Evaluation of Sockeye Salmon (*Oncorhynchus nerka*) Production from the Babine Lake Development Project

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Abstract

WEST, C. J., AND J. C. MASON. 1987. Evaluation of sockeye salmon (*Oncorhynchus nerka*) production from the Babine Lake Development Project, p. 176–190. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The Babine Lake Dèvelopment Project (BLDP) was initiated in 1962 and consists of three spawning channels on the Fulton River and Pinkut Creek systems, and associated river flow control works. The BLDP is intended to increase the number of sockeye salmon fry (*O. nerka*) rearing in the main basin of Babine Lake and ultimately, to increase the adult returns and commercial catch. A paucity of spawning area had been previously identified as the main factor limiting Babine sockeye production. Mean fecundity of BLDP stocks ranged from 3000 to 3500 eggs per female and was best estimated from body length. Length-independent, inter-annual variation in fecundity was related to the last year of ocean life. Egg retention and other spawning failures increased with female spawner density but did not exceed 3% over a wide range of densities. Egg-to-fry survival averaged 46% in the channels and 21% in the rivers, and was most affected by female spawning density. Efficiency of hydraulic sampling was 63% and the time course of pre-hatch mortality was nearly constant at a daily rate of 0.4–0.6%. Fry production remained efficient at densities as high as one female per 1.25 m^2 of spawning area, the relationship becoming asymptotic at approximately twice that density. The relationship between numbers of main basin smolt and BLDP fry is linear through high levels of production, with fry-to-smolt survival averaging 42.9 percent over 21 years. Adult returns of Fulton and Pinkut origin have increased nearly four-fold since the inception of the BLDP, and are now in excess of 1 M fish annually. Of these, an average of 825 800 are taken in Canadian and U.S. fisheries combined. Commercial landings (741 700/yr) of BLDP sockeye are worth more than $ 6.2 M/yr (1985 Canadian dollars). This amounts to a benefit:cost ratio of 3.02:1, applying a 10% discount rate. History of adult production from the BLDP is compared with abundance trends of non-enhanced stocks of Skeena sockeye.

Résumé

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Le projet de mise en valeur du lac Babine a débuté en 1962. Il est constitué de trois chenaux de frai, situés dans les bassins versants de la rivière Fulton et du ruisseau Pinkut, et des ouvrages connexes de régularisation du débit. Ce projet a pour objectif d'accroître le nombre d'alevins de saumon nerka (*O. nerka*) effectuant leur croissance dans le bassin principal du lac Babine et donc d'accroître les remontées d'adultes et les prises commerciales. On avait déjà déterminé que le manque de frayères constituait le principal facteur limitant la production du saumon nerka dans le lac Babine. La fécondité moyenne des stocks gérés par ce projet variait de 3 000 à 3 500 oeufs par femelle et était le mieux estimée à partir de la longueur corporelle. La variation interannuelle de la fécondité, indépendante de la longueur, était fonction de la dernière année passée en mer. La rétention des oeufs et d'autres facteurs d'échec du frai ont augmenté avec la densité des géniteurs femelles mais n'ont pas excédé 3 %, ceci pour une large gamme de densités. La survie d'oeufs à alevins s'élevait en moyenne à 46 % dans les chenaux et à 21 % dans les cours d'eau. Elle était surtout fonction de la densité des géniteurs femelles. Le rendement de l'échantillonnage hydraulique était de 63 % et le taux quotidien de la mortalité de pré-éclosion était pratiquement constant à 0,4–0,6 %. La production d'alevins est demeurée efficace à des densités aussi élevées qu'une femelle par 1,25 m^2 de superficie de frayère, cette relation devenant asymptotique lorsque la valeur de densité atteignait le double environ. La relation entre le nombre de smolts dans le bassin principal et d'alevins dans l'aire du projet est linéaire même aux niveaux de production élevés, la survie de alevins à smolts, notée au cours de 21 années, étant en moyenne de 42,9 %. Le nombre d'adultes revenant aux cours d'eau Fulton et Pinkut a pratiquement quadruplé depuis la création du projet et s'élève actuellement à plus de 1 million de poissons par an. De ceux-ci, 825 800 en moyenne sont capturés par les pêches canadiennes et américaines. Les débarquements commerciaux (741 700 poissons par an) de saumon nerka du projet ont une valeur qui dépasse les 6,2 millions de dollars par an (dollar canadien de 1985). Ces valeurs représentent un rapport avantages:coûts de 3,02:1 (taux d'actualisation de 10 %). Les auteurs comparent la production de poissons adultes obtenue ces dernières années grâce au projet aux tendances d'abondance des stocks de saumon nerka non mis en valeur de la rivière Skeena.

Introduction

From historic times, most sockeye of the Skeena River system have been produced in the tributary streams of the Babine-Nilkitkwa Lake system (Fig. 1). Fry typically rear in these lakes for 1 yr, then spend 1–3 yr at sea, returning predominantly at ages 3_2, 4_2, and 5_2. The Babine-Nilkitkwa stocks now constitute some 95% of the total production of sockeye in the Skeena River system.

The Fisheries Research Board of Canada began biological surveys on the Skeena sockeye stocks in the mid-1940's, to better elucidate stock and recruitment relations by improving escapement estimates. Spawning grounds of the Skeena sockeye comprise some 100 acres (less than 500 000 m^2). This led Brett (1952) to suggest "the possibilities of a well-planned farming program for fish culture". Johnson (1956; 1958; 1961) believed that the main basin of Babine Lake could support an additional seeding of some 350 M (million) fry. A conservative target of 100 M was set by the Fish Culture Section of the Department of Fisheries and two major tributaries of the main basin: Fulton River and Pinkut Creek (Fig. 1) were selected as development sites to achieve the production target of 100 M fry.

The Babine Lake Development Project (BLDP) associated with this production target presently consists of two spawning channels at Fulton River, one spawning channel at Pinkut Creek, and associated river flow control structures on each system. Channel no. 1 at Fulton River became operational

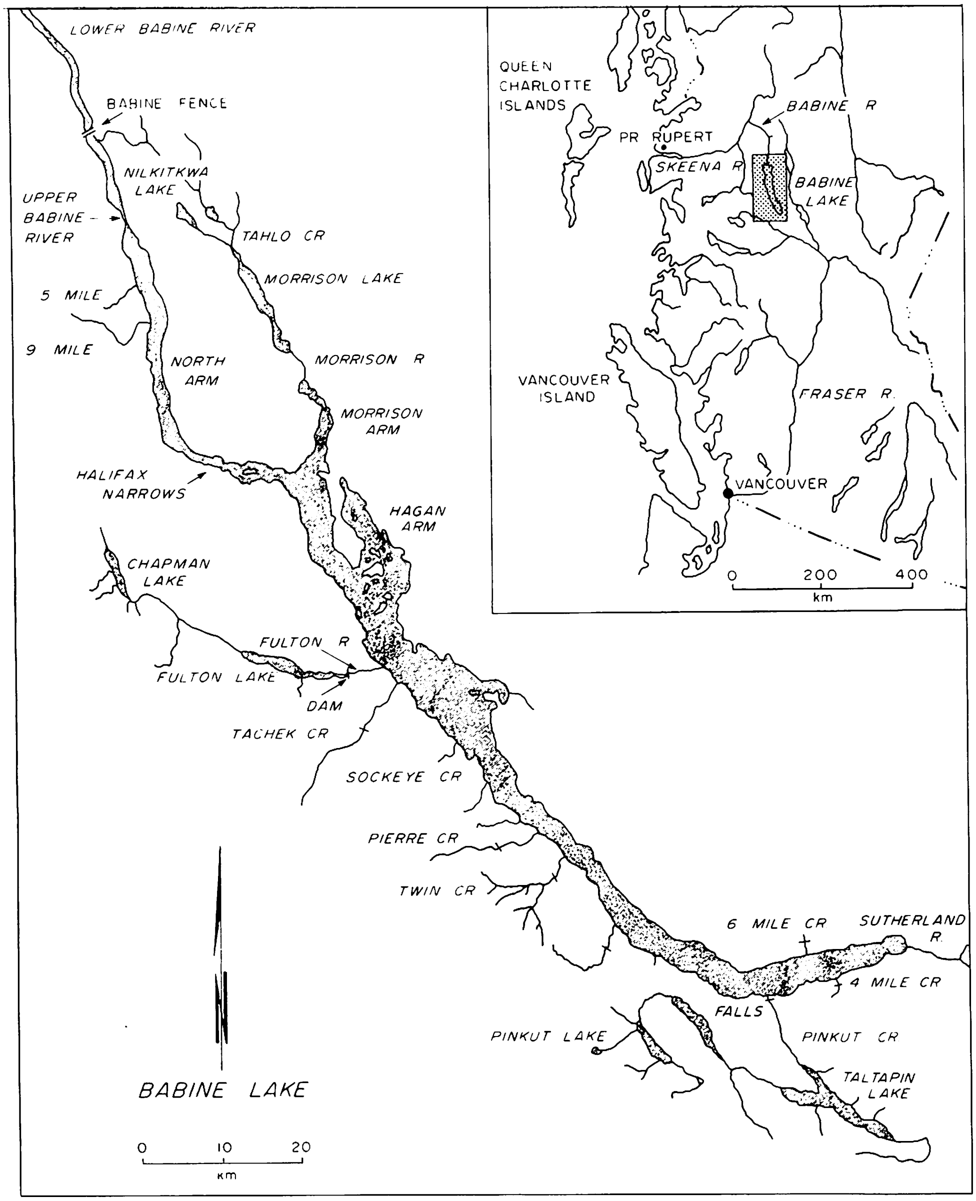

FIG. 1. Location of Fulton River and Pinkut Creek enhancement projects (BLDP) on Babine Lake, British Columbia.

