Babine Lake Sockeye Salmon (*Oncorhynchus nerka*) Enhancement Program: Testing some Major Assumptions

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The objective of the Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement project was to increase fry outputs (and thus, smolt outputs and adult returns) by expanding and improving available spawning beds through the use of artificial spawning channels and related water flow control facilities. The project proceeded on four basic assumptions: (1) the artificial spawning channels would prove an effective means of producing sockeye fry, (2) the fry produced would be as viable as those produced from natural spawning beds, (3) the lake nursery area had the capacity to support larger juvenile populations, and (4) increased smolt outputs would result in increased adult returns. A before and after study has allowed these assumptions to be tested. Egg-to-fry survival in the channels was close to 40%, as expected. Comparisons of wild and channel-produced fry did not reveal any substantial difference in their distribution, growth, and survival in the lake. Increases in the abundance of fry were followed by corresponding increases in the abundance of underyearlings in the lake and seaward migrating smolts. No significant change in the average size of the juveniles or their survival in the lake could be detected when population size increased. While the assumptions regarding juvenile production were found to be generally valid, adult returns did not meet expectations. This was due largely to the lack of response to increased smolt outputs from even-numbered brood years. Some options for future management are offered.

Le projet de mise en valeur du saumon nerka (*Oncorhynchus nerka*) du lac Babine avait pour objectif une production accrue d'alevins (et, partant, de smolts et de retours d'adultes) en élargissant et améliorant les frayères accessibles par le biais de chenaux de ponte artificiels et de diverses installations de contrôle du débit de l'eau. Le projet reposait sur quatre hypothèses fondamentales: (1) les chenaux de ponte artificiels sont un moyen efficace de produire des alevins de saumons, (2) les alevins produits sont aussi viables que ceux provenant de frayères naturelles, (3) la région d'alevinage du lac peut supporter de plus grandes populations de juvéniles et (4) une production accrue de smolts résulte en un plus grand nombre de retours d'adultes. On a pu vérifier ces hypothèses, grâce à des études menées avant et après la mise en œuvre du projet. La survie, de l'œuf à l'alevin, dans les chenaux se rapproche de 40%, tel qu'anticipé. Des comparaisons d'alevins produits dans la nature ou dans les chenaux n'indiquent pas de différence substantielle de leur distribution, croissance et survie dans le lac. Les augmentations du nombre d'alevins sont suivies d'augmentations correspondantes des poissons de moins d'un an dans le lac et de smolts émigrant vers la mer. L'augmentation de taille de la population ne semble pas être accompagnée de changement significatif de la taille moyenne des jeunes ou de leur survie dans le lac. Si les hypothèses touchant la production de juvéniles sont généralement valides, les retours d'adultes sont inférieurs à ce que l'on avait anticipé. Ceci est dû en grande partie au fait qu'une production accrue de smolts d'années paires n'a pas eu d'effet. Certaines options pour la gestion future sont sont offertes.

The Skeena River system is one of the major sockeye salmon (*Oncorhynchus nerka*) producers in British Columbia. Over the past 30 yr the average production of adult sockeye (catch plus spawning escapement) has been about 1.5 million annually. While numerous lakes in the drainage contribute to sockeye production, by far the largest and most important of these is the Babine Lake system, which contributes 90% or more of the total (Larkin and McDonald 1968).

Johnson (1956, 1958, 1961), after examining the distribution, abundance, and growth of juvenile sockeye in the various Babine Lake basins, concluded that the Main Lake basin was underutilized as a nursery area because of the limited capacity of adjacent spawning grounds to accommodate the number of spawning adults required to produce sufficient fry. This work led to an enhancement project (Anonymous 1965, 1968) aimed at increasing the number of fry entering the Main Lake. Three artificial spawning channels were built, two adjacent to the Fulton River and the third adjacent to Pinkut Creek (Fig. 1). The channels provided an additional 117 000 m² of spawning area expected to accommodate 220 000 spawners and produce an additional 125 million fry. In addition, water flow control structures were built at both locations to serve the spawning channels and to regulate river discharges with the expectation of increasing fry production in the existing natural spawning beds. The first spawning channel on Fulton River became operative in

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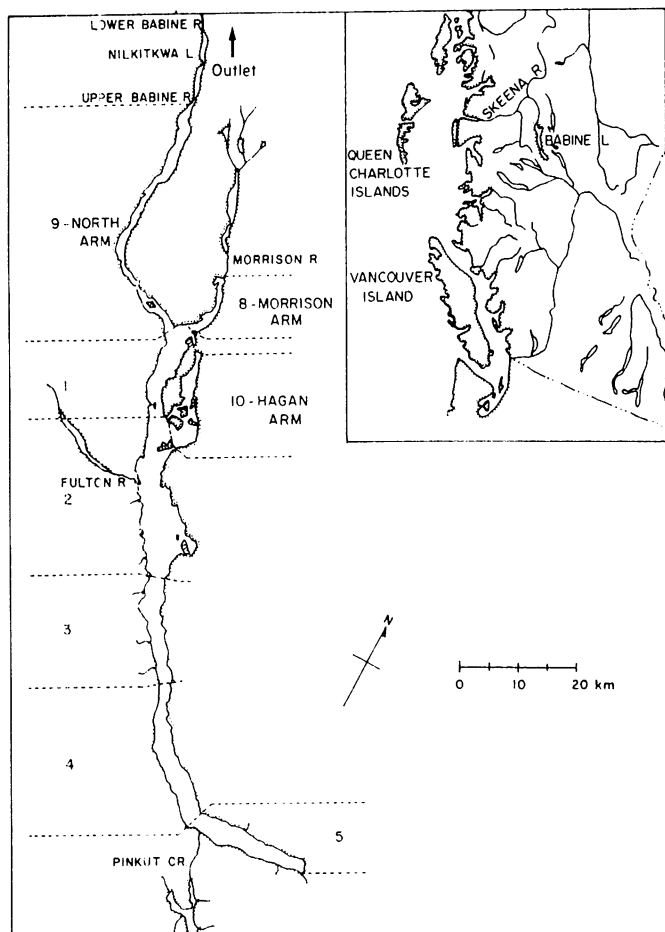
FIG. 1. Babine Lake system showing fishing areas.

This paper has been organized to address each of the four assumptions more or less in the order given above. Specifically, we will examine the following: (1) evidence of change in annual fry outputs as a result of the artificial spawning channels and subsequent changes in the abundance of underyearlings and seaward migrants, (2) comparisons of the distribution, growth, and survival in the lake of distinctively marked wild fry (from natural spawning grounds) and channel-produced fry to test the assumption of equal viability, (3) evidence of the dispersal and subsequent distribution of fry and juveniles in the lake to determine the extent to which the available lake nursery area is utilized, (4) the effects of increased population size and density on the size and growth of fry, to the seaward migrant stage, and (5) change in the abundance and age composition of returning adults in response to increased outputs of seaward migrants.

Background

Babine Lake, part of the Skeena River drainage, is one of the largest in British Columbia (Fig. 1). It is 150 km long and up to 7 km wide. This lake, together with the small and connecting Nilkitkwa Lake, provides about 500 km^2 of sockeye nursery area. The various lake basins are characterized as follows:

	Surface area (km^2)	Maximum depth (m)	Mean depth (m)
Main Lake	400.8	186	62.5
North Arm	54.4	46	20.1
Morrison Arm	17.7	31	11.4
Hagan Arm	17.7	83	28.4
Nilkitkwa Lake	4.9	21	7.8

1965. Flow control began on Fulton River and Pinkut Creek in 1968. Also, in this year the Pinkut Creek channel became operative. The first stage of Fulton channel No. 2 was completed in 1969. By 1971 all channels were fully operational.

The enhancement project proceeded on a number of important assumptions: (1) artificial spawning channels would prove to be an effective means of producing sockeye fry, and an egg-to-fry survival rate of 40% (at least double the observed rate from natural spawning beds) was anticipated as was an output of 125 million fry, (2) the viability of the fry produced would be comparable with that of fry produced naturally, (3) the Main Lake nursery area had the capacity to support the much larger juvenile population, and (4) an increase in the juvenile output from the lake would result in a corresponding increase in the number of returning adults. A catch of an additional 1 million adult sockeye was projected.

Monitoring the sockeye population at various life history stages before and after the enhancement project came "on-stream," provided an opportunity to examine these assumptions. Data on parent spawners and fry outputs are available from Ginetz (1977) and West (1978). Comparisons of the distribution, growth, and survival of channel-produced fry and wild life fry from natural spawning beds were made by McDonald (1969). Additional work hereto unpublished provides further comparisons and data bearing on the question of lake nursery area capacity. Finally, estimates of the annual number of seaward migrants and resulting adult returns are available to examine differences in sockeye production in pre- and post-enhancement years.

Details of the Babine Lake system's physical and chemical characteristics are provided by Johnson (1965a, 1965b), Narver and Anderson (1969), Stephens et al. (1969), McDonald and Scarsbrook (1969), and Stockner and Shortreed (1976).

Sockeye spawn mainly in September and October. The resultant fry emerge from the gravel the following spring (May and June) and migrate into the lake. Most remain in the lake 1 yr (underyearlings) then migrate to sea (smolts). A small percentage (<2%) spend 2 yr in the lake before seaward migration. Most return as maturing adults after spending 2 or 3 yr at sea.

Each year since 1946, sockeye returning to Babine Lake have been counted through a fence located on the Babine River, downstream of the spawning beds (Aro 1961; West 1978). Their numbers have ranged from 102 000 to 888 000 annually and averaged 668 000. Spawning takes place in all accessible streams but major spawnings occur in the upper and lower Babine River, Fulton and Morrison rivers, and Pinkut Creek. Spawning ground estimates for 1949–77 (West 1978) reveal that on average, 52% of the sockeye spawn in streams adjacent to the Main Lake, 44% in the Babine River adjacent to the North Arm, and 4% in Morrison Arm. Hagan Arm is devoid of adjacent spawning streams.

Some additional spawning has been observed to occur along the Main Lake shore but no quantitative information is available. Observed differences between annual fence counts and estimates of the number of spawners in the tributary streams suggest that up to 20% of the sockeye entering Babine may spawn in the lake.

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Distribution of Underyearlings

Past studies have revealed some important features of the distribution and behavior of juvenile sockeye in the lake. Johnson (1956, 1958, 1961, 1965b) concluded that dispersal of fry from their natal streams was limited and this, together with the multibasin nature of the lake, resulted in distinct populations in more or less distinct basins. His comparisons of population densities, food supply, and size of underyearlings among lake basins led him to propose that at high densities food became limited, growth was slowed, and compensatory mortality occurred.

However, McDonald (1969) found that in the Main Lake at least, distribution was not static but changed continuously through summer and fall. Fulton River fry dispersed rapidly into the lake, some as far as 71 km from the river by early July. Initially, underyearlings were found concentrated in the southern half of the Main Lake. As the season progressed the population shifted into central and northern areas.

McCart (1967) observed that in the North Arm as well as in the Main Lake, fry may disperse considerable distances from their natal stream. Fry from the Babine River were observed moving in schools along the shores of the North Arm as far as 32 km uplake, the most distant point of McCart's observations.

Whether underyearling distribution is more or less static, as described by Johnson, or dynamic, as described by McDonald and McCart, bears importantly on the question of lake nursery area capacity and the mechanisms that may determine it. Pertinent new information will be examined in this report to elucidate this question.

Kokanee

Kokanee, the nonanadromous form of *O. nerka*, are present in Babine Lake. They spawn, usually in their 4th yr, in most tributaries but most abundantly in small streams adjacent to the Main Lake. The abundance of spawners has varied greatly. Johnson (1958) cited reports of over 1 million spawners in 1955 and 1956, and H. W. D. Smith (Fisheries and Oceans, Vancouver, B.C., personal communication) observed about the same number in 1963. McCart (1970), after almost complete coverage of kokanee spawning streams from 1964 to 1967, estimated an average of 40 800 spawners per year (range 18 000–64 000). Comparable coverage by H. W. D. Smith in 1968 (personal communication) and by J. McDonald in 1969, 1970, and 1972 (unpublished data) revealed an average of 32 500 (range 26 000–35 000).

Mature kokanee are readily distinguished from sockeye by their relatively small size. However, no satisfactory way has been found to distinguish between juveniles of the two types. Although kokanee eggs and the resulting fry are smaller on average than those of sockeye (McCart 1970), the difference is not great enough to separate the two types subsequently in a mixed population of juveniles.

Johnson (1958) compared the potential egg depositions of kokanee and sockeye in the 1955 and 1956 brood years and estimated that as much as 70 and 39% of the ensuing juveniles in the Main lake could be the progeny of kokanee. The much smaller kokanee spawning populations in more recent years would reduce the proportions of juvenile kokanee accordingly. Comparisons of potential egg deposition of the two types for the 8 yr between 1964 and 1972, for which data are available, suggest that from 1 to 3% of the ensuing underyearlings in the Main Lake would be the progeny of kokanee.

