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Predator Control and Sockeye Salmon Production

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Abstract

Fairly intensive gill-netting in Cultus Lake was done from 1935 through 1942. Its influence upon the different predaceous fishes of the lake varied. Only the char quickly declined in abundance and remained scarce. Trout not only failed to decrease, but fluctuated upward during the years 1938-40. Coho varied sharply in numbers, but the changes in successive broods were related to the number of parent spawners which entered the lake, rather than to the netting program. Squawfish, the most numerous predator, were quickly decimated in their intermediate size range and such sizes never regained their original abundance. However the smaller squawfish were less affected, and the smallest nettable sizes increased greatly in 1940 and 1941, possibly because the original slaughter of large squawfish five years earlier restricted cannibalism.

Changes in mortality rate of sockeye over the same period involve the year-classes of 1933-40. These changes show little resemblance to changes in the apparent populations of salmonids, either individually or collectively, but they do parallel the size of the squawfish population, except for one year. This exception may be explicable as the result of an unfavorable effect, upon sockeye fry survival, of having a large population of year-old sockeye in the lake - for which there is some independent evidence.

Although netting of the kind and amounts done in 1938-42 did not suffice to prevent the upsurge of young squawfish in 1941-42 from increasing sockeye mortality to a normal level, the addition of various kinds of netting in summer and early autumn, along with increased winter and spring effort, would quite likely have done so. At least further attempts are warranted.

Production data for the lake suggest that its maximum capacity for sockeye growth over a year's time is about 45 metric tons, which yields 14 tons of smolts at normal survival rates, and 21 tons at the survival rates characteristic of the first years of predator control (broods of 1934-38). The minimum desirable smolt size is about 6 grams so the above difference of 7 tons corresponds to 1,200,000 smolts, which in turn could provide about 143,000 additional adult salmon to the fishery, worth $179,000 in 1952. Since the cost of control would be about $10,000 per year, this gives a measure of the possible benefit of an intensified netting program. However the reaction of squawfish and other species to netting had not reached any balance up to 1942, so any such future project would be experimental for a number of years at least.

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Introduction and Acknowledgement

Studies of sockeye salmon smolt production in Cultus Lake during the period 1927-1935 revealed the existence of heavy freshwater mortality, of the order of 96 per cent from the fry to the smolt or seaward migrant stage (Foerster, 1938). Having found also that many of these fry and fingerlings were eaten by piscivorous fish in the lake, an attempt was made to decrease the mortality rate by removing such fish with gill-nets. The fish netted during 1935-38 included 10,130 squawfish, 2300 trout, 760 char and 720 coho salmon. Concurrently the survival rate of young salmon in the lake increased about three-fold, and their average size also increased (Foerster and Ricker, 1941).

A cost analysis indicated that control of piscivorous fishes was a practical and profitable means of increasing production of adult salmon, provided the relation between control and increased survival was really one of cause and effect, and provided the initial success could be sustained over a longer period. The desirability of continued effort to determine these points was obvious (Foerster, 1944), but the program was not continued by the Fisheries Research Board because the Cultus Lake investigations were taken over by the International Pacific Salmon Fisheries Commission in 1938. The Commission, however, continued to expend considerable effort in removing predaceous fishes up to June of 1942; it also kept a record of the number and size of smolts produced through 1944; and it has continuously maintained a count of adult sockeye which enter the lake. All this information has recently been made available to the writers for the purpose of making an analysis of events in the lake subsequent to 1938. For this courtesy we are grateful to Mr. Loyd A. Royal, Director of the Salmon Commission.

Changes in Abundance of Predators

From 1938 through 1942, gill-netting was done in the lake from January or February through May or June, using gill-nets 150 feet long, either singly or in combinations. The catch is shown in Table I, along with January-June catches for earlier years. The total net-nights of fishing effort and the catch per 100 net-nights are also given.

In a netting program for predator control, two conflicting objectives present themselves. On the one hand, in a little-explored lake it is desirable to fish nets of many different meshes, sizes and types, and in

Table I. Number of fish caught by gill-nets, January-June, 1935-42, of the more important species, and catch per 100 net-nights. For 1938-42 these figures represent the total removal of piscivorous fishes from the lake, other than by angling. For complete yearly catches in 1935-37, see Foerster and Ricker, 1941, p. 317.

	Net-nights	Squaw-fish	Trout	Char	Coho	Suckers	Total piscivores
Total catch -							
1935	162	814[a]					
1936	2935	2960	348	138	184	684	3630
1937	3755	1447[b]	372	70	19	439	1908
1938	3548	1726	587	91	167	807	2571
1939	3604	1338	648	117	351	618	2454
1940	3245	2162	822	67	23	1076	3074
1941	2121	4647	397	28	643	847	5717
1942	4393	3065	390	54	304	1152	3813
Catch per 100 nights -							
1935		503					
1936		101	12	4.7	6.3	23	
1937		39	10	1.9	0.5	12	
1938		49	17	2.6	4.7	23	
1939		37	18	3.2	9.7	17	
1940		67	25	2.1	0.7	33	
1941		219	19	1.3	30.3	40	
1942		70	9	1.2	6.9	26	

[a] includes 452 tagged and released
[b] includes 286 tagged and released

many locations, to see which methods are most efficient. On the other hand, if the catches are to be used as indices of abundance of the fish populations, the strictest uniformity in all these respects is desirable, especially as between corresponding seasons of successive years.

The original plan of work at Cultus Lake for the most part emphasized exploration and diversity. Trials were made with floating nets having webbing 6, 9, 12, and 24 feet deep, and with bottom-set nets 6 and 9 feet deep. The total number of nets in use was varied, as was the relative number of different meshes, and also the frequency with which nets were attended. At the same time, in order to obtain comparative measures of populations, it was proposed to repeat, periodically, the kind and amount of netting that had been done during some limited portion or portions of the year. As an additional check upon the effectiveness of netting, squawfish were tagged in an effort to determine the fraction of the population being removed.

Rate of Removal of Squawfish

Squawfish were tagged using a strap tag applied to the upper part of the gill cover. The fish used were the livelier and least damaged of those taken in gill-nets.

The first experiment was made during the period June 6-21, 1935. Of 451 fish tagged, only 40 were retaken and 18 of these were not by normal fishing - 10 of them came to fence 7 in the outlet creek, where relatively few normal squawfish appear. Several were picked up dead in the lake, with gill-covers damaged or fungused. Figure 1 shows the percentage recaptured of different length-classes, excluding "strays" and all June recaptures. An important factor contributing to the poor return was less careful culling of the fish used for tagging than was used later. Fairly careful selection was used on June 6, the first day of tagging, and from that day's release 18 and 20 per cent recoveries were obtained for the two central length-classes, as compared with 4 and 3 per cent for all other days.

The second tagging experiment was done in the early winter of 1936-37 (November 10 - January 4, but mostly in December), and in the spring of 1937 (February 22 - May 22, mostly late March through May). Favouring better recoveries in this experiment were the cooler temperatures, much stricter culling, and the fact that the tagging was done just before or during the spring season of high catchability. Numbers tagged and recaptured are shown in Table II. The percentage recapture, in 1937, of winter-tagged fish is a minimal estimate of the 1937 rate of exploitation for squawfish of the length-classes concerned. In the better-represented classes the spring-tagged fish are less often retaken, as expected because of their being vulnerable for a shorter time. Fish of the 285-millimeter class were the ones most frequently retaken, both in the 1935 and the 1936-37 taggings (Fig. 1). The smaller rate of recovery of smaller fish presumably results largely from their lesser vulnerability, and perhaps to some extent from a possible greater rate of loss of or death from tags. The decrease in rate of recovery indicated for the largest fish is also probably chiefly the result of smaller vulnerability; but there might also be a greater natural mortality rate among them.