in 1965, Pinkut channel in 1968, and Fulton Channel no.2 became operational in two stages, in 1969 and in 1971. River flow control structures and permanent adult and fry counting fences were completed in 1968. These facilities and their operations were described by Ginetz (1976) and West (1977). The channels provide 116 500 m^2 of additional spawning area (Table 1) for 186 400 spawners and were expected, with river flow control, to supplement natural production by an additional 100 M fry. Spawning area at Pinkut Creek has been further augmented since 1973 by airlifting surplus spawners by helicopter to an area of approximately 26 700 m^2 of spawning grounds above impassable falls (Table 1). The combined accessible river spawning area is 115 000 m^2, nearly half of the total BLDP spawning area of 231 500 m^2. Sockeye utilize the alluvial fans of both Fulton River and Pinkut Creek when escapement to those systems is unusually high, thus making accurate counts difficult. The extent and outcome of spawning within the lake proper remains incompletely assessed.

TABLE 1. Spawning grounds within the Babine Lake Development Project (BLDP).

Location	Area (1000 m^2)
Fulton River	
Below fence	12.5
Above fence	62.7
Channel no. 1	10.0
Channel no. 2	73.1
Total	158.3
Pinkut Creek	
Pinkut Creek	
Above falls (airlift)	26.7
Fence to falls	10.0
Below fence	3.1
Channel	33.4
Total	73.2
Grand Total	231.5

The BLDP production target was established on the assumption that fry of river and channel origins were equally viable. It was anticipated that the 100 M additional fry would provide some 30 M smolts and 1.25 M adult sockeye, of which 1 M could be harvested in the commercial fisheries. This assumption was tested for the lake-rearing phase by McDonald (1969) and McDonald and Hume (1984) who showed that lacustrine distribution, survival, growth rate and smolt size of channel and river fry were essentially similar, and that the increased fry production has led to substantial increases in the smolt output. Record production of BLDP fry in recent years should allow assessment of the rearing capacity of Babine Lake at unprecedented levels of underyearling population.

In this presentation we examine fry production from the BLDP, some relevant factors affecting that production, and, using a stock reconstruction model, evaluate adult returns of both the BLDP and non-enhanced stocks.

Methods and Materials

Our analyses were grouped according to five consecutive life stages in the rivers: (1) controlling spawner population, (2) estimating egg depositon, (3) monitoring the incubation environment, (4) estimating production of fry, and (5) estimating adult returns.

CONTROL OF SPAWNER POPULATION

A range of operating protocols for seeding the channels and rivers during the past 15–20 yr has provided opportunities to evaluate the effects of variable timing, density, and sex ratio. We control spawner density in the rivers and channels by means of permanent fences, equipped with entry gates and counting stations. Within the channels, spawner entry into specific legs is controlled by adjustable weirs and flow bypass gates. At Pinkut Creek, surplus spawners are airlifted by helicopter to spawning grounds above impassable falls, as previously noted.

ESTIMATING EGG DEPOSITION

For each river system, three females within each centimetre of length are sacrificed at the peak of the run. Their otoliths are taken for age analysis and their eggs are counted individually. We then determine the relationship between number of eggs and female length (post-orbit to hypural plate) at age using regression analysis. Mean lengths of the female populations are then used to calculate mean fecundity, by age class, in each river and spawning channel. We examine fecundity in detail in RESULTS, reflecting nearly two decades of available data.

We estimate egg deposition from the age-specific product of number of females and mean fecundity, corrected for egg retention and complete spawning failure. The latter two statistics are obtained by sampling carcasses throughout the die-off period. The carcasses also provide lengths and otoliths for size and age composition analysis. Sex ratio in the channels is estimated from counts by sex as fish pass through the counting structures, and this ratio is also applied to the adjacent river spawners.

MONITORING THE INCUBATION ENVIRONMENT

Water temperature and volume are monitored continuously. Extensive chemical and physical analyses have been conducted intermittently for both surface and intra-gravel waters. Incubation history is determined by sampling eggs and alevins, using an hydraulic sampler (McNeil 1964) at the eyed stage in late November and again in late January or February at the time of hatching. A standardized hydraulic sampling design has been in place since 1973, and calls for random cross-channel sampling positions at fixed intervals and in representative areas of both rivers and spawning channels. Due to persistent ice cover in Pinkut channel, the January–February sampling was discontinued in 1979. Live and dead eggs and alevins recovered from sampling units of 929 cm^2 (1 ft^2) are recorded. Mean survival rates are calculated from estimates of egg deposition (method given above) and recovery of live eggs and alevins by hydraulic sampling. Confidence limits for mean catches are calculated by fitting catches to negative binomial distributions, using a maximum-likelihood method (Bissell 1972).

ESTIMATING PRODUCTION OF FRY

Prior to 1967, fry migrating downriver were estimated either by the Peterson mark–recapture method, or by a travelling, vertical sampler fished for pre-set time periods at specific locations. In the latter case, the catches were weighted by time, location, and area fished. Nightly migrations were estimated from the relationship over time between net catch, filtration volume, and estimated total river discharge. From 1967 onward, fry have been enumerated at the fences using fixed-position, converging throat traps (Tait and Kirkwood 1962) and, at Fulton channel no.1, with fan traps (Ginetz 1977). A total migration estimate is obtained by weighting the catches of index traps by time and cross-sectional area fished and summing the resulting nightly estimates over the period of migration. Fry trapping and estimation procedures are described in detail by Ginetz (1977). Egg-to-fry survival is calculated from the estimates of actual deposition and fry production by location.

ESTIMATING ADULT RETURNS

Previous attempts to assess adult returns by means of fin-clipping failed due to high rates of fin regeneration (McDonald 1969). We have estimated adult returns using computerized stock reconstruction techniques. Standardized run timing curves were developed for stocks passing the Babine Fence (Fig. 2). These curves were weighted by their annual escapements and, using the resulting composite curve at the Babine Fence, they were backcalculated to the Tyee Test Fishery (Fig. 2) then the weighted non-Babine stock timing curves were added.

Curves for non-Babine stocks (early and late timed groups) were developed for time of passage past the river fishing boundary, near the Tyee test fishing site. Run timing data were obtained from Aro and McDonald (1968), Smith and Jordan (1973), and Takagi and Smith (1973). More recent data were provided by Kadowaki (CDFO, Nanaimo, B.C. pers. comm.).

We used the curve of timing migration from the Area 4 fishery to the river boundary (Takagi and Smith 1973) to calculate the probable time that each stock spent in fishing Area 4 (Fig. 2). The contribution of each stock to the Area 4 fishery was then calculated from the proportional daily representation of stocks. Their contributions to the Canadian Area 3 X and 3 Y, and to the Alaska (Noyes I. and Cape

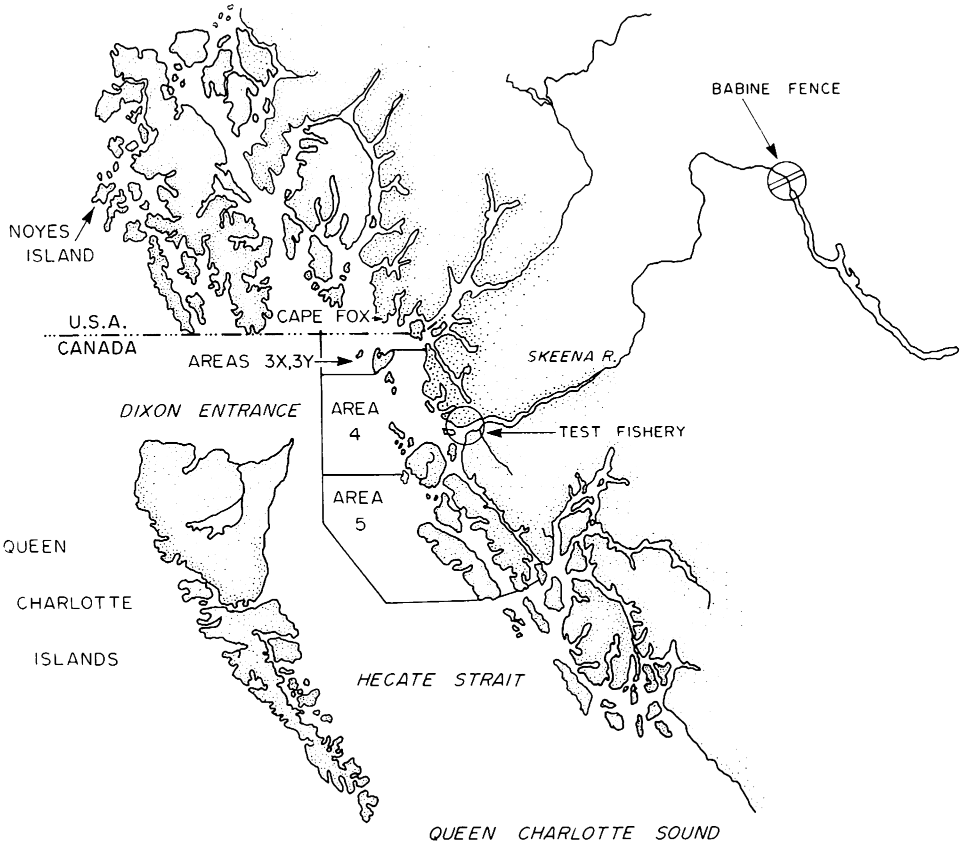

FIG. 2. Locations of the commercial fishing areas, the Skeena River test fishery, and the Babine Fence.