In this report, we will compare lake juvenile populations from the brood years 1965–67 with those of 1970–72 and 1976. For 5 of those 7 yr we can be confident that the presence of juvenile kokanee will have little effect on estimates of the distribution, growth, and survival of sockeye progeny. Unfortunately, no estimates of kokanee spawning populations are available for the remaining two brood years (1971 and 1976). Probably they were not large because unusually large numbers would have been noted during the course of annual counts of sockeye spawners.

Methods

Fry Outputs

Estimates of annual fry outputs from Fulton River and Pinkut Creek and their associated artificial spawning channels have been reported by Ginetz (1977) and West (1978). Methods varied from hydraulic sampling of eggs and alevins in the gravel to complete counts of fry migrants (Ginetz 1977). Most commonly, estimates were based on the catch of fry in traps operated periodically throughout downstream migration. Catches were extrapolated to take into account the volume of river or channel discharge not flowing through the traps and times of operation with respect to the diel periodicity of the migration. This procedure was checked periodically by independent estimates based on recovery in the traps of marked fry released upstream of the trapping sites.

Since fry outputs from other Main Lake streams are not monitored, we have estimated them on the basis of the number of parent spawners (West 1978) and the assumption that fry output per spawner was equal to the average estimated from natural spawning in the Fulton River and Pinkut Creek (233 fry per spawner). These estimates are gross, but when added to the much larger outputs recorded from Fulton River and Pinkut Creek and their spawning channels, the resulting totals are considered to provide useful estimates of the numbers of fry entering the Main Lake. These estimates, however, do not include fry that may have resulted from the unknown number of sockeye that spawn in the lake rather than in its tributaries. As a result, our estimates of Main Lake fry populations are probably conservative.

Lake Resident Juveniles (Underyearlings)

Underyearlings were captured from early summer through fall using a 10.7 m vessel equipped with a purse seine. The net was half-purse, 274.4 m long, with an effective fishing depth of 15.7 m. Mesh size varied from 0.48 cm in the bunt to 3.81 cm in the lead. details of the equipment and procedure are provided by Scarsbrook and McDonald (1970).

Seining was carried out in 1966–68, 1971–73, and again in 1977 in eight lake areas, which generally coincided with natural lake basins and prominent land features (Fig. 1). In 1966, set (fishing) locations were not predetermined but were distributed as widely throughout the lake as time and effort permitted. By using a map grid, set locations were randomly determined (Scarsbrook and McDonald 1970) in 1967, with the proviso that areas 1–5 and 9 would have 10 locations and areas 8 and 10 would have 5 locations each. The same set locations were used in subsequent years.

Seining was carried out routinely during three fishing periods each year: session I in late June and early July, session II in late August and early September, and session III in early October.

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Each session was usually of 10–15 d duration. Since underyearlings were only available in the surface layer at night (McDonald 1969, 1973), seining was confined to hours between times of evening and morning civil twilights for 55° north latitude.

Captured fish were recorded by species and samples were taken for length and weight measurements. After hardening in 10% formalin until stabilized (Parker 1963), fork length was measured to the nearest millimetre. From 1966 to 1968, mean weight was calculated by dividing the total sample weight by the number in the sample. In subsequent years, individual fish were weighed to the nearest 0.01 g.

In addition to the standard netting procedures described above, special seining was carried out on several occasions to provide ancillary information. Catches of underyearlings from these nonstandard sets have not been used in this analysis except for a number of marked fish, which were included in growth analysis.

Marking and Recovery

Two marking and recovery programs were carried out. The first involved fry from the 1965–67 brood years and was designed to compare wild and channel-produced fry. In a second program (1970 and 1971 brood years), fry from the Fulton and Pinkut systems were marked to compare their distribution, growth, and survival in the lake at pre- and post-enhancement population levels. In all cases, fry migrants were marked distinctively by excising one or the other or both pelvic fins. Recoveries were made by examining purse-seine catches in the lake and by examining seaward migrants. Methods and resulting data have been reported by Scarsbrook and McDonald (1970, 1972) and Coburn and McDonald (1972, 1973). Analysis of results of the 1965 brood year program was reported by McDonald (1969).

One of the assumptions upon which the marking programs were based was that the incidence of naturally missing fins was zero or at least not large enough to compromise comparison of the marked stocks. For the 1965–67 comparisons of wild and channel fry, right (wild) and left (channel) pelvic marks were used. Fry for the 1970 and 1971 broods were marked with the right pelvic (Pinkut Creek), left and double pelvic (Fulton River, 1970), and double pelvic only (Fulton River, 1971).

McDonald (1969) examined 3104 fry migrants from the unmarked 1965 brood and 4200 smolts from the unmarked 1964 brood without finding any missing pelvic fins. Another examination of 4650 smolts from the 1968 brood gave the same result. An extensive test of the incidence of natural marks was carried out on underyearlings of the 1972 brood. None of the fry of that brood year were marked. Examination of 81 733 underyearlings captured by purse seining in the lake resulted in 32 fish found with one or both pelvic fins missing. The numbers and types of natural "marks" found were as follows:

Type	No.	Marked:unmarked ratio
Right pelvic	13	1:6287
Left pelvic	16	1:5108
Double pelvic	3	1:27244
All	32	1:2554

The cause of the missing fins is unknown but deformities are a possibility as is fin loss from bacterial infection (fin rot).

Whatever the cause, it did not appear to discriminate between one fin or the other. The incidence of missing right and left pelvic fins was not significantly different ($\chi^2 = 0.310$, $P = 0.60$). The incidence of both pelvics missing was very low; presumably the chances of a fish losing the pair of fins were much less than those of losing only one.

The incidence of natural marks in the 1972 brood underyearlings was greater than that anticipated from the earlier but much smaller tests. However, while bothersome, the incidence is still very low and the presence of natural marks would make up a very small fraction of mark recoveries in years in which marking programs were carried out. For example, during the 5 yr of surveys, a total of 1284 marked fish were found among 205 120 underyearlings examined. Assuming that the 1972 brood incidence of naturally missing fins applied to all years (1:2554) then their estimated number in the 1284 marked fish would be 80, or 6%, of the total. The resulting error in interpretation of the marking and recovery data would be very small. Since the incidence of naturally missing right and left pelvic fins appears to be the same, comparisons of marked wild and channel fry would remain valid. However, estimates of survival rates of marked fry would be somewhat greater than the actual rates. The existence of natural marks demands caution when describing distribution of marked stocks, particularly in those lake areas where the marked to unmarked ratio was extremely low.

Seaward Migrants

The number of smolts migrating from Babine Lake has been estimated on a daily and seasonal basis for over 20 yr. Each day of the migration, smolts were tagged and released into the migrant population passing through Nilkitkwa Lake. Smolts captured in a trap about 5 km downstream were examined for tags (Jordan and Smith 1968). Procedures for estimating population size from the tag and recovery data are given by McDonald and Smith (1980).

This seaward migration is typically bimodal, with "early run" smolts originating from the North Arm and "late run" smolts from the Main Lake basin (Johnson and Groot 1963; McDonald 1969; McDonald and Smith 1980). The bimodality of the migration, together with differences in size between early and late smolts plus some behavioral changes noted by H. W. D. Smith (personal communication), has allowed separate estimates of smolt outputs from the North Arm and Main Lake. Estimates used in this report are from unpublished Department of Fisheries and Oceans files.

Returning Adults

Records of the annual catch and escapement of Skeena sockeye are kept by staff of the Department of Fisheries and Oceans. In addition, routine sampling and scale analysis is carried out to determine the age composition of each year's run so that adult returns can be related to brood year escapements. Available information does not allow a separate estimate of returns to Babine Lake, but since the Babine stock makes up more than 90% of the total, returns to the Skeena as a whole will provide close approximations.

Analysis

The number of years of observation required to examine changes in sockeye production before and after enhancement resulted in a large volume of data. To reduce the amount of

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TABLE 1. Abundance of Main Lake juvenile sockeye at various life history stages ($*P = 0.05$; $**P = 0.01$; $***P = 0.001$; NS, not significant).

Brood year	Pinkut and Fulton fry (millions)	Total fry (millions)	Underyearlings			Main lake smolts (millions)	Survival fry–smolts (%)
			Session I, July (lake index)	Session II, August (lake index)	Session III, October (lake index)		
1961	36.8	77.4				5.78	7.5
1962	46.7	72.1				29.35	40.7
1963	57.5	89.7				19.16	21.4
1964	29.0	47.0				13.78	29.3
1965	31.5	38.2	80.8	76.3	28.7	6.84	17.9
1966	53.2	61.2	102.7	84.3	29.5	18.10	29.6
1967	47.5	64.9	132.3	146.3	20.7	24.18	37.3
1968	75.7	98.4				34.63	37.2
1969	59.5	78.6				39.20	49.9
1970	114.9	134.7	167.1	193.1	113.9	44.56	33.1
1971	152.1	161.2	385.4	297.9	82.8	73.98	45.9
1972	158.5	170.6	328.6	198.9	106.7	61.13	35.8
1973	150.7	183.2				27.43	15.0
1974	107.0	134.9				36.12	26.8
1975	158.3	174.6				51.01	29.2
1976	228.8	232.5	340.5	212.7	150.6	70.92	30.5
1961–67 Mean	43.2	64.4	105.3	102.5	26.3	16.7	26.2
SD	10.91	17.64	25.85	39.20	4.87	8.66	11.52
1970–76 Mean	152.9	170.2	305.4	225.6	113.5	52.2	30.9
SD	39.53	33.31	95.39	48.86	28.10	17.50	9.37
t-test	7.079***	7.432***	3.463*	3.592*	5.198**	4.802***	0.83 (NS)

tabular material in the text, statistical analysis of underyearling density and abundance derived from catch per unit effort data and analysis of size data are presented in the appendix.

Comparison of pre- and post-channel fry and smolt production has been based on two series of brood years: 1961–67 and 1970–76. Although a small artificial spawning channel on Fulton River (channel No. 1) was operative in 1965–67, the number of fry produced did not appreciably change the total fry outputs into the Main Lake from those of previous years, and for our purposes 1965–67 has been considered representative of the preenhancement period. The years 1968 and 1969 were years of transition, with the Pinkut Creek channel operative in 1968 and the first stage of a second Fulton River channel operative in 1969. These 2 yr have been excluded from our comparisons. The spawning channels began to approach designed production in 1970.

Results

Change in Abundance

Fry production from the artificial spawning channels was close to the 40% projected. Data from West (1978) showed that the average egg-to-fry survival in Fulton channel No. 1 was 48.7% ($N = 11$ yr), 43.4% in Fulton channel No. 2 ($N = 8$ yr), and 30.1% in the Pinkut Channel ($N = 8$ yr). However, flow control over the natural spawning grounds in Fulton River or Pinkut Creek did not result in increased production. West (1978) reported pre- and post-flow control average egg-to-fry survivals at Fulton River of 20.8% ($N = 7$ yr) and 17.2% ($N =$

9 yr), respectively. The means are not significantly different ($t = 1.23$, $P > 0.20$). Similarly, means of 11.1% ($N = 5$ yr) and 14.9% ($N = 9$ yr) at Pinkut Creek were not significantly different ($t = 1.23$ $P > 0.20$).

As a result of channel production, there occurred a large increase in fry outputs from the two systems as channels were brought to full operation (Table 1). Average annual outputs increased significantly from 43.2 million (1961–67) to 152.9 million (1970–76), an increase of 3.5 times ($t = 7.079$, $P < 0.001$). For the Main Lake as a whole the increase was less, nearly threefold (means 64.4 million and 170.2 million, $t = 7.432$, $P < 0.001$).

Greater fry outputs were followed by larger Main Lake underyearling populations. The lake population index (see Appendix) in sessions I and II increased between two- and three-fold, while in session III, the increase was more than four times the earlier level (Table 1). All differences in pre- and post-enhancement means were significant ($P \leq 0.05$).

Average Main Lake smolt outputs increased more or less proportionately from 16.7 million to 52.2 million, a threefold increase ($t = 4.802$, $P = 0.001$). The increase for Babine System as a whole (i.e. including smolt production in the North Arm) was somewhat less, 30.1 million to 68.2 million (Table 12), an increase of 2.3 times.

Validity of Abundance Estimates

Because error limits are not available for the individual estimates of juvenile abundance, we have examined the relationships between the estimates at successive life history

TABLE 2. Relationship of abundance estimates of sockeye from one sampling period with estimates at later time periods.

Life history stage				P $(b = 0)$	r^2
X	Y	Linear regression			
Fry migrant	Session I	$Y =$	$43.653 + 1.566X$	<0.01	0.79
	Session II	$Y =$	$81.593 + 0.812X$	<0.05	0.58
	Session III	$Y =$	$2.579 + 0.655X$	<0.01	0.87
	Smolts	$Y =$	$6.278 + 0.302X$	<0.01	0.74
Session I	Session II	$Y =$	$52.453 + 0.548X$	<0.01	0.81
	Session III	$Y =$	$12.252 + 0.290X$	NS	0.53
	Smolts	$Y =$	$-2.284 + 0.205X$	<0.01	0.94
Session II	Session III	$Y =$	$1.803 + 0.430X$	NS	0.43
	Smolts	$Y = -13.092 + 0.323X$		<0.01	0.87
Session III	Smolts	$Y =$	$9.214 + 0.441X$	<0.05	0.69

stages given in Table 1. Evidence of a good relationship would support their validity whereas the absence of such a relationship would indicate that one or more of the estimates were very much in error or that annual variability in survival between life history stages was large.