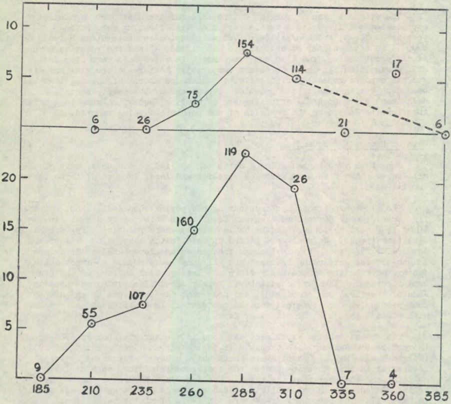


Fig. 1. Percentage of tags recovered in two squawfish tagging experiments, and the number tagged. Returns are complete to the end of 1936 for the 1935 tagging, and to the end of 1937 for the 1936-37 tagging.

Table II. Tags put on squawfish, 1936-37, and recoveries made. The fish are grouped into 25-millimeter classes, based upon fork length at time of tagging. (Those captured with tags lost are arranged by length at time of recovery.)

Mid-class size, mm.	185	210	235	260	285	310	335	360	Total
No. tagged, Nov 10 to Jan 4	9	38	25	71	64	11	1	3	222
No. tagged, less recoveries to Jan 4	9	38	25	68	62	10	1	3	216
Recaptured Jan 5 to Jun 30, 1937	0	2	1	11	17	1	0	0	32
Recaptured Jun 30 to Dec 31, 1937	0	0	0	1	0	0	0	0	1
Recaptured Jan 1 to Jun 30, 1938	0	0	0	3	3	1	0	0	7
Percentage recaptured in 1937	0	5	4	18	27	10	0	0	15
Total percentage recapture	0	5	4	22	32	20	0	0	19
No. tagged, Feb 22 to May 22	0	18	82	93	62	16	6	1	278
No. tagged less "strays"	0	17	82	92	57	16	6	1	271
Recaptured Feb 24 to Jul 31, 1937	-	1	4	10	9	4	0	0	28
Recaptured Aug 1 to Dec 31, 1937	-	0	3	2	1	0	0	0	6
Recaptured Jan 1 to Jun 30, 1938	-	0	3	2	3	1	0	0	9
Percentage recaptured in 1937	-	6	9	13	18	25	0	0	13
Total percentage recaptured	-	6	12	15	23	31	0	0	16
Recaptured with tag lost									
Jan 5 to Jun 30, 1937	0	0	1	0	1	0	0	0	2
Jan 1 to Jun 30, 1938	0	0	3	3	1	2	0	1	10

The average 1937 rate of removal of squawfish of 248-322 millimeters is evidently close to 25 per cent. In a year having intensive autumn fishing like 1936, it would probably have been higher, say 35 per cent. It is difficult to estimate how much these figures should be increased to take care of deaths from effects of tagging and losses of tags. The fish on which holes from lost tags were recognized are listed in Table II, but quite a number may have escaped attention. Taking these into account, a 40 per cent rate of removal in 1937, and 50 or 55 per cent in 1936, seem likely; even higher figures are quite possible.

Thus the tagging experiments indicate that gill-nets could and did take a large fraction of squawfish present, particularly in the intermediate length range (250-325 millimeters).

The only other fish tagged were 4 trout in 1936-37, none of which were recaptured.

Catches of the "Test-Periods" of 1935 and 1938

Over a period of 25 days in late May and June of 1938, nets were set and tended in a quantity and manner which exactly duplicated what had been done in 1935. The catches obtained in each mesh are shown in Table III of Foerster and Ricker (1941), and the size distribution of the fish is given in their Figure 4 (cf. also Table IV of this paper).

Considering the efforts of the two years as completely equivalent, it appeared that for squawfish the 1938 catch was reduced to about one-eighth (0.13) of that of 1935. The variations of decrease in catch with size of fish is approximately reciprocal to the variation of catchability with size, shown in Figure 1. Greatest reduction in catch was effected among fish of intermediate size; those taken in meshes 2.5-3 inches being only 1/25 as numerous as formerly. The small fish taken in the 2.25-inch mesh were one-fifth as numerous as in 1935, and it is probable that a 2-inch mesh would have shown much less reduction or none at all - these representing, of course, the young fish just entering the gill-net fishery. The big fish taken by nets larger than 3-inch mesh were little if any scarcer, doubtless partly because these meshes were little used after 1936. In the case of char, June inshore catches do not include many individuals but the 1938 catch was smaller than in 1935. For trout, the 1938 catch was only 38 per cent of that of 1935.

There is a possibility that the above catch comparisons might exaggerate differences between the two years, because whereas in 1938 the inshore region had been continuously fished to within two days of the start of the test period, in 1935 the nets were put into a practically unfished lake. To check on this, a comparison among the four weeks of the test period has been made (Table III). For trout and char there is in fact an increase with time in the ratio of 1938 to 1935 catch, but for squawfish and suckers this ratio is largest in the first week. Thus there is no reason to suspect bias in the 1935-1938 comparison for squawfish and suckers, and the whole of the data can be used. On the other hand, it is not unlikely that the salmonids were affected differently from the two warm-water species. Using the last two

Table III. Comparison of catches of "test" periods of 1935 and 1938, by weeks

	1st week		2nd week		3rd week		4th week	
	1935	1938	1935	1938	1935	1938	1935	1938
Squawfish	68	18	302	36	152	23	272	24
Char	6	0	4	1	6	2	3	4
Trout	9	1	15	3	9	7	12	7
Suckers	29	20	81	40	38	32	34	28

Table IV. Squawfish catches of the 1935 and 1938 test-net periods (columns 2 and 5), and the same adjusted for change in catchability with size, in two stages (cf. the text).

1	2	3	4	5	6	7	8	9
		- 1935 -			- 1938 -			
Mid-class length mm.	Actual catch	Weighted catch	Population estimate	Actual catch	Weighted catch	Population estimate	Percentage tag return	Factor
210	8	32	300	3	12	250	5.5	4.1
235	64	192	300	43	129	202	7.5	3.0
260	158	237	300	22	33	42	15.0	1.5
285	275	275	275	5	5	5	22.7	1
310	195	234	234	5	6	6	19.2	1.2
335	38	87	87	2	5	5	(10)	2.3
360	21	48	48	7	16	16	(10)	2.3
385	13	30	30	9	21	21	(10)	2.3
410	2	5	5	1	2	2	(10)	2.3
435	1	2	2	4	9	9	(10)	2.3
Totals	775	1142	1581	101	238	558		

weeks' data only, the estimated ratio of the 1938 to the 1935 trout population is 14:21, or 67 per cent. This is more in line with other indices than is the 38 per cent derived from the whole test period.