Fox) fisheries (Fig. 2) were estimated by applying the calculated representation of stocks in the Area 4 fishery to estimates of Skeena catch in these other areas. Skeena catch estimates were provided by L. Jantz (CDFO, Prince Rupert, B.C. pers. comm.). Native Food fishery catches of Skeena River sockeye were set in proportion to the escapements.

A Monte Carlo analysis to test the sensitivity of the model to assumptions about stock timing indicated 95% confidence limits of ± 6.5% on estimates of BLDP return. The results are consistent with numbers obtained by accurate counts of the Babine escapement, high resolution of stock timings from intensive tagging studies, and the predominance of Skeena stocks of sockeye in the Area 4 fishery where the principal harvesting of Skeena sockeye takes place.

Results

FECUNDITY

Fecundity of the various Babine stocks typically averages 3 100 eggs per female and is directly proportional to body length (Fig. 3). We used arithmetic values in our analysis following Rounsefell's (1957) finding that differences between the arithmetic and log-transformed values for fecundity of salmonids are of minor consequence.

For Fulton and Pinkut races (Fig. 3, Appendices I and II), comparing the statistically-significant fecundity versus length regressions of 4_2 and 5_2 females, the regression slopes of the 5_2's were generally lower but analysis of covariance

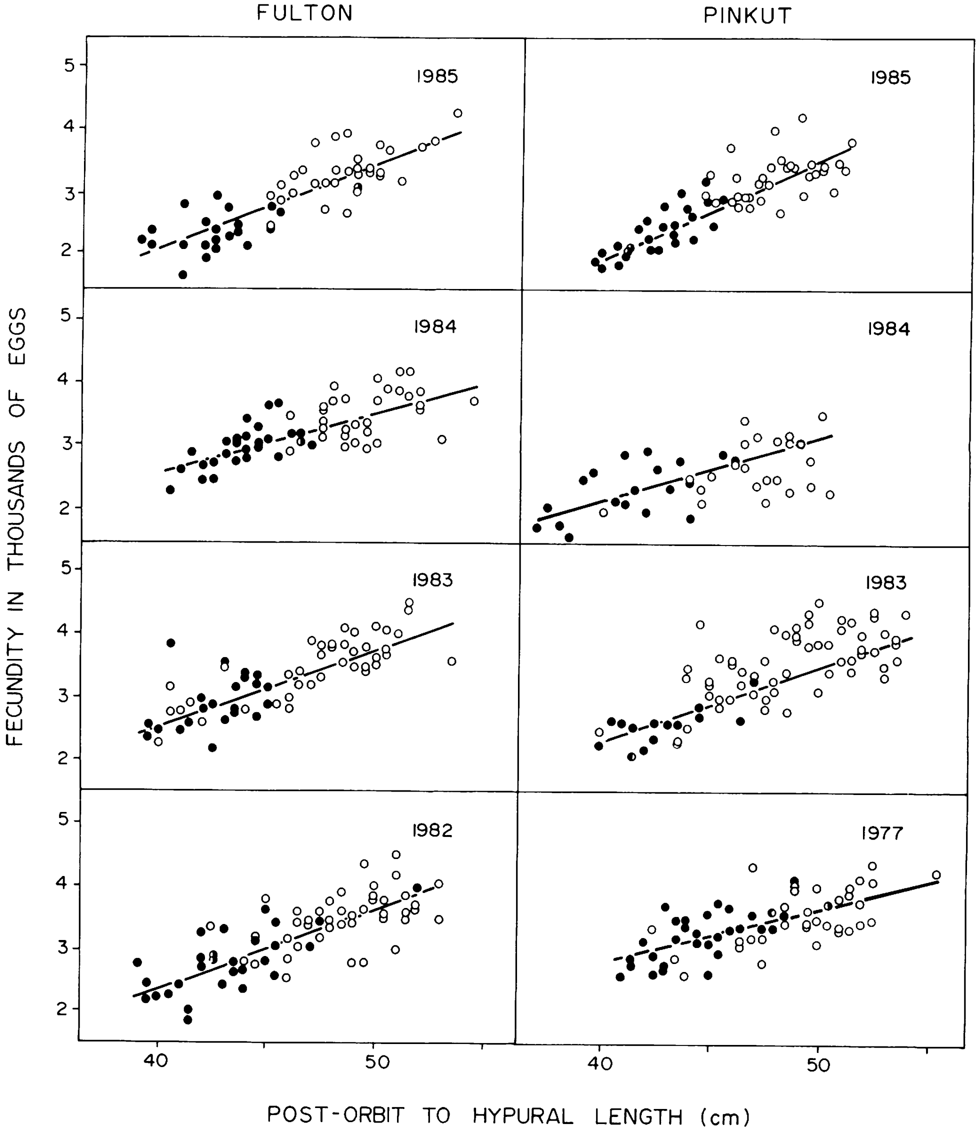

FIG. 3. Linear regressions for fecundity on length; Fulton River and Pinkut Creek sockeye stocks. Symbols as follows: ● — 4_2 females, ○ — 5_2 females.

revealed no statistical differences ($P<0.05$) in slopes or adjusted means in 10 of 11 cases. However, when the 4_2 and 5_2 age data were pooled by stock we did find significant ($P<0.05$) differences between years in adjusted mean fecundity. Annual variation amounted to ± 230 eggs, or 7.4% of the average fecundity. These differences were minor, however, compared to those found among races (non-specific ages) from several river systems as reported by Foerster (1968, p. 125).

Regression coefficients indicated that variation in length accounted for an average of 36% of the variation in fecundity in age-specific regressions, and 48% when age-classes and years were pooled. This variation is similar to the 31-32% reported by Rounsefell (1957) from six years of 4_2 data for the Cultus Lake stock, and the 37% value for Mathisen's four years of 4_2 plus 5_2 data for Pick Creek (Alaska) given by Koo (1968, page 219).

We found no evidence that age *per se* affected fecundity. For sockeye of common length, higher fecundities for younger ocean-age fish have been reported (Rounsefell 1957; Krogius cited in Foerster 1968). Our earlier analysis of covariance showed no dominance of either age class in terms of adjusted mean fecundity and slope. The average difference in adjusted mean fecundity was only three eggs in favor of the 4_2's.

We also tested for possible ocean effects by comparing fecundity-length regressions of 4_2 and 5_2 females from common brood years and from common years of return. While 5_2 females probably share their first 2 years of ocean life with 4_2's of the same brood, they probably share their last year (common year of return) with 4_2's of the subsequent brood. From analysis of covariance, four of nine comparisons by brood year indicated significant differences in slope or adjusted mean values while only one of eleven comparisons by year of return showed a significant difference (all $P<0.05$). This cursory search for possible ocean effects on fecundity suggests that fecundity is more closely associated with the last, rather than the penultimate, year of ocean life. Sea temperature has been negatively correlated with fecundity of pink salmon (*O. gorbuscha*) but freshwater history has not been shown to be of importance in this regard (Rounsefell 1957).

FACTORS AFFECTING EGG DEPOSITION

Magnitude and density of egg deposition are largely the direct outcome of the number of female spawners, their fecundity, and the amount of available spawning area. Deposition has ranged from 76 to 464 M eggs (six-fold) in Fulton River and 10 to 256 M (25-fold) in Pinkut Creek (Tables 2 and 3). The range in numbers of eggs deposited in the channels has been relatively narrow, as follows: Fulton Channel no. 1, 16–58 M (4-fold); Fulton Channel no. 2, 100–220 M (2-fold); Pinkut Channel, 31–100 M (3-fold). These ranges in deposition reflect the operational seeding priority of the channels over the rivers, and the preset targets for density of female spawners in channels. Hence the rivers are prone to greater annual fluctuations in female escapement.