Initially, two sets of regressions were calculated, one using the combined fry outputs from Fulton River and Pinkut Creek, the other using estimates of the total fry input to the Main Lake. No significant differences were found in the slopes of the two regressions. Because Fulton River and Pinkut Creek fry estimates are the most accurate and since the fry outputs from these streams make up most of the Main Lake total, regressions based on Fulton River and Pinkut Creek outputs only are presented here (Table 2).

All relationships were positive and in all but two, slopes were significantly greater than zero. If we ignore the two exceptions for the moment, the coefficients of determination (r^2) fell between 0.58 and 0.94, indicating a close relationship between the abundance estimates at successive life history stages. Both exceptions involved the abundance index for session III, suggesting that the estimates derived in October may be more unreliable than the others.

Survival Rates

Total juvenile populations

Based on estimates of total fry outputs into the Main Lake basin and resulting smolt outputs, survival rates ranged from 7.5 to 49.9% (Table 1). Average annual rates for the pre- and post-channel periods of 26.2 and 30.9 %, respectively, were not significantly different ($P > 0.40$).

Marked populations

The fry marking and recovery programs carried out over five brood years (Tables 3 and 4) provided opportunities for comparing wild and channel-produced fish (1965–67 brood years) and comparing survival rates in pre- and post-channel periods (1965–67 and 1970 and 1971 brood years). Also, survival rates for the marked populations could be compared with those derived from estimates of total fry output and smolt outputs from the Main Lake to test the validity of the two sets of estimates.

The relative survival of marked wild and channel fry was determined by comparing the marked ratio at time of release with those observed in underyearlings captured in the lake (sessions I–III) and finally among seaward migrating smolts (Table 3, 1965–67). The marked ratios found among the underyearlings varied considerably each year (due at least in part to the small number of recoveries in some instances), but no significant differences from the ratios at times of release were found when tested by chi-square ($P = 0.05$).

Comparisons of the ratios of marked seaward migrants given below are values for total, pooled, and heterogeneity chi-square (Sokal and Rohlf 1969) based on the numbers of marked wild and channel smolts observed daily throughout each annual migration:

Brood year	χ^2	df	P
1965			
Total	26.67	14	0.025
Pooled	2.61	1	0.090
Heterogeneity	24.06	13	0.030
1966			
Total	37.24	26	0.080
Pooled	13.25	1	0.005
Heterogeneity	23.99	25	0.500
1967			
Total	62.18	34	0.005
Pooled	23.71	1	0.005
Heterogeneity	38.47	33	0.250

Values of total chi-square were significant in 2 yr (1965 and 1967) and approached significance in the third, revealing day-to-day deviations from the expected ratio of wild and channel smolts during their migration. The significant pooled chi-squares in 1966 and 1967 indicate that the deviations were strongly in one direction. This was confirmed by the nonsignificant values of heterogeneity chi-square in those years. Thus, there were fewer than expected channel-produced smolts from the 1966 brood year and just the reverse from the 1967 brood. In 1965, pooled chi-square, while falling short of significance, suggests a tendency for fewer than expected wild smolts. However, the significant heterogeneity chi-square reveals that during the migration there were deviations from the expected ratio in both directions.

The above differences would, of course, be reflected in differences in the absolute survival rates of the two marked groups. Estimates of these survival rates can be made, since the number of marked fry released is known and the total number of marked smolts each year can be estimated by applying daily marked to unmarked ratios with daily estimates of smolt abundance and summing for the period of smolt migration (see Table 2 in McDonald 1969 for details of this procedure for 1965 brood year smolts). Survival rates are compared below (rates for the 1970 and 1971 brood years are included as a convenience for later discussion of pre- and post-channel periods):

Brood year	Group	No. marked and released	Estimated No. in smolt run	% survival
1965	Wild	203 754	25 895	12.7
	Fulton channel No. 1	299 363	42 848	14.3
1966	Wild	223 860	57 803	25.8
	Fulton channel No. 1	429 364	85 393	19.9
1967	Wild	325 727	95 308	29.3
	Fulton channel No. 1	341 607	113 367	33.2
1970	Fulton channel No. 2	366 661	91 503	25.0
	Pinkut channel	308 779	73 917	23.9
1971	Fulton channel No. 2	1 168 184	434 585	37.2
	Pinkut channel	550 062	140 623	25.6

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| Brood year | No. marked and released | | Lake area | No. recovered | | | | | | | |
| | Wild | Channel | | Session I | | Session II | | Session III | | Smolts | |
				Wild	Channel	Wild	Channel	Wild	Channel	Wild	Channel
1965	203 754	299 363	1	0	0	4	4	0	0		
			2	10	29	18	24	12	16		
			3	10	22	13	27	2	3		
			4	14	9	15	18	4	3		
			5	1	2	2	2	1	0	487	790
Total				35	62	52	75	19	22		
Marked ratios	0.405	0.595		0.361	0.639	0.409	0.591	0.463	0.537	0.381	0.619
1966	223 860	429 364	1	0	0	1	2	0	4		
			2	1	1	1	6	1	1		
			3	3	7	1	8	0	7		
			4	11	17	8	8	2	2		
			5	2	2	1	2	3	2	754	1222
Total				17	27	12	26	6	16		
Marked ratios	0.343	0.657		0.386	0.614	0.316	0.684	0.273	0.727	0.382	0.618
1967	325 727	341 607	1	1	0	8	6	0	2		
			2	0	3	10	10	1	1		
			3	18	22	2	4	1	5		
			4	23	37	18	15	2	0		
			5	14	8	6	2	1	0	1228	1551
Total				56	70	44	37	5	8		
Marked ratios	0.488	0.512		0.444	0.556	0.543	0.457	0.385	0.615	0.442	0.558

TABLE 4. Marking and recovery of fry from the Fulton and Pinkut channels, 1970 and 1971.

Brood year	Fulton channel No. 2	Pinkut channel	Lake area	Fulton	Pinkut	Fulton	Pinkut	Fulton	Pinkut	Fulton	Pinkut
1970	366 661	308 779	1	0	0	7	2	1	0		
			2	2	0	11	5	3	3		
			3	7	1	3	8	5	6		
			4	8	0	8	9	4	9		
			5	13	16	1	1	6	1	726	571
Total				30	17	30	25	19	19		
Marked ratios	0.543	0.457		0.638	0.362	0.545	0.455	0.500	0.500	0.560	0.440
1971	1 168 184	550 062	1	1	0	34	7	29	12		
			2	21	1	26	12	4	7		
			3	30	2	10	5	2	1		
			4	42	13	25	16	3	3		
			5	102	45	20	11	10	9	2214	683
Total				196	61	115	51	48	32		
Marked ratios	0.680	0.320		0.763	0.237	0.693	0.307	0.600	0.400	0.764	0.236

Annual rates for the 1965–67 brood years varied just over twofold for each group: from 12.7 to 29.3% and from 14.3 to 33.7% for wild and channel fry, respectively. However, the year-to-year change in the rate of one group was closely paralleled by that of the other, and when rates within years are compared they are similar. Clearly, the differences found by comparing marked ratios were too small to cause much difference in percent fry-to-smolt survival. In view of the small differences observed and the fact that they went both ways (a survival advantage for channel fry in 2 yr and for wild fry in 1 yr), we concluded that wild and channel-produced fry were similarly viable.

The fry-to-smolt survival rates of marked fish provide a second opportunity to compare rates for the pre- and post-channel periods, although the small number of brood years (5) for which information is available precludes meaningful statistical testing. Survival rates in the postchannel years of 1970 and 1971 were comparable with those in two prechannel years and greater than the rates in the third, supporting the conclusion arrived at using survival rates from total fry and smolt outputs, i.e. that there were no differences in survival between pre- and post-channel periods.

Validity of survival rates

The survival rates of marked fish and those of the total population were estimated independently of each other. The

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extent to which the two sets of estimates agree will provide a measure of their validity. Since there are two estimates for marked fry in each brood year (fry from two sources), it had to be decided which of the two (or the mean) should be used. It was decided that the rates from the source that produced the largest number of fry would be most representative. Data from West (1978) showed that by far the largest single source of fry was the Fulton River from 1965 to 1967 and Fulton channel No. 2 from 1970 and 1971. Regression analysis was carried out on the following pairs of survival rates:

	1965	1966	1967	1970	1971
Marked fry	12.7	25.8	29.3	25.0	37.2
Total fry	17.9	29.6	37.3	33.1	45.9

A high degree of association was found ($r^2 = 0.973$) when the estimates from marked fry were regressed on those derived from total fry and smolt outputs. A simple inspection of the paired values reveals that the rates for marked fish were consistently low by 4–9 percentage points. This is not surprising because some marking mortality could be expected. It is most likely that the higher rates estimated from total fry and smolt outputs are the more accurate.

Underyearling Distribution in the Main Lake

Total population

Distribution in terms of both density and abundance was examined for each fishing period using two-way analysis of variance with years and lake areas as treatment factors (Table A1). Estimates of relative density were derived from catch per unit of effort data (average catch per set) in each area, while estimates of relative abundance were calculated by weighting catches by area size as described in the appendix.

Looking first at densities in session I, significant differences were found among years and among lake areas within each year. However, the interaction term was not significant, showing that densities were distributed among the five lake areas in a similar way each year (i.e. no change before and after spawning channel operation). In sessions II and III, densities among years were again significantly different but differences among areas were significant only in session II. The significant interaction factor show that in contrast with session I, differences among areas varied from year to year.

Area densities were compared using Duncan's multiple range test modified for samples of unequal size (Table A2). During session I, in both pre- and post-channel years, there was a consistent increase in underyearling density from area 1 at the north end of the Main Lake to either area 4 or 5 in the south. In subsequent periods the north–south gradient was no longer apparent and no consistent pattern in distribution can be seen except in session II when the density in area 4 was either the greatest or second greatest. When pre- and post-channel years are compared, there is no evidence of a persistent change in distribution.

Distribution in terms of abundance was generally similar to that for density, revealing that differences in area densities were large enough to mask most of the effects of differences in area size. Significant differences in area indices occurred among years and among areas in all three fishing periods (Table A1). Again, the interaction terms demonstrate that distribution was consistent over the years during session I but variable in sessions II and III. When comparing area indices in session I (Table A3),
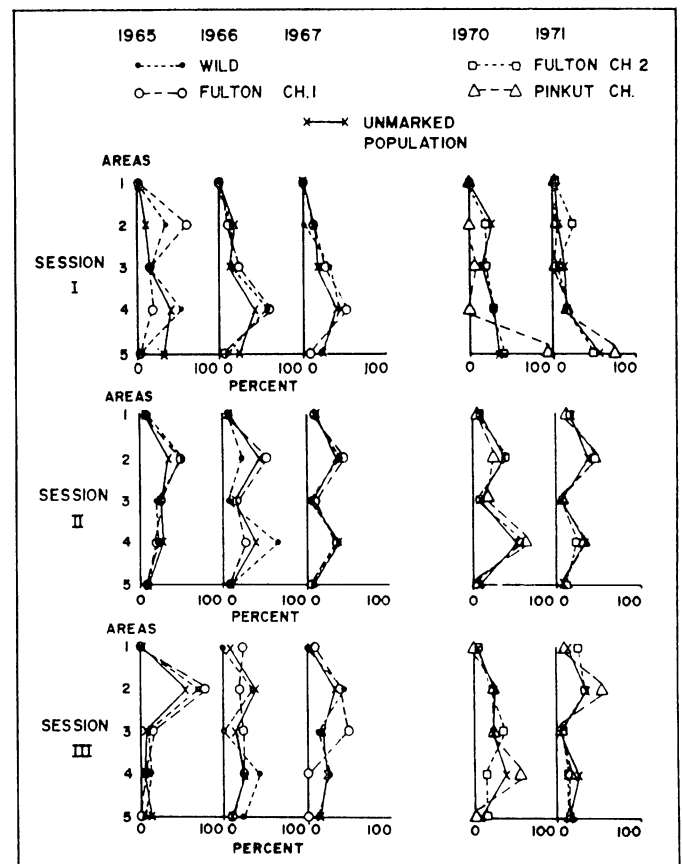

FIG. 2. Proportions of marked and unmarked underyearling sockeye in Main Lake areas by brood year and fishing period.

there was consistently fewer underyearlings in area 1 and greatest numbers usually in area 4 or 5. Later in the season, distribution was more variable although usually underyearlings were most abundant in areas 2 and 4.

Marked underyearlings

The proportions of marked fish in Main Lake areas were estimated by applying the marked to unmarked ratio observed in each area to the area index of abundance drawn from Table A3 (for an example of detailed calculations see those for the 1965 brood year in Table 6, McDonald 1969). The estimated proportions are shown in Fig. 2, along with those for the underlying population as a whole. These latter values are simply area indices of abundance expressed as percentages of the sum of the indices for Main Lake areas.