Change in Squawfish Population from 1935 to 1938

The squawfish population which is active in consuming young sockeye includes the fish down to about 175 mm. fork length. The nets used took squawfish less than 200 mm. only rarely (Foerster and Ricker, 1941, Fig. 1), even when 2-inch mesh was used, so that a group of small predators was scarcely touched at all. Among those that are caught in some numbers, the smaller ones are relatively much more numerous in the lake than is suggested by the length distribution of the catches, because they are less vulnerable. Fortunately there is an indication of the relative vulnerabilities of different sizes of squawfish in the variation in rate of return of tags, shown in Figure 1. These figures are not completely applicable to the test-net catches of 1935 and 1938 because no 2-inch mesh was used during the test periods, whereas it did contribute to the return of tags; however they can serve as a point of departure. In Table IV the catches of the two test periods are grouped at 25 mm. intervals and weighted by a factor proportional to the reciprocal of the rate of return from the 1936-37 tagging (columns 8 and 9), except that factors for fish of 335 mm. and larger are all based on an estimated 10 per cent rate of return. The result, shown in columns 3 and 6, gives length distributions more nearly representative of the lake's population over the catchable size range. However, as just explained, the adjustment is inadequate for the smaller squawfish, a fact which is indicated also by the rapid decrease in apparent number of small fish below 235 mm. As a rough correction, therefore, the length classes of 260 mm. and less are all assigned a 1935 abundance of 300 relative to the larger classes in the series. In 1938 these are all reduced in the ratio of the test-net catches of the two years, except that for the 210 mm. group, where very few fish were taken, an extrapolated higher value is used.

The indices of abundance estimated in this tenuous fashion are 1581 for 1935 and 558 for 1938. Over the three years there was a decrease of 1023, or 65 per cent. In spite of its limitations, this figure gives a much better picture of the decrease in the effective sockeye-eating population, achieved by netting, than does the figure 87 per cent taken from the gross catches. Indeed it is likely that the relative abundance figures assigned to the small fish in Table IV are too low, while fish less than 200 mm. have not been considered at all; hence the effect of netting on the "total" stock is probably still overestimated. On the other hand the 1938 squawfish were of very much smaller size, on the average, than those of 1935, and squawfish less than 225 mm. or so long eat fewer sockeye than do larger ones; hence 1:0.35 is perhaps as good an estimate as can be made of the ratio of the effective populations.

Characteristics of the General Netting Program

No repetition of the "test periods" was made after 1938, so that the story of population dynamics in later years comes from the regular netting program. Comparisons among years other than 1935 have one great advantage over those involving 1935, that the length composition of the squawfish taken was much more nearly the same in all years (Fig. 3), and consequently major adjustments of the kind made in Table IV are less necessary. On the other hand, from 1936 onward there were changes in age of the nets, and some changes in the total number set and in the relative number of each mesh. Consequently the problems which these variables involve must be considered.

Net competition

1. Suppose that a fish population is exploited by a fishery whose units of gear (nets, trawls, etc.) are scattered randomly over it, so that all fish are exposed to the possibility of capture at short intervals of time and there is no possibility of local depletion occurring. Further, the units of gear do not interfere with each other in respect to the mechanics of their operation. In such a situation any unit of gear reduces the catch of the others, and in a sense may be said to "compete" with them. The competition takes the form of a reduction in the size of the fish population as a whole; as the fishing season progresses each unit catches fewer fish, and with more gear present, the decrease is relatively more rapid. In this situation, catch-per-unit gear is proportional to the average population on hand during the fishing season.

2. If fishing gear is not dispersed orderly over the population, its action tends to produce local reductions in abundance greater than what the population as a whole is experiencing, leading to a different type of competition. Suppose that a population can be successfully fished over only a part of its range (near the shore of a lake, for example). Then the nets set near shore produce a local depletion of the supply; additional nets set in the same region increase the local depletion and catch-per-unit-effort will fall off in proportion to the local abundance. The magnitude of this fall is cushioned by the fact that some fish from the rest of the stock keep wandering into the fishing area and keep the supply there from dropping as far as it otherwise would. In this situation, catch-per-unit-effort does not vary as the average abundance of the whole stock, but tends to fall off more rapidly than that abundance, as fishing effort increases. Thus catch-per-unit-effort will fluctuate more violently, with change of effort between years, than does the corresponding average abundance of the whole stock.

3. Finally, if the setting of an additional unit of gear interferes directly with other gear, there exists competition which is independent of population abundance, even locally. For example, setting a new gill-net near one already in operation may scare fish away from the latter. Or much fishing of a schooling fish may disperse the schools and so reduce fishing success more than proportionally to actual decrease in abundance.

Competition of type 1 above can be considered normal and inevitable. It might be better not to call it competition at all, since the term is usually meant to suggest effects of types 2 or 3. Catch-per-unit-effort calculated from the whole season's activity of any fairly intensive fishery cannot be expected to reflect the initial abundance of the stock. If a measure of initial abundance is required, allowance must be made for the fact that fishing reduces the stock (Ricker, 1940; also below). Competition of types 2 and 3 may or may not be present in any given situation - it depends entirely on the nature of the fishery. In general, type 3 appears to be rather uncommon, but type 2 may be of rather wide occurrence, and may often exist where it is not suspected.

At Cultus Lake the nets were not set closely enough together to suggest significant competition of type 3. Type 2 competition may, however, be quite important, since the nets used never covered the whole of the range occupied by any fish. Insofar as type 2 competition exists, catch-per-unit-effort will, at the higher levels of effort, be relatively too low to be representative even of the average population present during fishing. Thus catch of squawfish per unit effort in June of 1936 was about one-tenth of that of 1935, but other indices suggest less reduction in total populations over that period. The discrepancy appears to be mainly the result of type 2 competition between the much larger numbers of nets used in 1936. From 1936 onward there was less change in number of nets in use during the first half of the year, so that most years are on much the same footing in that respect. However, attention should be called to the reduction of effort in 1941, as compared with 1940 or 1942 (Table I).

Total catch as an index of population

As rate of exploitation becomes large, catch-per-unit-effort becomes more and more difficult to interpret in terms of relative population abundance, so it is useful to examine any other possible indices. The use of total catch as an index of population has limitations which are the reverse of those applying to catch-per-unit-effort. Completely valueless in the presence of changing effort at low levels of exploitation, total catch becomes more and more useful as rate of exploitation increases, and at the extreme limit (complete removal) would be a completely accurate measure of stock initially on hand. That is, effects of competition of all three types above are automatically removed under such conditions. Of course, this limit is never reached, but for rates of exploitation in excess of, say, 50 per cent, it will often happen that total catch is a more useful statistic than catch-per-unit-effort. Since the annual rate of removal of the medium sized specimens of at least one predator, the squawfish, appears to have been of the order of 50 per cent, total catch is plotted along with indices based on catch-per-unit-effort.

Age of the nets

A final variable which can be given some consideration is the age of the nets in use. Our general experience was that nets decreased in usefulness only slowly, and in most years some replacements were made, so that average effectiveness of fishing probably did not vary greatly from year to year from this cause. Exceptions are 1935 and 1941, in both of which years an almost completely new set of nets was put into operation. Catch-per-unit-effort in these two years, therefore, is apt to be somewhat too high to be comparable with other years.

Indices of Abundance from the General Netting Program

Squawfish

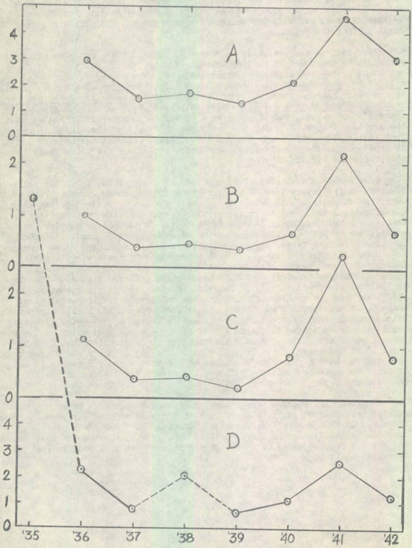
Since squawfish consume sockeye chiefly from October to April, it is the size of the winter and spring population which is of most interest. Recruitment and growth apparently occur entirely in summer, for the evidence from seasonal growth of the younger squawfish is that they do not grow in cool weather (Ricker, 1938a). Our comparative data are all from fishing during the first half of the year.