Deposition is secondarily affected by density-dependent changes in female reproductive behaviour and by water

TABLE 2. Egg deposition, fry production, and egg-to-fry survival in Lower Pinkut Creek (fence to falls), Upper Pinkut Creek (airlift area above falls), and spawning channel, 1964–85.

	Lower Pinkut Creek			Upper Pinkut Creek			Pinkut Channel		
Brood year	Eggs (M)	Fry (M)	Surv. (%)	Eggs (M)	Fry (M)	Surv. (%)	Eggs (M)	Fry (M)	Surv. (%)
1964	255.7	4.5	1.8	—	—	—	—	—	—
1965	53.2	6.9	13.0	—	—	—	—	—	—
1966	24.8	3.7	14.9	—	—	—	—	—	—
1967	40.9	2.7	6.6	—	—	—	—	—	—
1968[a]	19.0	1.9	10.0	—	—	—	30.8	10.4	33.8
1969	10.0	1.8	18.0	—	—	—	37.5	15.2	40.5
1970	16.5	3.3	20.0	—	—	—	37.9	22.0	58.0
1971	13.1	2.2	16.8	—	—	—	30.8	16.7	54.2
1972	21.5	3.0	14.0	—	—	—	96.6	29.0	30.0
1973	30.6	3.1	10.1	25.2	6.0	23.8	97.1	24.1	24.8
1974	30.7	3.0	9.8	49.5	4.6	9.3	93.4	8.3	8.9
1975	20.6	2.6	12.6	52.1	6.6	12.7	67.3	22.3	33.1
1976	35.7	8.1	22.7	48.4	10.9	22.5	under reconstruction		
1977	26.3	6.6	25.1		no airlift		99.5	53.6	53.9
1978	8.3	3.5	42.2		no airlift		50.4	15.1	30.0
1979	42.1	8.7	20.7	46.5	9.5	20.4	92.9	47.5	51.1
1980	31.7	10.8	34.1		no airlift		81.7	42.2	51.7
1981	81.8	20.4	24.9	86.8	21.6	24.9	69.6	57.7	82.9
1982	118.1	28.5	24.1	36.5	8.8	24.1	97.9	68.0	69.5
1983	25.7	7.6	29.6		no airlift		97.7	49.9	51.1
1984	69.6	14.3	20.5	48.4	8.7	17.9	73.2	46.6	63.7
1985	14.9	4.5	30.4	48.8	8.7	17.8	74.4	35.9	48.2
Mean	45.0	6.8	19.2	49.1	9.5	19.3	72.3	33.2	46.2
SD	53.78	6.62	9.62	16.46	4.93	5.41	25.69	18.34	18.15

[a] First year of flow control on Pinkut Creek.

TABLE 3. Egg deposition, fry production, and egg-to-fry survival in Fulton River and the two spawning channels, 1968–85. (M — millions).

Brood year	Fulton River Eggs (M)	Fulton River Fry (M)	Fulton River Surv. (%)	Channel 1 Eggs (M)	Channel 1 Fry (M)	Channel 1 Surv. (%)	Channel 2 Eggs (M)	Channel 2 Fry (M)	Channel 2 Surv. (%)
1964	187.0	24.5	13.1	—	—	—	—	—	—
1965[a]	189.0	23.6	12.5	1.2	1.0	82.0	—	—	—
1966	77.5	24.0	31.0	36.9	25.5	69.1	—	—	—
1967	171.6	28.8	16.8	31.9	16.0	50.2	—	—	—
1968[b]	213.6	38.7	18.1	57.7	24.7	42.8	—	—	—
1969	81.7	11.2	13.7	27.8	5.9	21.2	35.0	25.4	72.6
1970	189.9	38.9	20.5	43.3	13.4	30.9	101.7	37.3	36.7
1971	209.3	31.0	14.8	39.4	20.0	50.8	175.2	82.2	46.9
1972	167.4	33.4	20.0	44.6	23.2	52.0	220.4	69.9	31.7
1973	150.0	27.5	18.3	34.3	15.0	43.7	168.7	75.0	44.5
1974	131.5	27.7	21.1	23.6	15.0	63.6	137.6	48.5	35.2
1975	354.2	45.5	12.8	23.6	12.7	53.8	172.4	68.6	39.8
1976	289.3	50.1	17.3	30.3	17.8	58.7	212.8	141.8	66.6
1977	464.3	32.1	6.9	27.4	14.3	52.2	207.1	84.0	40.6
1978	75.9	33.6	44.3	21.7	8.3	38.2	185.6	62.8	33.8
1979	268.3	30.8	11.5	28.3	9.0	31.8	201.4	91.5	45.4
1980	93.9	32.3	34.4	16.3	8.0	49.1	133.3	68.4	51.3
1981	300.8	72.2	24.0	23.7	12.3	51.9	198.1	53.3	26.9
1982	337.4	43.1	12.8	25.6	9.6	37.5	210.6	54.0	26.8
1983	215.0	38.6	18.0	28.9	5.9	20.4	191.8	14.0	7.3
1984	269.7	41.3	15.3	23.7	9.3	39.2	163.2	99.9	61.2
1985	222.8	43.5	19.5	20.3	5.2	25.5	155.3	83.4	53.7
Mean	211.8	35.1	18.9	30.5	13.6	44.1	168.3	68.2	42.4
SD	98.37	12.09	8.39	9.89	6.21	13.51	46.62	29.85	15.99

[a] Eyed egg plant in Channel no. 1.

[b] First year of flow control on Fulton River.

temperature. The amount of egg retention and number of unspawned females was determined by examining adult carcasses following spawning. Regression analysis of the pooled Fulton data (two channels and river) indicated that egg retention and spawning abstention were positively and significantly correlated both with each other and with density of females ($P<0.001$). The relative increases in partially spawned and unspawned females as density increased were both quite low, considering the wide range of spawning densities observed. Both increases averaged less than 3% over all years.

Spawning abstention was also positively correlated ($P<0.001$) with mean water temperature in Fulton River during the first week of September, when the major entry of adults into the river commences. Without exception, all above-average abstentions took place at temperatures exceeding 16°C and reached 20% at 17°C. River temperatures, however, were not correlated significantly with incomplete spawning as reflected in partial retention of egg complement in either Fulton River or its channels. The positive correlation between spawning abstention and river temperature suggests a temperature-induced general stress or blocked behaviour involving commitment to spawning.

FACTORS INFLUENCING EGG-TO-FRY SURVIVAL

Egg-to-fry survival estimates were derived from estimates of eggs deposited and numbers of migrant fry obtained (Tables 2 and 3) as described above. We found only one significant correlation between estimates of survival from hydraulic sampling and estimates of either deposition in the fall, or of fry production (from trapping) in the spring. There was a statistically significant correlation in Channel no. 1 where both arithmetic and geometric mean recoveries of eggs obtained in late November were positively correlated ($P<0.05$) with deposition.

Despite the generally poor correlations, hydraulic sampling provides our only insight into egg mortality in the gravel. The method probably does allow one to detect unusual mortality prior to hatching, and also allows some appreciation of the time course of mortality. From the 12 yr of hydraulic sampling data for Fulton Channel no. 2 (1973–84), the mean survival to late February (25.3%, SD = 8.6) was only 63% of the mean egg-to-fry survival (40.1%, SD = 15.9) derived from estimates of egg deposition and fry production. Hence, sampling efficiency in these channels (63%) was much lower than 90% reported by McNeil (1964). The time course of mortality rate was nearly constant at a daily rate of 0.4–0.6%, using a sampling efficiency of 63% to correct the fall and spring catches from hydraulic sampling, and a conservative fertilization value of 90% based on several works reported in Foerster (1968) for sockeye eggs in natural redds. Recoveries of dead eggs ranged between 20 and 35%, and averaged 24.7% of the estimated deposition. Hence, their sampling efficiency appears to be much higher than for live eggs, approaching or exceeding McNeil's value of 90%. Similarly, more than 95% of the mean mortality (20.4%) over the winter period (90–95 days) was accounted for in the spring sampling.

