of fish in the returning stock that would be available for fishing if the number left to spawn in the years of return were to just equal the number of parent spawners. For example, in Fig. 2, when the parent spawners number 1.0 million, total returning stock would average about 2.2 million. If in the year of return an escapement equal to that of the parent year were to be allowed, then the fishery could take $2.2 - 1.0 = 1.2$ million fish. In Fig. 5a, estimated average yields for various numbers of parent spawners are illustrated. Since the total harvest is shared between the commercial fishery and the Indian food fishery, two yield curves have been shown; the top line representing the total yield and the bottom line indicating that part of the yield taken by the commercial fishery[6] alone. The data show that the maximum average total yield would be obtained from spawnings in the order of 0.9 million. Of the total yield of 1.4

[5]Cannery records and records of regulations as far back as 1917 indicate that the seasonal patterns of catch and effort did not change greatly from 1917 until recent times.

[6]The yield to the commercial fishery is estimated by assuming that the Indian fishery take is equal to 10% of the total escapement from the fishery.

million fish, the commercial fishery would take about 1.3 million. Spawning escapements greater and less than 0.9 million provide smaller average yields. As suggested by Fig. 5b, at spawning levels above about 1.25 million fish, the spawning stock would fail to reproduce itself and thus there would be no surplus for fishing[7].

Ignoring the effects of random environmental variations, the stock would be stabilized at various spawning levels by the imposition of different steady rates of exploitation (Ricker, 1954). In Fig. 5, the equilibrium points for various rates of exploitation are indicated by arrows.

Because the ascending limb of the reproduction curve is nearly straight, minor variations in the rate of exploitation would theoretically bring about drastic changes in the level at which the stock would stabilize. Thus, if the estimated commercial fishing exploitation rates varied in the relatively narrow range between 57% and 67%, the stock could reach equilibrium at spawning levels anywhere between 0.1 and 0.9 million spawners, with yields between 0.2 million and 1.3 million. This means that at commercial exploitation rates in the vicinity of 60%, the stock is very sensitive to small changes in fishing pressure. Since the maximum sustainable yield would be obtained theoretically by a commercial rate of exploitation in this same general range (57% as indicated in Fig. 5b), the problems involved in attempting to crop the stock at the optimum level through providing a constant annual rate of exploitation would be very great.

If the steady rate of exploitation were to exceed 70% for any considerable period, the stock would be reduced to a level close to extinction.

At commercial exploitation rates below about 57%, the stock would stabilize at levels of spawning associated with the descending limb of the curve. In this area, the curve is not particularly sensitive to minor changes in fishing pressure, but because of its precipitous slope would be very sensitive to random variations which provided higher returns than the average; i.e. if, with constant fishing rates below about 50%, fortuitous environmental conditions made the returning stock greater than expected, the resultant run would be pushed further down the descending limb and the return in the next generation would be drastically reduced.

As illustrated by Ricker (1958), when year-to-year variations in the success of survival are considered, the average yield obtainable from fish stocks is usually greater if the fishery is regulated to provide the optimum number of spawners rather than to apply the best constant rate of exploitation. This is especially true of sensitive stocks like the Skeena sockeye, where modest deviations from the average magnitude of the returning run can cause disastrous declines in yield if a constant fraction of the stock is taken every year. Furthermore, even if the returning stock conformed exactly to Fig. 3, it would in practice be very difficult to maintain the rate of exploitation within the narrow range required to provide a high yield. Thus best management of the Skeena stock involves varying the rate

[7]For the sake of simplicity in this discussion, the fish are considered to return to spawn at a single age. Values obtained for *average* yield under different fishing intensities and at different parent spawning levels are the same whether the returning stock is considered to be composed of one or several age-classes.