Four indices are presented in Figure 2, each of which has some merit as representing the trend of the population over the years. The total half-year catch (A) probably minimizes fluctuations which have occurred. The total catch divided by total net-nights (B) is of some value, but many of the nets included in the total take very few squawfish. The March-May catch per net-night for meshes 2 through 3 inches (C) includes only nets which catch appreciable numbers of squawfish, and it presents a picture of sharper fluctuations than the previous index. Finally, the catch per net-night of shore nets in May and June (D) is for meshes 2.25, 2.5 and 2.75 inches. Because few nets were used in those months of 1935 and 1938, catch-per-unit-effort for those years is unrepresentatively high.

Considered as estimates of population, graphs A, B, C, and D are consistent in their presentation of the direction of the trends from one year to the next. An estimate of the magnitude of these changes is subject to the many qualifications discussed above, particularly when an index of total (i.e. sockeye-eating) population is what is desired. In an earlier section the total populations of 1935 and 1938 were estimated as being in the ratio of 100:35, in spite of a much larger difference in catch-per-unit-effort. However very much less adjustment of catch-per-unit gear indices is necessary in making comparisons among years other than 1935, because the large body of highly vulnerable medium-sized fish of 1935 never again appears (Fig. 3). That is, the catches are predominantly of individuals recruited fairly recently. On the other hand the smallest fish, which are relatively invulnerable, were undoubtedly present in good numbers in all these years, but they contributed little to the catch or to the catch-per-unit-effort. A reasonable adjustment could be made by adding to graphs B-D of Figure 2 a quantity which is the same for all years after 1935. From considerations of length distribution this would be of the order of 0.5 of an ordinate unit for graphs B and C, and 1 unit for D. Such a procedure makes graphs B-D more closely resemble A, and in later comparisons A will be followed. A figure for 1935 is obtained from the test-net catches described earlier, as 1/0.35 = 2.9 times that for 1938.

The general history of the squawfish population consists of an original decline from 1935 to 1937, followed by little change or possibly some increase in 1938. In 1939 a slight decrease is indicated, but 1940 saw a sharp increase in abundance. This was followed by a greater increase in 1941, which brought the population up to a level not far from that of 1935. In 1942 it decreased again to about the level of 1940.

Fig. 2. Four indices of abundance of squawfish during the first half of the year. A. January-June catch by gill-nets. B. Total catch divided by number of net-nights. C. March-May catch per net-night for meshes 2 through 3 inches. D. Catch per net-night of shore nets in May and June, for meshes 2.25, 2.5 and 2.75 inches.



Not enough information is available to explain these changes with complete assurance, but it is probable that the young squawfish, like the young sockeye, experienced an increase in survival rate when piscivorous fishes were reduced in number. The most important consumers of age 0 squawfish are likely to be juvenile and older squawfish, which frequent the same inshore areas in summer. The year-class of 1936 would be the first brood of squawfish to benefit appreciably from predator control during the year it was hatched, which is presumably the time that it is most vulnerable to predation. Only in their fourth year of life do squawfish begin to enter the range of sizes taken by our nets (Ricker, 1938a), and the 1936 brood would start to appear in 1939. When a year older, all or nearly all are vulnerable to the gill-nets. Hence the rapid build-up of the nettable population in 1940 and 1941 could have resulted from improved survival of the young of the year-classes of 1936-37. To speculate on the reason for the decline in 1942 is not very profitable, but the fact that it did decline is encouraging. Perhaps the accumulating population of juvenile squawfish of the 1936 and 1937 broods began to again put serious pressure upon the fry, beginning with the year-class of 1938.

Although the number of smaller squawfish caught per unit of effort has fluctuated greatly, there has been no comparable change since 1937 in the numbers of the medium-sized and larger fish. In Figure 3 the size distributions of comparable "populations" of squawfish are shown over the years, formed by summing the length frequency distributions of catches of meshes 2.25, 2.5, 2.75, and 3 inches for a particular month, each mesh being given the same weight. The 1932-34 catches are lumped because little netting was done in those years. A frequency distribution of the kind shown in Figure 3 of course does not represent the size distribution of the lake's population, but it can show up changes in the latter. The original removal of medium-sized and fairly large fish in late 1935 and 1936 is apparent, and also the fact that the 1935 size distribution was not exceptional, but very similar to what had been taken in gangs of similar nets set sporadically in 1932-34. The smallest sizes of squawfish remain fairly common throughout because they were continuously recruited, and when the great increase of 1940 and 1941 took place, it entered at the smallest vulnerable sizes in 1940, and in 1941 moved into the lower-medium sizes (up to 250 mm.) in some numbers. In 1942 this brood was much reduced again, without having been able to appreciably repopulate the size-groups above 250 mm. which constituted the great bulk of the primitive population.

It is this last fact which chiefly distinguishes the observed changes in squawfish abundance from what would result from a purely natural fluctuation involving a series of weak year-classes followed by one or two strong ones. A year-class of the magnitude of the one entering the fishery in 1940 would have moved on through and been represented by a large body of fish of at least medium size (260-300 mm.) by 1942. The absence of any unusual quantity of such fish shows that the gill-nets are very effective in eliminating the great bulk of any brood, within a year after it grows into the vulnerable size range.

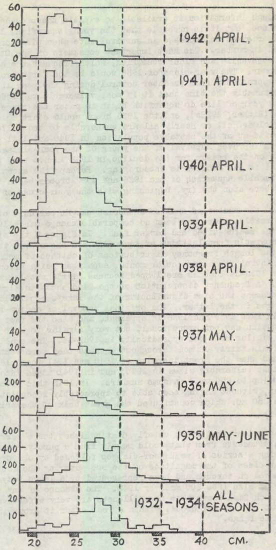


Fig. 3. Length frequencies of squawfish caught by meshes 2.25 through 3 inches.

Trout

Although small numbers of trout could always be caught in nets set near shore, especially in spring, it has been impossible to demonstrate that the netting program affected their abundance. Trout are also taken by angling and no records of that catch are at hand. It is quite likely that the catch by angling exceeded the net catch in most years.

Comparisons of April trout catches per net-night for 1936-38 were presented in the earlier paper; these can now be continued to 1940, and for some meshes to 1941 or 1942 (Table V, Fig. 4). No significant trend downward or upward is apparent, although there are considerable fluctuations in the catches of individual meshes.

The total trout catch (Table I, Fig. 4) was about the same in 1936, 1937, 1941 and 1942, but during the intervening years 1938-40 it rose to higher levels. The total spring catch divided by total net-nights is similar, but gives higher values for 1940 and 1941, while the low value for 1942 is apparently chiefly the result of more deep-water fishing in that year.

Possible changes in length-frequency were searched for by constructing a "population" consisting of the catches of the 2.25-, 2.5-, 2.75- and 3-inch meshes in each year (solid histograms, Fig. 5). The distributions are suggestive of three principal age groups in the fishery, probably ages III, IV and V. The catches of smaller and larger meshes add to the picture (superimposed open histograms) but are not available for all years. Age II fish were present in the catch in small numbers, particularly in years when 2-inch mesh was used; the modal size for this age would apparently be about 200 mm. There is some indication of variation in strength of the different year-classes, and the larger catches of 1938-40 might be largely attributable to a single strong brood.