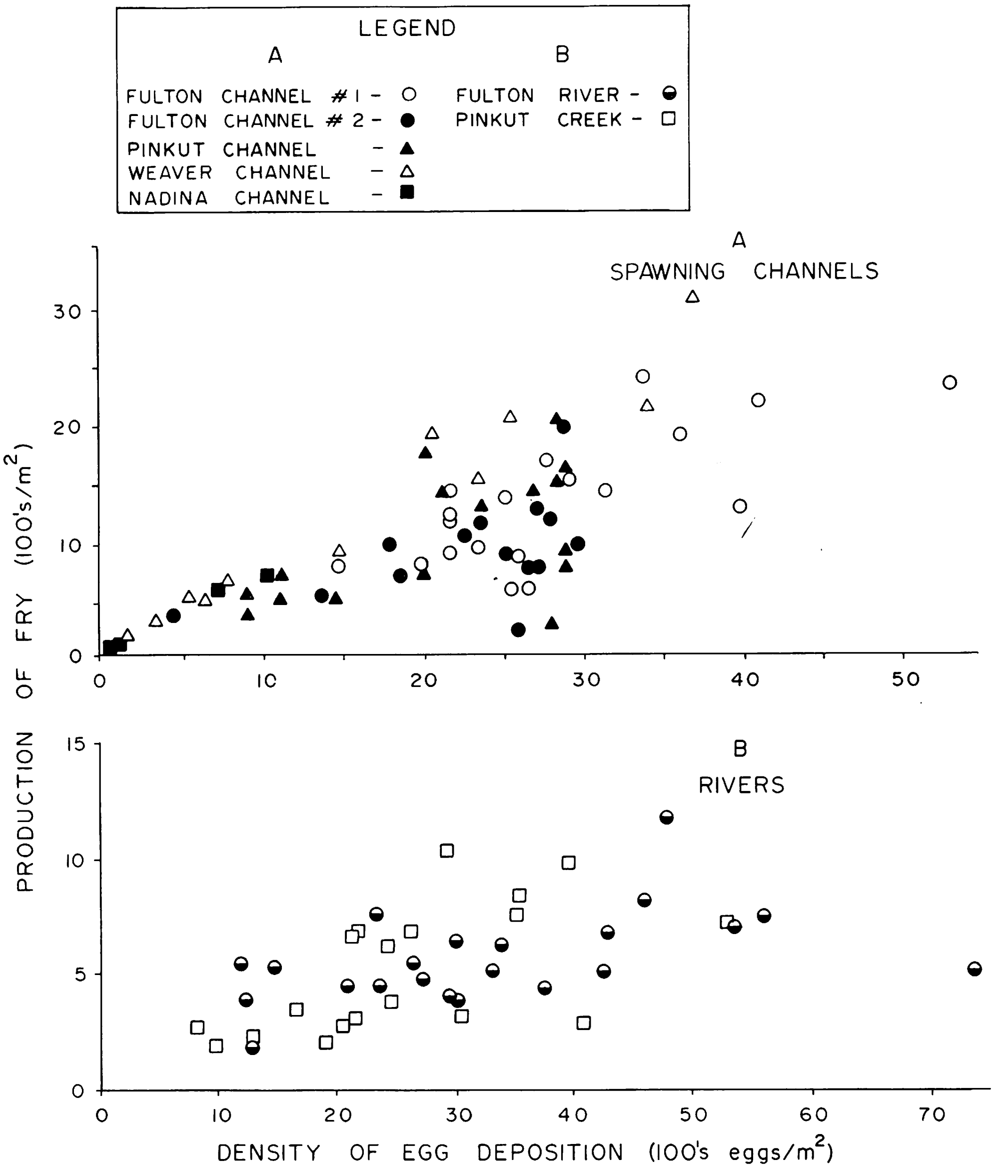

FIG. 4. Production of sockeye fry relative to mean density of eggs at time of deposition in five spawning channels (A) and two rivers (B) in British Columbia. Note differences in scale.

We found significant positive correlations ($P<0.05$–<0.01) between egg density and fry production (Fig. 4.) in both channels and rivers. We advocate general ceilings on egg deposition in the vicinity of 3 000–4 000 eggs/m^2 for both channels and rivers. Within the the BLDP, Fulton Channel no. 1 approached the production ceiling in the first year of operation. A production of 2 350 fry/m^2 was recorded from a density of 3 400 eggs/m^2 and an egg-to-fry survival of 69.1%. We have included fry production data from Nadina River and Weaver Creek (Fraser River stocks) in Fig. 4 by way of comparison. These two sockeye channels were built and operated until 1986 by the International Pacific Salmon Fisheries Commission (Cooper 1977).

Maximum egg-to-fry survival in the several channels has been similar over the usual range (2 000–3 000 eggs/m^2) of egg density (Fig. 5). The wide range in percent surviving at intermediate densities suggests a highly variable but density-dependent mortality mechanism controlling production of fry. The fry production versus egg density plots for channels and rivers have similar form (Fig. 4), but egg-to-fry survival in the two rivers is about halved ($P<0.01$) despite the controlled flow. Fry production in both environments may be approaching maxima at densities greater than 3 000 eggs/m^2, roughly equivalent to a spawning area of 1 m^2/female.

We found no relationship between percent survival and egg density for any of the BLDP channels (Fig. 5A) although significant negative correlations at the 1% and 5% levels were found for Fulton River and Pinkut Creek, respectively (Fig. 5B). Pooling the channel data to expand the range of egg density failed to reduce the ambiguity.

There are at least two major sources of egg mortality: superimposition and siltation. Wave spawning (wherein the spawning beds are used by two or more successive "waves" of spawners) in relation to superimposition was investigated by Ginetz (1972). Pinkut channel was subjected to siltation during the early years of operation. Erosion of the berms through the action of anchor ice and spawning activity, and

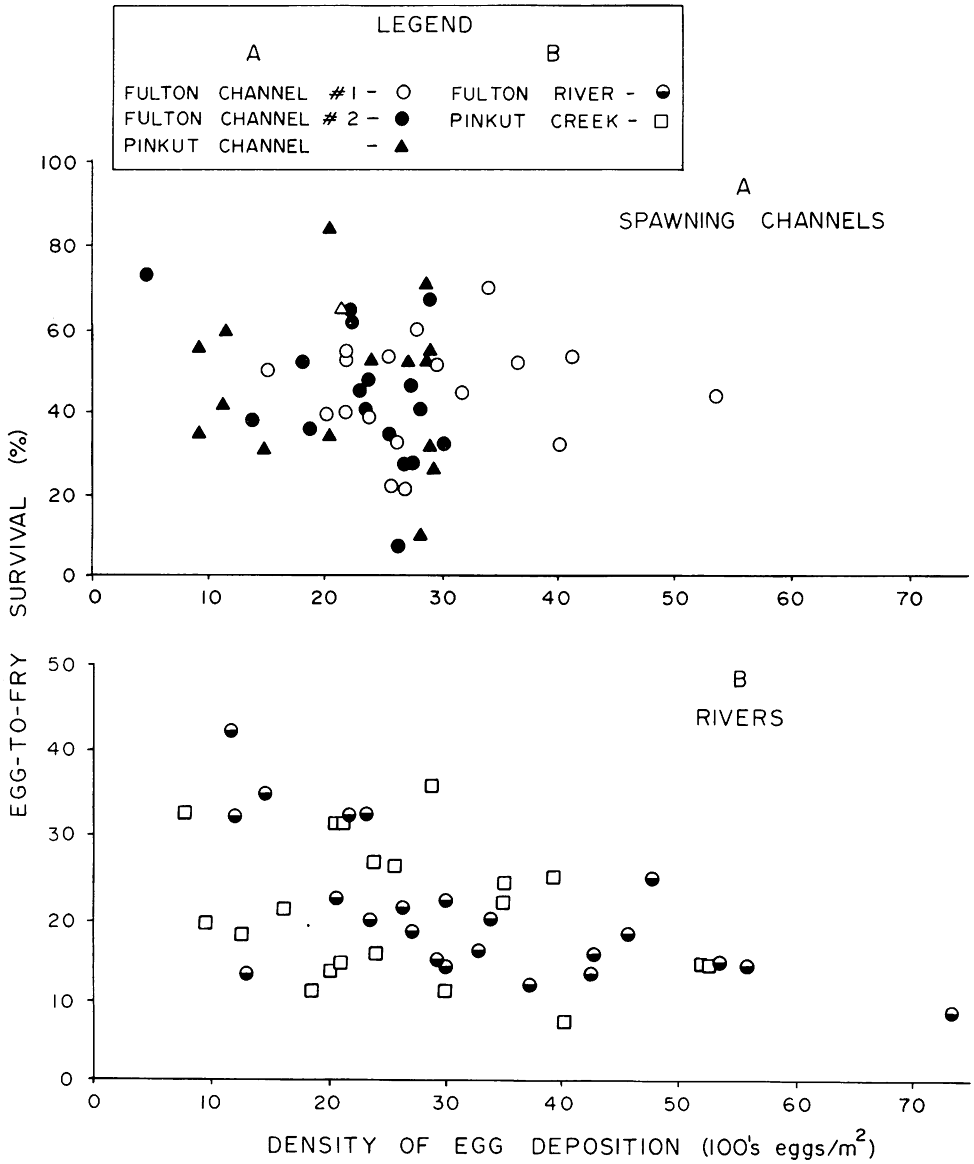

FIG. 5. Relative survival of sockeye fry (%) in relation to mean density of eggs at time of deposition in spawning channels (A) and rivers (B) of the BLDP Project. Note differences in scale.

high sediment loads due to low settling basin capacity, served to reduce survival from a range of 58–25% (mean of 35.4% in 1968–73) to less than 9% in 1974 (Table 2), although mean survival was exceeded in two early years. Following channel reconstruction, the addition of two more settling basins, and intensified annual gravel cleaning, survival of the ensuing 9 brood years (1977–84) has averaged 55.8% and has reached 83% at comparable egg densities. The differences in mean survival and in fry production before and after reconstruction were significant ($P<0.05$).