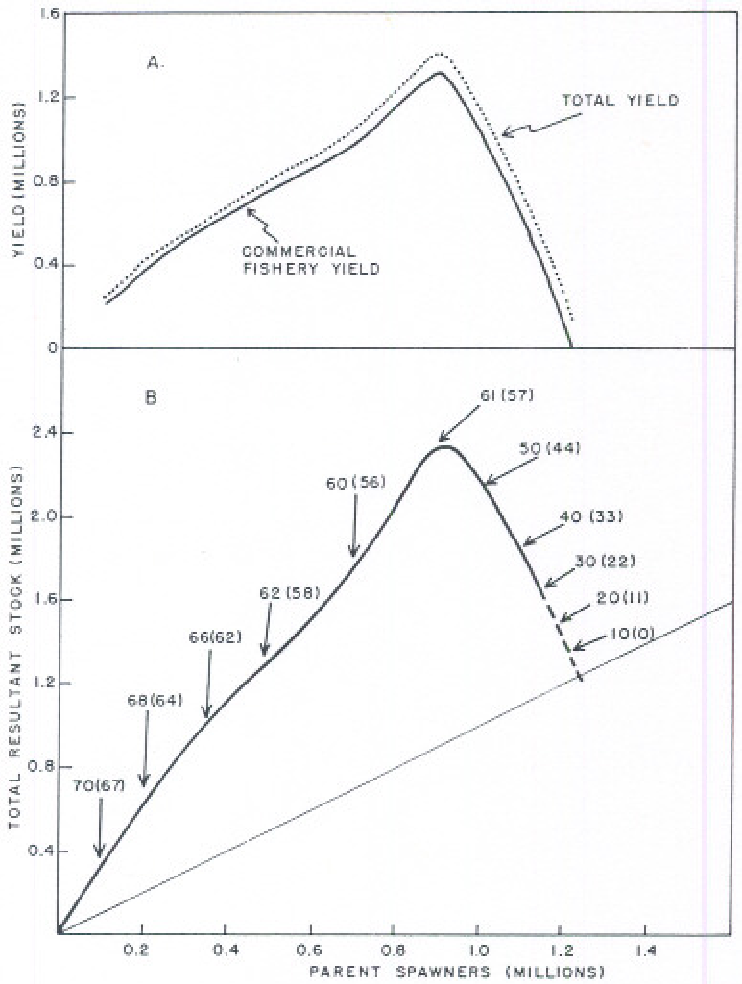

FIGURE 5. Relation between exploitation, stock level, and yield for Skeena 4_2 and 5_2 sockeye. A. Variation in equilibrium yield with size of parental spawning. B. Rate of exploitation, as percentage, associated with stabilization of stock at various numbers of parent spawners. Unbracketed figures in the body of the graph indicate total rates of exploitation (commercial fishery plus Indian food fishery); figures in brackets indicate rates of exploitation exerted by the commercial fishery alone.

of utilization as the size of the stock varies, in order to provide something close to the optimum number of spawners—about 900,000—each year.

Actually, as mentioned earlier, even higher sustained yields might be obtained from the Skeena sockeye population if individual parts of the composite stock (considered as a unit stock in the present paper) were managed as separate units.

The observed fluctuations in the commercial yield of Skeena sockeye over the past 50 years have followed a pattern that would be expected as a consequence of the interaction of the observed changes in rate of exploitation with the spawner-return relationship. The average yield to the fishery in the period from 1910 to the early-1920's (Fig. 1) remained fairly constant at a level of about 100,000 cases (about 1.0 million fish). The rates of exploitation applied to the parent stocks of these runs hovered around 55%. According to the reproduction curve, commercial exploitation rates of this order would be expected to stabilize the stock at levels near the top of the ascending limb (Fig. 5) and would be expected to provide average yields of about 1 million fish.

From the early 1920's to the mid-1930's the catch fell. In the period during which the parents of the fish contributing to these catches were being exploited, the rate of exploitation had risen to slightly over 60% (Table I), a removal rate which would be expected to move the equilibrium point on the curve toward the left and downward, and to provide smaller yields than in the former period.

From the mid-1930's to early 1940's, the rate of exploitation declined and levelled off in the vicinity of 50%, and the decline of the catch was arrested. The observed respite in fishing increased the average size of the spawning escapements, with the result that the stock would respond by moving upward along the ascending limb of the curve of Fig. 5. However several generations would be required before the stock would become stabilized at higher levels and provide the corresponding average yields.

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