Whatever the details of the fluctuations in trout population may have been, there is in Figure 4 no trace of any persistent depletion of fish of intermediate and large size within a year or two of the start of the predator control campaign, such as shown in Figure 3 for squawfish. If the total catch picture is representative, the increase of 1938-40 comes after the right interval to suggest increased survival of trout fry following the initial decrease in squawfish abundance. However that would not account for the decline of 1941-42.

Char

The abundance of char, as measured by total catch or catch-per-net-night, reached a relatively low level as early as 1936 (Foerster and Ricker, 1941) and since that time has shown no recovery (Table I). The smallest catch was 28 fish in 1941, and the rise to 54 in 1942 was chiefly the result of increased deep-water fishing in the first four months of the year.

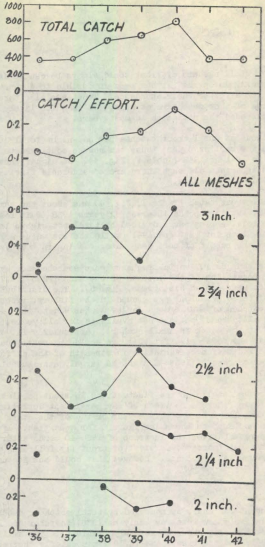


Fig. 4. January-June catch of trout; total catch divided by total net-nights; and April catches, per net-nights, of meshes 2-3 inches.

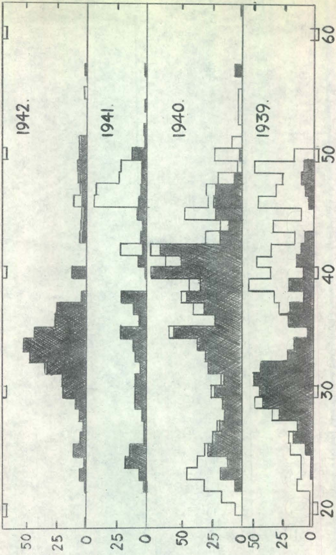


Fig. 5. Length frequency distributions of trout caught in meshes 2.25 through 3 inches (solid histograms) and in all meshes (open histograms).

Table V. (1) Catch per net-night of trout in April, and (2) number of net-nights used. Nets of 2-inch mesh are 12 feet deep set floating; all other nets are either 6 or 9 feet deep, set on the bottom. All sets are at shore.

Mesh (inches)	3		2.75		2.5		2.25		2	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
1936	0.149	138	0.431	160	0.246	384	0.151	86	0.100	100
1937	0.580	112	0.089	326	0.038	158	-	-	-	-
1938	0.585	181	0.165	103	0.118	178	-	-	0.268	242
1939	0.222	81	0.200	85	0.375	88	0.345	58	0.139	108
1940	0.872	39	0.129	171	0.163	190	0.271	151	0.178	62
1941	-	-	-	-	0.091	22	0.288	66	-	-
1942	0.500	62	0.080	25	-	-	0.182	22	-	-

Coho

The coho taken by the nets were almost wholly of the "residual" type, and their abundance depended mostly on the number of adult anadromous coho which entered the lake each year (Foerster and Ricker, MS). Coho become large enough to eat sockeye fingerlings some time in the autumn of their second year, and they were caught mostly in the spring of their third year. Total catches (A) and catch-per-unit-effort (B) are shown in Figure 6. Evidently 1941 was the year of greatest population.

Control of coho is much easier than for any other predator. It is only necessary to prevent adults from entering the lake in order to reduce their population to a negligible level. There need be no reluctance to do this on the ground of diminishing the supply of adult coho, since it was found that coho which enter the lake contribute very few smolts to the marine stock (loc. cit.).

Other species

Squawfish, trout, char and coho appear to be the only species which regularly eat fingerling sockeye. Several other species have been observed to take very young alevins. These include sculpins (*Cottus asper*), Rocky Mountain whitefish (*Prosopium williamsoni*), and older sockeye. Occasional sculpins were taken in our nets, but there is little likelihood that their abundance was affected. The whitefish has remained rare throughout, as has the peamouth chub (*Mylocheilus caurinus*) which is not yet shown to be a salmon predator. Suckers (*Catostomus macrocheilus*) are common, but were not found to eat salmon eggs or young. The abundance of sockeye larger than fingerling size has fluctuated in response to the size and growth rate of their successive broods; their possible effect on survival of fry is discussed below.

Factors Influencing Survival of Sockeye

Sockeye Mortality before Predator Control

Before comparing the changes in predator populations with sockeye mortality and survival, it is necessary to consider what changes occurred in survival prior to predator control. The complete history of survival in the lake is given in Table VI and plotted in Figure 7. Comparisons are hampered by the fact that artificial propagation was used in some years, but the best adjustment possible is made for this in columns 9 and 11 of the Table. During the years 1925-33, before predator control, there was some variation in survival rate, though it is much less than what occurred later. Consideration of the characteristics of the populations concerned permits two tentative hypotheses concerning the cause of a part of this variability. It is suggested that (1) when very large numbers of spawners enter the lake, survival from unspawned egg to yearling is poor; and (2) any fairly large carry-over of yearlings which fail to migrate at age I depresses the survival rate of the following brood. On this basis the pre-control broods are divided as follows:

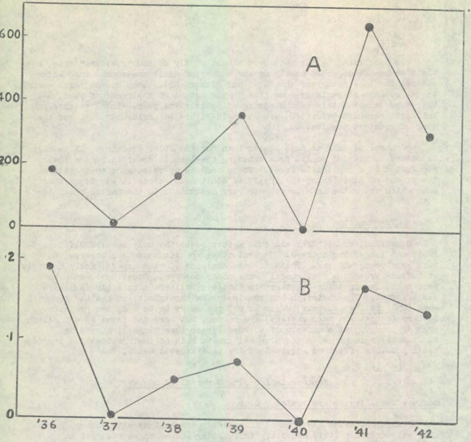


Fig. 6. A. Catch of age II coho in spring. B. Catch per net-night of meshes 2.25 through 3 inches.

Table VI. Smolts produced by natural propagation (N), eyed-egg planting (E), and fry distribution (F) with the number of eggs in unspawned females, of eyed-eggs planted, or of fry distributed shown in column 3. The "yearling stock", column 7, is an estimate of yearlings in the lake just prior to smolt migration, being the yearling smolts, plus the next year's two-year-old smolts multiplied by a factor based upon an estimate of survival from the yearling to two-year-old ages during the year concerned: this factor was 3 for broods (1933-37) which had a high survival rate at that stage, and 10 for all other broods. In columns 9 and 11 the percentage survivals in the years of artificial propagation are adjusted to the basis of natural propagation, on the basis of the ratios of the average instantaneous mortality rates for each type of propagation prior to 1934.