FRY AND SMOLT PRODUCTION

From the onset of the BLDP, fry production has steadily increased from initial levels of about 40 M to levels commonly exceeding 200 M in the last decade (Fig. 6). Total production of fry has averaged around 190 M (1970–85) of which approximately 130 M (68%) were produced in the channels (Tables 2 and 3). Thus, production in the channels alone is 30% greater than their design target of 100 M fry. Fry production from the two streams, Fulton and Pinkut, (excluding the production from airlifts) has increased since the onset of flow control from an average of 29.6 M to an average of 44.7 M. The spawning grounds above the Pinkut Creek falls have produced an average of 9.9 M fry during the years when surplus escapement justified the airlift. Egg-to-fry survival in upper and lower Pinkut, as indicated by hydraulic sampling, were comparable during those years (Table 3).

Estimated production from both the small Babine streams and from estimated numbers of lake spawners was based on 233 fry/spawner after McDonald and Hume (1984). Fry production (1974–85) from small streams probably declined from that of earlier years, due to reduced escapement. Assumed production from lake spawners rose meanwhile, particularly during the later years of this period, and has averaged about 300 M fry from the last 6 broods (Fig. 6). If, indeed, lake spawners do produce viable fry at such a rate as 233 fry/spawner, their reproductive role could be important. If not, this assumption serves only to underestimate

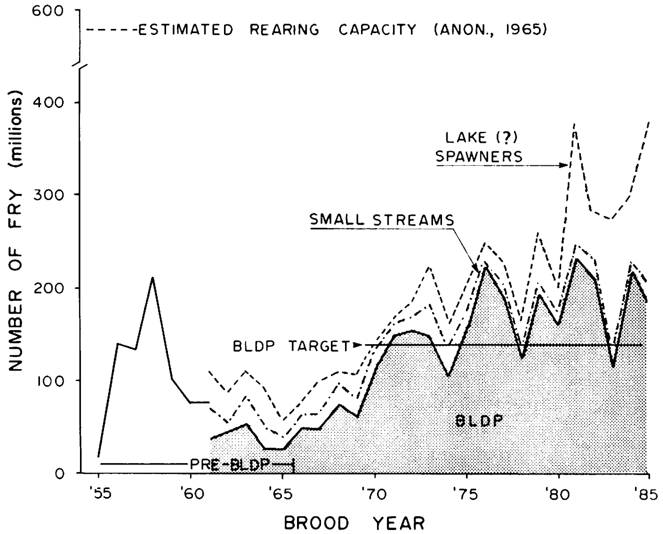

FIG. 6. Numbers of sockeye fry entering the main basin of Babine Lake, British Columbia, 1955–84, and their origins. Estimates of fry for the pre-1961 years are based on August estimates of fry population from Anon. (1965), assuming a 50% survival during the intervening months from emergence.

fry-to-smolt survival in the main lake. The pre-1961 production estimates are based on August population estimates (Anonymous 1965) adjusted upward by applying a generous survival rate of 0.5 between time of lake entry and late summer.

The relationship between fry and smolt production in Fig. 7 is reasonably linear ($r = 0.808$, df = 20, $P < 0.001$), suggesting that fry-to-smolt survival is quite uniform (40–45%) for fry inputs exceeding 100 M. The linearity of this regression relationship suggests that there is no compensatory mortality mechanism serving to reduce fry-to-smolt survival even at recent, high levels of fry production.

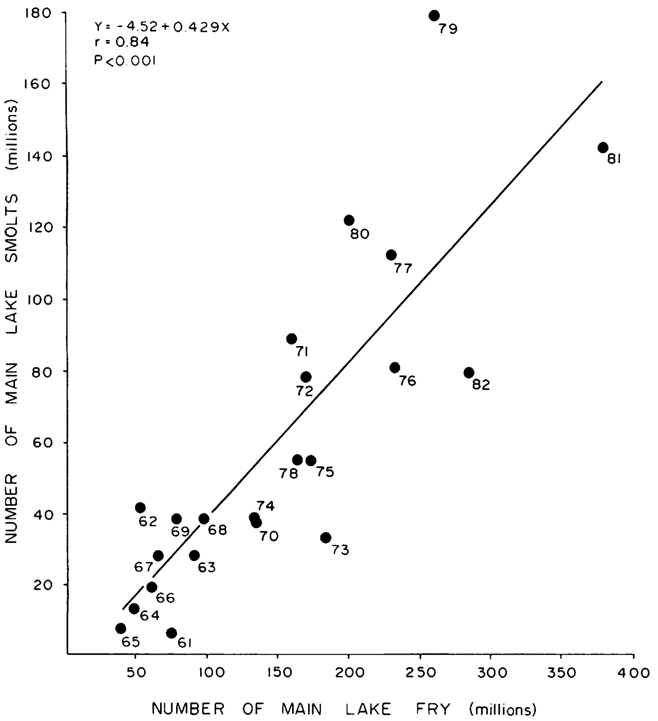

FIG. 7. Size of the sockeye smolt run from the main basin of Babine Lake, British Columbia, 1961–82 brood years, relative to the fry from the BLDP and small streams, excluding potential fry from lake spawners.

ADULT RETURNS, LANDINGS, AND ESCAPEMENTS

Total returns, landings, and escapements of Skeena sockeye derived from the stock reconstruction model have been averaged over two time periods: 1958–1971 (pre-BLDP) and 1973–85 (BLDP), see Table 4. Data for 1972 were omitted to equalize the number of years in the two time periods and to recognize that 1973 marks the 4-yr-old return of brood year 1969 whose fry production reached the halfway point in the BLDP target of 100 M additional fry.

Total Skeena sockeye returns have increased by 87%, from 1 322 241 in the first time period to 2 476 361 fish in the second period, and total landings (Canada and USA) have more than doubled, from 633 685 to 1 357 837. Overall (1958–85), annual total returns and landings of Babine stocks have both doubled but returns to Babine River and the small tributary streams have decreased by 22 and 28%, respectively. Of the non-Babine stocks, returns of the "late timing" group have not declined but the "early" group has declined significantly (56%), at least partly because of intense exploitation during 1973–76 (Fig. 8). The non-Babine stocks underwent extensive decline in the 1950's, almost two decades prior to the first, increasing returns to the BLDP. Since that time, the early stock grouping showed an evident decline during the late 1960's to late 1970's from >30 000 to <10 000, then recovered to moderate escapement levels (~20 000) thereafter, accompanied by marked reductions in harvest rate.

The estimated landings of BLDP sockeye from the various fisheries are given in Table 5. Some 68% of these landings (both time periods) were taken in Area 4 (40–41% of the return), the remaining landings (5–7% in each) were from the Alaska, Areas 3 X and 3 Y, and Native Food fisheries. Since the BLDP, the average return of Fulton plus Pinkut sockeye has increased nearly four-fold, from 358 000 to 1 359 000. More than 1 M fish have been added to the average annual pre-BLDP runs. The Native Food fishery has shown the lowest rate of increase, and the fishery in 3 X and 3 Y has shown the highest.

Discussion

Fry production has exceeded the design target of each BLDP facility illustrating that large spawning channels can be effective producers of sockeye fry. Some factors which may determine fry production have been identified but the associated processes and their interactions that dictate production levels require clarification if we are to maximize production without sacrificing quality. For example, fry production approaches a maximum of 1000 fry/m^2 in the rivers and 2 500 fry/m^2 in the channels when deposition is about 3 000 eggs/m^2 or more (Fig. 4). This corresponds to a density of 1 female/m^2.

At routine egg densities of 2 000-3 000 eggs/m^2, egg-to-fry survival has averaged 46.3% in the channels compared to 20.8% in the rivers. This significant difference ($P < 0.01$) reflects the combined benefits of selected gravel size, control of water flow and spawner density, and reduced silta-

TABLE 4. Estimated average returns, landings (U.S. plus Canadian commercial plus Native food), and spawning escapements of Skeena River sockeye stock groupings during 1958–71 (pre-BLDP) and 1973–85 (BLDP), from the Skeena stock reconstruction model.