The marking program of 1965–67 was designed specifically to compare wild and channel-produced fry. In Fig. 2, their distributions can be seen to be similar to each other and to the distribution of the total underyearling population. Some of the observed differences between wild and channel fish may be more apparent than real. For example, the proportions in session III, for 1966 and 1967, were calculated from a small number of mark recoveries (see Table 3), and considerable error is likely. On the other hand, differences seen in session I, 1965, were attributed to differences in times of lake entry between the two marked groups (McDonald 1969). The similarities, however, far outweigh the differences and strongly support the conclusion that the origin of the fry, whether wild or channel, did not have any substantial effect on their distribution in the lake.

The programs of 1970 and 1971 in which fry from the Fulton and Pinkut systems were marked served two purposes. First, the

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1970 and 1971 distributions of Fulton fish can be compared with that described above for prechannel years 1965–67. Second, the distribution and extent of mixing of juveniles from Fulton and Pinkut can be examined.

Fulton fry were distributed in much the same way in pre- and post-channel years (Fig. 2). The dispersal of most fry into southern lake areas continued in 1970 and 1971, confirming that this movement is a consistent feature of the Fulton stock. Distributions in session II were comparable as well, while those in session III remained variable.

Mixing of Fulton and Pinkut juveniles occurred in all three fishing periods. In session I, mixing was confined mostly to area 5, which is adjacent to Pinkut Creek. The limited dispersal of Pinkut fish compared with that of Fulton fish probably results from the relatively late time of lake entry by Pinkut fry (West 1968) and thus less time to disperse. The similarity in distribution of the two stocks during session II and to a lesser extent in session III is striking. The two stocks were found in almost equal proportion in all lake areas, indicating that they were distributed as a single population.

Comparisons of Size and Growth

Marked wild and channel juveniles

Data are available to compare the sizes of the two groups from fry migrant to smolt migrant stages (Table 5). Values for fry migrants were weighted to daily abundance and cannot be tested statistically but the means indicate little difference in length or weight. Mean lengths of wild fry were between 27.80 and 28.21 mm, while those for channel fry were between 27.21 and 28.31 mm. In 1966, wild fry were slightly longer and heavier. In 1967, channel fry were slightly longer but only equalled wild fry in weight. West (1978) reported the mean lengths of fry from the same two sources for the brood years 1965 and 1966. His data arose from samples of fry migrants drawn completely

independently of this study. Differences in mean length were consistent with those observed for marked fry. West found that the mean lengths of wild and channel fry from the 1965 brood year were not significantly different ($P > 0.05$). However, in 1966, wild fry were found to be longer than their channel counterparts ($P = 0.002$).

Comparisons at subsequent stages reveal that channel fry were consistently smaller throughout the period of lake residence and again at time of seaward migration (Table 5; Fig. 3). While the differences were not very large (channel fish were 88–99 and 80–98% of wild fish in length and weight, respectively), in most cases the means were significantly different ($P < 0.05$).

On the other hand, growth rates of wild and channel fry were similar (Table 6). Fastest growth in length was reached between sessions I and II (July–August) when rates approached 1%/d. Growth in weight was greatest from time of lake entry to session II and varied from 2.7 to 3.4%/d. As would be expected, growth rates slowed in the fall and fell sharply over winter when growth in length was less than 0.1%/d and growth in weight did not exceed 0.21%/d. The overwinter rates may be a poor description of growth in that period. Probably, most growth would have occurred in late fall and/or early spring just before seaward migration.

Direct comparisons of the growth of wild and channel-produced juveniles were made by covariance analysis using sizes of marked fish recovered from sessions I, II, and III. This period, from late June or early July to October, spans most of the first growing season. The length and weight of individual mark recoveries were converted to natural logarithms. Recovery dates were assigned time values (days) based on May 1 equal to day 1. Results are summarized below (a = computed sizes of the fry (logarithms) on day 0 (April 30); b = instantaneous rates of increase in length and weight with 1 d as the unit of time; **P = 0.01):

Brood year	Source	Length				Weight				df
		a	b	a	b	a	b	a	b	
				F value				F value		
1965	Wild	3.121	0.0069	58.26**	1.73					1 305
	Channel	2.962	0.0074							
1966	Wild	3.041	0.0083	33.54**	1.84	−2.49	0.0262	34.28**	2.01	1 399
	Channel	3.032	0.0076			−2.51	0.0239			
1967	Wild	3.056	0.0084	27.79**	0.01	−2.49	0.0269	25.29**	0.00	1 361
	Channel	2.992	0.0084			−2.71	0.0268			

Over the 3 yr there were no significant differences in the slopes (growth rates) of the regressions for wild and channel fish. Each year, however, the intercepts were significantly different, confirming that channel-produced underyearlings were consistently smaller than their wild counterparts.

This difference did not appear to have resulted from differences in initial size (of fry) or different growth rates but rather from different times of lake entry. The migrations of channel fry were consistently later than those of wild fry (by 9–14 d), and periods of growth in the lake prior to sampling in session I differed accordingly. Mean growing periods to session I were

44 and 32 d for wild and channel fry, respectively (from Table 6), giving wild fry a distinct advantage. For example, assuming an initial length of 28 mm and a growth rate of 0.008 mm/d (the approximate mean of observed values), the size a wild fry would attain by session I would be 39.80 mm, while that for channel fry would be 36.16 mm. The difference of 3.64 mm is close to the actual differences observed in the three brood-years used for the comparisons (Table 5). Since growth rates remained comparable at subsequent life history stages, the size advantage gained initially by wild fry was maintained through to seaward migration.

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TABLE 5. Mean size of marked wild and channel juveniles from fry to smolt stages.

| Brood year	Stage	No. in sample		Mean fork length (mm)			Mean weight (g)		
		Wild	Channel	Wild	Channel	t	Wild	Channel	t
1965	Fry	450	450	28.21	28.19				
	Session I	55	75	35.96	31.69	5.663***			
	Session II	51	75	52.88	47.12	2.077*			
	Session III	27	27	69.85	65.89	6.833***			
	Smolt	487	790	78.90	76.94	6.853***			
1966	Fry	1000	950	27.80	27.21		0.172	0.155	
	Session I	30	39	38.57	36.11	2.247*	0.645	0.517	2.280*
	Session II	79	134	63.37	58.57	4.256***	2.888	2.325	3.979***
	Session III	11	26	69.68	66.75	1.275	3.914	3.230	1.421
	Smolt	754	1222	80.42	78.22	8.450***	5.543	5.128	7.870***
1967	Fry	700	699	27.84	28.31		0.156	0.156	
	Session I	57	72	37.49	35.33	2.901**	0.550	0.441	2.810**
	Session II	45	38	60.91	56.97	2.630**	2.490	2.050	2.740**
	Session III	5	8	72.40	71.25	0.300	4.229	3.831	0.700
	Smolt	1228	1551	81.14	80.36	3.880***	5.158	5.038	2.910**
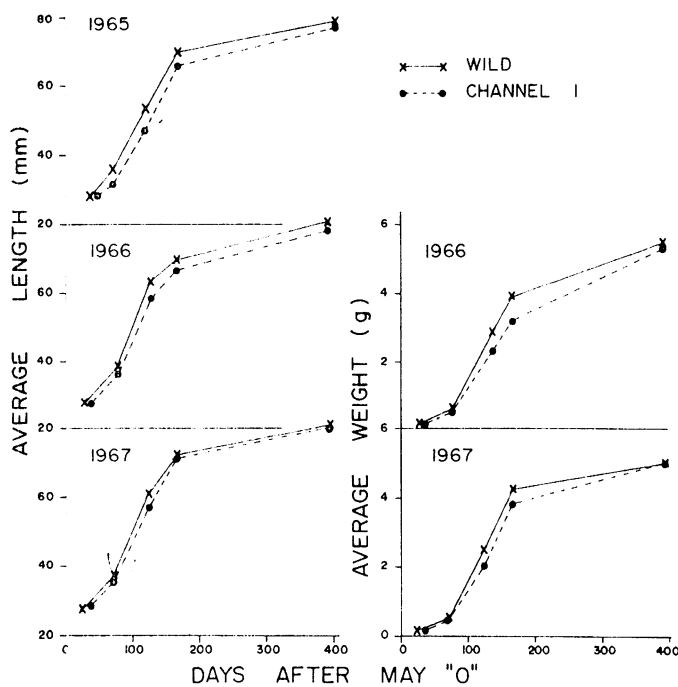
FIG. 3. Size comparisons of marked wild and channel juvenile sockeye, fry to smolt stage, 1965–67.

Juveniles in pre- and post-channel years

Size of fry migrants — Fry from Pinkut Creek and Fulton River and their associated spawning channels were sampled at frequent intervals during their downstream migration (Ginetz 1977). The samples of usually 50 fish were randomly subsampled in proportion to the abundance of fry migrants, and weighted mean lengths and weights of fry entering the main lake each year from these sources were calculated. Available data allow comparisons of two prechannel years (1965 and 1967) and seven postchannel years (1970–76). Annual mean lengths and weights ranged from 29.3 to 30.2 mm and from 0.135 to 0.154 g, respectively (Table 7). Although some significant differences between means occurred, there was no pattern over the years that would suggest differences between pre- and post-channel periods. In terms of length, fry from the two

prechannel years were not significantly different from those in three of seven postchannel years. In terms of weight, fry from the 1966 brood were not significantly different from those of the postchannel years 1972 and 1974, and the 1965 mean did not differ significantly from those of six of the seven postchannel years.

There is evidence however, that fry in prechannel years tended to be heavier per unit length. It can be noted from the table that while their mean lengths were among the least, their mean weights were among the greatest. Stage of development of wild and channel migrants was compared (Table 7) using the index of Bams (1967) where

$$K_d = \frac{10\sqrt[3]{\text{weight in mg}}}{\text{length in mm}}.$$

Indices for 1965 and 1966 were greater than those for most other years, revealing that prechannel fry were less advanced and contained relatively large amounts of heavy (as compared with body tissue) yolk sac material.

Size of underyearlings — Mean sizes of underyearling in Main Lake areas 1–5 were compared. Two-way analysis of variance was applied to length data for each fishing session using years and areas as the two factors (Table A4). Significant differences among years and areas occurred in all three fishing periods. Interactions between areas and years were significant ($P < 0.001$), showing that differences among areas changed from year to year.

A more detailed analysis of each year's data and each session was undertaken using Duncan's multiple range test (Tables A5). During session I, underyearlings in area 1 were always larger than those in any other area. In the prechannel years (1965–67), underyearlings in area 2 or 5 were smallest and those in areas 3 and 4 were intermediate in size. In postchannel years, a distinct north–south gradient can be seen with mean lengths and weights decreasing progressively from area 1 to area 5. In session II, underyearlings in area 1 remained relatively large (6 of 7 yr). A north–south trend in size occurred in prechannel years 1966 and 1967 (whereas it was absent in session I) and in postchannel

TABLE 6. Instantaneous growth rates of marked wild and channel juveniles (SI, SII, SII = sessions I, II, and III).

Brood year	Stage	Central dates	t (d)	Growth in length		Growth in weight	
				Wild	Channel	Wild	Channel
1965	Fry–SI	June 6–July 11	35	0.0069			
		June 17–July 11	24		0.0034		
	SI–SII	July 11–Aug. 28	48	0.0080	0.0083		
	SI–SIII	Aug. 28–Oct. 16	49	0.0057	0.0068		
	SIII–smolt	Oct. 16–June 8	235	0.0005	0.0007		
1966	Fry–SI	May 29–July 17	49	0.0067		0.0270	
		June 6–July 17	35		0.0081		0.0344
	SI–SII	July 17–Sept. 6	51	0.0098	0.0095	0.0294	0.0295
	SI–SIII	Sept. 6–Oct. 14	38	0.0025	0.0035	0.0080	0.0086
	SIII–smolt	Oct. 14–May 27	225	0.0006		0.0016	
		Oct. 14–May 28	226		0.0007		0.0021
1967	Fry–SI	May 25–July 11	47	0.0063		0.0268	
		June 6–July 11	38		0.0058		0.0273
	SI–SII	July 11–Sept. 1	52	0.0093	0.0092	0.0291	0.0296
	SII–SIII	Sept. 1–Oct. 14	43	0.0041	0.0052	0.0123	0.0145
	SIII–smolt	Oct. 14–May 30	228	0.0005		0.0009	
		Oct. 14–May 29	227		0.0005		0.0012

TABLE 7. Mean length, weight, and K_d of newly emerged downstream migrant fry from the Pinkut and Fulton systems. Means that are underlined are not significantly different from each other ($P > 0.05$).

Brood year	1975	1965	1976	1966	1972	1971	1974	1973	1970
N	365	273	337	509	681	202	319	380	1135
Length (mm)	29.3	29.3	29.4	29.5	29.5	29.8	29.8	29.9	30.0

Brood year	1976	1970	1971	1974	1975	1965	1973	1972	1966
N	337	1135	202	265	365	272	380	681	509
Weight (g)	0.142	0.147	0.147	0.148	0.148	0.150	0.152	0.153	0.154

Brood year	1970	1974	1971	1976	1973	1975	1965	1972	1966
N	1135	265	202	337	380	365	272	681	509
K_d	1.756	1.766	1.770	1.775	1.783	1.803	1.808	1.811	1.815

years 1970 and 1972. The distribution of means in 1971 and 1976 differed from those in other years in that underyearlings in area 5 rather than being the smallest were either the largest or second largest. In session III, the distribution of means was similar in prechannel years and also in 1970 and 1972. In each of these years there was generally a progressive decrease in size from north to south. In 1971 and 1976, however, the reverse was true, with the largest underyearlings occurring in area 5 and the smallest in area 1.