1	2	3	4	5	6	7	8	9	10	11	12	
Brood year	Kind of propagation	Eggs or fry available	Yearling smolts	Two-year-old smolts	Total smolts	"Yearling stock"	Yield of smolts Actual	Yield of smolts Adjusted	Yield of yearling stock Actual	Yield of yearling stock Adjusted	Instantaneous mortality rate[a]	Average weight of yearling smolts
		thousands	thousands	thousands	thousands	thousands	%	%	%	%		grams
1924	N	-	-	66.7	-	-	-	-	-	-	-	-
1925	N	17,474	183	1.7	185	200	1.059	-	1.145	-	4.470	8.10
1926	F	5,916	336	8.6	345	422	5.832	2.254	7.133	2.949	3.524	5.04
1927	N	250,000	2456	67.0	2523	3126	1.009	-	1.250	-	4.382	3.06
1928	E	2,649	38	5.2	43	90	1.623	0.578	3.398	1.456	4.229	6.55
1929	F	9,093	350	0.2	350	352	3.849	1.295	3.871	1.305	4.339	7.10
1930	N	24,939	788	15.9	804	947	3.224	-	3.797	-	3.271	7.32
1931	N+F	62,292[b]	1528	63.3	1591	2161	-	2.205	-	2.995	3.508	3.67
1932	F	4,825	122	14.2	134	264	2.777	0.837	5.472	2.070	3.877	6.53
1933	E	4,372	242	1.4	243	246	5.558	2.696	5.627	2.738	3.598	7.55
1934[d]	E	5,590	502	1.0	503	505	8.998	4.923	9.034	4.948	3.006	8.83
1935[d]	N	38,600	3089	22.9	3112	3158	8.062	-	8.181	-	2.503	5.96
1936[d]	F	12,141	1617	20.4	1637	1678	13.483	6.898	13.821	7.137	2.641	6.82[c]
1937[d]	N	2,880	196	0.1	196	197	6.805	-	6.840	-	2.682	11.60[c]
1938[d]	N	32,740	1375	1.0	1376	1385	4.202	-	4.230	-	3.163	9.73[c]
1939	N	220,400	3958	20.7	3979	4165	1.805	-	1.890	-	3.969	2.69
1940	N	232,000	1752	12.0	1764	1872	0.760	-	0.807	-	4.820	5.31
1941	N	38,500	691	2.6	694	717	1.803	-	1.862	-	3.983	7.76
1942	N	104,900	2012	-	-	-	1.918+	-	1.918+	-	3.954-	7.48

a Based on yearling stock, adjusted to terms of natural propagation where necessary (from columns 10 & 11).
b Includes 56,261,000 eggs and 6,031,000 fry.
c Estimated from mean length.
d These year-classes are presumed to have benefitted substantially from predator control.

1. Broods which stem from natural propagation of unusually large numbers of spawners: 1927.

2. Broods which lived, as fry and fingerlings, with large populations of yearlings: 1925, 1928, 1932.

3. Broods not included above: 1926, 1929, 1930, 1931, 1933.

Notice first the four years of natural propagation, indicated by open circles in Figure 7. A brood having very large population (1927) and a brood which lived with a large carry-over of yearlings (1925) both suffered much greater mortality than two broods (1930 and 1931) which lacked these probable disadvantages. The years of artificial propagation, shown by black circles in Figure 7, are less consistent with the hypotheses, perhaps because of greater possibilities for variation in hatching conditions (eyed eggs) or viability of fry. Of the years of fry distribution, 1926 has a low and 1928 a high mortality rate, as postulated, but 1929 is also high. For eyed-egg planting, estimated mortality for 1932 was intermediate, but was greater than for the "unhandicapped" year-class 1933.

There are of course not enough years' data to establish these hypotheses in any statistical sense, but they accord with common-sense notions of what may happen in the lake. Poor survival of a very large population could result from crowding of spawning beds or competition among fry, while a large group of year-old fish in the lake could be an even greater handicap for an oncoming brood. In addition, there is considerable likelihood that the brood of 1927, which produced very small yearling smolts, produced also unusually large numbers of lake-maturing residual sockeye. This devolves from the fact that residuals are derived mainly from the smaller fish of any brood (Ricker, 1938). They were produced fairly numerously by the 1931 year-class, which had moderately small smolts, but unfortunately no netting was done in the lake when the abundance of the 1927 year-class residuals could have been checked.

Turning now to the years of predator control, we find that from 1934 to 1938 there were no exceptionally large spawning runs and no large numbers of two-year-old smolts. However 1939 and 1940 both had large adult runs, almost equal to 1927, so mortality might be expected to be greater than usual. In addition, the 1940 brood may have had considerable competition from that of 1939. Two-year-old smolts in 1942 are listed as only moderately numerous but the probability of numerous residuals of the 1939 brood is even greater than for 1927, since the yearling smolts were smaller (Table VI)[1].

Predator Abundance and Sockeye Mortality

In order to estimate changes in effective total predator abundance, it would be necessary to know both the relative abundance of the different

[1] Another possibility is that two-year-old smolts of the 1939 year-class were more numerous than shown in Table VI. Their size was small, overlapping broadly that of the yearling smolts with which they migrated, and apparently some difficulty was encountered in separating the two ages by scale markings.

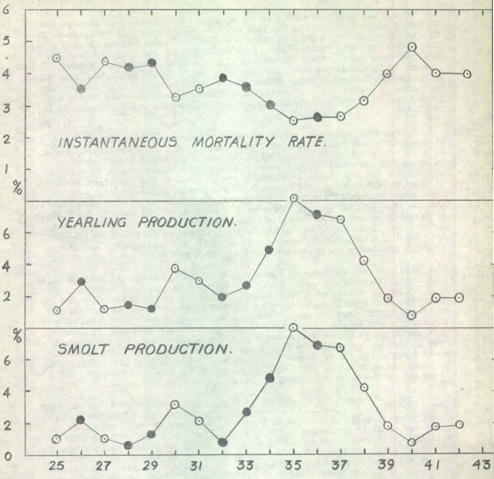


Fig. 7. Estimates of sockeye mortality and survival. Years of artificial propagation, here adjusted to the basis of natural propagation, are indicated by solid dots. (For details see Table VI.)

species and their relative effectiveness in killing sockeye. As regards the latter, stomach contents suggest that over the whole year a trout is equivalent to about 5 squawfish, a coho to about 4 squawfish, and a char to about 3 squawfish. Coho eat more sockeye than trout do in spring, but probably less during the previous summer and autumn because of their small size then. Although apparently less numerous than the squawfish, the salmonid population thus might outweigh the latter in total effectiveness as predators. Unfortunately the only idea of the relative abundance of the several species comes from the number caught by the nets, since no information on relative vulnerability is available.

Consumption of sockeye by individual predators was found to be proportional to the abundance of the sockeye, except possibly at the lowest levels of sockeye population (Ricker, 1941). In such a situation the mathematical relation between predators and sockeye is that the instantaneous mortality rate of the sockeye should be directly proportional to the effective abundance of the predators (Ricker and Foerster, 1948, p. 205; Ricker, 1952). This instantaneous rate is plotted in the lower half of Figure 8. The first two and the last two years shown represent the usual mortality rate in the absence of predator control; this is close to 4, corresponding to survival of about 1.9 per cent from unspawned egg to yearling. The year-classes from 1934 to 1940 exhibit a marked fluctuation, with which we must compare the changes in predator populations that occurred over the same period.

Most interest attaches to a comparison of sockeye mortality and squawfish abundance, since far more squawfish were caught than any other species, and only squawfish seem to have been seriously affected by the netting program. An estimate of squawfish abundance is plotted along with sockeye mortality in Figure 8. Apart from the year-class of 1940, there is a general similarity between the two graphs. This resemblance is consistent with the hypothesis that variation in the squawfish stock has been a major cause of the fluctuation in sockeye survival rate over the years concerned. The fluctuations in sockeye mortality are of course on a much smaller scale than the fluctuations in squawfish population, since not all predation is done by squawfish, and since some sockeye probably die from causes other than predation.