Stock grouping	1958–71	1973–85	Magnitude of change
Fulton/Pinkut (BLDP)			
Returns	358 410	1 359 558	3.79
Landings	212 441	825 729	3.89
Escapements	145 969	533 829	3.66
Babine River			
Returns	562 388	410 949	−0.27
Landings	303 846	242 845	−0.20
Escapements	258 542	168 104	−0.35
Babine Lake			
Returns	284 789	529 411	1.86
Landings	144 797	334 089	2.31
Escapements	116 267	195 322	1.40
Babine streams			
Returns	141 440	94 285	−0.33
Landings	60 319	36 361	−0.40
Escapements	81 121	57 924	−0.29
Babine Totals			
Returns	1 347 027	2 394 203	1.78
Landings	721 403	1 439 024	1.99
Escapements	625 624	955 179	1.53
Early non-Babine streams			
Returns	55 377	21 145	−0.62
Landings	27 165	7 236	−0.73
Escapements	28 212	13 909	−0.51
Late non-Babine streams			
Returns	41 658	37 565	−0.10
Landings	21 936	23 265	1.16
Escapements	19 722	14 300	−0.28
None-Babine Totals			
Returns	97 035	58 710	−0.40
Landings	49 101	30 501	−0.38
Escapements	47 934	28 209	−0.41
Skeena R. Totals			
Returns	1 444 062	2 452 914	1.70
Landings	770 504	1 469 526	1.91
Escapements	673 558	983 388	1.46

tion. The two to three-fold range in channel survival, however, is equivalent to that for the rivers at similar egg densities, and do not stem from errors in estimating fecundity, egg deposition, or fry production which do not exceed 10%. Hence, we suggest that positive and negative factors common to both environments: biological factors such as spawner interaction, redd superimposition, sex ratio and proportion of jack sockeye, reproductive state of spawners, gamete viability or disease; and physical factors such as temperature (effects on spawner activity, on fertilization and embryo development etc.), and scouring of the gravel bed by anchor ice may have quantitatively similar impacts on survival in both channels and rivers.

Egg-to-fry survival in the spawning channels is about half that routinely found in alternate hatchery technologies so we have considerable incentive to quantify the biological factors identified above, and to determine their potential interactions and effects as they may affect fry production. Operationally, successive wave spawning that leads to redd superimposition is minimized by loading the channel sections one at a time, and preventing upstream movement of later arriving fish into fully loaded sections.

A fishery for jacks at the Babine Fence exerts some influence on the proportion of jack sockeye in the BLDP escapements but does not otherwise affect the sex ratios of the component stocks. Sex ratio could also be controlled at section fences within the BLDP but we have insufficient manpower to assess the effects of such manipulation on egg-to-fry survival and fry production at present. We aim to stabilize density of female spawners at 1/1.25 m^2 for five years and to increase experimentation in production operations. Extensive manipulation of spawning population in the BLDP could only be justified if it leads to an improved understanding of the underlying causes of variability in survival to the migrant fry stage.

LAKE REARING CAPACITY AND SMOLT YIELD

Fry densities observed in the North Arm of Babine Lake and in Nilkitkwa Lake (Fig. 1), led Johnson (1958) to conclude that to achieve comparable densities in the main basin would require an input of some 600 M fry, ostensibly without exceeding the rearing capacity. Thus, the current combined production of 250–300 M fry from the BLDP and wild

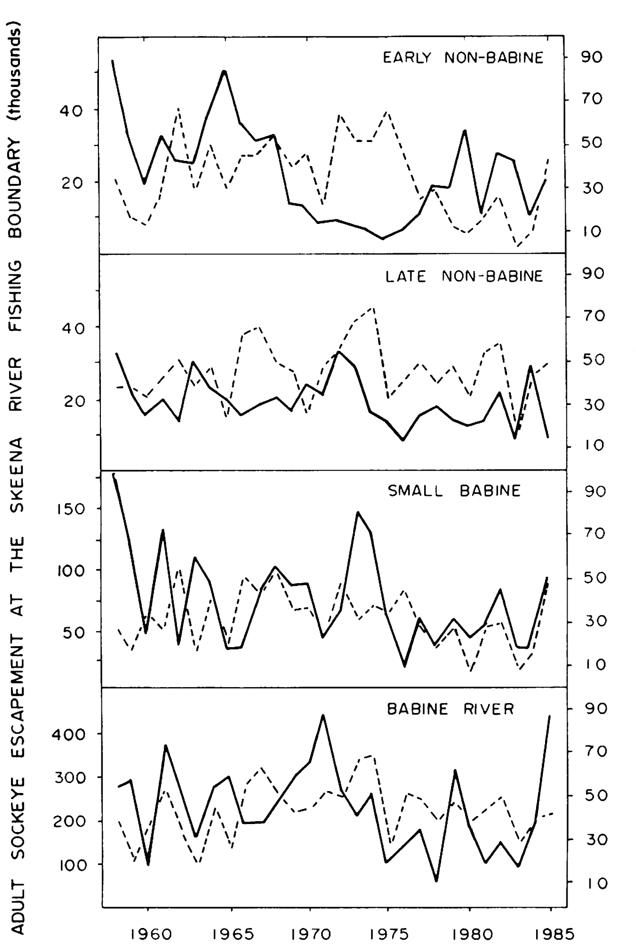

FIG. 8. Annual harvest rates in Area 4 (dashed lines) for the non-enhanced stocks of Skeena sockeye, and their escapements past the Skeena River Fishing Boundary (solid lines), 1958–85.

Babine stocks (300 M includes the potential production from lake spawners) would be expected to utilize about half of Johnson's estimated rearing capacity in the main basin.

The persistent linear relationship between fry and smolt production in the main basin suggests that rearing capacity has not been exceeded. Declining mean size of smolts since BY1969 (Macdonald et al. 1987) could be interpreted as evidence that the rising production of fry and smolts is challenging food resources. These authors have shown a clear link, within cohorts, between smolt length and subsequent survival to return, and smolt size is known to affect marine survival of other salmonids. However, mortality assumptions associated with smolt size relations within cohorts should be applied with caution to size relations between cohorts. Intense gradients of size-selective mortality within a juvenile population may cause only small differences in mortality rates among populations differing slightly in mean size (West and Larkin 1987). Thus, mortality attributable to annual variations in mean size of Babine smolts may be of minor consequence, considering that the range in mean annual length of Babine smolts during the past 25 years only amounts to some 10% of the smallest mean length. In contrast, range in mean annual length exceeds 35% in smolts from Chilko Lake (Fraser River system) where size is not correlated with 25 years of adult return (I. Williams, CDFO, Cultus Lake, B.C. pers. comm.).

Whether or not the length and weight trends in Babine smolts persist or will affect adult return remains conjectural. Smolt biomass is increasing in Babine Lake and it may be profitable to accept reduced survivals, in favour of increased overall returns. The processes producing the more than four-fold range in smolt biomass from similar, high numbers of fry should command our attention since mean smolt size and size of smolt population are not correlated.

HARVEST AND CONSERVATION PROBLEMS

Traditional mixed-stock fishery problems are well documented on the Skeena. Larkin and McDonald (1968) suggest that the non-Babine stocks are inherently less productive than are the Babine stocks and warrant lower harvest rates. Following the Babine Slide in 1951 and a consequent shift of harvest pressure, the non-Babine stocks underwent an extensive decline in the mid-1950's. Failure of these stocks to rebuild (prior to the first BLDP returns in the early 1970's) was noted by Ricker and Smith (1975) who speculated that lake productivity could have declined due to reduced fertilization from the carcasses of diminished escapements. The largest single stock reduction (>100 000 fish) among non-enhanced, Skeena sockeye has occurred in the Babine River stock (Table 4). This decline may be partially due to circumstances unrelated to the BLDP since the latter half of the Babine River run occurs coincidentally with the Babine River pink salmon run. Babine pinks have increased from a few thousand fish in the early 1950's to several hundred thousand in recent years and are now subject to an expanding commercial fishery. This fishery is creating an interception problem for the Babine River sockeye.

TABLE 5. Average contribution of BLDP and all Skeena sockeye (in parentheses) to the Canadian and Alaskan fisheries and to the spawning escapement, for the periods 1958–71 and 1973–85.

Fisheries and escapements	1000's of Fish				Magnitude of Increase (x)
	Pre-BLDP (1958–71)		BLDP (1973–85)		
Alaska Fishery	20.0	(77.3)	85.5	(151.6)	4.3
Canada Fisheries					
Area 3 X, 3 Y	20.4	(82.2)	95.1	(161.9)	4.7
Area 4	144.5	(566.3)	561.1	(1031.0)	3.9
Native Food Fishery	27.5	(44.7)	84.1	(125.0)	3.1
Escapement	146.0	(673.6)	533.8	(983.4)	3.7
Total	358.4	(1 444.1)	1 359.6	(2 452.9)	3.8

Fishery managers are at present coping with this harvesting problem by maintaining low exploitation rates on non-enhanced stocks. Thus, an average annual escapement surplus to spawning needs of the BLDP (369 000) of 165 000 reflects managements efforts to protect other stocks and species. Exploitation of the Pinkut stock has been reduced from 45 to 35% since the intense period of 1972–75, and the Fulton stock has been held to 50% exploitation. Fishing closures early in the commercial fishing season provide almost complete protection for the earliest returning stocks.

Maintaining harvest rates below those which the BLDP stocks can sustain, and thus protecting non-enhanced stocks, is an achievable goal. However, the present high rate of production and average over-escapements of 200 000 sockeye to the BLDP, point to the need to examine supplemental upriver harvesting strategies. As previously stated, the present jack sockeye fishery at the Babine Fence could be expanded to include adults of Fulton and Pinkut origin, or a male-only fishery.