The analysis clearly shows that the mean size of underyearlings in the Main Lake differed considerably from area to area in all fishing periods and in all years. Usually, the largest underyearlings were found in area 1 and the smallest in area 5, often with a progressive decrease in size from north to south. Exceptions to this pattern were seen in 1971 and 1976 when by fall (session III) a strong south–north gradient was established, exactly the reverse of other years.

Further examination of underyearling size in pre- and post-channel periods was carried out by comparing annual means for the Main Lake as a whole (areas 1–5 combined). Differences in mean length were tested (Table A6). In session 1, underyearlings in postchannel years were significantly larger than those in prechannel years. As the season progressed,

postchannel means continued to be relatively large except for the 1970 means, which changed in rank from third largest to the smallest in session II and second smallest in session III. Otherwise, ranking did not change substantially and the means of the postchannel years, 1971, 1972, and 1976, remained the largest. The differences were significant in session II but in session III, 1972 and 1976 means were not significantly different from that of 1965, the highest ranking prechannel mean.

Differences in mean weight could not be statistically tested, but the means were distributed over the years in much the same way as mean lengths, suggesting that in three of the four postchannel years, underyearlings were not only longer but also heavier. To examine this contention, length–weight relationships were compared (Table A7). Significant differences in length–weight relationships occurred among years. However, differences occurred at least as frequently within pre- and post-channel periods as they did between the two periods. In session I, only one of four coefficients for postchannel years was significantly different from those of prechannel years. In session II, no significant differences between the two periods were found, while in session III, differences occurred between combinations of pre- and post-channel years.
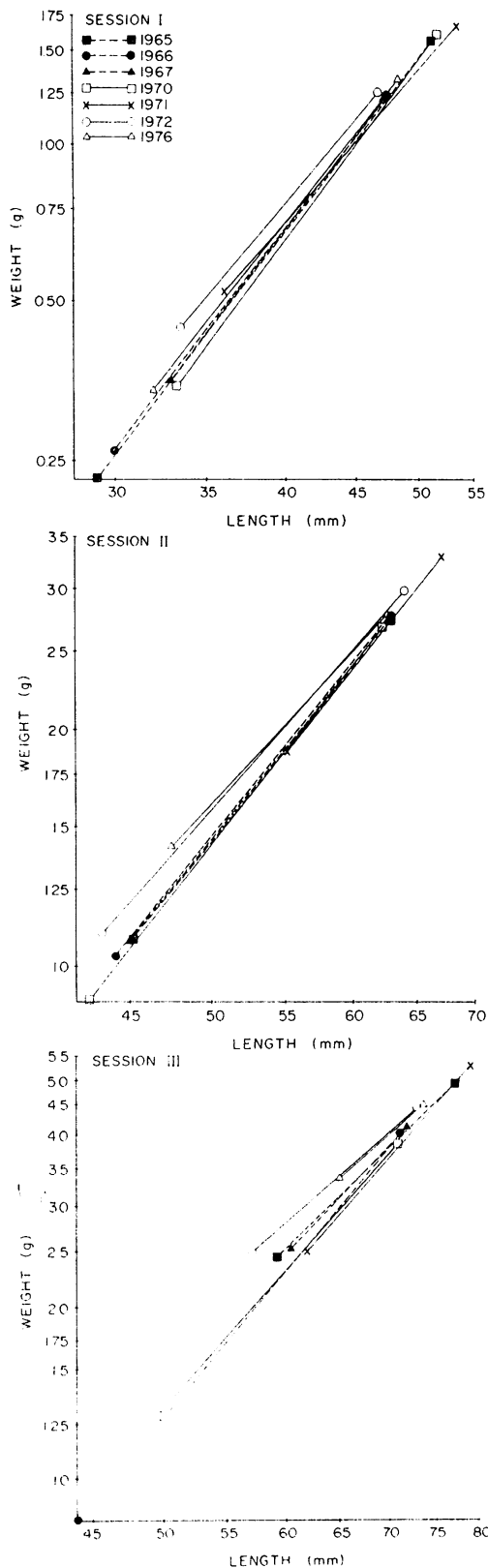
FIG. 4. Relation between length and weight of Main Lake underyearlings by brood years and fishing periods.

Differences and similarities in weight per unit length can be seen by inspection of the regression lines shown in Fig. 4. Most striking are the greater elevations of the lines for 1972 (session I) and 1972 and 1976 (sessions II and III). Postchannel underyearlings were not only longer in 3 out of 4 yr than prechannel
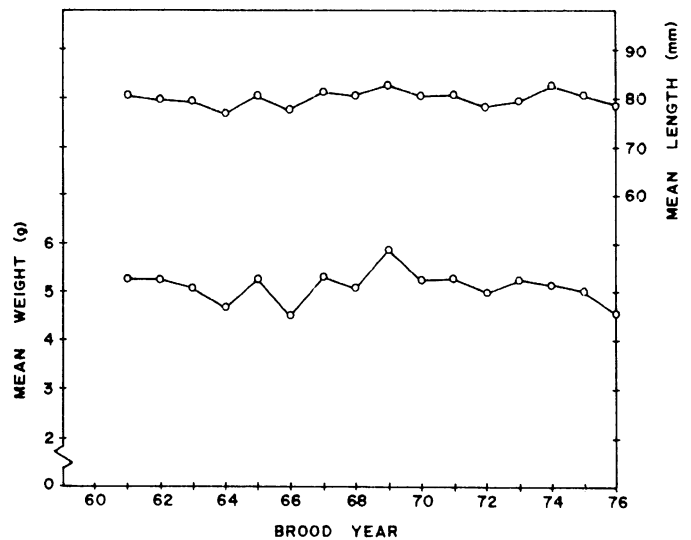

FIG. 5. Mean length and weight of Main Lake smolts, 1961–76 brood years.

underyearlings but in 2 yr (1972 and 1976), they were heavier per unit length.

Size of seaward migrants — Main Lake smolts were sampled daily during their annual migrations from Babine Lake. Mean lengths and weights were weighted to abundance (daily abundance estimates from tag and recovery procedures) to provide estimates of annual means for the brood years 1961–76. Mean length ranged from 76.72 to 82.57 mm and mean weight from 4.57 to 5.84 g (Fig. 5). During the 16-yr period no trend in size was apparent. Linear regressions of length and weight on brood years and smolt abundance were calculated with the following results:

	b	F
Years with weight	−0.0109	0.3399
Years with length	0.0537	0.3717
Abundance with weight	−0.0015	0.1330
Abundance with length	0.0050	0.0624

In all cases, slopes did not differ from zero ($P < 0.01$), demonstrating no significant change in size between pre- and post-channel periods.

Comparisons of annual growth rates — Mean weight and length at the various life history stages were plotted to illustrate annual growth patterns (Fig. 6). Dates shown are the midpoints of annual fry and smolt migrations and of sampling periods for underyearlings. Instantaneous growth rates were calculated to permit more precise comparison of growth among years (Table 8). Annual growth patterns were similar to these already described for marked fish with rapid growth in spring and summer slowing in fall and slowing still further over winter. In all but 1 yr (1972), relative increases in weight were greatest from May to July, and in all years relative increases in length were greatest from July through August. Growth rates in the periods between fry migration and session III, while variable, do not suggest any change from pre- to post-channel years. Rates for 1965–67 were all within the range of those observed in later years. However, overwinter growth rates in three of four postchannel years were relatively low, about one-half the rates in prechannel years. As a result of this slow overwinter growth, the
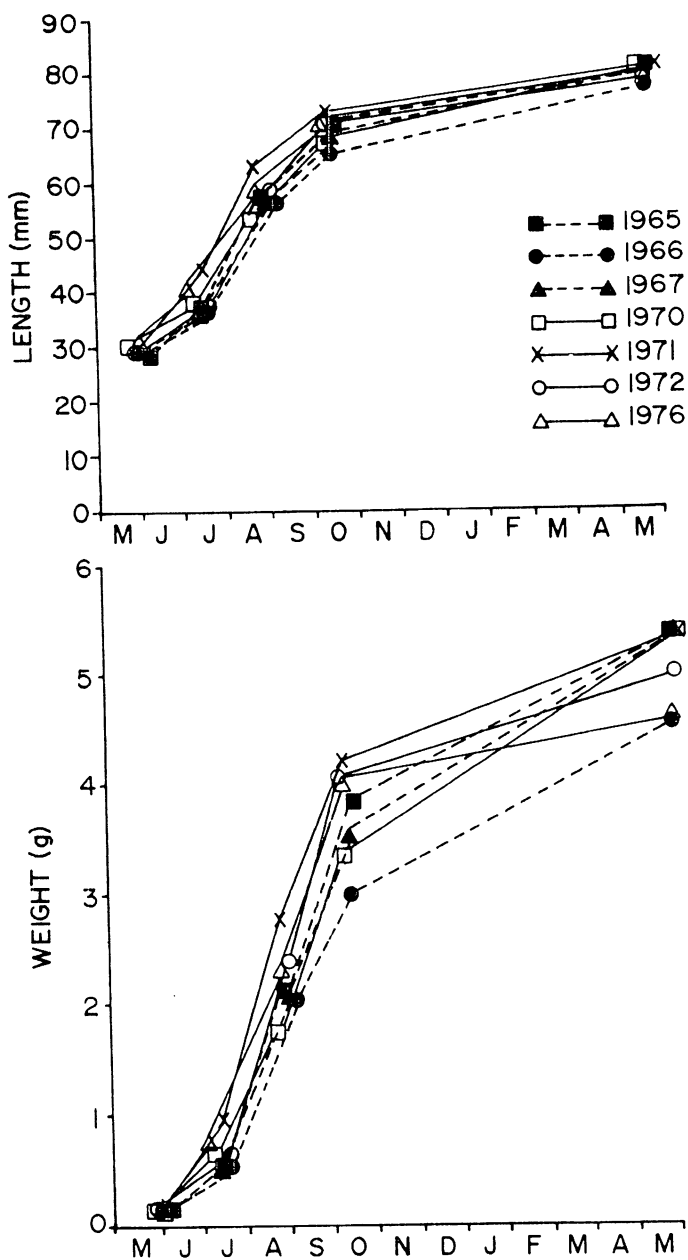
FIG. 6. Increase in mean length and weight from fry to smolt stage in Babine's Main Lake.

index of the biomass of fall underyearlings. The biomass index was calculated by multiplying the mean weight of underyearlings in session III (Table A6) by the lake index of abundance (Table 1). This analysis suggested an inverse relationship between growth and biomass ($r^2 = 0.528$) but fell short of significance ($t = 2.324$, $df = 5$, $0.05 < P < 0.10$).

For the early and late summer periods (sessions I and II), area mean weights were regressed against $\log_{10}$ of area densities (Table 9). In Session I, the regression coefficients were all negative and in three of the four postchannel years were significantly less than zero. When the probability values for all 7 yr were combined and a single test of significance computed, the resulting value was significant ($P < 0.01$), indicating an inverse relationship between size and density. There was no suggestion of a similar relationship in sessions II and III and, in fact, in 4 of 7 yr the slopes were positive.

Any relationship (or the lack of one) between size and density must be examined cautiously. It was demonstrated earlier that change throughout summer and fall was a consistent feature of underyearling distribution. Consequently, there is no assurance that underyearling size in a particular area, at a particular time, will accurately reflect growing conditions (including underyearling density) in that area. Instead, their size may more accurately reflect conditions in the area or areas they occupied previously. This is particularly true of underyearlings sampled in session I in areas 3–5, which contained many immigrants from the Fulton River and channels. McDonald (1969) estimated that dispersal of Fulton fish into these areas occurred at a rate between 1.0 and 1.3 km/d. New estimates of their travel rates were derived from mark–recovery data (Table 4) and based on the distance from the Fulton River at which 50% of the marked fish were found and the number of days between middates of mark releases and recoveries in session I. Travel rates of eight marked groups over 5 yr ranged from 0.7 to 1.3 km/d and averaged 1.0 km/d (Table 10). At this average rate, travel to the nearest boundaries of areas 3, 4, and 5 would take 16, 36, and 59 d, respectively. Because the period between lake entry (mainly from mid-May to mid-June) and sampling in session I was only about 40–70 d, many of the underyearlings of Fulton origin found in these areas, and particularly in the more distant areas 4 and 5, would be recent arrivals and their size largely determined by conditions enroute.