A similar comparison of sockeye mortality with measures of trout and coho abundance (Figs. 4, 6) cannot be said to suggest any relation between them. Total salmonid catch is entered on Figure 8, but again no relationship is indicated. Adding the salmonids to the squawfish graph does perhaps improve slightly the degree of correspondence of the latter with the sockeye mortality, but does nothing to change the aberration at the right end. In any event, simple addition of catches or catch-per-unit-effort's of the different predators is arbitrary because their relative vulnerabilities are unknown, and because of their differences in efficiency as sockeye catchers. On the whole, what is known of predators other than squawfish indicates that while they probably make at least a fairly important contribution to the total predation upon sockeye, they are not important contributors to the changes in sockeye mortality indicated in Figure 8.

In the previous section it was noted that the year-classes 1934-38 were free of two handicaps which seem to increase mortality rate - these being

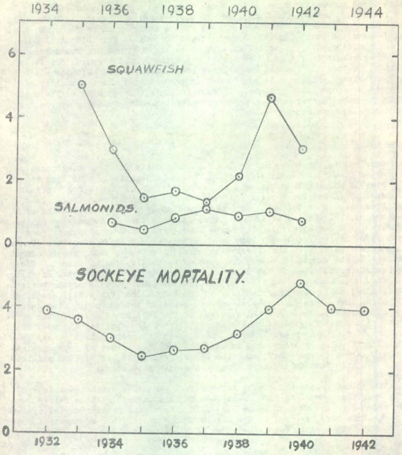


Fig. 8. Above: Estimates of spring populations of squawfish and of salmonids, in the years shown at the top, based on total catches (except in 1935). Below: Instantaneous mortality rate of sockeye of the year-classes attacked by the predators above, adjusted to terms of natural propagation in all years.

extra large population size, and a large companion population of yearlings. The year 1939, however, had the first of these handicaps, while 1940 probably had both. Adjustments for these effects on the lower graph of Figure 8 would lower the point for 1939 somewhat, and lower that for 1940 still more. In a comparison with the squawfish line above, this adjustment would make for better agreement in the relative positions of the last two years, but it is doubtful whether the overall resemblance would be improved. With or without such adjustment, Figure 8 is not enough to prove that sockeye mortality was affected by squawfish abundance. It does indicate that this is sufficiently likely to make further work on predator control a most promising approach to increasing sockeye stocks.

Ocean Mortality

Survival in the ocean and on the fishing grounds is of interest here only insofar as it may have been affected by freshwater survival. The last column of Table VII shows the approximate percentage return of smolts for the year-classes 1937-42 and for earlier years of natural propagation. The years of high freshwater survival which followed immediately on the introduction of predator control (broods of 1935-38) were characterized by average or better-than-average ocean survival. The three subsequent years of normal or poor freshwater survival (1939-41) were accompanied by poor ocean survival. There is no reason to suspect that freshwater survival rate, as such, should affect survival in the ocean. However, one type of connection can be traced. The low freshwater survival of the 1939 and 1940 broods apparently resulted partly from the large number of eggs deposited, and the same crowding of the environment reduced smolt size, particularly in the 1939 brood (Table VI). Foerster (MS) shows that there is a general inverse relation between smolt size and percentage return, and the ocean survival of the 1939 brood was much the worst on record. However, size of smolts accounts for only a part of the poor ocean survival of the three years 1939-41, and to a considerable extent it may be merely fortuitous. Whatever the causes, the combined effect of poor survival in the lake and in the ocean, upon the large spawning stocks of 1939 and 1940, was to cut them down to ordinary size in a single generation.

After 1942, ocean and freshwater survival cannot be estimated independently, but their combined effect has been to hold all cycles at a fairly steady density (column 8 of Table VII). If natural and fishing mortality outside the lake have reverted to the levels of the middle 1930's, survival from egg to smolt must again be of the order of 1.5-2 per cent.

Discussion

Probable Effectiveness of More Intensive Netting

In summarizing the actual and potential value of predator control on Cultus Lake, it is desirable not only to know what has happened, but to assess what might have happened if control work had been rigorously continued or itensified.

Table VII. Parent stock, smolts and adults produced, in years of natural propagation.

Brood year	Parent stock Male	Parent stock Female	Parent stock Total	Adults produced Age III	Adults produced Age IV[a]	Adults produced Total	Ratio of adults to parents	Smolts	Ratio of adults to smolts
								thousands	%
1925	1540	3883	5423	0?	6364	6364	1.2	250	2.5
1927	26049	56376	82425	1678	37473	39151	0.47	2460	1.6
1930	4853	5542	10395	607	19621	20228	1.9	779	2.6
1935	5615	10174	15789	3908	71676	75584	4.8	3112	2.4
1937	2234	827	3061	492	13977	14469	4.7	217	6.7
1938	5511	7831	13342	4187	36959	41146	3.1	1375	3.0
1939	21624	51565	73189	346	11827	12173	0.17	3979	0.31
1940	-	-	74121	48	14036	14084	0.19	1752	0.80
1941	5515	13649	18164	164	5034	5198	0.29	694	0.75
1942	12758	24547	37305	4197	33084	37281	1.00	2012	1.9
1943	3931	7944	11875	200	8720	8920	0.75	-	-
1944	4871	9329	14200	178	12772	12950	0.91	-	-
1945	5622	3683	9331	314	9059	9373	1.00	-	-
1946	12182	21105	33284	242	29928	30170	0.91	-	-
1947	3043	5855	8898	667	12697	13184	1.5	-	-

[a] Includes a small number of Age-V fish of the previous cycle.

It is likely that control could be made more effective by prosecuting it during times of year in addition to January-June, as far as possible. The possibilities are perhaps limited, but not unimportant. Gill-netting during summer runs into difficulty because of the crowds of vacationists on the lake, and from mid-October to late December it is impractical because of the adult salmon in the lake. However the addition of six week's intensive netting in September and early October would take a large bite out of the squawfish which have just grown into the vulnerable size range during the summer, and so prevent them having several months' contact with the fingerling sockeye. Winter and spring fishing gets the squawfish only after 3-8 months' damage has already been done, though of course such fishing would have to be continued, and it could be intensified. In summer, it is possible that less conspicuous gear could be used, submerged trap-nets for example, and these might prove more effective at all seasons, specially for the smaller squawfish. Another possibility that could be explored is that of using rotenone locally in shallow water in summer, where it would be likely to kill cyprinids, but not salmonids other than a few coho fry.

By these various means it is likely that the squawfish could be brought under some kind of steady control which would permit much higher sockeye survival rates than those of 1940-42. If in addition the coho were practically eliminated by barring access of adults to the lake, it is quite possible that sockeye survival rates of the order of those of the 1934-37 broods could be maintained indefinitely, that is, about 7 per cent survival from unspawned egg to smolt, or 300 smolts per female.

Value in Terms of Additional Sockeye Caught

In the earlier report a balance sheet was presented of costs and benefits of predator control up to 1938. As of 1952, the cost of control on the scale contemplated would be up to about $10,000 per year, while the value of the adult sockeye to fishermen is now 25 cents per pound, or about $1.25 per fish.

Apart from changes in money values, new consideration of the cost picture is necessary because of the higher level of sockeye stock now present in the lake. The former evaluation was appropriate to a period when all four runs of sockeye could be and were being rapidly increased. Now, however, there are important indications that the maximum productivity of the lake for sockeye was achieved by the broods of 1935 and 1936, and the attempt to surpass this level of productivity with the large 1939 and 1940 broods resulted in a debacle, just as did the earlier attempt of 1927. Thus an estimate of the productivity potential of the lake must now be made.