Low productivity of even-numbered brood years from the Babine system prompted McDonald and Hume (1984) to suggest a reduction in even-year escapements and a complimentary increase in landings. If returning pink salmon (*O. gorbuscha*) are active predators on sockeye smolts as hypothesized by Ricker (1982) and Peterman (1982), there is an obvious risk in making any significant reductions in escapement, and consequent smolt production from even-year broods. Any depensatory mortality stemming from adult pinks would then be amplified, particularly if the implicated pinks were from the Babine River stock. However, further speculation on this odd–even year hypothesis may be pointless since the inclusion of more recent data dissolves the regression relationships presented by McDonald and Hume (1984).

The BLDP currently contributes a yearly average of 656 200 sockeye worth some $ 5.5 M (landed value — Canadian) to the commercial Canadian fisheries. Total BLDP construction costs of $ 12 M (1965–71 construction years) with annual operating costs of $ 0.65 M and a discount rate of 10% give a benefit: cost ratio of 3.02:1 (E. Blewet, CDFO, Vancouver, per. comm.). This is an outstanding performance for a sockeye salmon enhancement project.

RESEARCH NEEDS

Spawning channels are designed to optimize the spawning and incubation environments and increase the production of viable fry. In both design and operation, the focus of attention has been on the physico-chemical environment and the fact that egg-to-fry survival in the Babine channels has been twice that of the adjoining rivers suggests the importance of improved abiotic conditions. Egg-to-fry survivals vary widely in both channels and rivers at normal operating densities but the source of this variability is unknown. Hydraulic sampling results indicate that major losses occur before the eyed stage. Improving egg-to-fry survival from long term averages of 40–55% to 65–70%, which has been attained a number of times (Fig. 5), is an attractive target for research.

Continued poor knowledge of juvenile sockeye dynamics in the coastal zone *sensu* Parker (1968) relative to adult returns is of particular concern. Babine smolt production has increased from a mean of 31.2 M before inception of the BLDP to 81.8 M afterward, but smolt-to-adult survival has decreased from 5.1 to 3.0% in the corresponding periods. The cause of the decline in post-lacustrine survival is unknown but could be due to compenstory mechanisms within the stocks, e.g. mortality in the river during seaward migration, in the estuary, or further seaward in the coastal zone (Ricker 1962; Peterman 1982).

Changes in ocean productivity could also affect survival (Ricker 1968). We note that returns of Bristol Bay (Alaska) sockeye stocks have increased threefold from some 10 M during the 1970's to about 30 M during the 1980's, with a 60 M return in 1980 being the largest in the past 25 years (Eggers and Rogers 1987). However, factors other than ocean productivity may have contributed to this increase, and there has been no corresponding increase in the return rate of the unenhanced Babine River sockeye or that of the substantial Rivers Inlet stocks on the Central B.C. coast. Therefore, there is no clear evidence of ocean productivity changes affecting the BLDP stocks.

Finally, the Babine lake spawner assemblage requires critical examination. Surveys (McDonald 1963 and 1964) revealed lake spawners in some Babine Lake areas, prompting the Skeena Salmon Management Committee to identify assessment of lake fry production as a high priority information need for fisheries management. At present, lake spawner estimates are derived from numerical differences between the total stock counts at the Babine Fence and the summed escapement estimates for the BLDP, Babine River, and small tributary streams. Thus, the estimates include all uncounted surplusses of the BLDP which might be forced to spawn in sub-optimal areas, *bona fide* lake spawners, lake mortalities of diverse Babine origin, and errors in estimating escapements to the unenhanced streams. Hence, this lake spawning assemblage is an accounting convenience of unknown reproductive significance.

The number of sockeye categorized as lake spawners has increased from an average of 142 000 (1951–71) to 305 000 (1973–85), peaking at 732 000 in 1985. The increasing size of this assemblage is added cause for concern. By assigning a reproductive success of 233 fry/spawner as for stream spawning populations we would greatly increase estimates of fry inputs to the main lake in recent years. However, if the majority of these adults originate in the BLDP and are therefore surplus to spawning needs there, and are of little reproductive consequence elsewhere in the system, they would constitute a harvestable surplus of considerable interest to fisheries management and industry alike.

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Appendix I

Regression statistics for fecundity on post-orbit hypural length (mm) of Fulton River sockeye for 12 years of return, 1964–85. * = P<0.05, ** = P<0.025, *** = P<0.01, **** = P<0.005, ***** = P<0.001, NS — not significant.

Year	Age	Mean fecundity	Regression $a + b$	s_{yx}	n	r	P
1964	4.2	2948	−2290.4 + 11.74	87.7	14	0.75	****
	5.2	3406	−1741.0 + 3.39	103.2	11	0.17	NS
1965	4.2	2657	−1572.3 + 9.86	73.1	12	0.52	NS
	5.2	3320	−899.7 + 8.88	74.7	16	0.61	**
1966	4.2	3186	−754.6 + 5.39	61.9	21	0.42	NS
	5.2	3810	−519.4 + 8.61	103.9	9	0.58	NS
1974	4.2	2937	−692.1 + 8.22	50.9	48	0.45	****
	5.2	3717	−853.2 + 9.10	108.5	26	0.27	NS
1975	4.2	3002	−1006.1 + 8.72	59.9	47	0.41	****
	5.2	3728	−932.0 + 9.16	99.0	29	0.41	*

Appendix I. (Continued)

Year	Age	Mean fecundity	Regression $a + b$	s_{yx}	n	r	P
1977	4.2	3069	–3383.9 + 13.73	48.3	71	0.62	*****
	5.2	3685	–4269.9 + 15.27	86.1	25	0.61	****
1978	4.2	3185	–1685.4 + 10.77	70.6	21	0.60	****
	5.2	4056	–4973.8 + 1.81	83.2	27	0.11	NS
1979	4.2	3216	–1714.3 + 10.82	65.8	41	0.54	*****
	5.2	4531			1		
1980	4.2	3046	–2038.0 + 11.41	67.5	24	0.61	****
	5.2	3526	–2491.7 + 12.52	55.1	36	0.77	*****
1982	4.2	2720	–3388.2 + 14.16	70.7	29	0.74	*****
	5.2	3470	–621.9 + 8.42	57.8	43	0.50	*****
1983	4.2	2875	–1434.7 + 10.10	73.9	25	0.44	*
	5.2	3476	–2098.7 + 11.79	48.4	40	0.80	*****
1984	4.2	2965	–2481.8 + 12.41	44.7	29	0.66	*****
	5.2	3479	–246.3 + 7.54	60.4	32	0.42	*
1985	4.2	2363	–155.6 + 5.95	62.0	22	0.34	NS
	5.2	3288	–2341.7 + 11.60	50.5	35	0.63	*****
Pooled	4.2	2972	–1811.9 + 10.67	19.1	404	0.59	*****
	5.2	3568	–1244.7 + 9.77	23.1	330	0.56	*****
	4.2+5.2	3240	–2152.0 + 11.52	14.9	734	0.71	*****

Appendix II

Regression statistics for fecundity on post-orbit hypural length (mm) of Pinkut Creek sockeye for 9 yr of return, period 1966–85. Symbols as in Appendix I.

Year	Age	Mean fecundity	Regression $a + b$	s_{yx}	n	r	P
1966	4.2	2897	–2681.7 + 12.82	68.8	23	0.53	***
	5.2	3355	–519.0 + 5.72	147.8	5	0.30	NS
1974	4.2	2970	–1786.6 + 10.52	49.7	25	0.61	****
	5.2	3622	–5263.5 – 3.23	86.4	6	0.44	NS
1975	4.2	2929	–5842.7 + 20.42	61.6	30	0.80	*****
	5.2	3466	–2028.9 + 2.99	121.1	15	0.11	NS
1976	4.2	2932	–3787.8 + 15.22	52.6	39	0.61	*****
	5.2	3274	–3871.3 + 14.66	114.5	10	0.76	**
1977	4.2	3233	–1792.0 + 11.18	49.6	33	0.68	*****
	5.2	3605	–934.7 + 9.08	65.0	31	0.48	***
1979	4.2	3080	–1906.7 + 11.44	90.8	31	0.42	**
	5.2	3864	–6301.4 + 20.33	199.8	3	0.83	NS
1982	4.2	2542	–3119.5 + 13.24	84.6	16	0.63	***
	5.2	3358	–1640.6 + 10.28	52.6	61	0.64	*****
1984	4.2	2333	–1608.5 + 9.53	81.4	19	0.59	****
	5.2	2710	–952.1 + 7.78	83.3	24	0.41	*
1985	4.2	2422	–5046.2 + 17.63	44.1	26	0.80	*****
	5.2	3296	–641.2 + 8.24	54.0	34	0.44	***
Pooled	4.2	2865	–3793.0 + 15.28	24.2	242	0.68	*****
	5.2	3326	–2013.5 + 10.99	30.7	189	0.58	*****
	4.2+5.2	3067	–2015.8 + 11.10	19.5	431	0.69	*****