A further complication with respect to density-dependent effects apparent in session I can result from mixing of juveniles from different spawning stocks when these juveniles differ in initial size (as fry) and in times of lake entry. Such differences together with differences in abundance will influence the mean size of underyearlings observed later in the lake. The mixing of juveniles from the Fulton and Pinkut systems in area 5, and to a lesser extent in area 4, was confirmed by mark recoveries (Table 4) and is surely an annual feature of underyearling distribution in session I. Data from West (1978) allow comparisons of the size of fry migrants from the two systems and of their peak migration dates in the four postchannel years. Mean weights and peak migration dates of fry produced from the natural spawning grounds and spawning channels were weighted according to the number of fry produced from each to arrive at an overall mean value for each system (Table 11). Fry from the Pinkut system were consistently smaller than those from Fulton and migration was later except in 1976 when, according to West, rising water temperatures and discharge resulted in an unprecedented early migration. While the differences in mean size were not large, in combination with their later time of lake entry (except for 1976),

progeny of the 1971, 1972, and 1976 brood years that were large as underyearlings were comparable in size with those in other years by the time of seaward migration. In contrast, the progeny of the 1970 brood that were small as underyearlings, experienced fast growth over winter, and by the time of seaward migration they were amongst the largest.

Size and Density Relationships

The differences in overwinter growth rates noted above and some consistent trends in the distribution of underyearling size and density that were evident during the summer months suggest that density-dependent mechanisms may have been operative in the Main Lake. Overwinter growth rates were low in three postchannel years when, by fall, underyearlings were both relatively abundant and large in size. To test for compensatory growth, we regressed overwinter growth rates against an

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TABLE 8. Instantaneous growth rates for Main Lake juveniles (G_W = instantaneous growth in ln g/d; G_L = instantaneous growth in ln mm/d).

		Brood year							Mean	
		1965	1966	1967	1970	1971	1972	1976	1965–67	1970–76
Emerging fry–	G_W	0.0365	0.0291–	—	0.0270	0.0368	0.0266	0.0433	0.0328	0.0334
session I	G_L	0.0064	0.0048	—	0.0046	0.0077	0.0046	0.0080	0.0056	0.0062
(May–July)										
Session I–II	G_W	0.0284	0.0272	0.0284	0.0256	0.0256	0.0290	0.0256	0.0280	0.0265
(July–Aug)	G_L	0.0092	0.0082	0.0089	0.0079	0.0086	0.0099	0.0082	0.0089	0.0086
Session II–III	G_W	0.0122	0.0099	0.0123	0.0134	0.0085	0.0149	0.0121	0.0115	0.0122
(Aug.–Oct.)	G_L	0.0042	0.0040	0.0043	0.0048	0.0030	0.0049	0.0041	0.0041	0.0042
Session III–	G_W	0.0014	0.0018	0.0019	0.0020	0.0010	0.0009	0.0005	0.0017	0.0011
smolt run	G_L	0.0006	0.0007	0.0008	0.0007	0.0004	0.0004	0.0004	0.0007	0.0005
(Oct.–June)										

TABLE 9. Regression coefficients (b) of mean weight and density of underyearlings in Main Lake areas. Also shown are the coefficients of determination (r^2) and the probability of the regression coefficients being equal to zero (P).

Brood year	Session I			Session II			Session III		
	b	r^2	P	b	r^2	P	b	r^2	P
1965	−0.307	0.192	9,468	+0.082	0.009	>0.750	−0.388	0.035	>0.750
1966	−0.205	0.552	0.146	+0.309	0.082	0.663	+1.132	0.105	0.612
1967	−0.137	0.502	0.183	+0.344	0.074	0.678	−0.155	0.049	0.728
1970	−0.410	0.988	<0.0001***	−0.000	0.000	>0.750	+0.130	0.042	0.742
1971	−0.223	0.651	0.083	−0.178	0.026	>0.750	−0.465	0.014	>0.750
1972	−0.249	0.954	0.002**	+0.662	0.198	0.462	+0.825	0.253	0.407
1976	−0.361	0.905	0.006**	−0.083	0.058	0.505	+0.108	0.012	>0.75
$-2\Sigma \ln P$			50.217***			1.202 (NS)			2.166 (NS)

TABLE 10. Estimated travel rates of marked Fulton River and channel fry into southern lake basins.

	Middates			Time out (d)		Distance traveled (km)		Travel time (km/d)	
	Marked fry release								
Brood year	River	Channel	Recoveries	River	Channel	River	Channel	River	Channel
1965	June 6	June 17	July 11	35	24	35.6	16.1	1.0	0.7
1966	May 29	June 12	July 17	49	35	46.9	46.9	1.0	1.3
1967	May 25	June 5	July 11	47	36	46.9	35.6	1.0	1.0
1970		May 24	July 8		45		46.9		1.0
1971		May 25	July 13		49		58.7		1.2

the size that Pinkut fry would attain by session I would be considerably less than that of Fulton fry, with the result that the mean size of underyearlings in areas of mixing (mostly in area 5) would be less than that observed in areas occupied only by Fulton fish. The extent of this reduction cannot be quantified with available data. It will certainly vary from year to year depending on size and time differences at lake entry and the relative abundance of the two stocks.

The influence of progeny from other spawning stocks on mean size is even less certain. Fry from numerous small streams tributary to the Main Lake contribute to the underyearling population. However, their spawning stocks and resulting fry outputs are small relative to those of Fulton and Pinkut and any effect on underyearling size would be small as well.

There is a possibility, however, that progeny from the large spawning stock of the Babine River and that of the Morrison River may emigrate to the Main Lake and influence mean size, particularly in area 1, which lies immediately uplake of North and Morrison arms. Both mark–recovery data and abundance indices have demonstrated that this area is sparsely populated in

TABLE 11. Comparisons of size and migration times of sockeye fry from the Fulton and Pinkut systems.

Brood year	Average weight (g)		Peak migration date	
	Fulton	Pinkut	Fulton	Pinkut
1970	0.149	0.141	May 18	May 28
1971	0.148	0.138	May 27	May 31
1972	0.154	0.152	May 27	May 29
1976	0.143	0.136	May 25	May 5

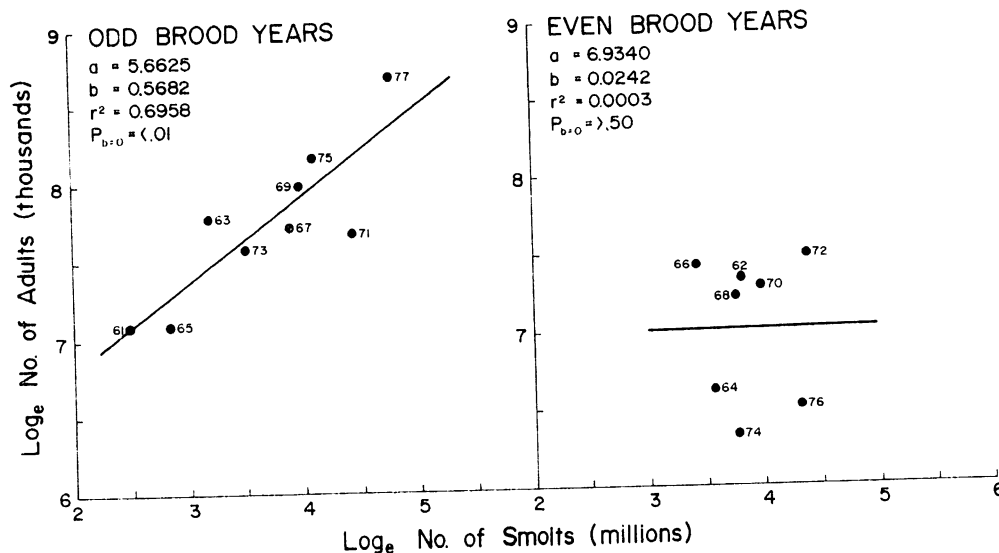Can. J. Fish. Aquat. Sci., Vol. 41, 1984

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FIG. 7. Relation between smolt outputs and adult returns of Babine Lake sockeye for even- and odd-numbered brood years.

TABLE 12. Mean lengths (mm) and weights (g) of underyearlings in each lake basin. Mean lengths underlined are not significantly different from each other ($P > 0.05$).

Brood year	Basin	Session I		
		Main Lake	North Arm	Morrison Arm
1966	Mean weight	0.50	—	1.52
	Mean length	36.0	48.6	50.7
1967	Mean weight	0.47	1.18	1.19
	Mean length	35.6	46.6	47.4
1970	Mean weight	0.54	0.89	—
	Mean length	37.5	43.6	—
1971	Mean weight	0.96	1.26	1.52
	Mean length	44.1	48.0	51.7
1972	Mean weight	0.63	1.14	1.59
	Mean length	37.3	44.6	49.9
1976	Mean weight	0.65	0.81	0.88
	Mean length	38.9	41.6	42.0

session 1 by juveniles from the Fulton system. The movement of only small numbers of fish from the two arms into area 1 could have a strong influence on the mean body size of the composite population.

As noted earlier, McCart (1967) observed during May and June schools of fry migrating from the Babine River as far as 32 km uplake and only 11 km from the Main Lake. If the dispersal of these fry is as far ranging and as rapid as that observed for Fulton fry, the presence of some Babine River fry in area 1 by early June could be expected. The presence of fry from the Morrison River only 10 km away is even more likely.

Data are available from six brood years to provide comparisons of underyearling size in the two lake arms and Main Lake during session 1 (Table 12). North Arm and Morrison Arm fish were substantially and significantly larger with mean lengths between 107 and 141% those of Main Lake fish. The presence in area 1 of relatively larger underyearlings from one or both of the lake arms could account either completely or at least in part for the large mean size observed in this area relative to other Main Lake areas.

The evidence for stock mixing in area 1 is far from conclusive

but is sufficient to suggest that the relatively large size of underyearlings in this area may be the result of stock mixing rather than the effect of low population density. While the situation in area 1 remains unclear, there is more convincing evidence that the small size of underyearlings in densely populated area 5 is due at least in part to the mixture of Fulton and Pinkut stocks.

Adult Returns

Smolts outputs and adult returns by age group and in total from prechannel brood years (1961–67) and postchannel brood years (1970–71) were compared (Table 13). Preliminary estimates for 1977 are courtesy of R. Kadowaki (Fisheries and Oceans, Prince Rupert, B.C., personal communication). Remaining estimates are from various Department of Fisheries and Oceans sources.

The mean total return of 2 249 700 adults in the postchannel period exceeded the prechannel mean by 667 000. The means, however, were not significantly different ($P > 0.20$). Also, no significant difference was seen in mean numbers of 4-yr-olds (1.2) and 5-yr-olds (1.3). However, 3-yr-old jack sockeye (1.1) were more abundant in the postchannel period ($P < 0.05$). When expressed as a percentage of the total return, the mean proportion of jacks produced in the postchannel period was 10.5% as compared with 5.9% in the earlier period, a significant difference ($t = 2.627$, $P < 0.055$).

Peterman (1978, 1982) concluded that the relationship between smolt outputs and adult returns was density dependent with no significant increase in returns when smolt outputs increased. Peterman also pointed out that the survival rates of smolts produced from odd-numbered brood years were usually greater than those for smolts from even-numbered brood years. This difference is readily apparent by inspection of rates given in Table 13. The average survival rate of 6.4% in odd-numbered brood years was more than double the average rate of 2.6% in even-numbered brood years ($t = 3.663$, $P < 0.005$).

In view of the apparently different smolt to adult relationship between even- and odd-year broods, we have examined each separately. A strong positive relationship was found between smolt abundance and adult returns from the odd-numbered

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Brood year	Smolts (millions)			Adult returns (thousands)				Smolt-to-adult survival (%)
	Main Lake	North Arm	Total	1.1	1.2	1.3	Total	
1961	5.78	6.75	12.53	60.0	649.3	488.8	1198.1	9.6
1962	29.38	16.54	45.89	64.0	548.2	940.9	1553.1	3.4
1963	19.16	4.51	23.67	182.0	975.2	1275.9	2433.2	10.3
1964	13.78	21.53	35.31	29.3	199.6	510.7	739.7	2.1
1965	6.84	9.73	16.57	53.4	746.0	402.4	1201.8	7.3
1966	18.10	12.79	30.89	154.0	822.8	704.1	1680.9	5.4
1967	24.18	22.01	46.19	166.0	1040.7	1067.0	2273.6	4.9
1968	34.63	8.38	43.01	54.6	369.5	963.5	1387.6	3.2
1969	39.20	13.31	52.51	258.7	1131.8	1505.2	2895.7	5.5
1970	45.56	8.78	54.34	233.4	849.2	370.5	1453.1	2.7
1971	73.98	14.77	88.75	254.3	1104.0	798.6	2157.0	2.4
1972	61.13	19.00	80.13	137.0	548.2	1092.9	1778.1	2.2
1973	27.43	6.62	34.05	255.5	958.4	739.3	1953.1	5.7
1974	36.12	6.86	42.98	45.4	223.1	294.3	562.8	1.3
1975	51.01	10.03	61.04	296.3	2332.5	838.7	3467.5	5.7
1976	70.92	5.04	75.96	93.4	223.2	354.4	671.0	0.9
1977	99.19	9.03	108.22	233.9	2714.7	2240.0	5955	5.5
1961–67 mean			30.13	101.2	711.7	770.0	1582.9	6.1
1970–77 mean			68.18	193.7	1119.2	841.1	2249.7	3.3
t			3.628	2.269	1.111	0.267	0.954	2.764
P			<0.05	<0.05	>0.20	>0.50	>0.20	<0.025

brood years (Fig. 7). The relationship, when tested by the conservative Varley and Gradwell (1963, 1968) method, as used by Peterman (1978), is curvilinear, indicating density dependence with the rate of adult returns decreasing as smolt abundance increases. However, the degree of density dependence is small enough to permit an increasing surplus of returning adults from smolt outputs several times the preenhancement level. For example, the predicted return from the postchannel average smolt output of about 70 million is 3 million adults. Allowing for brood stock requirements (no more than 1 million spawners), the surplus (available catch) of 2 million more than exceeds the initial target of the enhancement program.