The most noticeable effect of large broods in the lake is the fact that the individual fish become small (Foerster, 1944). This is of direct importance because large smolts produce more adults than do smaller smolts; for example, ocean survival is estimated to be doubled over the range of smolt size from 4 to 7 grams (Foerster, MS). Another serious result of small yearling size is that an increased fraction of the stock does not migrate at age I. The fish carried over require an additional year's nourishment from the lake and suffer additional mortality estimated at about 90% under natural conditions (Ricker and Foerster, 1948). For these handicaps only partial and poor compensation is afforded by the larger size attained by the survivors when they finally do migrate as 2-year-old smolts. Also, some such fish fail to migrate at all. In that event they are a complete loss to the fishery; they become a continuing drain on the lake's plankton supply, and they also eat some sockeye fry of later broods. As noted earlier, the number of non-migrating sockeye produced by year-classes having very small smolts may have been very damaging. From the history of known year-classes (Table VI) a tentative desirable minimum size limit for smolts, above which these unfavorable effects are largely avoided, can be set at an average weight of 6 grams.

We know that smolt weight is inversely related to size of the brood. What is the best indicator of brood size for this purpose? Is it the abundance of the brood at the yearling stage, or is it its abundance when just beginning lake life as fry? Unfortunately there is no direct count of fry for most years, but number of eggs in females can be used as an indirect measure of initial abundance of each brood. Using data for the eleven years of natural propagation (Table VI), relationships can be computed as follows:

Quantities related	Correlation	Standard regression coefficient
Average weight of yearling smolts (W) and estimated total number of yearlings (N)	-0.819	
The same, with (E) (see below) eliminated	-0.778	-0.572
Weight of yearling smolts (W) and number of eggs in their parents (E)	-0.754	
The same, with (N) eliminated	-0.485	-0.355
Multiple correlation of (W) with (N) and (E)	0.858	

The two variates between them account for a satisfactorily large fraction, approximately 74 per cent, of the variability in smolt size. Number of eggs and number of yearlings have a positive correlation of 0.697, so the partial correlation of each with smolt size is numerically less than the simple correlation. The standard regression coefficients suggest that number of yearlings is more closely related to smolt size than is the number of eggs from which they sprang. However, since percentage hatch of eggs probably varies, it is possible that if an index of initial number of fry were available, it would be as good or better than number of smolts as an index of resulting smolt size. Actually the two standard regression coefficients each have a standard error of 0.252, and hence do not differ significantly. We conclude that both number of yearlings and number of fry have some independent effect upon smolt size, which is of the same general order of magnitude for each.

Two contrasting hypothetical situations may be put forth in order to show the bearing of the above computations upon the role which predator control might play in the future. Firstly, suppose that the limit of productivity of the lake could be completely described in terms of a maximum number of smolts of adequate size which it could produce annually. As a basis for discussion, consider the figure 2,000,000 smolts, weighing 12 metric tons, as a possible average potential "sustained yield". These smolts could be produced in two ways: in the presence of a normal predator population there would be a normal egg-to-smolt survival rate of say 2 per cent, so that 100,000,000 eggs would have to be laid, from about 24,000 females. Alternatively, the same smolts could be produced under conditions of predator control at a survival rate of say 7 per cent; this would require 29,000,000 eggs from 7000 females. From an economic point of view, the difference between the two procedures is that in the latter case, 17,000 additional females and accompanying males could be spared to the fishery. Males being commonly about half as numerous as females at Cultus, this would represent 25,000 fish altogether, worth about $30,000 at 1952 prices. Since the commercial fishery normally operates with a considerable oversupply of gear and personnel, this $30,000 could be almost wholly net gain. However, it is not likely that control operations could be justified on this basis. The difference between benefit and cost is only $20,000, and there is no way of assigning the cost of the benefits to the particular fishermen to whom they accrue. More important, there is no way of seeing that exactly the right number of fish is taken by the fishery, in order that the correct number of spawners will reach the lake. To regulate spawning as envisaged, it would usually be necessary to have a certain surplus reach the lake, and those which had to be destroyed at the lake after the quota was achieved would be of relatively little commercial value.

A second view of the lake's limit of productivity would be that it could support and bring to migration the survivors of some fixed number of sockeye <u>fry</u> each year. For argument let us say it could support the fry produced from the eggs in 15,000 female spawners, i.e., 63,000,000 eggs. At the "normal" survival rate this yields 1,300,000 smolts. At a 7 per cent survival rate the yield is 4,400,000 smolts. The gain in this case is 3,100,000 smolts, of which 10 per cent or 310,000 survive to adults. At prevailing levels of effort possibly 80 per cent of the latter would be caught by the fishery, giving 250,000 fish worth about $300,000.

However, neither of the two kinds of assumptions contrasted above is realistic in the light of the correlations examined earlier. It appears that both the number of fry initially present, and the number of yearlings produced, must be taken into consideration in setting a limit to the lake's sockeye output. This suggests that the total drain on the lake's sockeye food production might be a more fundamental limiting factor, and this in turn should be fairly closely related to the actual increment in weight of all sockeye in the lake during the year. Ricker and Foerster (1948) have computed this production of sockeye in the lake for a number of years, defining production as the total sockeye flesh formed, including what dies or is eaten in the lake as well as that which survives to migration time. It was found that sockeye production, in weight units, was about 3.2 times as great as yearling stock in years before predator control, and 2.1 times as great during control (l.c., Table V). Thus for any given limit of production there would be 1.5 times as great a weight of migrants with control, as without it. The limit of production suggested in 1948, from information up to 1938, was about 45 metric tons, and as it turned out, production by the large populations of the early forties did not exceed this figure. A total production of this magnitude yields 14 tons of smolts without control and 21 tons with it. Estimating the minimum permissible average size for smolts at 6 grams, as before, this gives 2,300,000 and 3,500,000 smolts respectively, yielding 230,000 and 350,000 adults. Without control, 27,000 females or 41,000 of both sexes would be needed for reproduction, and 230,000 - 41,000 = 189,000 could go to the fishery. With control, only 6000 male and 12,000 female spawners would be needed, and the fishery could take 350,000 - 18,000 = 332,000. The net gain from control would, therefore be an extra catch of 332,000 - 189,000 = 143,000 fish worth $179,000, provided the rate of exploitation could be accurately adjusted. Necessary leeway in the latter respect would tend to reduce these figures somewhat.

An estimate similar to the above can be made using the hypothesis that it is the lake's production of sockeye in summer which best reflects the limited food available and used, summer being the time that most growth is made. In that event the difference between control and no control is somewhat greater, and the possible difference in catch is of the order of 180,000 fish.

The above figures give an idea of the magnitudes of the possible benefits from renewed and continued reduction of predator populations to the level encountered by the 1934-37 year-classes. Further experiment is needed, however, to see whether this level could or could not be maintained, or whether it could be lowered even farther. Another feature of any renewed experiment at the lake should be limitation of spawning at some level considerably below that of the disastrous years 1939 and 1940. Indeed such limitation may become necessary even without control, if it is desired to avoid renewed dominance of the lake by one of the four cycles. The wide gap between cost of predator removal and the prospects for increased catch seem to warrant renewed effort along these lines, whether at Cultus Lake or elsewhere.

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