While the productivity of the odd-numbered brood years has met expectations, even-numbered brood years have performed poorly. Adult returns varied widely but did not indicate any response (positive or negative) to smolt abundance within the range observed.

Discussion

There is considerable evidence to show that the basic assumptions regarding juvenile production were valid or nearly so. The artificial spawning channels proved to be effective producers of sockeye fry with egg-to-fry survival rates close to the 40% anticipated. One shortcoming was the lack of response in production to flow control over the formerly natural spawning beds of Fulton River and Pinkut Creek. Some increase in egg-to-fry survival was expected (the amount was never specified) but survival rates did not increase. The end result was an average increase in fry output into the Main Lake of 106 million, less than the 125 million projected, but still sufficient to increase the juvenile population nearly threefold.

Two lines of evidence are available to examine the hypothesis that channel-produced fry were as viable as wild fry. Compari-

son of marked fry revealed little difference in the survival rates of the two types through to the smolt stage. The small differences observed were probably more apparent than real, reflecting sources of error inherent in marking and recovery methods. Results from marking and recovery were confirmed by observed changes in the total abundance of Main Lake juvenile populations from prechannel to postchannel years. The nearly threefold increase in mean fry output was followed by roughly equivalent increases in the abundance of underyearlings and seaward migrating smolts.

Comparison of the size and growth rates of 1965–67 brood year juveniles produced from the Fulton River (wild fry) and the first Fulton River spawning channel revealed that growth rates were similar, but channel-produced fish were smaller on the average as underyearlings and again as smolts. The difference was attributed to later fry migrations from the channel and consequently a reduced growing period in the lake.

The 1965–67 comparison, however, cannot be considered representative of later years. With flow control in 1968, and with the large second Fulton River channel and the Pinkut Creek channel in operation, all sockeye production in the two systems was subject to some form of manipulation influencing fry migration time. West (1978) noted flow control, increased water temperatures, and adult "loading" (i.e. manipulation of times of entry of parent spawners into the facilities) as factors influencing fry migration time. Data from West (1978, Table 8) show that since 1970, migrations of channel fry have generally peaked during the 3rd or 4th wk of May or about 2–4 wk earlier than in the 1965–67 period. The increased growing period in the lake provided by earlier migrations served to eliminate any disadvantage in size of channel-produced fish. As a result, underyearlings in postchannel years were equal to or exceeded the size of prechannel underyearlings and their mean size as smolts was not significantly different.

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Lake Capacity

Johnson (1958, 1961, 1965b), after comparing the size and density of underyearlings in various parts of the Babine Lake system, found an inverse relationship between size and density. He concluded that growth was density dependent, with food supply and also possibly space the limiting factors. The relatively low density and large size of underyearlings he observed in the Main Lake basin led to the hypothesis that the Main Lake nursery area was underutilized and could support a much larger juvenile population.

Johnson's interpretation of compensatory growth depended on his assumption that dispersal of young from their natal streams was limited and that once pelagic, they remained as discrete populations in discrete lake basins. While this may be the case in a very general sense in that the interchange of Main Lake and North Arm population does not appear to be very great (McDonald 1969 and unpublished data), fry in the Main Lake dispersed widely from their natal streams, and McCart (1967) observed that fry from the Babine River dispersed throughout much of the North Arm. The situation with respect to Nilkitkwa Lake, which separates the upper and lower Babine River spawning grounds, is less clear but judging by McCart's observations of the size and movements of Babine River fry, the population in Nilkitkwa Lake is largely transitory and most fry eventually migrate upstream into the North Arm.

Movement patterns similar to those in the Babine system have been reported in other sockeye-producing lakes. Hartman and Burgner (1972), when reviewing sockeye production in Alaskan systems, noted widespread fry dispersal in each of the five Wood Rover lakes and also in very large Lake Iliamna. In the Naknek River system, which consists of a chain of four lakes, these authors reported that both interbasin (i.e. within lake) and interlake migrations occurred. Goodlad et al. (1974) reported fry dispersal followed by changes in underyearling distribution in Fraser, Chilko, and Shuswap lakes of the Fraser River drainage.

Two of the reports cited above included estimates of underyearling size observed at various locations in the nursery area. McCart (1967), after sampling in early July, found a direct relationship between the average length of underyearlings in Babine's North Arm and the distance from their point of origin (Babine River). This size trend then broke down, suggesting that considerable mixing was taking place. A similar trend in size with distance was reported by Hartman and Burgner (1972) in the Wood River lakes. Samples taken in late summer revealed that average length of sockeye juveniles increased from the west end (where most fry originated) to the east end of these lakes. They concluded that size differences within each lake were the result of more widespread dispersal of the older and larger fish, which were the first to emerge from the spawning beds. Growth rates calculated from these data would be apparent only and not representative of different rates for different lake areas.

Widespread dispersal of growing juveniles appears to be characteristic of moderate to large-sized lake basins. In the two documented cases where the fry originated from a single source (or at least a fairly localized one), there was a trend of increasing size with distance "uplake." The dispersal of fry from their point of lake entry where they would be most abundant (at least initially) into distant and less populated lake areas would result in a second trend; that of decreasing population density with distance from their source. A similar trend can be seen in Johnson's (1958, 1961, 1965b) North Arm data. The trends of increasing size and decreasing density with distance when combined would produce an inverse relationship between size and density, which could be construed wrongly as density effects on growth.

There are good grounds for caution when interpreting size and density relationships that may be seen when comparing data obtained from different areas within a nursery lake. In Babine's Main Lake and probably also in the North Arm and in Nilkitkwa Lake, density effects will be confused by fry dispersal followed by changes in distribution of the population during their growing period. At any one time and place of sampling, underyearling size will be the net result or balance of densities, food supply, and other factors influencing growth that were encountered previously. The situation in the Main Lake is even further confused by the mixing of juvenile stocks that differ in the size of fry and times of lake entry.

These complexities preclude the use of current information to arrive at a point estimate of the carrying capacity of the Main Lake. However, by using the criteria of juvenile size and survival rate, we can indicate whether this capacity has been exceeded by the larger postchannel population. After a nearly threefold increase in average abundance, underyearlings remained at least comparable in size and no significant change in the mean size of smolts was found to occur. Two independent lines of evidence were available to compare fry-to-smolt survival rates of pre- and post-channel populations. The mean rates based on total fry and smolt outputs of 26.5 and 30.7% were not significantly different. Comparison of the rates calculated for marked fry supported this conclusion. The absence of any reduction in size and survival rate supports the hypothesis that the Main Lake nursery area was capable of supporting the larger juvenile populations. However, it should be noted that in years when, by fall, juveniles were relatively large in size and number, overwinter growth tended to be slowed, suggesting that the overwinter carrying capacity of the lake may have been approached.

Adult Returns

The final assumption was that larger juvenile outputs would result in increased adult returns. The response from odd-numbered brood years has been about as expected. While the relationship between smolt output and adult return is curvilinear, it still allows a large surplus of adults from smolt outputs more than two or three times the preenhancement level. Gains from odd-numbered brood years, however, have been largely offset by the consistently low productivity of even-numbered brood years.

Available evidence does not suggest that the difference in even- and odd-year productivity originates in the lake. As noted by Peterman (1982) and Ricker (1982), there is no consistent difference in the mean size of smolts from even- and odd-year broods, which might explain different survival rates either en route to the sea or in it. The only other available measure of smolt quality that might bear on their survival is the degree of infestation by the internal parasite *Eubothrium salvelini*. This parasite is found every year in large numbers of Babine smolts. Its presence is associated with reduced size and vigor of the host (Smith 1973). Annual infection rates recorded by Smith and updated by N. Boyce (Fisheries and Oceans, Ottawa, Ont., personal communication) do not reveal any significant differ-

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ence in mean rates of 33 and 29% ($P = 0.50$) for even- and odd-numbered brood years, respectively. While the incidence of *Eubothrium* may reduce the marine survival of Babine results, as Smith suggested, the presence of the parasite does not appear to account for the difference in odd- and even-year survival rates.

Peterman (1982) suggested that the marine survival of Babine smolts is density dependent and, further, that this dependence may be due to interaction with pink salmon (*Oncorhynchus gorbuscha*). Pink salmon have an invariable 2-yr life cycle, and along the north coast of British Columbia they are generally more abundant in even-numbered years. Peterman suggested two likely mechanisms. Large populations of juvenile pinks (from even-year parents) may serve as a buffer to predation on odd-year broods of sockeye smolts. These same pink salmon as incoming adults may actively prey on the outgoing even-year broods of sockeye smolts. Ricker (1982) also considered the possibility of predation of adult pink salmon but pointed out the difficulty of reconciling this hypothesis with past highly successful even-year broods of sockeye. There is of course no certainty that the even- and odd-year phenomenon observed in Babine sockeye during the past 20 yr or so existed during the earlier history of the run. Returns up to 1919 were characterized by a distinct 5-yr cycle of abundance and through the 1930's and 1940's by a 4-yr cycle (Larkin and McDonald 1968). It is difficult to relate either a 4- or 5-yr cycle with consistent superiority of even- or odd-numbered brood years.

Obviously, further information is required to clearly identify the mechanisms that are currently suppressing Babine sockeye production from even-numbered brood years. In the meantime, alternate management strategies should be considered. The current practice of attaining large brood stocks and smolt outputs from both even and odd years has not provided the expected increase in adult returns and shows little promise of doing so in the future. Returning to entirely natural production is one strategy that could be considered but one that would probably be politically unacceptable and possibly biologically unrealistic. Manipulation of brood stocks since the enhancement program began 17 yr ago has no doubt altered some of their biological characteristics that bear on reproduction. The difference in times of fry migration resulting from manipulating the "loading" of parent spawners was noted earlier. Such changes could result in decreased survival rates and even lower adult returns if enhancement facilities were abandoned.

A second strategy would be to make the best of the current even- and odd-year phenomenon until such time as the factors suppressing odd-year productivity are identified and corrective measures implemented. Under this strategy, odd-year brood stocks and smolt outputs would be maintained at current leves or even increased to take full advantage of their high productivity. In the relatively unproductive even years, brood stocks (and thus, resulting smolt outputs) would be reduced and then maintained at a moderate level by appropriate regulation of the fishery. In this way, more of the 5-yr-old adults from productive even-year broods but returning in even-numbered years could be added to the catch.

Whatever strategy may be adopted, it seems imperative that it proceed on an experimental basis and with close monitoring of the Babine stocks. Only in this way can adverse effects on the stocks be detected and ameliorated should the strategy be inappropriate. Close monitoring will also be required to identify future opportunities to increase production.

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Appendix

Tests for differences in density, abundance, and body size of underyearling sockeye among lake areas and among years are presented.

Density and Abundance

Estimates of the relative density and abundance of underyearlings in the five Main Lake areas were based on catch per unit

TABLE A1. Two-way analysis of variance of estimated area density and abundance in the Main Lake using years and lake areas as the independent factors.

Source	df	Fishing period	F Density	F Abundance
Years	6	Session I	19.61***	19.65***
Areas	4		107.57***	12.08***
Interaction	24		1.52 (NS)	1.51 (NS)
Within	295			
Years	6	Session II	10.62***	10.47***
Areas	4		11.66***	28.66***
Interaction	24		2.80***	2.75***
Within	349			
Years	6	Session III	32.63***	31.49**
Areas	4		1.78 (NS)	22.12***
Interaction	24		2.10**	2.08**
Within	324			

effort by seine-net. If it is assumed that underyearling availability and gear efficiency remains constant, then catch per unit effort will be proportional to density. Each estimate of density was usually based on 10 sets. Catches were transformed to $\log_{10}$ to normalize their distribution.

Comparisons of density and abundance were made only within fishing sessions because seasonal changes in the availability of underyearlings to the gear could be expected to occur from one session to another due to increased fish size and possible changes in behavior.

Differences among lake area densities were tested by analysis of variance using years and areas as treatments (Table A1). This was followed by a multiple pairwise comparison of means (Table A2) using Duncan's multiple range test (Duncan 1955).

Because lake areas differed in size, area densities could not be used directly to estimate relative abundance. Instead, an area index was calculated by weighting catches by lake surface area and then finding the geometric mean. Differences among area indices were then tested by analysis of variance (Table A1) and Duncan's multiple range test (Table A3).

An index of abundance for the five main lake areas combined (as given in Table 1) was derived by summing areas indices and dividing by a constant to reduce the indices to a convenient number.

Size

The same statistical procedures were used to test for differences in underyearling length. Two-way analysis of variance showed that significant differences occurred among lake areas and years (Table A4). This was followed by tests for differences among lake areas during each fishing session each year (Table A5). Finally, mean underyearling lengths for the Main Lake as a whole (areas 1–5 combined) were tested for differences in pre- and post-enhancement years (Table A6). These means were calculated after subsampling lake area samples in proportion to abundance indices.

The relationship between length and weight was examined by regression analysis using logarithms of mean lengths and weights of underyearlings sampled from catches made in usually 50 sets each fishing session (Table A7). Differences in the relationship among years were tested by covariance analysis and the simultaneous test procedure (Sokal and Rohlf 1969).

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TABLE A2. Geometric mean catch per set for Main Lake areas during three fishing periods. Means that are underlined are not significantly different from each other ($P = 0.05$).

Brood year		Lowest				Highest
Session I						
1965	Area	1	2	3	4	5
	Mean	15.8	21.1	94.6	173.2	185.2
1966	Area	1	2	3	5	4
	Mean	12.5	45.9	103.5	161.8	249.2
1967	Area	1	2	3	5	4
	Mean	17.9	40.1	214.2	231.7	292.2
1970	Area	1	2	3	4	5
	Mean	19.5	100.1	192.9	237.6	381.9
1971	Area	1	2	3	4	5
	Mean	54.2	131.1	276.0	346.3	1576.8
1972	Area	1	2	3	4	5
	Mean	26.3	165.9	265.8	377.0	1067.6
1976	Area	1	2	3	4	5
	Mean	38.7	231.5	483.5	545.8	547.9
Session II						
1965	Area	1	5	2	4	3
	Mean	31.9	49.4	57.6	110.5	153.7
1966	Area	1	5	3	2	4
	Mean	36.3	37.1	71.0	79.7	175.4
1967	Area	5	3	1	2	4
	Mean	64.9	74.9	120.4	130.6	311.3
1970	Area	5	1	3	2	4
	Mean	63.3	93.6	121.8	146.6	516.6
1971	Area	3	5	2	1	4
	Mean	125.9	183.6	261.3	419.6	506.2
1972	Area	5	1	3	4	2
	Mean	117.2	143.6	158.8	218.1	245.3
1976	Area	2	3	1	5	4
	Mean	36.7	71.0	224.4	357.8	531.7
Session III						
1965	Area	1	4	3	5	2
	Mean	12.5	13.9	20.2	25.1	43.2
1966	Area	5	1	2	3	4
	Mean	20.2	25.0	26.7	33.2	43.8
1967	Area	1	2	5	4	3
	Mean	10.0	16.4	22.0	27.6	34.7
1970	Area	1	5	2	3	4
	Mean	54.7	67.2	62.9	216.5	244.5
1971	Area	3	2	5	1	4
	Mean	52.5	74.1	81.6	97.0	114.7
1972	Area	3	5	2	4	1
	Mean	63.4	68.2	100.4	143.3	162.5
1976	Area	3	1	2	4	5
	Mean	84.1	114.4	142.8	182.5	223.9

TABLE A3. Area index (of abundance) for Main Lake areas during fishing periods. Indices that are underlined are not significantly different from each other ($P = 0.05$).

Brood year		Lowest				Highest
Session I						
1965	Area	1	2	3	5	4
	Mean	188	871	1115	2589	3115
1966	Area	1	3	2	5	4
	Mean	146	1242	1919	2262	4484
1967	Area	1	2	3	5	4
	Mean	210	1678	2569	3226	5253
1970	Area	1	3	2	4	5
	Mean	230	2314	4183	4275	5344
1971	Area	1	3	2	4	5
	Mean	645	3301	5495	6222	22065
1972	Area	1	3	4	2	5
	Mean	313	3187	6783	6956	14936
1976	Area	1	3	5	2	4
	Mean	463	5800	7619	9680	9817
Session II						
1965	Area	1	5	3	4	2
	Mean	381	685	1840	1975	2342
1966	Area	1	5	3	4	2
	Mean	432	512	846	3152	3341
1970	Area	5	1	3	2	4
	Mean	881	1110	1449	6043	9282
1971	Area	3	5	1	4	2
	Mean	1509	2558	5028	9105	10958
1972	Area	5	1	3	4	2
	Mean	1627	1698	1859	3908	10261
1976	Area	3	2	1	5	4
	Mean	846	1521	2671	4986	9564
Session III						
1965	Area	1	4	3	5	2
	Mean	148	233	238	347	1769
1966	Area	5	1	3	4	2
	Mean	253	284	383	786	1093
1967	Area	1	5	3	4	2
	Mean	91	303	413	481	685
1970	Area	1	5	3	2	4
	Mean	651	853	2592	1616	4399
1971	Area	3	5	1	4	2
	Mean	629	1131	1154	2059	3094
1972	Area	3	5	1	4	2
	Mean	759	942	1948	2575	4202
1976	Area	3	1	5	4	2
	Mean	1006	1370	3120	3282	5984

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TABLE A4. Two-way analysis of variance of the lengths of under-yearlings resident in the main lake areas using years and areas as the independent factors.

Source	df	SS	MS	F
Session I				
Years	6	65 097.64	10 849.61	395.284***
Areas	4	52 662.88	13 165.72	479.667***
Interaction	24	22 746.75	947.78	34.531***
Within	13 962	383 223.34	27.45	
Session II				
Years	6	55 687.78	9 281.30	164.574***
Areas	4	29 184.75	7 296.19	129.375***
Interaction	24	31 476.75	1 311.53	23.256***
Within	17 121	965 552.10	56.39	
Session III				
Years	6	56 587.31	9 431.22	157.333***
Areas	4	6 881.78	1 720.44	28.701***
Interaction	24	32 782.81	1 365.95	22.787***
Within	13 109	785 806.00	59.94	

TABLE A5. Mean lengths (mm) and weights (g) of underyearlings resident in each Main Lake area. Mean lengths that are underlined are not significantly different from each other ($P > 0.05$).

		Smallest				Largest
Session I						
1965	Area	2	5	3	4	1
	Sample size	255	394	376	350	101
	Mean weight	0.32	0.50	0.52	0.60	1.25
	Mean length	32.0	35.6	37.5	38.1	48.9
1966	Area	5	2	3	4	1
	Sample size	500	260	490	500	154
	Mean weight	0.43	0.45	0.51	0.53	0.78
	Mean length	34.5	34.5	36.5	37.0	40.4
1967	Area	5	2	4	3	1
	Sample size	500	466	500	500	217
	Mean weight	0.46	0.45	0.46	0.49	0.70
	Mean length	34.9	35.2	35.7	36.1	40.5
1970	Area	5	4	3	2	1
	Sample size	201	200	200	200	157
	Mean weight	0.45	0.52	0.53	0.64	0.97
	Mean length	35.6	37.3	37.4	39.8	43.8
1971	Area	5	4	3	2	1
	Sample size	199	220	180	200	190
	Mean weight	0.89	0.91	1.03	1.24	1.14
	Mean length	43.1	43.1	45.6	45.9	46.7
1972	Area	5	3	4	2	1
	Sample size	498	500	499	500	267
	Mean weight	0.54	0.65	0.70	0.72	0.95
	Mean length	35.6	37.7	38.7	39.3	42.9
1976	Area	5	4	3	2	1
	Sample size	879	1002	1000	883	46.0
	Mean weight	0.50	0.64	0.67	0.73	1.01
	Mean length	36.2	38.8	39.3	40.5	44.4
Session II						
1965	Area	5	2	3	4	1
	Sample size	567	977	880	928	342
	Mean weight	1.76	2.01	2.09	2.32	2.32
	Mean length	53.7	56.3	57.4	59.1	59.4

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TABLE A5. (*Concluded*)

		Smallest				Largest
1966	Area	5	4	3	2	1
	Sample size	330	500	431	464	367
	Mean weight	1.45	1.99	2.04	2.17	2.20
	Mean length	50.0	55.9	56.3	57.7	58.2
1967	Area	5	4	3	2	1
	Sample size	500	500	500	500	500
	Mean weight	1.52	1.94	2.05	2.16	2.45
	Mean length	52.0	55.2	56.7	57.8	59.6
1970	Area	5	2	3	4	1
	Sample size	193	186	193	200	189
	Mean weight	1.52	1.64	1.69	1.72	2.11
	Mean length	50.8	53.0	53.0	53.5	56.8
1971	Area	3	4	1	2	5
	Sample size	202	235	200	179	180
	Mean weight	2.56	2.64	2.67	2.81	3.06
	Mean length	61.3	61.4	62.3	63.9	64.4
1972	Area	5	3	4	2	1
	Sample size	429	453	469	491	400
	Mean weight	2.09	2.21	2.43	2.40	2.59
	Mean length	55.2	57.7	59.1	59.2	60.8
1976	Area	2	4	3	5	1
	Sample size	430	1313	624	1229	1015
	Mean weight	2.44	2.15	2.13	2.31	2.50
	Mean length	57.0	57.5	57.5	58.3	59.5

Session III

1965	Area	5	4	3	2	1
	Sample size	357	398	352	463	130
	Mean weight	3.05	3.60	3.80	3.97	4.25
	Mean length	64.9	68.7	70.4	71.2	71.9
1966	Area	5	4	3	2	1
	Sample size	292	414	304	298	276
	Mean weight	2.20	2.85	3.08	3.14	3.37
	Mean length	62.7	64.4	65.2	66.7	67.5
1967	Area	5	3	4	1	2
	Sample size	266	359	311	159	181
	Mean weight	3.09	3.49	3.50	3.52	3.68
	Mean length	65.4	67.3	67.7	69.1	69.3
1970	Area	5	3	4	2	1
	Sample size	173	200	200	194	188
	Mean weight	2.42	3.47	3.30	3.53	3.56
	Mean length	60.8	68.2	68.4	68.4	68.5
1971	Area	1	2	4	3	5
	Sample size	201	156	179	200	165
	Mean weight	3.58	3.97	4.43	4.35	4.93
	Mean length	70.0	72.4	73.9	74.5	76.3
1972	Area	5	4	3	1	2
	Sample size	379	500	448	500	473
	Mean weight	3.45	4.03	4.06	4.13	4.20
	Mean length	66.8	69.9	70.0	70.8	71.0
1976	Area	1	2	3	4	5
	Sample size	823	899	741	1047	931
	Mean weight	3.80	3.91	4.18	4.16	4.09
	Mean length	68.6	69.4	71.2	71.4	71.5

TABLE A6. Mean lengths (mm) and weights (g) of underyearlings resident in the Main Lake during each fishing session. Mean lengths that are underlined are not significantly different from each other ($P > 0.05$).

Session I

Brood year	1967	1966	1965	1972	1970	1976	1971
Middate	July 11	July 17	July 11	July 8	July 13	July 18	July 4
Sample size	1239	1129	887	1072	615	3048	341
Mean weight	0.47	0.50	0.54	0.63	0.64	0.65	0.96
Mean length	35.6	36.0	36.8	37.3	37.5	38.9	44.1

Session II

Brood year	1970	1966	1967	1965	1976	1972	1971
Middate	Aug. 22	Sept. 7	Sept. 1	Aug. 28	Aug. 22	Sept. 2	Aug. 23
Sample size	404	1150	1283	3160	2842	925	477
Mean weight	1.71	2.04	2.06	2.10	2.27	2.38	2.74
Mean length	53.4	56.4	56.5	57.2	58.0	58.8	62.8

Session III

Brood year	1966	1970	1967	1965	1972	1976	1971
Middate	Oct. 15	Oct. 11	Oct. 14	Oct. 16	Oct. 8	Oct. 8	Oct. 12
Sample size	766	495	527	685	1177	2216	511
Mean weight	2.98	3.34	3.50	3.82	4.07	4.01	4.20
2Mean length	65.6	67.8	68.0	70.2	70.2	70.3	73.0

TABLE A7. Results of covariance analysis and the simultaneous test procedure on the regression coefficients of the length and weight relationships for each session and year. Slopes that are underlined are not significantly different ($P > 0.05$). $W = \log_{10}$ weight (g); $L = \log_{10}$ length (mm).

	SS	df	MS	F
Session I				
Regressions	0.01894	6	0.00316	4.493***
Intercepts	0.15040	6	0.02507	35.679
Residual	0.22692	332	0.00070	
Total	0.39626	344		

Common regression line: $W = -5.580 + 3.277L$

Brood year	1971	1972	1976	1966	1965	1967	1970
Slope	2.948	3.089	3.273	3.365	3.376	3.425	3.497

	SS	df	MS	F
Session II				
Regression	0.00577	6	0.00096	3.059**
Intercepts	0.04693	6	0.00782	24.891
Residual	0.11690	372	0.0031	
Total	0.16860	384		

Common regression line: $W = -4.218 + 2.792L$

Brood year	1976	1972	1965	1966	1967	1971	1970
Slope	2.437	2.571	2.792	2.803	2.815	2.867	2.885

	SS	df	MS	F
Session III				
Regression	0.02257	6	0.00376	13.760***
Intercepts	0.07701	6	0.01283	46.949
Residual	0.09377	343	0.00027	
Total	0.19335	365		

Common regression line: $W = -4.358 + 3.005L$

Brood year	1972	1976	1965	1967	1970	1971	1966
Slope	2.359	2.378	2.632	2.800	3.044	3.056	3.238

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